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Review Article

The Role of Optic Flow and Gaze Direction on Postural Control

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Abstract

Objective: The observers use the optic flow to control self-motion. However, the current state of knowledge indicates that it is difficult to understand how optic flow is used by the visual system without a direct measurement of the changes in the flow patterns caused by eye movements during natural behaviour. The purpose of this literature review is to highlight the importance of the integration between optic flow and eye movements for postural control. *Methods*: A literature review of the electronic papers through July 2022 was independently performed by three investigators. The selection of the studies was made by a search on PubMed, Scopus, and Google Scholar with two groups of selected keywords. We excluded papers performed on subjects with pathologies, children, and the elderly. *Results*: The results of this literature analysis highlight that eye movements are required to drive visual motion processing and heading perception in both static and dynamic contexts. *Conclusion*: Although we now know many neural mechanisms that process heading direction from the optic flow field, a consideration of optic flow patterns relative to gaze direction provides more detailed information on how the retinal flow field is used to control body balance.

Keywords:

Optic Flow; Eye Movements; Heading Perception; Visual Perception; Self-Motion; Body Sway; Posture; Quite Stance; Eye Position; Motor System.

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1- Introduction

The optic flow stimuli projected on the retina during self-motion are important for both navigating in the environment and maintaining posture [1, 2]. The visual input is continually integrated with other signals regarding the position of the eyes and the position and movements of body segments in relation to each other to guide self-motion and maintain balance [3]. The quite stance is the state in which a person, slightly displaced from his/her equilibrium position, tends to return to it through small body fluctuations. Postural responses are unconscious and automatic and adapt to the continuous changes of the surrounding environment. Numerous studies have focused on the analysis of visually guided balance, studying the spontaneous oscillation of the body revealed by the trajectory of the center of pressure (COP) and the ankle joint in response to changes in the visual field [4–6]. The presence of a visual stimulus significantly affects posture. Indeed, the speed of body oscillation is lower in the presence of visual stimuli compared to the absence of them [7].

Postural control is a fundamental motor skill. Several studies demonstrated that the control of stance requires the integration of different sensory modalities such as visual, vestibular and proprioceptive information [8-13]. The integration of such signals generates the typical body oscillation defined as "body sway". The body sway is regulated by the neuromotor system, which plays an important role in maintaining stability, especially under circumstances where voluntary movements are required to sustain or regain balance [14]. This reflects the regulatory activity of the several control loops for the stabilization of an unstable structure, such as the human body [15, 16]. It has been shown that the stimulation of the retina caused by a moving room affects the control of posture by evoking an observer swinging in synchrony with the room [7]. These studies have shown that optic flow stimuli are very important for the maintenance

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of static equilibrium in the upright position. In this regard, when a person receives inconsistent information about the movement of his/her own body, he/she unconsciously tries to correct the posture, thus risking to accentuate the body sway or even lose balance. Furthermore, posturographic analysis with the force platform showed that the subjects attempted to react, at the onset of the visual stimulus, with anticipatory postural adjustment, especially in the antero-posterior and vertical directions [17].

The visual control of posture is a wide field of study and one of the most important aspect is the understanding on how the information of the visual flow provided by self-motion influences the postural control during locomotion. The knowledge within the field of the postural control is accelerating at a high speed while at the same time it remains fragmented and interdisciplinary. This makes it hard to keep up with state-of-the-art and to be at the forefront of research, as well as to assess the collective evidence in the field. Even though it is known that optic flow and eye movement signals interact for generating the spatial representation of extrapersonal space, their effects during quiet standing in healthy adults have yet to be reviewed. Thus, the primary aim of this review is to point out the importance of the integration between optic flow and eye movement signals in the postural control field of study. The secondary aim was to examine the integrative mechanisms of optic flow and eye position on postural control in a healthy population.

The results of this narrative analysis describe the search and the key findings by summarizing studies. We deeply analyze the optic flow neural processing, the integration between eye movements and optic flow, the postural control and the integrative mechanisms between postural control and optic flow. We discuss the importance of the integrative mechanisms between optic flow and eye position for postural control.

