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ORGANIZATION OF SPATIAL FREQUENCY IN CAT STRIATE CORTEX

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Abstract—Primary visual cortex, the first cortical stage of visual information processing, is represented by diverse functional maps that demonstrate the selectivity for specific visual features such as spatial frequency (SF). Although the local organization of SF maps in cat area 17 (A17) has been largely investigated, the global arrangement remains elusive. To address this unclear aspect, we evaluated the organization of SF maps within A17 by intrinsic signal optical imaging and extracellular electrophysiological recording. Our results explicitly showed that SF organization in cat A17 displayed a global asymmetrical unimodal distribution. In particular, we found the highest SF preference within the global distribution concentrated around the horizontal meridian. These results significantly contribute to a more comprehensive understanding of the SF organization in visual cortex.

Key words: cat, striate cortex, A17, spatial frequency, optical imaging, electrophysiology.

INTRODUCTION

The visual properties of columnar organized visual attributes, such as orientation and retinotopy in cat primary visual cortex (V1), were first described by the pioneering work of Hubel and Wiesel (Hubel and Wiesel, 1959, 1963). In the following decades, psychometric studies on the visual recognition rules of spatial frequency (SF) suggested that the human visual system contains sensory channels selectively sensitive to different SFs (Sachs et al., 1971; Stromeyer et al., 1972). Further anatomical and physiological experiments aimed to elucidate the origin of distinct SF representations. Studies in cats defined two principal afferent pathways named X and Y pathways (Sherman, 1985). X cells possess small visual receptive fields and respond preferentially to high SF and low temporal frequency (TF), while Y cells with big receptive fields prefer low SF and process visual information of the basic visual forms (Derrington and Fuchs, 1979; Stone et al., 1979; Shapley and Lennie, 1985; Sherman, 1985). These features may suggest that the presence of high- and low-SF selectivity in V1 is due to the anisotropic X/Y inputs from the lateral geniculate nucleus (Shoham et al., 1997).

SF patch arrangement in a local region of the cat visual cortices has been characterized by numerous experiments (Bonhoeffer et al., 1995; Hübener et al., 1997; Grinvald et al., 1986; Shoham et al., 1997; Everson et al., 1998; Issa et al., 2000). Recent studies discovered a global anteroposterior SF gradient within cat area 17 (A17) (Tani et al., 2012; Ribot et al., 2013). However, this global distribution of SF preference is in contradiction with the fact that the cortical region representing the area centralis should exhibit higher spatial resolution than that representing the peripheral visual fields (Tusa et al., 1978; Movshon et al., 1978b). Together with the retinotopic organization of A17, we questioned the smooth gradient distribution of SF preference.

To address this question, we used a combination of intrinsic signal optical imaging and extracellular electrophysiological recording to characterize the organization of SF maps in the cat striate cortex.

EXPERIMENTAL PROCEDURES

Six healthy adult cats, weighing 2–3 kg, were studied in this experiment. All surgical and experimental procedures were conducted in accordance with protocols approved by the Animal Care and Use Committee at University of Science and Technology of China (USTC).

Surgical procedure

Cats were initially anesthetized by intramuscular injection of ketamine (25 mg/kg). Lidocaine was applied to all wounds to reduce local pain. Tracheal and venous catheterizations were performed. The cat was then placed into the Horsley–Clarke stereotaxic apparatus mounted on a vibration isolation table. During the subsequent experiments, cats were treated with pentobarbital sodium (20 mg/kg/h, i.v.) to maintain a constant level of anesthesia. Gallamine triethiodide (10 mg/kg/h, i.v.) was used to keep muscle paralyzed. Electrocardiogram, temperature, and expired carbon dioxide (CO_2) were monitored during the experiments. Artificial respiration was performed by a ventilator to

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Abbreviations: A17, area 17; A18, area 18; DSI, direction selectivity index; HWHH, half-width at half-height; OSI, orientation selectivity index; ROI, region of interest; SF, spatial frequency; TF, temporal frequency.

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keep the respiration frequency at a constant rate of ~23 breaths/min and the end-tidal CO_2 around 4%. The body temperature was maintained at 37.5 °C through a feedback-controlled heating pad. Miosis was alleviated by tropicamide (0.25%). Nictitating membrane was retracted by phenylephrine hydrochloride (1%). Corrective or plano contact lenses were chosen, by streak retinoscopy, and mounted to focus the eyes on the stimulus monitor. Dexamethasone (2 mg/ml), penicillin (0.1 g/ml) and atropine (1 mg/ml) were intramuscularly injected every 12 h to prevent for brain edema, infection and hypersecretion of mucus in the respiratory tract, respectively. The craniotomy was performed according to the position in the Horsley–Clarke coordinate (e.g. A5–P15, L0–L10). For intrinsic signal optical imaging, a customized steel chamber was immobilized onto the skull by dental acrylic, filled with silicone oil (Sigma–Aldrich, DMPS-5X) and sealed with a polycarbonate cover slip. We had the dura cleaned and chamber refilled every few hours to ensure the imaging quality. For electrophysiological recording, a customized plastic chamber was placed, filled with agar (3% agar in 0.9% saline) and sealed with silicon oil.

