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Neural
Networks

Neural Networks 12 (1999) 1325–1329

www.elsevier.com/locate/neunet

Current Opinions

How stereovision interacts with optic flow perception: neural mechanisms

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Received 6 January 1999; accepted 26 May 1999

Abstract

Optic flow, the global visual motion experienced during self-movement, supplies important navigational information. Optic flow analysis in the visual system is aided by several other visual and non-visual signals. Recent psychophysical findings demonstrate an interaction of optic flow perception and stereoscopic depth vision. Retinal disparity strongly affects an optic flow illusion, which can be related to the mechanisms of visual self-motion detection. To investigate the neuronal basis of this interaction, we tested several hypotheses by introducing different disparity contributions in a detailed neurobiological model of optic flow processing in monkey cortex. The disparity-dependent modification, which accounted best for the data suggests a specific contribution of a subset of stereoscopically modulated cortical neurons present in areas MT and MST. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Optic flow; Heading; Perception; Stereo; Binocular disparity; Neural model; Cortical mechanism

1. Introduction

Human perception is based on a multitude of sensory signals that are integrated with each other in the central nervous system. This paper is concerned with the interaction of two specific visual signals, binocular disparity and visual motion in the perception of complex optic flow patterns. Optic flow arises whenever an animal moves in its environment. During linear forward motion, the optic flow consists of a radial pattern with all motion flowing out from the focus of expansion, which indicates the direction of heading (Gibson, 1950). Eye movements distort this simple pattern of retinal image motion (Warren & Hannon, 1990). In this case, the visual system may combine the optic flow with the extra-retinal eye movement signals to cope with the visual effects of eye movements (Royden, Crowell & Banks, 1994), or it may use the distorted patterns of retinal flow directly (Warren & Hannon, 1990; van den Berg, 1993).

The precise structure of the retinal flow pattern depends not only on the translation and eye-rotation of the observer, but also on the three-dimensional (3D) layout of the visual scene. Information about the depth layout, acquired for instance by stereovision, can influence optic flow perception. We have recently found a clear interaction of stereoscopic disparity and optic flow perception in a stimulus that

induces an illusory transformation of optic flow fields (Grigo & Lappe, 1998). The illusory flow stimulus consists of two equal sized groups of random dots, with one group forming a radial (expansion) pattern with the singular point centered on the screen. The second group performs a global unidirectional motion (Fig. 1(A)). Human subjects perceive the center of expansion displaced from its true location in the direction of the unidirectional motion by as much as 20° (Duffy & Wurtz, 1993; Grigo & Lappe, 1998; Pack & Mingolla, 1998).

A possible explanation for this effect was derived from simulations of a biologically plausible network model of optic flow processing in the primate visual cortex (Lappe & Rauschecker, 1995). This explanation links the illusory shift to mechanisms of heading detection from optic flow in the presence of eye movements. Following these model simulations, the illusory stimulus can be viewed as the approximate instantaneous result of the following egomotion scenario (Fig. 1(B)). The observer approaches a transparent frontoparallel plane, indicated by the broken line, at an oblique path. In addition, the observer performs an eye rotation to keep watch on one individual element of the plane. Then, the motion of all points on this plane conforms with a purely radial motion centered at the direction of gaze (Warren & Hannon, 1990). A second plane (solid line) is added farther from the subject. As a result of the greater distance, points in this plane exhibit a much smaller radial motion component. Instead, these points appear to move in an approximately unidirectional fashion due to eye rotation.

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Nomenclature

θ	optic flow vector
T/R	observer translation/rotation
Z	distance
R	residual function
δ	binocular disparity
$w(\delta)$	weight function

The combination of this egomotion with the two planes approximately results in the transparent motion pattern shown in Fig. 1(A). Therefore, the complete stimulus in (A) suggests a heading direction towards the right of the center of the radial motion. This heading direction is consistent with the average location of the perceived center of the radial motion reported by human subjects. In this view, the unidirectional motion is interpreted as a visual reafferent (eye-)rotation signal which triggers a compensational mechanism that shifts the perceived location of the focus of expansion (Duffy & Wurtz, 1993; Lappe & Rauschecker, 1995; Pack & Mingolla, 1998). However, such an interpretation in terms of self-motion implicitly assumes a specific 3D layout of the dots in space (Fig. 1(B)).