2- Methods

An extensive review of the electronic literature was performed by three investigators (M.R., M.P., A.P.). The discussed studies were selected by a search in PubMed, Scopus, and Google Scholar following the PRISMA statements [18]. The selected keywords belonged to the following two groups: 1) optic flow, eye movements, angle of gaze, postural control, integration mechanisms, AND 2) human, monkey. The criteria for exclusion were: 1) studies performed on subjects with pathologies or retinal dysfunction, 2) studies performed on children and elderly subjects, 3) studies non-specifically related at uncovering the functional link between optic flow and body sway. The search period covered years from inception to July 2022. Potential publications were selected by screening titles and abstracts. Only articles published in peer-reviewed journals and in English language were considered.

3- Results

The search of selected databases provided a total of 3568 references. Out of these, 3271 articles were discarded after abstract review because they were not specifically related to the aim of this review. The full text of the remaining 297 citations were examined in detail, leaving 102 papers related to the topic of this work (Figure 1).

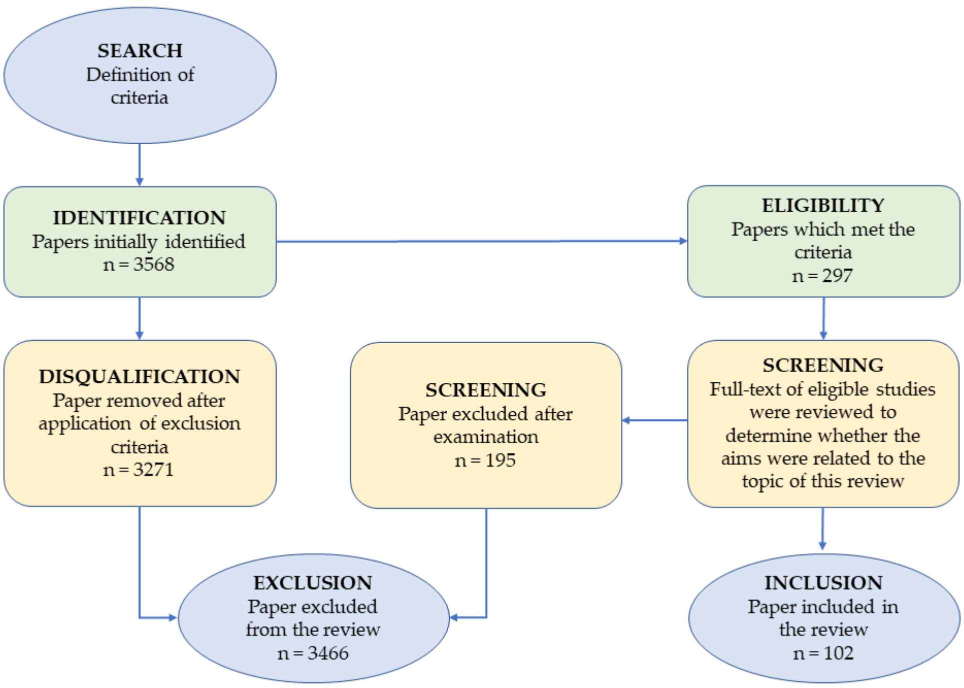

Figure 1. Flow diagram of study selection process

3-1- Optic Flow Neural Processing

James J. Gibson, with his ground-breaking work, introduced the concept of optic flow during World War II. He defined optic flow as the information carried by light resulting from environmental structure and the human's path through the world [2, 19, 20]. When we move in the environment, the retina undergoes a whole field stimulation, the optic flow, which depends on speed and direction of our movement and on the structure of the visual scene. The optic flow originates from a single central point, the focus of expansion (FOE) that corresponds to the final destination of self-motion (Figure 2).

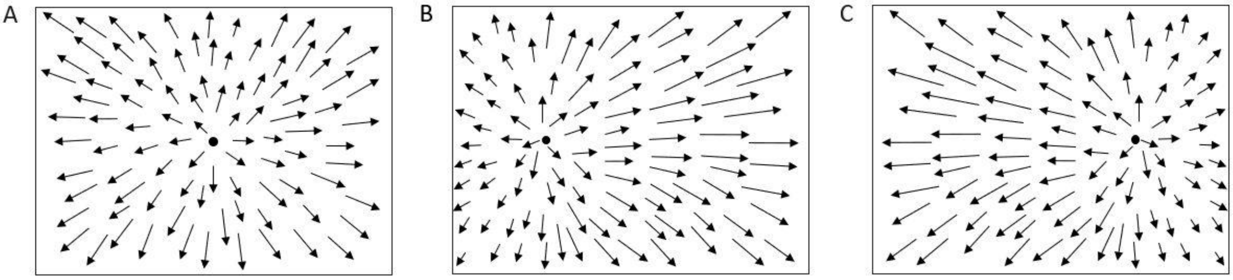

Figure 2. Schematic drawing of optic flow fields. Arrows represents the direction of moving elements presented in the visual field. The dot represents the focus of expansion (FOE). A. Optic flow representing forward motion in which the observer moves straight ahead. B. Optic flow representing forward motion to the left. C. Optic flow representing forward motion to the right.

