

The Common and Distinct Orientation Adaptation Effect at Pinwheel Centers in Areas 21a and 17 of Cats

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Abstract—Cortices are non-uniform in their capacity for adaptive changes. In cat area 17, pinwheel centers of the orientation map demonstrated much greater selectivity shifts after the orientation adaptation than the iso-orientation domains (Dragoi et al., 2001a). However, whether this heterogeneity exists in other visual cortical regions remains unclear. Similar to area 17, area 21a neurons in cats are well known to be functionally clustered according to their orientation preference in iso-orientation domains that converge at pinwheel centers but with a higher pinwheel density (Huang et al., 2006). In this study, we simultaneously measured the adaptation effects on the orientation maps in area 17 and area 21a of anesthetized cats by intrinsic signal optical imaging. We found that in area 21a, the adaptation-induced selectivity shifts were significantly larger at pinwheel centers, similar to the findings in area 17. However, at either pinwheel centers or iso-orientation domains, the selectivity shifts in area 21a were all consistently greater than those in area 17, even though the heterogeneity in the orientation distribution was similar in the two areas. More importantly, in our short-term adaptation protocol, orientation adaptation in area 17 resulted in mostly repulsive shifts at the pinwheel center region, while in area 21a, it induced both repulsive and attractive effects. These results suggest that both common and distinct strategies exist for orientation adaptation across cortices and sub-regions. © 2018 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: intrinsic signal optical imaging, area 21a, visual adaptation, pinwheel centers, attractive shift, repulsive shift.

INTRODUCTION

Cortical neurons processing the sensory information within fine-scale networks adjust their responses continuously according to real-time dynamic inputs from the environment (Hebb, 1949; Grossberg, 2013; Miller and Buschman, 2013). Adaptation is the process of self-adjustment of the sensory system based on the content in the temporal and spatial dimensions of prior experiences (Kohn, 2007; Webster, 2011, 2015) and reflects a kind of functional plasticity.

Previous studies in cat area 17 showed that the sensitivity of the change in preferred orientation depends on the location of neurons in the orientation map (Dragoi et al., 2001a). Neurons in iso-orientation domains had small preferred orientation shifts after orientation adaptation, whereas the selectivity of neurons located at or near pinwheel centers shifted strongly

(Dragoi et al., 2001a). The recurrent network based on the local intra-cortical inputs (Martin and Suarez, 1995; Schummers et al., 2002; Mariño et al., 2005; Ozeki et al., 2009; Stimberg et al., 2009; Adesnik et al., 2012; Shushruth et al., 2012; Priebe, 2016; Angelucci et al., 2017) could be heterogeneous due to the spatial layout of orientation columns and thus serve as a possible neural mechanism of orientation adaptation in area 17 (Dragoi et al., 2001a). It is known that area 21a has a similar organization of preferred orientation, with both pinwheel centers and iso-orientation domains (Huang et al., 2006; Villeneuve et al., 2009). However, little is known about whether area 21a will follow a similar intra-cortical mechanism and thus demonstrate spatially heterogeneous orientation adaptation effects.

In addition to the intra-cortical recurrent network, various other factors may also influence the adaptation effect. Our previous work showed that the selectivity shifts in preference of area 21a were greater than those of area 17 as a whole (Li et al., 2017), and consistent findings were observed between the lateral geniculate nucleus (LGN) and primary visual cortex (V1) (Dhruv and Carandini, 2014) and between the V1 and middle temporal visual area (MT) (Kohn and Movshon, 2003, 2004; Patterson et al., 2014b), suggesting a cascading effect across different regions along the bottom-up visual

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Abbreviations: IPS, inside the pinwheel surround region; LGN, lateral geniculate nucleus; OPC, outside the pinwheel center region; OPS, outside the pinwheel surround region.

system (Dhruv and Carandini, 2014; Larsson et al., 2016). In addition, adaptation might induce the neuronal preference to be either away from (repulsive) or toward (attractive) the adapter depending on the cortical regions (Kohn and Movshon, 2004), stimulus size (Wissig and Kohn, 2012; Patterson et al., 2013), and stimulus duration (Yao and Dan, 2001; Ghisovan et al., 2008, 2009; Patterson et al., 2013). These factors might sometimes be intermingled with the influence of the intra-cortical network. For example, there is a higher pinwheel center density in area 21a (Huang et al., 2006; Li et al., 2017). If a local region at pinwheel centers has greater plasticity in area 21a, similar to the case in area 17 (Dragoi et al., 2001a), the overall enhanced adaptation effect from area 17 to area 21a may be explained by the local intra-cortical network instead of a bottom-up, feed-forward mechanism. It is thus crucial to design the experiment to differentiate these factors in both areas 17 and 21a.