Visual stimuli

Full-screen visual stimuli were created by MATLAB using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). A high refresh rate (1920*1080 pixels, 144 Hz) LCD monitor was placed 30 cm in front of the animals' eyes. Gamma correction was performed to maintain the mean luminance of monitor at 32 cd/m^2. Drifting sinusoidal gratings and rotating square wave gratings were used. The contrast of gratings was maintained at one. The SF of drifting gratings used for intrinsic signal optical imaging was set from 0.05 to 2.4 cycle per degree (0.05, 0.1, 0.2, 0.4, 0.8, 1.2, 1.6, 2.0 and 2.4 cpd). For conventional optical imaging, the drifting sinusoidal gratings moved back and forth perpendicularly to each orientation (0° to 157.5° in steps of 22.5°; 2 s for each direction). The inter-stimulus interval was 13 s. For Fourier optical imaging (Kalatsky and Stryker, 2003), square wave gratings with different SFs was centered at the central fixation point rotated in full-screen. The angular speed of rotation was two rotations per minute. For electrophysiological recording, all stimuli were displayed in a circular window covering the receptive field. Preferred orientation and direction tunings were studied using sinusoidal gratings at five orientations moving in orthogonal directions (0° to 270° in steps of 30°). Preferred TF was examined using four stimulus TFs (1, 2, 4 and 8 Hz). Optimally directed sinusoidal gratings with preferred TFs were used for further SF-tuning tests. Nine different SFs (0.1, 0.2, 0.4, 0.8, 1.2, 1.6, 2.0, 2.4 and 2.8 cpd) were tested. Each stimulus contained 5 cycles of drifting sinusoidal gratings. Trials were interspersed with gray blank stimuli of 2 s.

Intrinsic signal optical imaging and data analysis

In this study, classical (Bonhoeffer and Grinvald, 1991) and modified paradigm (Kalatsky and Stryker, 2003) intrinsic signal optical imaging were used. Three cats underwent both imaging paradigms, while other two cats were studied using the classical imaging. Our customized optical imaging system was described earlier (An et al., 2014b). The recorded area was illuminated by a 550-nm green light to obtain the surface vasculature patterns or a 630-nm red light to acquire evoked response. A CCD camera (Dalsa, Pantera 1M60) was used to collect experimental data. The resolution of imaging was ~17 μm/pixel.

For conventional imaging, each trial had a pair of complementary visual stimuli. For example, gratings with orientations of 0° and 90° were considered as a pair of complementary stimuli. Before the stimulus onset, cortex condition was recorded at 16 frames per second for 1 s under the 630-nm red light. The response during this second was averaged and defined as the blank frame. Next, visual responses to stimuli were recorded at the same rate for a period of 8 s. Data were typically averaged over 32 or 64 trials. Frames taken from the 2nd to the 6th second after the stimulus onset were averaged. The response signal was then subtracted and divided by the blank frame to generate the differential-condition map of reflectance change ($\Delta R/R$). Some images were high-pass filtered (33 pixels or 561 μm in radius) and smoothed (kernel of nine pixels or 153 μm in radius) using a circular averaging filter to avoid signal distortion. The border between areas 17 and 18 was determined based on the different responsive amplitudes between SF 0.15 cpd and 0.5 cpd (for classical imaging) or SF 0.1 cpd and 0.8 cpd (for Fourier imaging and some classical imaging) (Bonhoeffer et al., 1995; Ohki et al., 2000). Vector summation method (Blasdel and Salama, 1986) was used to construct the orientation preference map and orientation selectivity strength map.

For Fourier optical imaging, drifting gratings were rotated in full screen with different SFs. Fourier analysis was used to extract two matrices pixel by pixel: one for the response strength to different stimulus frequencies and the other one representing the phase of stimulus orientations. Maximal intensity map for each SF was constructed by detecting the maximum response to graphically represent the response strength for each stimulus SF over the cortical region. The color-coded preferred SF map of recorded cortical region was constructed by calculating the maximum response to all SFs.

To test the similarity or difference between two orientation preference maps, the responsive area in the maps were subtracted pixel by pixel. The angle difference was analyzed and shown using histograms. Control was obtained through subtracting the shuffled version of the responsive area in one map from the corresponding area in another map. The variability between measured and control angular differences was detected by a one-tailed Student's t-test. $P < 0.05$ was considered statistically significant.

Electrophysiological recording and data analysis

We performed single-unit recording after intrinsic signal optical imaging in 5 adult animals as described in our