Direction of motion maps in the visual cortex: a wire length minimization approach

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Abstract

In the visual cortex, many neurons respond preferentially to one direction of motion. Maps of direction preference vary in appearance between species and cortical areas. We propose that the observed variability in map appearance reflect the variability in intra-cortical circuits as a consequence of wire length minimization. This hypothesis allows us to bypass a detailed developmental analysis of map formation. We solve the layout optimization problem numerically for various intra-cortical circuits and obtain direction preference maps that reproduce the observed variability in map appearance. These results allow one to infer intra-cortical connectivity from the appearance of direction preference maps. © 2002 Published by Elsevier Science B.V.

Keywords: Visual cortex; Wire length; Maps

1. Introduction

In mammalian visual cortex many neurons respond preferentially to edges of certain orientation. Many of these neurons show preference for direction of motion. Spatial organization of orientation and direction preference maps has been revealed electrophysiologically [1,16] and optically [11,15,17]. Map appearance shows variability between cortical areas and species. Previously, we proposed that variability in orientation preference map appearance reflect variability in the statistics of intra-cortical connectivity in accordance with wire length minimization hypothesis [10].

In this paper, we study how statistics of intra-cortical connectivity affects the appearance of direction preference maps. We base our theory on the wire length

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minimization hypothesis [2,4–7,12,13]. This hypothesis asserts that placing connected neurons far from each other in the brain is costly in terms of evolutionary fitness. Therefore, evolution was constrained to come up with developmental rules which respect wiring constraints and place connected neurons as close as possible. This allows us to bypass a detailed developmental analysis and arrive at direction preference maps by solving a layout optimization problem, wherein the neurons of various direction preferences should be arranged to minimize the length of connections required to support their function.

2. Model

We consider neurons characterized by direction preference and arranged on a square lattice. To describe intra-cortical circuitry we introduce a connection function, which specifies the number of connections each neuron establishes with other neurons as a function of the direction preference difference between them. Based on recent experimental results [14] we take the connection function to be bimodal: one peak is around $0°$ direction difference (similar direction preference), the other peak is around $180°$ direction difference (opposite direction preference). For various parameters of the connection function, such as the relative amplitude of the two peaks and the amplitude of the uniform background, we search for a layout, which minimizes the total length of connections specified by the connection function.

3. Results

We use a previously developed simulated annealing algorithm [10] to find optimized layouts for different connection functions. When the two peaks of the connection function are of the same amplitude, neurons with similar axis of motion preference form clusters, in which neurons of opposite direction preference are intermixed uniformly (Fig. 1). We use the orthogonality relation between direction and orientation preferences of a neuron to obtain the corresponding orientation map. In this case, the orientation preference map is continuous with occasional $90°$ fractures and $180°$ pinwheels. The mixing of neurons with opposite direction preference combined with clustering by orientation preference is reminiscent of the electrophysiological and optical imaging experiments in macaque area 17 [3,8].

When the ratio of the same to opposite peak amplitude is about four, neurons still form axis of motion clusters (Fig. 2). However, these clusters segregate into regions of opposite direction preference. Boundaries between these regions zigzag through clusters. In the cortical plane, direction preference changes frequently by $180°$, while axis of motion remains more continuous. This is similar to electrophysiological measurements in macaque area MT [1].

When the same direction preference peak is much higher than the opposite direction peak, Figs. 3 and 4, direction preference maps are continuous with occasional fractures. The fractures terminate at pinwheels around which direction preference changes
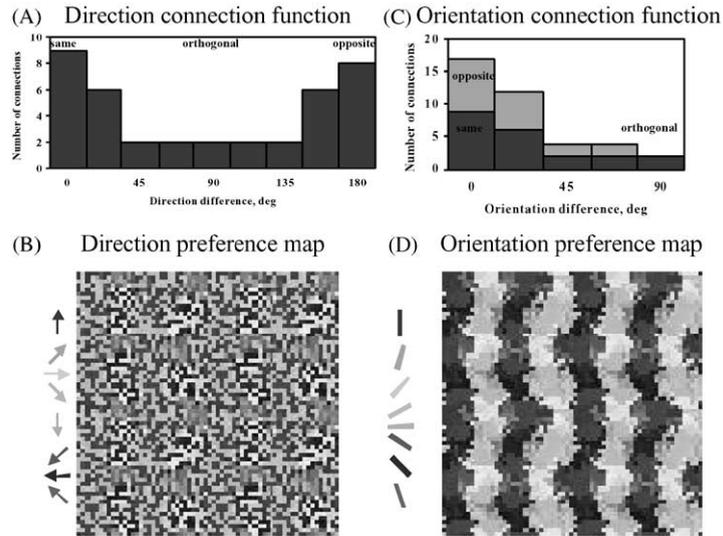
Fig. 1. (A) Direction connection function with peaks of similar amplitude. (B) Optimized direction preference map. (C) Corresponding orientation connection function following from (A). (D) Corresponding orientation preference map obtained from (B) through the orthogonality relation.
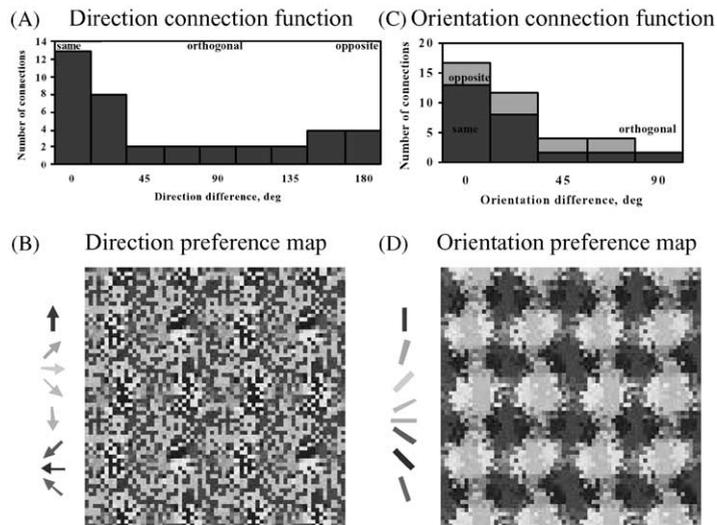