When the observer moves straight forward, all elements existing in the visual field move radially from the FOE to the periphery (Figure 2-a), while when the observer moves to the left, the elements are directed to the right (Figure 2-b) and when the observer moves to the right the elements move to the left (Figure 2-c). The gradient speed of the optic flow field depends on the distance between the FOE and the observer; objects near to him/her move faster in the retinal projection than the objects further away. The integration of optic flow with other sensory signals permits to create the neural maps for driving self-motion, generating a motor action and/or maintaining postural stability.

The research field on optic flow started decades ago. In both human and animal brains there are specific areas whose neurons are dedicated to optic flow processing, especially regarding heading estimation, time-to-contact estimation, and obstacle avoidance. The optic flow studies in monkeys are of great importance because this animal model allows the experimenters to study the activity of single neurons. Thanks to the neurophysiological studies, we now have a deep knowledge on the neural network mechanisms for optic flow processing.

Within the visual system, the first cortical region showing optic flow responsiveness is the medial superior temporal (MST) area. The first studies of Tanaka and Saito showed that area MST possesses neurons with the ability to process whole events of visual motion by integrating the elemental motion information extracted by previously activated areas (i.e. the middle temporal (MT) area or earlier areas) [21]. The authors discussed the possibility that the type of motion, direction and speed of the animal movement and the external space are represented by the activity of these neurons [22, 23]. Duffy & Wurtz made several important studies in the 1990s describing neuronal mechanisms for optic flow perception in MST cells, like the presence of direction-selective inhibitory or direction-selective excitatory responses [24, 25]. Starting from these studies on MST neurons, several investigations aimed at uncovering optic flow responsiveness in other brain regions. Besides area MST, other cortical areas encode optic flow signals like the superior temporal polysensory area (STP) [26-28], the caudal part of area PE (area PEc) [29], the dorsal prelunate (DP) area and area 7a [30, 31], the ventral intraparietal (VIP) area [32, 33], the primary motor cortex (area M1) [34], the visual posterior Sylvian (VPS) area in the parieto-insular vestibular cortex [35] and the cerebellum [36].

In humans, several neuroimaging studies have demonstrated that passive viewing of optic flow stimuli activates higher-level motion areas [37]. Thus, the human brain needs a large cortical network to encode self-motion perception. This network includes the homologues of area MST [38-40], area VIP [41], area PEc [42], the parieto-insular vestibular cortex [43, 44] and area V6 in the parieto-occipital sulcus [45, 46].

It has to be noted that the laboratory studies performed on monkeys required the animals to orient the gaze toward a fixation point with the restrained head (database search using "freely viewing monkey AND optic flow" retrieved no results). Of course, this is not an ecological situation, however, to date, it is the only way to study the neuronal responsiveness to specific stimuli on animal model.

3-2- Eye Movements and Optic Flow

Besides optic flow, the majority of the above-mentioned areas also process eye movements' signals [47-55]. The presence of eye movement and optic flow neurons in the same region is very important given that heading perception requires their integration. Raffi et al. [56] performed an experiment aimed at assessing if angle of gaze and/or head rotation modify the spatial representation of the FOE. By varying FOE, fixation point and head position in space, the authors found combined effects between head and eye position upon the selectivity for optic flow stimuli. These results suggested that area PEc optic flow neurons use different reference coordinate frames depending on the eye/head position in space underlying some neuronal mechanisms for multiple extraretinal inputs integration.

When the gaze is directed toward the FOE, i.e., we fixate the final destination of our motion, optic flow processing is relatively simple. However, during daily life, the gaze is very rarely directed to the FOE of the flow field and we are perfectly able to navigate in the environment moving the eyes across the visual field. Eye-movements have long been considered a serious issue in understanding the visual control of self-motion because they transform the optic flow in retinal flow (i.e., a complex combination of translation and rotation components).

