Receptive field structure of heading detectors

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Abstract

We looked for common constraints among proposed physiologically-based heading models [1-4] at the level of local motion detectors. First of all, we find that a *circular* RF structure, as proposed in the velocity gain field model [1], also emerges in the subunits of the population model [2]. Such circular RF structure is also evident when determining the contributing directions of most active motion sensors in the template model [3]. Secondly, we find that further restrictions on the population model lead to *local motion-opponency*, as found in the motion-opponency model [4]. Thirdly, we find that a *bi-circular* RF structure, as proposed by the velocity gain field model [1], can also be constructed for units in the population model. These similarities in the RF structure suggest common principles underlying human visual heading perception.

1 Introduction

The image flow created by camera movement relative to the world provides useful feedback on the camera's heading. As seen in Fig. 1a, the heading (circle) corresponds to the center of flow. However, the flow field is not only influenced by heading, but also by translation speed, distances of scene points and rotation. For example, addition of flow due to rotation (Fig. 1b) results in flow that has a center displaced towards the right (Fig. 1c). A number of physiologically-based models [1-4] have been proposed on how the visual systems arrives at detectors that are insensitive to parameters other than heading. Basically, these models assume heading is encoded by a set of heading-specific units that each respond best to a specific pattern of flow, similar to neurons in brain area MST, and each receive input from a set of local motion sensors, as found in brain area MT. We looked for similarities in the models at the level of their receptive field (RF) structure, i.e. the set of preferred motions and their contribution to a heading-selective unit.

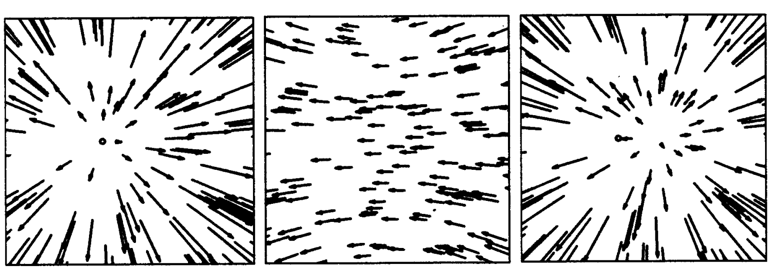

Figure 1 *Image flow due to observer translation (a, left), observer rotation (b, middle), and the combination thereof (c, right).*

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Supported by SFB509 and HFSP

Figure 2 *Bi-circular receptive field structure of a unit in the velocity gain field model, that prefers heading 10° towards the left (circle) and simultaneous rotation about the vertical axis. Vectors indicate preferred direction and magnitude of local motion inputs.*

2 RF structure of units in the velocity gain field model

The velocity gain model [1] makes clear suggestions on the RF structure, derived from assumptions how invariance for translational speed and eye rotation is obtained. The model is based on templates [3], but allows the use of extra-retinal rotation velocity signals to arrive at rotation invariance. Invariance for any flow caused by translation along the unit's preferred heading [1], requires that only the *circular* component of flow is sampled (Fig. 2), i.e. motion along circles centered on the unit's preferred heading. Rotation invariance for each heading-specific unit is obtained by subtracting a series of activities that forms a Taylor's expansion of the unit's response with respect to rotational flow. This means that to first order, a unit's change in activity due to eye rotation is compensated by subtracting a visual derivative activity that reflects how much the unit's response changes per change in rotation velocity, multiplied by an estimate of the rotation velocity. Such rotation derivative unit can be constructed by subtracting two heading-specific units responses, each Gaussian-tuned to rotation, but having opposite preferred rotation velocities. The RF structure of a rotation-tuned unit, which we refer to as *bi-circular* flow, is shown in Fig. 2. The circularly-oriented vectors vary in direction, pointing clockwise or counterclockwise, depending on the side of the image plane. Their preferred magnitude is proportional to the unit's preferred rotational flow, decreasing towards the axis perpendicular to the rotation axis.

3 RF structure of units in the population model

We examined to what extent the above proposed properties of the RF structure appear in the population model. To this end, we reconstructed the RF-structure of local MT-inputs to heading-specific units in the population model. We here present results obtained for an implementation of the model, under the assumption that the camera fixates a stationary object during the translation, while no rotation about the line of sight occurs.

The population model [2,6] is a neural implementation of the subspace algorithm by Heeger and Jepson [5]. This algorithm computes a residual function $R(\mathbf{T}_j)$ for a range of possible preferred heading directions. The residual function is minimized when flow vectors measured at m image locations, described as one array, are perpendicular to the columns of a matrix $\mathbf{C}^{\perp}(\mathbf{T}_j)$. This matrix is computed from the preferred 3-D translation vector $\mathbf{T}_j$ and the m image locations. Thus, by finding the matrix that minimizes the residue, the algorithm has solved the heading, irrespective of the 3D-rotation vector and unknown depths of points.

