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SPATIOTEMPORAL PROFILES OF NEURONS RECEPTIVE FIELDS IN THE CAT POSTEROMEDIAL LATERAL SUPRASYLVIAN CORTEX

M. PICHÉ, [†] **S. THOMAS** [†] **AND C. CASANOVA** [*]

École d'optométrie, Université de Montréal, Montréal, Québec, Canada

Abstract—The cortical area located in the lateral portion of the posteromedial suprasylvian sulcus (PMLS) is considered a key area for motion processing. It receives major projections from areas 17 and 18 but also from the lateral posterior-pulvinar complex where neurons exhibit, for the most part, complex receptive fields (RF). Based on these inputs, complex-like RFs would be expected for PMLS neurons and results from hand-plot mapping support this idea. However, PMLS neurons' first-order spatiotemporal RF profiles and their role in shaping neuronal response characteristics is currently unknown. In this study, the first-order spatiotemporal characteristics of PMLS cells were revealed using reverse correlation analysis, based on responses elicited by coarse white noise stimuli. Experiments were carried out in adult anesthetized cats. Detailed RF profiles were obtained by analyzing bright and dark subfields separately. Results indicate that the average maximal spike probability is higher for dark subfields than for their paired bright subfields. Spatial RF analysis shows that neurons exhibit oval RF subfields and that their size is larger for dark subfields. The majority of cells have complex-like profiles, with spatially overlapping RF subfields. Temporal analysis showed that for the majority of cells, subfields are coincidentally activated; however, a subset of neurons exhibit time-dissociated subfield peak activity windows. Correlation analysis between spatial and temporal parameters of RF subfields and their neuron's response characteristics to gratings was also performed. The data show that the direction index is positively correlated with subfield size difference and negatively correlated with spatial subfield overlap. Modulation index is negatively correlated with the degree of temporal subfield activity overlap. We conclude that first-order RF structures are important functional factors that shape PMLS neurons response characteristics.

Key words: reverse correlation, PMLS, electrophysiology, extrastriate cortex, visual pathways.

INTRODUCTION

The processing of visual information across cortical areas is thought to be carried out in a sequential manner, along two parallel pathways (Stone et al., 1979; Lennie, 1980). Based mainly on neuroanatomical findings, cortical hierarchies have been proposed for both pathways. Along the putative dorsal stream in cats (Lomber, 2001), the posteromedial lateral suprasylvian cortex (PMLS) receives inputs from cortical areas 17 and 18 (Maciewicz, 1974; Symonds and Rosenquist, 1984; Einstein and Fitzpatrick, 1991; Lowenstein and Somogyi, 1991; Shipp and Grant, 1991; Norita et al., 1996). These inputs originate from the supragranular layers where the vast majority of neurons are known to be complex cells (Hubel and Wiesel, 1965; Gilbert, 1977; Ferster, 1981; Martinez et al., 2005). Building upon these inputs, the receptive fields (RFs) of PMLS neurons would be expected to respond to more complex stimulus features. Physiological investigations of PMLS neurons support this idea, as larger RFs have been described in PMLS than in area 17 (Hubel and Wiesel, 1969; Spear and Baumann, 1975; Zumbroich and Blakemore, 1987). Additionally, global motion stimuli evoke direction selective responses in PMLS while this is not the case in area 17 (Toyama et al., 1990; Kim et al., 1997; Mulligan et al., 1997; Brosseau-Lachaine et al., 2001; Villeneuve et al., 2006). The RF features of PMLS neurons could also result from the integration of other input sources. For example, the LP-pulvinar thalamic complex densely innervates layer IV of PMLS cortex (Rauschecker et al., 1987b) and could play an important role in modulating the RFs properties of PMLS neurons.

While the response properties of neurons in PMLS have been described by several groups (for a review: Spear, 1991, for more recent work: Sherk and Mulligan, 1992; Minville and Casanova, 1998; Merabet et al., 2000; Brosseau-Lachaine et al., 2001; Sherk and Kim, 2002; Villeneuve et al., 2006), the spatiotemporal structure of their RFs is relatively unknown (Borghuis

[*]Corresponding author. Address: Visual Neuroscience Laboratory, School of Optometry, Université de Montréal, CP 6128, succ. Centre-ville, Montréal, Quebec H3C 3J7, Canada. Tel: +1-514-343-2407; fax: +1-514-343-2382.

E-mail address: christian.casanova@umontreal.ca (C. Casanova).

URL: http://www.opto.umontreal.ca/neurosciences (C. Casanova).

[†] Both authors contributed equally to this work.

Abbreviations: DI, direction index; LGN, lateral geniculate nucleus; MI, modulation index; OA, overlapping area; PLLS, posterolateral suprasylvian sulcus; PMLS, posteromedial suprasylvian sulcus; PPI, peak probability index; RF, receptive field; SEM, standard error of mean; SD, standard deviation; SF, spatial frequency; SOI, spatial overlap index; SSI, subfield size index; TOI, temporal overlap index; TF, temporal frequency.

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et al., 2003), especially in regard to their first-order structure.

