

The Scatter of Retinal Position Affects the Formation of Orientation Map

Chong Jiao^a, Ming Li^b and Dewen Hu^c

College of Intelligence Science and Technology, National University of Defense Technology, Changsha, Hunan, China

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Abstract: The neurons in the primary visual cortex of mammals have been found to have significant orientation selectivity. In the higher mammals, the neurons with similar preferred orientation clustered together to form a pinwheel-like pattern, which is thought as a strategy to reduce wiring cost. In contrast, the preferred orientation of neurons in rodents are randomly distributed, which is termed as salt-and-pepper map. Why the mammals have such two distinct organizational pattern remains to be explored and this will be important for understanding the principles of the visual information processing in cortex. In this paper, we used a multidimensional scaling (MDS) model to study the spatial distribution of the preferred orientation and retinotopic position with the objective of minimizing wiring cost. Our results suggested that the scatter of retinotopic position in an orientation column was a critical factor on the formation of pinwheel map or salt-and-pepper map; higher mammals with ordered retinotopic position tend to have continuous map while rodents with relatively larger scatter of retinotopic position tend to have random map.

1 INTRODUCTION

Even though the deep learning (LeCun et al. 2015) technology has achieved incredible performance on many vision tasks, it still suffers from problems such as overfitting and lack of explanation (Krizhevsky et al. 2017). The study on the information processing in the biological visual system will provide an opportunity to solve these problems and will be an important step towards general artificial intelligence (Bashivan et al. 2019, George et al. 2017). This paper focus on the organization of orientation map in the primary visual cortex of mammals. Neurons in the primary visual cortex of mammals have significant orientation selectivity (Hubel and Wiesel 1962, Hubel and Wiesel 1959); only the light stimuli at the preferred orientation could evoke the response of neurons most effectively. In the higher mammals including carnivorous and primates, the neurons with similar orientation will cluster together to form a highly ordered pinwheel-like pattern (Bonhoeffer and Grinvald 1991, Ohki et al. 2006). Specifically, the orientation preference of neurons gradually changes

across the cortex to form pinwheel-like patters where orientation changes from 0 degree to 180 degrees around the pinwheel center, clockwise or anticlockwise. In contrast, the neurons in the primary visual cortex of rodents are randomly distributed irrespective of the orientation preference (Ohki et al. 2005), which is termed as salt-and-pepper map. The study on why this distinct orientation map exist in the mammals will help us understand the principles of visual information processing in the cortex.

There have been many models developed to study the origin of pinwheel map, such as the simple spin model (Cowan and Friedman 1990), dimension reduction model (Durbin and Mitchison 1990) and the coordinated map including multi-features (Yu et al. 2005). These models achieved realistic map like the experimental findings. However, they did not explain why the rodents lacks orientation map. Recently, Weigand proposed a multi-dimensional (MDS) model to study the difference of orientation map in rodents and higher mammals (Weigand et al. 2017), and suggested the number of cells could be an important factor leading to the difference of orientation map. However, their model did not agree

^a <https://orcid.org/0000-0002-3504-9707>

^b <https://orcid.org/0000-0002-9471-9897>

^c <https://orcid.org/0000-0001-7357-0053>

with the experimental observation very well (Ibbotson and Jung 2020) because they overlooked other features of neurons; for instance, retinotopic position was also an prominent feature of neurons in the primary visual cortex..

In this paper, we extend the MDS model to study the map of retinotopic position and orientation preference simultaneously. We optimized the spatial distribution of these two tuning properties by minimizing the wiring cost, equivalently speaking, by putting neurons with similar tuning preference together. Our results suggested that the competition between retinotopic position and orientation could explain the emergence of pinwheel map and salt-and-pepper map. Specifically, the scatter of retinotopic position in an orientation column was a critical factor on the formation of pinwheel map or salt-and-pepper map; higher mammals with ordered retinotopic position tend to have continuous map of orientation while rodents with relatively larger scatter of retinotopic position tend to have random map.

2 METHODS

From the view of dimension reduction framework (Durbin and Mitchison 1990), the visual map can be thought as a projection from high dimensional feature space onto the two dimensional cortex surface. Similar features should be mapped in close vicinity to reduce wiring cost (Weigand et al. 2017) and enhance robust computation (Stringer et al. 2019). This motivated us to compare the optimal placement of orientation preference of neurons with the observed orientation map in the experiments, which will help us to understand the mechanisms behind the neuronal map. Specifically, we tried to obtain the optimal

orientation map by placing neurons according to their tuning similarity and studied which factor leads to the emergence of pinwheel-like map like in higher mammals or random map like in rodents. MDS is a classical method to transform the inputs from the high dimensional space to subspace while preserving the distance in the original space (Borg and Groenen 2005), which has been successfully used to study the spatial distribution of orientation preference (Weigand et al. 2017). However, they only considered the spatial distribution according to the orientation similarity but ignoring the contribution of other tuning properties to the final spatial distribution. In fact, the feature maps, especially the retinotopic position and orientation preferences, are strongly dependent (Durbin and Mitchison 1990, Yu et al. 2005).