2. Disparity dependence of the illusory shift

Information about the depth layout of the visual scene is inherent in the stimulus in the form of motion parallax. Depth information would also be normally available from stereoscopic vision. When the unidirectional and the radial dot motion are presented in different relative depth arrangements, a strong and highly significant modulation of the illusory perception is observed (Grigo & Lappe, 1998). Specifically, when the unidirectional motion is presented in front of the radial motion, the magnitude of the perceived shift is decreased by 75%. A slight decrease also occurs when the unidirectional motion is presented in the rear.

This result fits well with the explanation of the illusion given above. The optic flow stimulus can be attributed to the combination of three factors—a self-translation in a direction offset from the center of the radial motion, a simultaneous self-rotation (such as an eye movement), and a visual environment in which one set of dots (those that translate) are far away, while the other set of dots (those that move radially) are near. If binocular disparity signals the unidirectional motion behind the radial motion, stereoscopic and motion information is consistent. A conflict arises when binocular disparity signals the unidirectional motion in front of the radial motion. In this case, the egomotion scenario derived from the pure visual motion cannot be completely valid and the perceived shift is reduced.

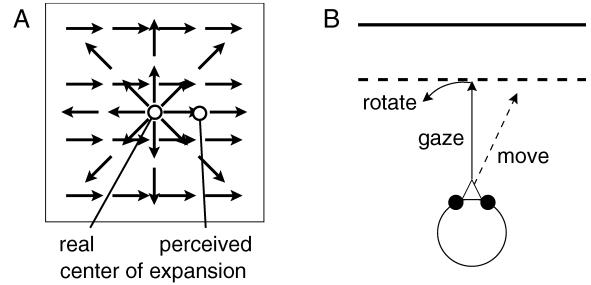


Fig. 1. (A) Illustration of the illusory optic flow stimulus and the human perception; (B) schematic depiction of a corresponding egomotion scenario.

3. Modeling the disparity dependence

The above considerations provide a qualitative explanation for the experimental results, accounting mainly for the observed decrease when unidirectional motion was in front. To quantitatively account for the data and to get an idea for possible neural mechanisms for the interaction, we tried to model the results. In the visual cortex of the macaque monkey, cells in the medial superior temporal (MST) area respond selectively to optic flow fields (Duffy & Wurtz, 1991). Their selectivity for the location of the focus of expansion in an optic flow pattern could allow them to represent the direction of heading (Lappe, Bremmer, Pekel, Thiele & Hoffman, 1996). Area MST receives its major input from the middle temporal (MT) area, which contains neurons that are sensitive to motion and disparity (Maunsell & van Essen, 1983; Bradley, Qiann & Anderson, 1995).

The present modeling is based on the model of Lappe and Rauschecker, who previously replicated the results of the two-dimensional (2D) experiment correctly (Lappe & Rauschecker, 1995), but did not include any disparity-related input. Here we add several hypothetical mechanisms of disparity influence and compare them in computer simulations with our experimental results. A detailed description of the 2D model can be found in Lappe and Rauschecker (1993) and Lappe (1998). Only a few basic properties are necessary to understand the added disparity dependencies. The model consists of two layers of neurons. The first layer encodes the optic flow field in populations of direction-selective neurons that mimic cells in area MT of primate cortex. The second layer computes the direction of heading in populations of neurons resembling cells from area MST. In its synaptic connections, the network implements a least-squares algorithm for heading detection. This algorithm computes a difference measure or residual function, R , between a number of input flow vectors, θ_i , and a set of candidate flow vectors, $\hat{\theta}(T, \Omega, Z_i)$. These candidate flow fields depend on the unknown self-motion parameters (translation, T , and rotation, Ω) and an unknown environmental layout, i.e. a set of unknown distances, Z_i , of the visible points from the observer. The least-squares residual