Fig. 2. (A) Direction connection function with peaks of different amplitude. (B) Optimized direction preference map. (C) Corresponding orientation connection function following from (A). (D) Corresponding orientation preference map obtained from (B) through the orthogonality relation.
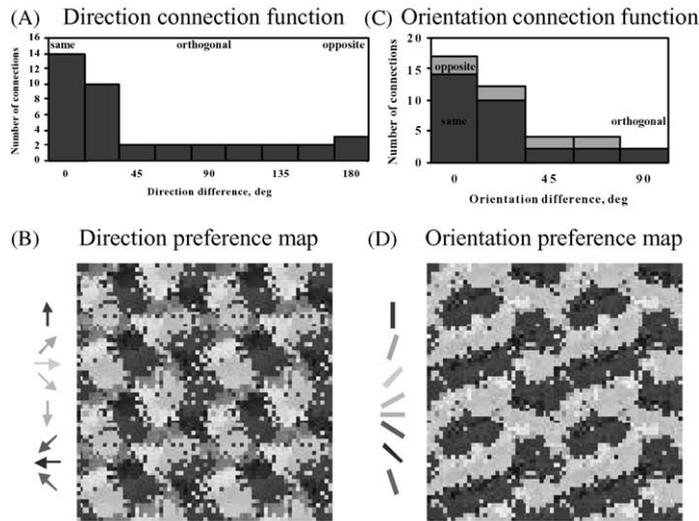
Fig. 3. (A) Direction connection function where same direction peak is much higher than the opposite direction one. (B) Optimized direction preference map. (C) Corresponding orientation connection function following from (A). (D) Corresponding orientation preference map obtained from (B) through the orthogonality relation.
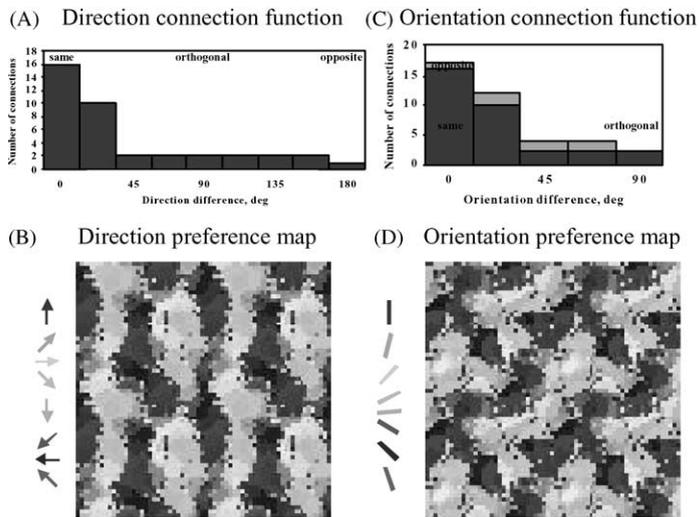

Fig. 4. (A) Direction connection function with the same direction peak only. (B) Optimized direction preference map. (C) Corresponding orientation connection function following from (A). (D) Corresponding orientation preference map obtained from (B) through the orthogonality relation.
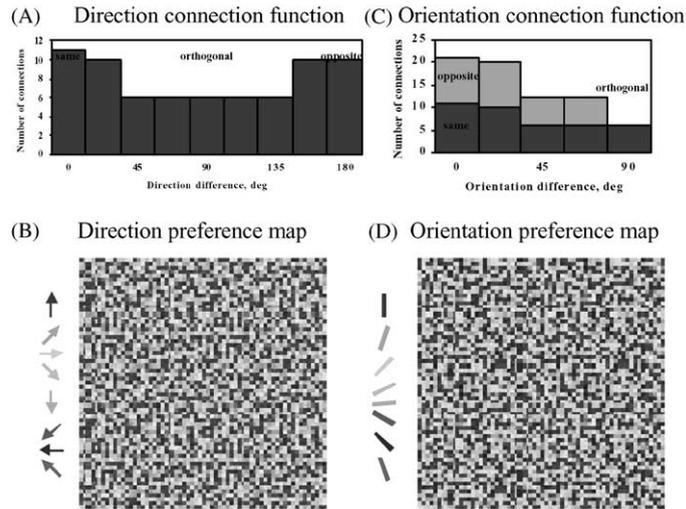
Fig. 5. (A) Direction connection function with large uniform background. (B) Optimized direction preference map. (C) Corresponding orientation connection function following from (A). (D) Corresponding orientation preference map obtained from (B) through the orthogonality relation.

gradually by $180°$ and jumps by $180°$ at the fracture. Since preferred orientation is orthogonal to direction this implies smooth orientation maps with occasional $180°$ pinwheels consistent with observations in ferret area 17 [17], cat areas 17 [9,16] and 18 [15], and owl monkey MT [11].

Finally, when the uniform background of the connection function is large, we get a *Salt& Pepper* layout both for direction and orientation preference maps (Fig. 5).

4. Conclusion

We obtain direction preference maps for different statistics of intra-cortical connectivity by using wire length minimization approach. We propose that the observed variability in map appearance between cortical areas and species may be due to differences in intra-cortical connectivity. Thus, we establish a link between connectivity and map appearance. This link allows one to infer statistics of intra-cortical connectivity from the appearance of direction preference maps.

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