It is generally considered that eye movements help capture optic-flow information necessary to perceive self-motion. Royden et al. examined heading judgments during eye movements and found that people require extra-retinal information about eye position to accurately perceive heading [57, 58]. Knoll et al. showed that in both human and non-human primates, optic flow triggers intuitive and uninstructed eye movements toward the FOE [59]. Chow et al. performed an experiment in which the subjects viewed expanding or contracting optic flow made by moving dots that could randomly shift [60]. The authors found that 84% of observers tracked the FOE with their eyes without being instructed to do that. These results highlight that eye movements are required to drive visual motion processing and heading perception in dynamic contexts.

Our ability to estimate heading direction from optic flow despite gaze shift results from a comparison of visual information with internal reference signals predicting the visual consequences of an eye movement. Haarmeier et al. demonstrated that the reference signal predicting the effects of smooth-pursuit eye movements is continuously calibrated on the basis of direction-selective interactions between the pursuit motor command and the rotational flow induced by the eye movement [61]. Self-motion perception remains stable when the optic-flow information changes by gaze shifts. This has been interpreted that extraretinal signals are involved in compensating for retinal changes. However, Kuang et al. recently hypothesized that accurate heading perception can be achieved from optic-flow-based visual strategy acquired through experience, independent of extraretinal mechanism [62]. The authors asked to the participants to judge optic flow direction in three task conditions: 1) in the *fixation* condition, subjects fixated a cross presented in the center of the screen and had to judge if the direction of optic flow was left or right; 2) in the *pursuit* condition, subjects made smooth-pursuit eye movements to keep track of the cross which moved leftward or rightward relative to the straight-head direction; 3) in the *simulated* condition, the cross was stationary upon a distorted optic-flow pattern, which was the vectoral summation of a normal optic flow and a global laminar motion as if the eyes had moved. In this way, the retinal image motions in the simulated condition were kept identical to those in the real-pursuit condition. Thus, the only difference between the pursuit and simulated conditions was that the latter did not have an eye-movement-related extraretinal signal. The participants performed a pretraining session (baseline) and six training sessions in the next two days, followed by a retest in the post-training session on the final day. In the pre- and post-training sessions, there was no feedback about the correct answer, while in the training sessions, feedback was provided on a trial-by-trial basis. The authors found that behavioral training can enforce the exploitation of retinal cues to compensate for the retinal changes without the contribution from the extraretinal signals, suggesting that self-motion perception is a flexible and adaptive process which might depend on neural plasticity.

Durant and Zanker studied the effects of eye movements on motion information during walking, showing that eye movements improved the optic flow information even when large wide retinal changes were experimentally created [63]. Clemens et al. demonstrated that eye-movement signals influence self-motion perception even in absence of visual stimulation [64].

3-3- Postural Control

Upright standing is one of humankind's most important evolutionary achievements. A well-stabilized posture is necessary to provide support for voluntary limb, head, or trunk movements. Postural control and balance involve the control of the body's position in space for stability and orientation and require a combination of feedforward and feedback mechanisms (i.e., production of movements or muscular contractions) that help in keeping the body upright in space. The feedforward mechanisms include signals which anticipate potential postural disturbances arising as a consequence of a body movement [65]. The feedback mechanisms involve movements of the head through the vestibular system in the inner ear, visual feedback, and feedback about pressure changes through the support surfaces of the body. The organization of the feedback-control mechanisms is still unknown and whether these mechanisms play a dominant or a minor role in postural control has still to be clarified. It has been reported that feedback control alone is insufficient to explain human postural control [9]. However, some other studies suggested an important role for predictive mechanisms [66] or have concluded that nonlinear mechanisms combining open- and closed-loop control are used for stance control [15].

The human balance is regulated by the neuromotor system that produces the body sway [16, 67]. The body sway is considered as a consequence of noise within the human neuromotor system, as a reflection of an active search process [15, 16, 67], and as an output of a control process of stabilization of an unstable structure, the human body [68]. Visual, proprioceptive, and vestibular systems clearly contribute to postural control [7, 13, 69, 70]. However, it is not completely clear how the information from these senses is computed and combined to generate an appropriate posture when there are conflicting input from different sensory systems. It is possible that sensory cues are linearly combined, so that each sensory system detects an “error” indicating the deviation of body orientation from some reference position [71].