In this paper, we extend the method to study the spatial distribution of both the orientation preference and retinotopic position simultaneously. The method is illustrated in Figure 1. The receptive field properties (including retinotopic position, orientation, spatial frequency et al) are represented by a vector v_i . We defined the connection probability of two neurons based on their tuning similarity as in equation (1).

$$\rho(i, j) = a + b * e^{-\frac{\|v_i - v_j\|_2^2}{\sigma^2}} \quad (1)$$

Where a is the constant connection probability between two arbitrary neurons, b is the gain of the selectivity. The feature selectivity is controlled by the parameter σ , which is illustrated in figure 2. With a random process defined with the connection probability, we could obtain the binary connection matrix C .

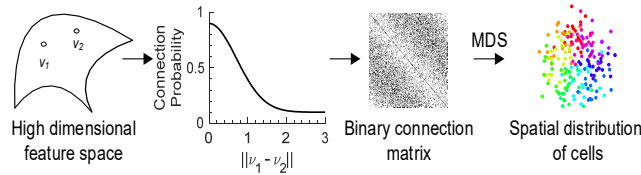


Figure 1: Method to obtain the optimal spatial distribution with MDS model.

To get the dissimilarities of each paired neurons, we used Jaccard distance in equation (2) as the feature distance, which was the same as in previous study (Weigand et al. 2017).

$$JD = 1 - \frac{|C_i \cap C_j|}{|C_i \cup C_j|} \quad (2)$$

Where C_i is the set of all other neurons which has a connection with neuron i . With the dissimilarities defined for each pair of neurons, we could use the metric MDS to get the spatial distribution of these neurons in a two-dimensional space. the whole process was illustrated in Figure 1. Our method is an modification to the method in

(Weigand et al. 2017) to support the high dimensional feature space rather than only orientation for the original method.

In this paper, we studied the retinotopic position and orientation preference simultaneously. The feature vector can be defined as a 4-dimensional vector as $(x, y, r * \cos(2\theta), r * \sin(2\theta))$, where x and y denote the cartesian coordinates of retinotopic position, θ denotes the preferred orientation and r is the orientation selectivity. The MDS operation was implemented by the *mdscale* function in Matlab.

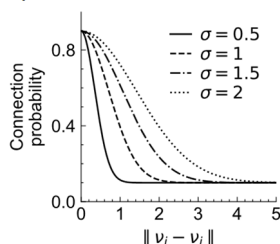


Figure 2: Connection probability function with different feature selectivity.

3 EXPERIMENTAL RESULTS

3.1 Spatial Distribution of Orientation Preference

We first studied the spatial distribution when only considering the orientation preference. With the method in section 2, we first defined the feature vector as $(r * \cos(2\theta), r * \sin(2\theta))$, where θ denotes the preferred orientation. We studied the impact of orientation selectivity σ and the number of cells N on the final spatial distribution. All the preferred orientation was uniformly distributed in $(0, \pi)$.

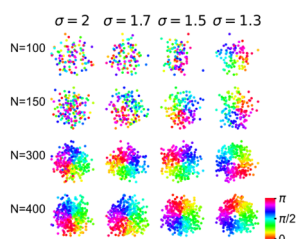


Figure 3: Pinwheel patterns emerges with increasing number of cells or greater orientation selectivity.

With the MDS transformation (see Methods), the results are illustrated in Figure 3. The color of each cell is assigned according to their orientation preference, which was illustrated in the bottom right

corner. It can be seen in Figure 3 that increasing the selectivity (decreasing σ , from left to right) will lead to the emergence of pinwheel map. In addition, increasing the number of cells (from top to bottom) will also result in the appearance of pinwheel pattern. Our results is similar to the report in(Weigand et al. 2017), which proved our adaptation to multidimension model was valid. However, this results was not fully consistent with the experimental observation (Ibbotson and Jung 2020). Part of the reason was that this modelling methods ignored the interdependence of cortex maps, which had been found in the experimental results. For instance, the orientation, ocular dominance, and spatial frequency domains has been demonstrated a clear influence of each other (Yu et al. 2005). This motivated us to model multi-features simultaneously.