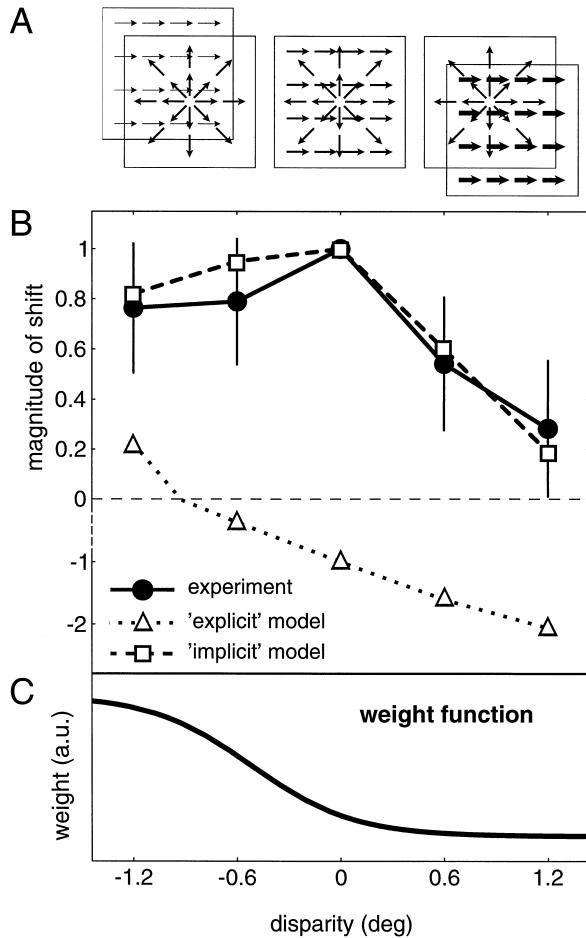


Fig. 2. Disparity dependence of the optic flow illusion—(A) the two motion patterns are separated in depth by relative disparity (Grigo & Lappe, 1998); (B) disparity dependence of the perceived shift: experiment (points), absolute depth ('explicit') model (triangles) and disparity weight ('implicit') model (squares). Note the different scaling for negative shifts; (C) weight function that optimally reproduced the experimental results.

function is thus given by

$$R(T, \Omega, Z) = \sum_i \|\theta_i - \hat{\theta}(T, \Omega, Z_i)\|^2.$$

The network evaluates this function and then proceeds to find those self-motion parameters that minimize it (Lappe & Rauschecker, 1993). The model proposes a computational map of heading space. This map is composed of populations of MST-like optic flow sensitive neurons. Each such population represents one specific heading T_j , its total activity is inversely related to $R(T_j, \Omega, Z)$. The best-matching heading is identified by the maximum activity across the different populations. Each population consists of several neurons that receive input from different subsets of MT neurons. The connection strengths are chosen such that each neuron evaluates part of $R(T_j, \Omega, Z)$ based on its current inputs from MT. However, true selectivity for a specific heading is established only at the population level.

In the following, disparity information is introduced into this model in three distinct ways.

3.1. Disparity-based preprocessing in MT

Neurons in area MT perform a disparity-based spatial integration of visual motion (Bradley et al., 1995). In a previous model, this effectively implemented a cortical preprocessing of the optic flow field in the following way (see Lappe (1996) for details). Each first layer neuron averages the motion inside its receptive field. This gives a spatial smoothing of the flow field. The averaging includes only motion signals with disparities near the preferred disparity of a neuron, thereby restricting the smoothing to motion signals from within a common depth range. Such a preprocessing results in an increased robustness against noise and is consistent with human performance in noisy 3D flow fields (Lappe, 1996). However, the disparity modulation in individual neurons is symmetric around the respective preferred disparity of each neuron. In contrast, the experimental data on the illusion show an asymmetric dependence on disparity, i.e. a foreground/background separation. Thus, the disparity-based preprocessing in MT cannot account for the data.