It has been suggested that the central nervous system contains an internal forward model that can predict the effects of motor commands [72, 73]. The internal model can capture the neuromuscular inputs and outputs in order to simulate subsequent sensory consequences providing timely estimates of new sensory information, even in the absence of actual sensory input due to temporal delays associated with feedback control. For example, an internal model could predict a future state (e.g., body position and/or velocity), given the current state and motor command [74]. Several authors have investigated the simple feedback model to simulate upright stance in humans [71, 75-77]. In this model the standing position looks like an inverted pendulum where the feet are still and the head is free to move. On the other hand, the body is multi-segmented with a number of joints where rotation can occur. Thus, describing the upright position in terms of one single link between ankle and head (as in a pendulum) is incorrect. The study of the postural control within the inverted pendulum model allowed scientists to describe three strategies for achieving the upright stance: the ankle, the hip and the stepping strategies [11, 78]. In order to maintain a stable standing position, the ankle strategy restores the body by changing the angle of the ankle joint, while keeping the other joints rigid. Feedback from various sensory organs can activate ankle muscles to correct the body alignment. This strategy is mainly used when external disturbances are small. On the other hand, the hip strategy is used to maintain the postural stability under bigger disturbances. In this strategy the ankle and hip joints are controlled cooperatively. When the external disturbances are so large for the ankle or the hip strategies, the body balance is restored by moving the feet to an appropriate position under the stepping strategy.

3-4- Postural Control and Optic Flow

Several studies have shown that moving visual fields can induce a power sense of self-motion [15, 16, 67, 68]. When the visual input is ambiguous the body sway increases, corresponding to an active search process by the neuromotor regulation system. The complex task that requires the maintenance of postural stability has been studied by numerous investigators to elucidate the relative contributions of each sensory system during standing.

Lee & Aronson [79] demonstrated how the manipulation of optic flow can affect postural stability. The authors developed the swinging room paradigm so to manipulate the environment. The swinging room produced a convincing sense of vection to the observer. The subjects were instructed to stand inside a moving room that was swinging in forward and backward directions. A sway meter was used to quantify the postural oscillations (body sway) of each participant. The authors found that body sway was manipulated by the movement of the room in which the subjects stood. The results showed that adults increased antero-posterior oscillations and that such oscillations were in phase with the room when the misleading visual information was presented [79].

Several studies demonstrated that optic flow stimuli can elicit postural responses [1, 7, 79-84]. Specific spatial and temporal properties of the optic flow, such as geometric structure [70, 85], amplitude [13, 71], velocity [8, 86-88], frequency [8, 88] and location in the visual field [87, 89, 90] can influence posture.

In a moving visual environment, postural stability requires the dynamic coupling of vision and postural control system [13, 17]. In the nervous system, the retinal input related to self-motion is integrated with proprioceptive and vestibular signals in order to assess direction and speed of self-movement, guide the locomotion, and maintain the correct posture [91]. The optic flow structure apparently interacts with the stimulated retinal field in controlling stance [85-88, 92]. Optic flow stimuli are crucial for the maintenance of quiet stance in the upright position when integrated with other sensory signals like vestibular and proprioceptive [71]. Visual input changes, such as from forward to backward motion or from dark to light environment, require an updating of the sensory integration to provide the premotor and motor cortices with precise and reliable information about both the extrapersonal environment and internal state. Such updating results in leg muscles activation to produce a compensating motor response. It has been proposed that the postural reflex activity of the leg muscles evoked by postural and vestibular disturbances, could be organized to minimize future disturbance rather than to correct a past one [93].

In the upright position, the body sway may be produced by the illusory self-movement perception or by an automatic response integrated at a subcortical level. Temporal correlation between stimulus onset and the build-up of postural response is quite important to understand the neural mechanisms. Palmisano et al. asked to their subjects to step onto the force plate in order to study individual differences in the influence of vision on postural stability. Results showed that spontaneous postural sway was significantly greater during eyes-closed (as opposed to open) conditions, and oscillating displays induced significantly more compelling vection than smooth displays. Fujimoto and Ashida investigated postural responses (head displacements) and self-motion perception to radial and lateral optic flows while sitting and standing by using a head mounted display [94]. The authors found that head displacement directions varied across postures. In standing posture, radial optic flow produced the opposed head displacement against the perceived vection direction [94]. Obereisenbuchner et al. measured behavioral, neurophysiological and head motion responses in healthy participants to radially expanding optic flow stimuli, simulating forward transitional motion, which were either initiated by the participant's own button-press ("*self-initiated flow*") or by the computer ("*passive flow*") [95]. The authors found that the visual system is capable to affect behavior by predicting optic flow when self-initiated.