3.2 The Spatial Distribution of Retinotopic Position

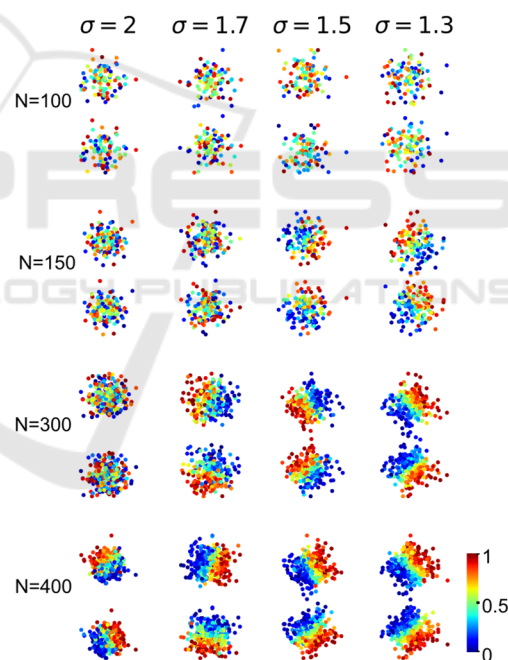


Figure 4: The spatial distribution of retinotopic position becomes ordered with increasing number of cells or feature selectivity.

Besides the orientation, one of the most prominent features is the retinotopic position. Thus, we further studied the distribution of retinotopic position with the same method. The feature space is a two-dimensional vector defined as (x, y) , which are the cartesian coordinates of retinotopic position respectively. In this model, both of x and y were

uniformly distributed in the range of (0, 1). The results are illustrated in figure 4. The colors from blue to red corresponds to the value of 0 to 1. For each parameter combination, top panel denotes the distribution of x and the bottom panel denotes the distribution of y. It can be seen in Figure 4 that the ordered map appeared when increasing the number of cells (from top to bottom) or increasing the feature selectivity (from left to right), which was similar to the results on the orientation distribution. An interesting finding is that the gradient of x and y is near orthogonal to each other in the ordered map (bottom right) even though we did not constrain their relation explicitly, which suggested our model could capture the dependent relations of different features.

3.3 Mapping the Orientation and Retinotopic Position Simultaneously

We further studied the spatial distribution of retinotopic position and preferred orientation simultaneously to study the interdependence of both cortex maps. The feature space is defined as $(x, y, r * \cos(2\theta), r * \sin(2\theta))$ (see Methods). The range of the retinotopic position reflect the scatter of retinotopic position in the orientation column. Thus, we define the domain of x and y as (0, SZ), where SZ defined the scatter of retinotopic position in the orientation column. We set the number of cells $N=300$ and feature selectivity $\sigma = 1.2$. With this configuration, both distribution of retinotopic position and orientation should appear as an ordered map if we consider these features independently (see Figure 3 and Figure 4). We want to know the impact of SZ on the optimal spatial distribution. The results can be seen in Figure 5 that, when increasing the SZ, the retinotopic position gradually dominates the spatial distribution of neurons and the pinwheel map of orientation in the first row became randomly distributed.

This situation was reminiscent of the experimental results that rodents tend to have greater scatter of retinotopic position compared to cat or Macaque (Marshel et al. 2011, Schuett et al. 2002, Van den Bergh et al. 2010), which suggested the scatter of retinotopic position might be an important factor to the emergence of orientation map.

To quantify the pinwheel pattern, we used the correlation coefficients between preferred orientation and azimuth in the spatial distribution. This index was also used by the previous research (Ohki et al. 2006, Weigand et al. 2017). To obtain the correlation coefficients between orientation and azimuth, we

denoted the preferred orientation at the azimuth of π as $\pi/2$, and the subtract this orientation to obtain the preferred orientation relative to this angle. To reduce the estimation error, we only consider the cells which lie at the azimuth in the range of $(\pi/4, 7\pi/4)$. The results were shown in Figure 6 and it can be seen that the linear correlation gradually disappeared when increasing the SZ, which was in agreement with the observation in Figure 5.