3.2. Explicit use of stereoscopic depth information in the heading detection algorithm

The second hypothesis assumes that the true distances of the stimulus dots from the observer are known and explicitly used in the calculations. For the least-squares minimization this reduces the number of unknowns. The residual function simply becomes

$$\tilde{R}(T, \Omega) = \sum_i \|\theta_i - \hat{\theta}(T, \Omega)\|^2.$$

As a quick test to see whether this could explain the experimental findings, the minimization can be performed analytically by differentiation and equating with zero (Koenderink & van Doorn, 1987). Solving for T and Ω and finally expressing the assumed distances as relative disparity between the two dot motions, the computation leads to an analytical curve for the predicted magnitude and direction of the shift (Fig. 2(B), triangles). However, this curve failed to reproduce the experimental data (Fig. 2(B), points). Rather, for unidirectional motion in front of radial expansion and even for the coplanar case, a shift in the opposite direction from that found experimentally would be predicted. Thus, we conclude that binocular depth information does not contribute explicitly to optic flow processing.

3.3. Implicit use of disparity by disparity-dependent weighting of motion signals

The third hypothesis assumes a disparity-dependent weighting function in the minimization such that more

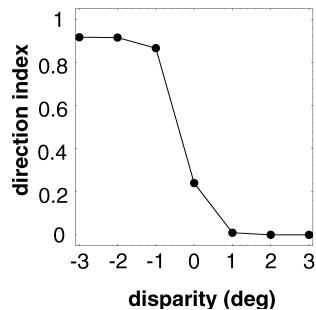


Fig. 3. Disparity dependence of the direction selectivity of a typical model neuron.

distant flow vectors contribute more to the optic flow processing than the near ones. This is a specific neural implementation of the assumption that distant points may provide more reliable optic flow information than near points.

The residual function becomes

$$\bar{R}(T, \Omega, Z) = \sum_i w(\delta_i) \|\theta_i - \hat{\theta}(T, \Omega, Z_i)\|^2,$$

where $w(\delta_i)$ denotes the weight as a function of relative disparity between the two motion patterns. This mechanism could account for the data (Fig. 2(B), squares). Just assuming a simple sigmoid weighting function (Fig. 2(C)), our experimental findings were easily reproduced. Surprisingly, this function is very similar to the disparity-dependence of a special class of neurons, the so-called 'far-neurons', which are found in areas MT (Maunsell & Van Essen, 1983) and MST (Roy & Wurtz, 1990). This suggests that far-neurons might have a special role in the processing of 3D optic flow-fields. This implication is discussed in the remainder of this paper.

4. Implications of disparity-based weighting of motion signals for single MST neurons

As our model consists of a neural network, it is possible to ask what the consequences of disparity-based weighting would be on single optic flow processing neurons. The

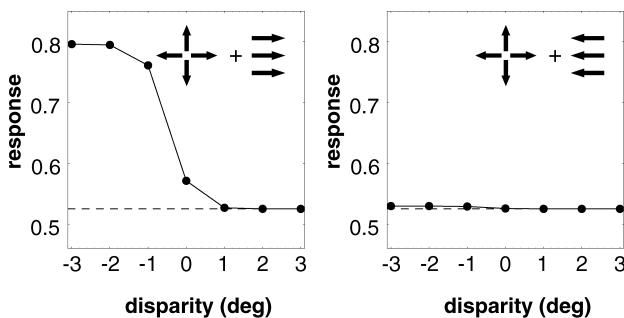


Fig. 4. Disparity dependence of the response of a typical model neuron to the disparate illusory stimuli.

second layer of the model corresponds to area MST in monkey cortex. Most of the second layer neurons respond more strongly and more selectively to stimuli presented with uncrossed disparities, i.e. further distant than the plane of fixation. Fig. 3 illustrates this for the selectivity to full-field unidirectional motion in a single frontoparallel plane. The direction selectivity index (response in preferred direction minus response in anti-preferred direction divided by their sum, $(\text{pref} - \text{anti})/(\text{pref} + \text{anti})$) of a typical model neuron as a function of disparity is also shown in the figure. The evident modulation of the direction index reflects the behavior of 'far-sensitive' neurons observed in MST (Roy & Wurtz, 1990) which respond to far stimuli in preferred direction but do not respond above spontaneous activity level to motion in anti-preferred direction in any disparity condition. Hence, the direction index of these neurons depends on the disparity, in a manner similar to Fig. 3. Our simulations would predict that these neurons form the basis of the perceptual effect of disparity in optic flow processing.