In this study, we simultaneously imaged the orientation maps in areas 17 and 21a when an identical adaptation protocol was presented and then analyzed the orientation adaptation effects at pinwheel centers, as well as in regions far away from the pinwheel centers. We found that in both areas 17 and 21a, there were greater selectivity shifts at the pinwheel centers. However, the magnitudes of the shifts in area 21a were significantly larger than those in area 17, both at the pinwheel centers and in the regions away from pinwheel centers. In addition, the direction of the selectivity shift (repulsive / attractive) also differed in those two areas.

EXPERIMENTAL PROCEDURES

Study approval

Nine adult cats (either sex, age: 1–2 years old, body weight: 2.5–3.5 kg) with no optical or retinal abnormalities served as subjects. All experiments involving animals were carried out in accordance with the approved guidelines, and all animal experimental protocols were approved by the Animal Care and Use Committee of Fudan University.

Animal preparation

Anesthesia was induced by intramuscular injection of ketamine HCl (20 mg/kg) and sustained by 2.0–3.0% isoflurane (RWD Life Science Co., China) during the surgery. Then, noninvasive tracheal and intravenous cannula intubation was performed under sterile preparations. After the surgery, 1.0–2.0% isoflurane and gallamine triethiodide (8–10 mg/kg/h) were infused intravenously to maintain necessary anesthesia and paralysis. Artificial respiration was performed (6025, UGO Basile, Italy), and expired pCO₂ was maintained at approximately 3.8%. The body temperature was maintained at 38.0 °C by the automatic temperature control system (BME-461A, Institute of Biomedical Engineering, CAMS). Electroencephalograms (EEGs) and electrocardiograms (ECGs) were monitored

throughout the experiment to ensure adequate anesthesia. Pupils were maximally dilated with atropine (1%) and fitted with appropriate contact lenses to protect the cornea from dryness and to correct the visual acuity. Neosynephrine (5%) was administered to retract the nictitating membranes. A craniotomy and durotomy were performed at Horsley–Clarke coordinates P0–P10, L0–L12 to expose both areas 17 and 21a. In this work, the large window was useful to obtain a large orientation map of both areas 21a and 17 in one imaging field, and to identify the location of area 21a based on the relationship to the lateral suprasylvian and lateral sulci (Tusa and Palmer, 1980; Van Der Gucht et al., 2001). In addition, the methods to structurally and functionally determine the imaging site of area 21 and area 17 were identical to those used in our previous work (Li et al., 2017). In brief, area 21a is located in the middle part of the caudal suprasylvian gyrus, defined by anatomical connections and retinotopic organization in cats and bounded medially and caudally by area 19 (Tusa and Palmer, 1980; Van Der Gucht et al., 2001). To ensure our recording location in area 21a, an electrode was left in the recorded area 21a, and we reconstructed the electrode track to confirm the imaging location (Li et al., 2017). Furthermore, we used orientation maps with different spatial frequencies to precisely distinguish areas 17 and 18 (Hung et al., 2001). The location of the 17/18 border is clearly differentiated by subtraction of the low (0.1 cycle/°) and high spatial frequency responses (0.5 cycle/°) (Li et al., 2017).

The dura was removed under light microscopy and replaced with an artificial dura (0.005-in. Silicon Sheeting, Specialty Manufacturing Inc., USA). It was then covered with 3% agar (Type 1 Low EEO, Sigma–Aldrich, USA) in 0.9% saline and sealed with a transparent cover glass. This chronic transparent window was cemented to the skull by super dental bond (Super-Bond C&B, Sun Medical Co., Japan). After 3 days of recovery, we imaged and compared the orientation maps (Fig. 1E, color-coded preferred orientation map) for the two areas simultaneously.

Stimuli

The visual stimuli were sine wave gratings generated by MATLAB programs based on Psychtoolbox (Brainard, 1997) and presented on a CRT monitor. The cats were stimulated binocularly with full screen at a viewing distance of 57 cm. To optimize the functional maps of areas 17 and 21a simultaneously (Villeneuve et al., 2009), we selected the same stimulus parameters for two areas: spatial frequency, 0.3 cycle/°; temporal frequency, 2 Hz.

The procedures of intrinsic signal optical imaging were described in our previous studies (Huang et al., 2006; Shen et al., 2006; Yu et al., 2008; Tong et al., 2011; Chen et al., 2014; Li et al., 2017). We adopted the classic top-up adaptation protocol (Movshon and Lennie, 1979; Carandini et al., 1998; Dragoi et al., 2000; Kohn and Movshon, 2003, 2004; Engel, 2005), and the stimulus protocols were in line with the one used in our previous

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