

How To Use Non-Visual Information for Optic Flow Processing in Monkey Visual Cortical Area MSTd

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1 Visual and non-visual information in MSTd

Area MSTd, part of the visual motion pathway in monkey cortex, contains cells that respond selectively to various large-field, random-dot, optic flow patterns [2] [9] [12]. It receives major input from area MT which contains cells directionally selective for local motions. An earlier network model proposes a way to achieve the visual response properties of MSTd neurons from the output of MT-like neurons [5] and links these properties to the psychophysics of human heading detection from optic flow [6] [7]. However, human heading detection has been shown to sometimes depend on non-visual eye movement information [11] [13] [14], and area MSTd has been found to contain extraretinal eye movement [8] as well as eye position [1] information. For instance, pursuit neurons in MSTd fire during smooth pursuit even in the absence of visual stimulation. Many other MSTd cells show a different behavior possibly related to non-visual input: They distinguish between active, self-induced visual motion resulting from active eye movements in a stationary environment and passive, externally-induced visual motion resulting from movements in the outside world, a finding not present in area MT [3].

In this paper we incorporate extraretinal information into the network model in a biologically plausible way by introducing an independent population of pursuit neurons, enabling the model to account for important psychophysical data. We show that the model neurons then attain the active/passive properties described for MSTd. However, we also show that these neuronal properties can be achieved visually without the need for extraretinal input, thereby posing the question, whether the active/passive distinction in MSTd is necessarily a reflection of some non-visual input or whether it may be due to complex optic flow processing allowing for such a differentiation.

2 Detecting egomotion visually

The network model is a biologically plausible implementation of a least-square algorithm of heading detection from optic flow. This algorithm computes the most likely heading direction \mathbf{T} by minimizing a residual function

$$R(\mathbf{T}) = \|\Theta^t \mathbf{C}^\perp(\mathbf{T})\|^2, \quad (1)$$

in which Θ is a collection of several optic flow vectors θ_i , and $\mathbf{C}^\perp(\mathbf{T})$ is a matrix depending on the visual field locations of these flow vectors [4]. The network implements this minimization in a two-layer scheme. The first layer represents the optic flow input by direction selective neurons modelled after

cells in area MT. Several neurons with different preferred directions \mathbf{e}_{ik} and tuning functions s_{ik} are assumed to form a population encoding of an optic flow vector

$$\boldsymbol{\theta}_i = \sum_{k=1}^n s_{ik} \mathbf{e}_{ik}. \quad (2)$$

Their outputs feed into a second layer which contains cell populations that each represents one direction \mathbf{T}_j and becomes maximally excited when $R(\mathbf{T}_j) = 0$, so that the peak of activity in this layer signals the best matching direction of heading. However, a single neuron l within population j evaluates only part of the argument of $R(\mathbf{T}_j)$. Its output activity is described by

$$u_{jl} = g\left(\sum_{i=1}^m \sum_{k=1}^n J_{ijkl} s_{ik} - \mu\right), \quad (3)$$

where $g(x)$ is a sigmoid function, μ a threshold, and J_{ijkl} the synaptic connection from a first layer cells ik . The synaptic strengths are chosen to satisfy

$$\sum_{i=1}^m \sum_{k=1}^n J_{ijkl} s_{ik} = \boldsymbol{\Theta}^t \mathbf{C}_l^\perp(\mathbf{T}_j), \quad (4)$$

and the threshold μ is chosen such that the population activity $U_j = \sum_l u_{jl}$ peaks when $R(\mathbf{T}_j) = 0$ [6].

3 Combining visual and non-visual input

This visual-only heading detection system is complemented by a separate population of pursuit neurons with preferred directions \mathbf{e}_k and directional tuning functions p_k . They provide the second layer cells with the direction and — up to a scalar gain factor γ — the speed of a pursuit eye movement. Thus, the eye rotation is encoded as

$$\boldsymbol{\Omega} = \gamma \sum_{k=1}^n p_k \mathbf{e}_k. \quad (5)$$

The second layer neurons use this information to subtract the eye movement related visual motion from the input flow field. The component of the optic flow that is a result of the pursuit eye movement can be written as

$$\boldsymbol{\theta}_i^p = \gamma \sum_{q=1}^3 \sum_{k=1}^n w_{iq} p_k \mathbf{e}_k \quad (6)$$

with suitable coefficients w_{iq} . Taking the input from the pursuit neurons into account the activity of a single second layer neuron becomes

$$u_{jl} = g\left(\sum_{i=1}^m \sum_{k=1}^n J_{ijkl} s_{ik} + \sum_{k=1}^n J_{jkl}^p p_k - \mu\right). \quad (7)$$