What responses would be expected from MST neurons in the case of the disparate illusory stimuli? In the co-planar (2D) case, model and MST neurons respond to the illusory stimulus (Lappe & Duffy, 1998; Duffy & Wurtz, 1997). Their response is different from the response to radial expansion alone. Model neuron simulations in the case of disparate (3D) illusory stimuli predict that the difference between the responses in the two conditions become smaller when the unidirectional motion is presented with near disparities. Fig. 4 shows the disparity dependence of an example neuron's response to the disparate illusory stimuli for the two directions of overlapping horizontal motion. For uncrossed and zero disparities, a direction specific influence of the overlapping unidirectional motion can be observed. In contrast, for crossed disparities the response does not depend on the direction of the horizontal motion. In both cases it approaches the firing rate observed with radial motion alone (broken line).

A special disparity-dependent behavior was described for MST neurons and hypothetically linked to the visual control of self-motion (Roy & Wurtz, 1990). Some MST neurons appear to reverse their preferred direction for full-field unidirectional motion depending on the relative disparity between the motion pattern and the fixation point. Such a neuron might, for instance, prefer leftward motion for near disparities and rightward motion for far disparities. In our simulations, such neurons were not observed. This suggests that such a behavior is not necessary for the observed disparity dependence of the optic flow illusion, which can be explained simply by neuronal selectivity for far disparities.

5. Conclusion

Our experimental findings demonstrate that stereoscopic vision and optic flow processing clearly interact. This

interaction is consistent with computational requirements of the analysis of self-motion. Our modeling studies point out that in optic flow analysis, the visual system lays special emphasis on distant motion signals. This finding fits with previous studies which suggest that the furthest points in a flow field display are used to estimate egorotation (van den Berg & Brenner, 1994a) or to cause the sensation of self-motion (vection) (Ohmi, Howard & Landolt, 1987) or related effects (Heckmann & Howard, 1991), respectively. In a previous study on stereoscopic influence on self-motion perception, van den Berg and Brenner (1994b) suggested that disparity can provide a depth ordering, which the visual system uses in analyzing optic flow. However, their findings might also be explained by a general stereoscopically mediated noise reduction mechanism in area MT (Bradley et al., 1995; Lappe, 1996), which uses only the depth separation, and not the depth order. Our results favor a contribution of depth order, rather than depth separation effects to optic flow processing.

The modeling results also show that the psychophysically observed disparity dependence of optic flow processing is inconsistent with an explicit use of stereoscopic depth information in optic flow analysis. If we assume that the known depth distances are directly used in the computation of the direction of heading, a different behavior of the illusory shift than was observed experimentally would be expected. In contrast, the disparity-dependent weighting, which reproduces the experimental observations, is merely a modulatory process. The analysis of the optic flow remains purely based on visual motion, with the contribution of single motion signals defined by disparity.

Based on functional arguments from computer simulations, we propose that already at the level of area MT, neuronal disparity sensitivity may be used for optic flow analysis. This is added to the other features of area MT that can be used in a preprocessing of the optic flow field, such as a preference for centrifugal motion (Albright, 1989), an increase of preferred speeds with eccentricity (Maunsell & Van Essen, 1983), and a disparity selectivity that enhances the representation of noisy flow fields (Bradley et al., 1995; Lappe, 1996). Far-sensitive MT neurons can provide a disparity-weighted motion signal to be used for disparity-dependent optic flow processing in area MST, while a band-pass (tuned) disparity selectivity in MT can reduce motion noise (Lappe, 1996).

Our simulations suggest that the optic flow processing in MST might also rely predominantly on far-sensitive neurons. Their disparity sensitivity is sufficient to model the illusory perception. These model predictions would have to be tested in experiments on single MST neurons with stereoscopically presented optic flow patterns.

Acknowledgements

This work was supported by DFG SFB 509.

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