4- Discussion

The revised studies clearly indicate that the eye position contributes to processing the visual judgments via orientation of the ground plane [96] and perceived distance [97]. The integration of multiple sensory inputs is important for the perception of a dynamic environment when controlling the body sway. The precise eye position in a specific time depends on the perception that the brain has of the body posture and the head's relative position to the body. Roll and colleagues showed that the stimulation of the extraocular muscles evoked precise postural changes that underlie the relationship between eye position and postural control [98-100].

The oculomotor strategy used to interact with the external world requires the stabilization of the eyes relative to the extrapersonal space to process an image that could be used for the control of action. All vertebrates utilize saccadic eye movements to rapidly move the gaze to a new location and ocular fixation to keep the gaze stable. This oculomotor strategy suggests that the input to the visual system is structured by our ability to rapidly direct the gaze to a salient stimulus and then fixate such a stimulus as we move in the environment. Raffi et al. investigated the effects of eye position on postural muscles and body sway when subjects viewed radial optic flow stimuli [82]. The authors manipulated the dot speed and the eye position to simulate specific headings combined with different gaze directions. The results showed that the different combinations of optic flow and eye position modulated the body sway, suggesting that the integration of gaze direction and optic flow is a necessary process for body sway control.

Balance control and the maintenance of the right trajectory have to be accomplished by integrating the sensory signals and rhythmic activity of the central pattern generator. During walking, changes in gaze directions are required for many processes, such as to avoid obstacle collisions or to select salient stimuli from the environment. Therefore, the adoption of the desired heading during self-motion is expected to be hampered during eye movements. Here we discuss the results of two studies on how we maintain the correct trajectory during self-motion when our gaze direction does not match our heading direction. Schubert et al. performed one of the first studies assuming incongruity between optic flow and retinal flow [101]. In their experiment, the author tested the effect of eye rotation on heading with subjects walking on a treadmill. The authors found a systematic optic flow effect inducing lateral body sway and a worsening of heading due to incongruent retinal flow components. The data suggested that during locomotion, both retinal and extraretinal information are integrated to control postural oscillation. Jeschke et al., using virtual reality, recently showed that gaze direction affects walking speed [102]. Specifically, the authors found that participants walked faster when their gaze was directed toward a stimulus placed at eye level or just above it.

The visual system is an important source of information about self-motion. Optic flow originates from a change in distance between the observer's eyes and the elements of the visual field: such distance systematically varies with postural sway. The optic flow is integrated with oculomotor signals and other sensory modalities for crating neural representations of the extrapersonal space suitable for motor control. As reviewed in this paper, the factors that affect postural control have so far not been adequately studied using experimental manipulation of both "optic flow" and "eye movements". Therefore, it is far from clear how visual and oculomotor signals affect postural control.

5- Conclusion

Gibson in the 1950', started from the view that heading direction is perceived by a radial expansion pattern originating from the FOE of the flow field [2]. In the following years, it became generally accepted that the optic flow patterns were used by the observers to control self-motion. Since then, a large amount of research investigated the topic. The current state of knowledge indicates that it is difficult to understand the way optic flow is used by the visual system without a direct measurement of the retinal flow generated during natural behavior. The examination of the retinal flow in experiments with eye position and optic flow manipulations suggests a change in emphasis and reinterpretation of the perceptuomotor role of optic flow, emphasizing its role in postural balance (and for completeness, steering and walking are not the object of the present review). Although we now know many neural mechanisms involved in heading perception, a consideration of optic flow patterns relative to gaze direction provides more detailed information on how the retinal flow field is used to control real-world self-motion.

6- Declarations

6-1- Author Contributions

Conceptualization, M.R., A.P., and M.P.; methodology, M.R., A.P., and M.P.; investigation, M.R., A.P., and M.P; writing—original draft preparation, M.R. and M.P.; writing—review and editing, A.P.; project administration, M.R.; funding acquisition, M.R. All authors have read and agreed to the published version of the manuscript.

6-2- Data Availability Statement

Data sharing is not applicable to this article.

6-3- Funding

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6-4- Institutional Review Board Statement

Not applicable.

6-5- Informed Consent Statement

Not applicable.

6-6- Conflicts of Interest

The authors declare that there is no conflict of interest regarding the publication of this manuscript. In addition, the ethical issues, including plagiarism, informed consent, misconduct, data fabrication and/or falsification, double publication and/or submission, and redundancies have been completely observed by the authors.

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