To implement the subspace algorithm, the population model uses two layers of units. The first layer represents MT-like local motion sensors that fire linearly with speed and have cosine-like direction tuning. The MST-like units in the second layer compute the

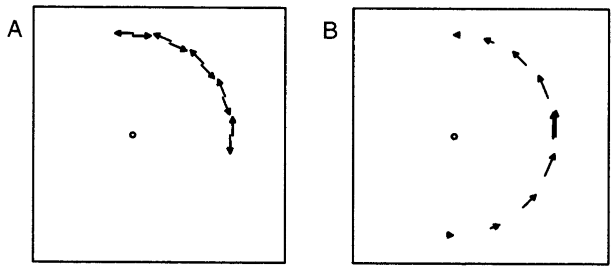

Figure 3 *Circular receptive field structure of pairs of MT-like units in the population model, each encoding heading 10° towards the left (circle). Vectors indicate the preferred direction and the preferred strength of the synapse to the 2nd layer unit. Vectors when pairs are a) taken from same image location, or b) from image locations 90° rotated clockwise about heading point.*

likelihood that the residual function for a specific heading is zero. To reduce the number of connections per unit, the residual function $R(\mathbf{T}_j)$ is partitioned into smaller subresidues based on only few image flow vectors. Thus, the likelihood for a specific heading to be correctly represented is given by the sum of a population of responses.

Given the image locations and the preferred translation, one can reconstruct the RF structure of a second layer unit. Each pair of elements in a column of $\mathbf{C}^{\perp}(\mathbf{T}_j)$ forms a vector, of which the direction represents the preferred motion direction, and the magnitude represents the synaptic strength of its connection to a second layer unit. The matrix $\mathbf{C}^{\perp}(\mathbf{T}_j)$ is computed from the orthogonal complement of a $(2m \times m+3)$ matrix $\mathbf{C}(\mathbf{T}_j)$ [5]. On the assumption that only fixational eye movements occur, the matrix further reduces to a $(2m \times m+1)$ matrix [6]. Thus, given only a pair of MT-units inputs ($m = 2$), the matrix $\mathbf{C}^{\perp}(\mathbf{T}_j)$ reduces to one column of length $m = 4$.

The orthogonal complement of the 4×3 matrix was solved in Mathematica on a Macintosh G4, by first computing the nullspace of the inverse matrix of $\mathbf{C}(\mathbf{T}_j)$, and then constructing an orthonormal basis for this using Gram-Schmidt orthogonalisation. We were able to compute the orientation and magnitude of the two MT-inputs analytically. Instead of presenting the mathematics, we here describe the main results.

3.1 Circularity

Independent of the location of the two MT-inputs, their preferred local motion is always directed along a circle centered on the heading point. Fig. 3 shows two examples of the circular RF structures, for 5 pairs of MT-inputs that represent the same heading and have been chosen to lie on a circle.

3.2 Motion-opponency

Mathematically it turns out that when the positions of a pair of motion sensors overlap, the preferred directions are always opposite, having equal magnitudes (Fig. 3a). For motion vectors that are spatially separated, the preferred magnitude and directions of two motion inputs to a 2nd-layer unit depend on each other. Dividing the image plane along the heading-fixation axis, we find that preferred motions are directed clockwise or counterclockwise if the pair is split across image sides, while opponent preferred motions again emerge when the pair is located at the same side. Thus, the population model is able to incorporate motion-opponent detectors that respond strongly to locally opposite motion, like the input of head-specific units in the motion-opponency model [4].

3.3 Bi-circularity

For pairs chosen so that each local motion input has its counter part at an image location 90° rotated about the heading point (Fig. 3b), a bi-circular RF-structure very similar to that proposed for rotation-tuned units in the velocity gain field model can be constructed (compare with Fig. 2). Note, however, the largest magnitude occurs along the line through the fixation and heading point, whereas the largest magnitude for a velocity gain field unit is found along the vertical line through the fixation point, i.e. the projection of the rotation axis onto the image plane. Thus, the bi-circular RF-structure of the unit in the population model resembles a rotation-tuned unit in the velocity gain model that is Gaussian-tuned to rotation about the horizontal axis. Such rotation-tuning we can explain, because this implementation of the population model assumes rotation invariance only for rotations that keep the point of interest in the center of the image plane, in this case rotation about the vertical given leftward heading. The unit is therefore likely to be sensitive to rotation about the horizontal and torsional axis.

4 Discussion

We mathematically showed that a circular RF structure, such as proposed by the velocity gain model, also occurs in the population model. Furthermore, we showed that by placing restrictions on the population model, other RF structure properties such as motion-opponency and bi-circularity emerge that are found in other models as well.

A circular RF structure is also implicitly present in the template model by Perrone and Stone [3]. In their model, the local motion input is the activity of the most active sensor in a collection of motion sensors, each tuned to a different ego-translation speed, but with the same preferred ego-rotation and heading direction. The contributing response will only be sensitive to the heading direction and rotation, but not to the translational component of the flow. The resulting response could therefore be represented by a motion sensor having circularly-oriented preferred motion.

A circular RF structure is found to be a prominent property in three models, supporting the counterintuitive, but computationally sensible idea, that it is not the radial flow structure, but the structure perpendicular to it, that contributes to the response of heading-sensitive units in the human brain. This suggests that testing selectivity for expanding motion might be a bad indicator for determining a cells preferred heading, and that selectivity for circular flow, common in brain area MST, has a direct link to heading detection mechanisms.

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