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Pinwheel-dipole configuration in cat early visual cortex

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ABSTRACT

In the early visual cortex, information is processed within functional maps whose layouts are thought to underlie visual perception. However, the precise organization of these functional maps as well as their interrelationships remain unsettled. Here, we show that spatial frequency representation in cat early visual cortex exhibits singularities around which the map organizes like an electric dipole potential. These singularities are precisely co-located with singularities of the orientation map: the pinwheel centers. To show this, we used high resolution intrinsic optical imaging in cat areas 17 and 18. First, we show that a majority of pinwheel centers exhibit in their neighborhood both semi-global maximum and minimum in the spatial frequency map (i.e. extreme values of the spatial frequency in a hypercolumn). This contradicts pioneering studies suggesting that pinwheel centers are placed at the locus of a single spatial frequency extremum. Based on an analogy with electromagnetism, we proposed a mathematical model for a dipolar structure, accurately fitting optical imaging data. We conclude that a majority of orientation pinwheel centers form spatial frequency dipoles in cat early visual cortex. Given the functional specificities of neurons at singularities in the visual cortex, it is argued that the dipolar organization of spatial frequency around pinwheel centers could be fundamental for visual processing.

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Introduction

The brain contains the representations of multiple sensory features that form continuous and orderly maps. These maps subtend perception, yet the principles governing their organization remain fundamentally unknown. Uncovering the fine structure of maps can reveal their underlying organizing principles and shed new light on how the brain processes the sensory information.

The early visual cortex (V1 and V2) of higher mammals provides a particularly appropriate cortical area to investigate these questions. Its neurons are selective locally to several attributes of the visual scene, such as the orientation (OR) of a stimulus (Hubel and Wiesel, 1959) and its spatial frequency (SF) (Movshon et al., 1978). Neurons with similar functional properties are clustered vertically and form functional maps parallel to the cortical surface. The organization of the OR map has been extensively studied in the past 20 years: it consists of regular zones where preferred OR varies smoothly, together with singularities, the *pinwheel centers* (PCs), in the vicinity of which all ORs are represented (Bonhoeffer et al., 1995).

In contrast, the existence and the organization of the SF map have been the subject of long-standing debates over the last decades. Evidence however accumulates that SF is organized in a continuous manner in several mammals, including cat (Issa et al., 2000; Villeneuve et al., 2009; Tani et al., 2012; Ribot et al., 2013; but see Sirovich and Uglesich, 2004) and monkey (Nauhaus et al., 2012). Yet, how the layout of the SF map is constrained to the OR map and how these constrained might subtend visual perception remain disputed. In cat, for instance, pioneering investigations have suggested that OR PCs are situated preferentially at local SF extrema (Shoham et al., 1997; Issa et al., 2000, 2008). These results fit with the uniform coverage hypothesis (Swindale et al., 2000) according to which all combinations of the attributes should be uniformly represented in the cortex. On the other hand, it was recently argued that these findings might be the result of high-pass filtering methods leading to extreme SF values being over-representation at PC (Ribot et al., 2013). Instead, these new data based on recent intrinsic optical imaging techniques (Kalatsky and Stryker, 2003) have rather suggested that SF gradients were sharp in these cortical locations (Ribot et al., 2013), arguing against uniform coverage hypothesis at PCs.

In this study, we reexamined this issue, and used high-resolution intrinsic optical imaging in cat visual cortex area 17 (A17) and area 18 (A18) to map the SF structure near OR PCs. First, we show that at a majority of pinwheel locations, the SF representation covers a wide range of SFs, with values including semi-global minima and maxima

Abbreviations: OR, Orientation; SF, Spatial frequency; PC, Pinwheel center; A17, Area 17; A18, Area 18.

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found over a hypercolumn. This intriguing property prompted a more accurate description of the structure of the SF representation. To this purpose, we introduced a mathematical model for a dipolar structure and show that it could be accurately fitted to the SF map near a majority of PCs. The functional role of this pinwheel-dipole configuration is then discussed and it is proposed that representing a large range of SFs close to PCs is beneficial for visual perception.

Materials and methods

Five adult cats (two males, three females), aged between 24 and 72 weeks and born from different litters in our colony, were studied. They were all in good health and had no apparent malformations or pathologies. All experiments were performed in accordance with the relevant institutional and national guidelines and regulations i.e. those of the Collège de France, the CNRS and the DDPP (JO 87-848, consolidated after revision on May 30, 2001, Certificate no. 75–1754, French "Ministère de l'Agriculture et de la Pêche"). They also conformed to the relevant regulatory standards recommended by the European Community Directive (Directive 2010/63/UE) and the US National Institutes of Health Guidelines.