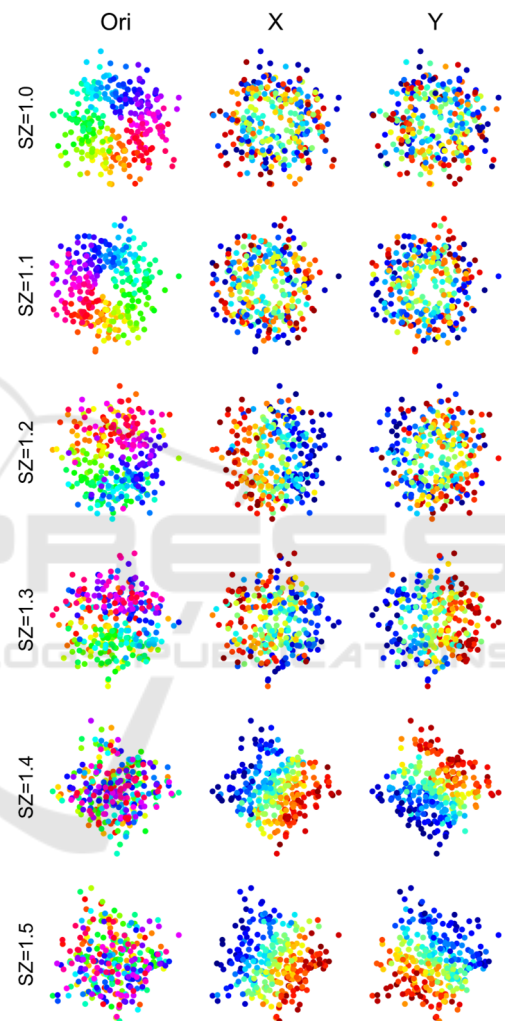


Figure 5. The spatial distribution of tuning preferences including orientation (Ori) and retinotopical position (X and Y) changes with the scatter size in an orientation column.

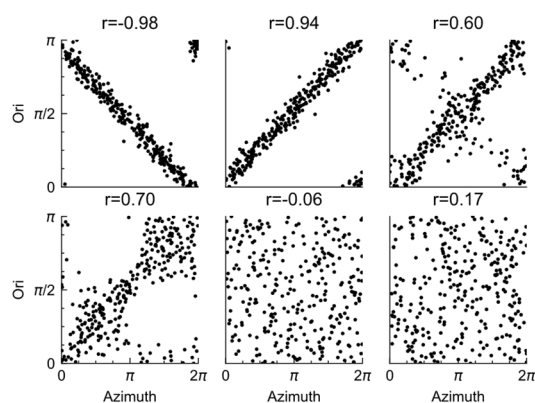


Figure 6. The scatter plot of preferred orientation (Ori) versus azimuth for different scatter size.

We further explored the change of the squared of correlation coefficients (R^2) with the scatter (SZ). We computed the corresponding R^2 for SZ in the range of (1.0, 1.5) and repeat 15 times for each parameter configuration. Figure 7 gave the variation curve of R^2 with the change of SZ. It was clear that the R^2 had a sharp decrease when the SZ exceed some value, which suggested a transition of orientation map from pinwheel-like pattern to a totally random map.

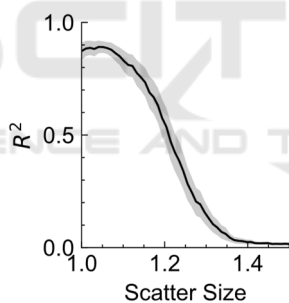


Figure 7. The squared correlation coefficients (R^2) decreases with scatter size; the shadow area indicates standard bias; the sharp decrease of R^2 indicates a transition from pinwheel-like map to a totally random map.

4 CONCLUSIONS

In this paper, we extend the MDS model (Weigand et al. 2017) to study the optimal placement of retinotopic position and orientation simultaneously with the objective of minimizing wiring cost. Our first result revealed that the feature selectivity and the number of cells were both important factors for the emergence of ordered map, which was consistent with previous study (Weigand et al. 2017). Moreover, we further extended this model and found that when

considered the orientation preference and retinotopic position simultaneously, the scatter of retinotopic position had great impact on the appearance of pinwheel map. In particular, when the scatter of retinotopic position exceed some threshold, the pinwheel map sharply disappeared and deteriorated into a random map. In fact, the study on mouse retinotopic mapping indeed showed a larger scatter compared with cat (Garrett et al. 2014). Our results also were in consistent with the report that the central-to-peripheral ratio (CP ratio) of retinal cell density can be used to predict the pinwheel map (Ibbotson and Jung 2020). The central vision tends to have greater cortical magnification factor and less scatter. This means that mammals with higher CP ratio will have less scatter in the central vision thus having a greater chance to form pinwheel map. Recent study on mouse also found a cortex region with enhanced spatial resolution like the fovea of higher mammals (van Beest et al. 2021), which suggested that the functional architecture of visual cortex of higher mammals and rodents might not have huge difference as previously thought. Our results implied that the pinwheel map of higher mammals and random map of rodents might emerge with the scatter of retinotopic position even though they have no difference in the organizational principles.

However, a through survey and quantitative estimate of the degrees of scatter for mammals is required to obtain a solid conclusion. Besides the retinotopic position and orientation, the ocular dominance and spatial frequency are also important features for neurons in the primary visual cortex. Experimental studies suggested that these functional maps had subtle interdependent relations (Nauhaus et al. 2016, Nauhaus et al. 2012). A comprehensive model including all of these factors might provide insights about the organization of cortex map of mammals.

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