Instead of eq. 4 the calculation of the synaptic connections then proceeds with

$$\sum_{i=1}^m \sum_{k=1}^n J_{ijkl} s_{ik} + \sum_{k=1}^n J_{jkl}^p p_k = (\boldsymbol{\Theta} - \gamma \boldsymbol{\Theta}^p)^t \mathbf{C}_l^\perp(\mathbf{T}_j). \quad (8)$$

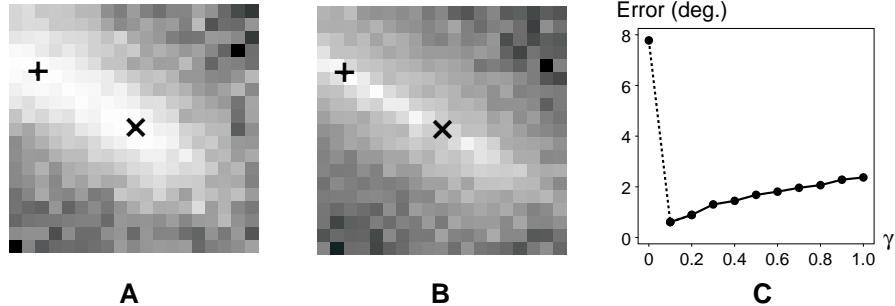


Figure 1:

A: Output activities of the second layer populations in response to an optic flow input when approaching a frontoparallel plane while performing an eye movement. Non-visual eye movement information was not available to the network ($\gamma = 0$). B: Same situation with the non-visual information switched on ($\gamma = 1$). C: Mean error of 100 simulation runs as a function of gain γ .

4 Using non-visual information: system level

Humans cannot accurately determine their direction of heading when an optic flow field corresponding to approaching a frontoparallel plane is confounded by the visual effects of a simulated eye movement [10]. When real eye movements are performed instead the task is solved easily [14]. The model was tested with such flow stimuli (Fig. 1). Without the input from the pursuit neurons ($\gamma = 0$) the network erroneously computes a direction towards the visual field center (\times) instead of the correct direction ($+$). When the pursuit information is present ($\gamma > 0$) the network identifies the direction of heading ($+$) correctly. This behavior is consistent with the data reported for humans [10] [14]. However, accurate information about the speed of the eye movement is not required, since the network works best with $\gamma < 1$ (Fig. 1C). The sharp drop between $\gamma = 0$ and $\gamma = 0.1$ in Fig. 1C shows that the eye movement information is only necessary to resolve the ambiguity present in the flow field. Similar to humans, in many cases other than this restricted situation the network functions with visual input only, and does not depend on extraretinal information at all [6].

In conclusion the model reproduces a characteristic human deficiency in processing certain retinal optic flow fields as well as its disappearance when non-visual eye movement information is available.

5 Using non-visual information: neuron level

Similar to cells in MSTd the neurons in the second layer of the model respond selectively to various optic flow patterns [6]. In the model different degrees of selectivity which have been described in MSTd [2] can be achieved by introducing biologically plausible constraints on the eye movements [5]. Fig. 2 shows that by using extraretinal eye movement information the second layer neurons can also distinguish between active, self-induced stimulation (as happens during smooth pursuit over a lit background) and passive, externally induced stimulation (when a visual pattern is moved across the receptive field). However, the dependence of this distinction on the non-visual input is also influenced by said eye movement constraints. The neuron in Fig. 2A-B loses its selectivity

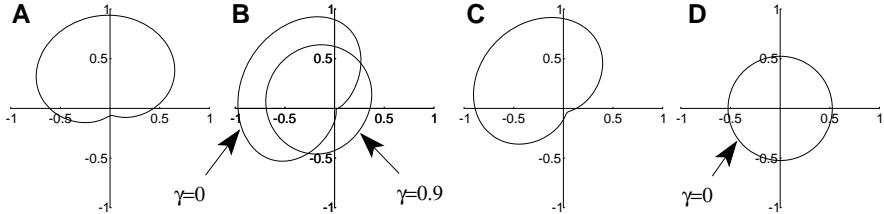


Figure 2:

A: Polar plot of passive direction selectivity of a second layer neuron preferring upward motion. B: Responses induced by an optic flow pattern experienced during active pursuit without ($\gamma = 0$) and with ($\gamma = 0.9$) non-visual input. C-D: Passive (C) and active (D) responses of a different neuron.

for the direction of an active pursuit only if $\gamma \gg 0$, whereas the neuron in Fig. 2C-D is not selective for the direction of an active pursuit even when no eye movement information is present ($\gamma = 0$). The synaptic weights of the latter neuron were calculated using eq. (8), while in constructing the former neuron eq. (8) was modified, as described in [5], by assuming that only smooth pursuit eye movements to fixate a environmental target were to be performed.

Thus we conclude that in addition to several visual properties of MSTd cells [5] [6] the model can also generate cells with the ability to discriminate self-induced from externally-induced visual motion. However, the model shows that this ability must not necessarily depend on non-visual input, leaving this question to future experimental work.

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