Surgical procedure

On the day of the optical imaging experiment, animals were anaesthetized with Saffan® (initial, i.m., 1.2 mg/kg; supplements, 1:1 in saline, i.v. as needed). After tracheal and venous cannulation, electrocardiogram, temperature and expired CO_2 probes were placed for continuous monitoring. Animals were installed in a Horsley-Clarke stereotaxic frame and prepared for acute recordings. The scalp was incised in the sagittal plane, and a large craniotomy was performed overlying areas 17 and 18 of both hemispheres. The nictitating membranes were then retracted with eye drops (Neosynephrine® 5%, Ciba Vision Ophthalmics, France) and the pupils dilated with atropine eye drops (Atropine 1%, MSD-Chibret, France). Scleral lenses were placed to protect the cornea and focus the eyes on a tangent screen at a distance of 28.5 cm. The size of the lenses was adapted to the eye of each cat. Animals were then paralyzed with an infusion of Pavulon (0.2 ml/kg, i.e., 0.4 mg/kg i.v.) and breathing was assisted artificially through a tracheal cannula with a 3:2 mixture of N_2O and O_2 containing 0.5–1.0% isoflurane. The respiration frequency was adjusted to around 18 per minute and the volume adapted to the ratio of exhaled CO_2 (pCO_2 was maintained at 4%). Paralysis was maintained throughout the recording by continuous infusion of a mixture of Pavulon (0.1 ml/kg/h) diluted in glucose (5%) and NaCl (0.9 g/l). At the end of the recording session, the animal was given a lethal dose of pentobarbital. The experiments lasted less than 12 h.

Optical imaging

The cortex was illuminated at 545 nm to reveal the vascular pattern of the cortical surface and at 700 nm to record the intrinsic signals. The focal plane was adjusted to 500 μm below the cortical surface. The optic discs were plotted by tapetal reflection on a sheet of paper covering the tangent screen. The centre of the screen was situated 8 cm (~15°) below the middle of the two optic discs, that is, ~8.5° into the lower visual field (Bishop et al., 1962). Intrinsic optical signals were recorded while the animal was exposed to visual stimuli displayed on a CRT monitor. The size of the display subtended a visual angle of ~75° × 56°. The image had a resolution of 14 pixels per degree and the refresh rate was 88 Hz. Frames were acquired by CCD video camera (1 M60, Dalsa, Colorado Springs, USA) at the rate of 40 frames per second and were stored after binning by 2 × 2 pixels spatially and by 12 frames temporally using the LongDaq system (Optical Imaging Inc., New York, USA). In three animals, images were acquired at a resolution of approximately 15.3 μm/pixel via a 50 × 50 mm tandem lens configuration. To illustrate the fine representation of SF around OR PC (Fig. 5 and Fig. S3), a 135 × 50 mm configuration was used to reach a spatial resolution of 5.9 μm/pixel.

Stimulation

Full-screen visual stimuli were presented continuously to the animal. Each stimulus consisted of sine-wave gratings drifting in one direction and rotating in a counter-clockwise manner (Kalatsky and Stryker, 2003). The angular speed of the rotation was 2 rotations per min. The temporal frequency of the drift was 2 Hz (Khaytin et al., 2008, Ribot et al., 2008). The contrast was set at 50% to ensure the production of smooth sine wave gratings (Xu et al., 2007). Thirty SFs ranging linearly in a logarithmic scale from 0.039 to 3.043 cycle/degree (cpd) were presented in random order. Ten full rotations were presented for each SF. At the end of the last rotation, the first frame of the first rotation for the next SF was presented without interruption. The total duration of the recording was 2.5 h.

Image processing

Data analysis was based on the method developed by Kalatsky and Stryker (2003) to extract periodic signals from intrinsic data in Fourier space. First, data were pre-processed to remove slow-varying components. A common approach for this is high-pass filtering of images (Vanni et al., 2010). However, since SF representation is anisotropic in both A17 and A18, active domains may have very different sizes depending on the stimulus SF. High-pass filtering is thus risky since it spatially limits the size of the activated areas. Here, we used a multivariate analysis technique, the generalized indicator function method (Yokoo et al., 2001; Ribot et al., 2006) that does not require any assumptions about the spatial characteristics of the activity patterns. This method was originally developed for bloc design experiments, but can be applied as such for periodic stimulation paradigms (one frame corresponds to one stimulus). It identifies the stimulus-related activity patterns (signals), without prior knowledge about the signal and noise characteristics. The extracted signals, that is, the generalized indicator functions, are determined by maximizing the weighted difference between the signal variance and the noise variance. This algorithm efficiently extracts stimulus-related activity patterns from noisy signals originating mainly from blood vessels and spatially slowly varying fluctuations inherent in the recorded signals. This procedure was applied to raw data for each SF separately. A low-pass filter with a Gaussian kernel of around 30 μm half width was also applied for smoothing the data.

To construct the OR map, a Fourier transform was performed on the temporal signal of each pixel for all SFs together. The phase at the frequency of rotation was calculated to obtain the preferred OR (plus the hemodynamic delay) at each pixel (Kalatsky and Stryker, 2003). This operation was motivated by the observation that preferred orientation in A17 is invariant to the SF of stimulation (Webster and De Valois, 1985; Issa et al., 2000; Ribot et al., 2013). The hemodynamic delay (approximately 2.5 s) was subtracted from all OR maps.

Then intrinsic signals related to each SF were considered separately. For each pixel, a smooth cosine function whose phase was equal to the preferred OR at this pixel and whose frequency was equal to twice the frequency of rotation, was fit to the data. This operation was motivated by the fact that signal-to-noise ratio around PCs is weak compared to regular domains. The calculation of the orientation maps through a direct Fourier transform for each SF could thus lead to some local artifacts at these cortical locations. The fitting thus helps limiting these artifacts by solely keeping the relevant signal modulation at the preferred orientation. As a result, magnitude maps for preferred ORs were obtained for each stimulus SF. These maps are referred as "maximal intensity maps". Pixels with negative values, which corresponded to interpolation peaking at orthogonal ORs, were rectified to zero. Then, values were rescaled for each pixel by setting the greatest value among all SFs to 100 (Fig. S1).

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