Thus, we studied spatial and temporal characteristics of RFs in PMLS using coarse white noise stimuli and reverse correlation analysis as previously done in areas 17 and 18 (Jones and Palmer, 1987; Szulborski and Palmer, 1990; DeAngelis et al., 1993, 1995; Ringach et al., 1997) and in the LP-pulvinar complex (Casanova et al., 2008). Here, first-order spatial and temporal profiles of bright and dark subfields from PMLS neurons are described. We found that the majority of cells had spatially overlapping subfields, with the average area of dark subfields larger than its bright counterpart. Temporal profiles indicated that the majority of cells have temporally coinciding activity, but careful analysis revealed the presence of cells with distinct time-dissociated subfield peak activity windows. Correlations between response properties of cells to drifting sine wave gratings and characteristics from their spatial and temporal profiles were calculated. It was found that first-order RF structures correlated well with direction and modulation indices, traditionally associated with second-order RF structures (Borghuis et al., 2003).

EXPERIMENTAL PROCEDURES

Animal preparation

All procedures were performed in accordance with the directives of the Canadian Council for the Protection of Animals and the Ethics review board of the Université de Montréal. Adult cats (2.5–4.5 kg) were premedicated with atropine (0.1 mg/kg) and Atravet (1 mg/kg). 30 min later, anesthesia was induced with isoflurane (5%), in a 50:50 (vol/vol) mixture of O_2 and N_2O, subsequently lowered to 2%. Pulse and blood O_2 saturation levels were monitored with an oxymeter. A local anesthetic (lidocaine hydrochloride 2%) was applied to incision and pressure points. A polyethylene tube was inserted into the cephalic vein for intravenous administration of drugs, and a tracheotomy was performed prior to transferring the animal to the stereotaxic apparatus.

Following administration of gallamine triethiodide (10 mg/kg/h) in lactated Ringer's solution, animals were artificially ventilated with isoflurane (2%) in a mixture of N_2O/O_2 (70:30). Expired level of CO_2 was maintained between 28 and 32 mmHg by adjusting the tidal volume and respiratory rate. Rectal temperature was monitored and maintained at approximately 38 °C. The electrocardiogram (ECG) and electroencephalogram (EEG) were continuously monitored. Pupils were dilated and nictitating membranes retracted with atropine (1%) and phenylephrine hydrochloride (2.5%), respectively. The eyes were then protected with contact lenses with the appropriate refractive power. A craniotomy (Horsley-Clarke coordinates AP: −3 to +4, ML: 10 to 15) exposed a portion of the medial lateral suprasylvian sulcus as defined by Palmer et al. (1978). Varnished tungsten microelectrodes (3–5 MΩ, H.-J. Winston, Winston-Salem, North Carolina) were angled at approximately 40° in order to follow the slant of the sulcus. The craniotomy was filled with warm agar and covered with melted wax in order to create a sealed chamber. Since isoflurane has a strong depressive effect on the amplitude of the visual responses (Villeneuve and Casanova, 2003), it was replaced by halothane (0.5–1%) during recording sessions.

Electrolytic lesions were performed at several points along each successful penetration. Upon termination of the experiment, the animals were intravenously administered pentobarbital sodium (Euthanyl: 240 mg/ml, 110 mg/kg) and then perfused through the left ventricle with phosphate buffer solution and fixative (4% paraformaldehyde). Using a cryostat, coronal serial sections (40 μm) that included the cortex surrounding the suprasylvian sulcus were cut and Nissl stained.

Recordings

Electrophysiological signals were amplified, band-pass filtered (300 Hz–10 kHz) and fed to a window discriminator (WPI 121, WPI Inc., Sarasota, USA) to isolate action potentials from the background neuronal activity using an amplitude threshold, manually determined. The analog signal, digitized action potentials, and stimulus presentation time stamps were fed into a CED 1401 plus data acquisition board and acquired with Spike2 v5 (CED, Cambridge, UK). Using Spike2, single units were isolated by shape discrimination, when applicable. Data sampling was performed at 25 kHz and saved for later analysis, although online analysis was also carried out in order to direct further tests.

Visual stimulation

Prior to stimulation, RFs and ocular dominance were qualitatively assessed with a hand held light source displaced on the screen. Subsequent stimulations were monocular. Stimuli were back projected onto a translucent screen placed 57 cm in front of the animal, and the stimulated area covered 75° × 92° of visual angle. Hence, the reverse correlation stimulus was not limited to a small area in and around the RF but rather covered a large portion of the visual field. This large area of stimulation thus encompassed any region of the RF that was missed in hand mapping.

Stimuli were generated by custom software written under Python v2.3.4 (www.python.org), running on a Pentium III 930 MHz with a NVIDIA GeForce2 GTS graphics card. Stimuli consisted of a 25 cd/m^2 gray background, upon which single white (hereafter bright: 50 cd/m^2) or black (hereafter dark: ≈0 cd/m^2) squares were presented. Each neuron was tested with a series of stimuli in which the size and duration got progressively and independently smaller and/or shorter in successive stimulation blocks. A stimulus block consisted of brief presentations of a bright or dark square at different positions in the display area, with position and polarity (bright or dark) randomized, until 30 trials of each position and polarity had occurred. There was no delay between the disappearance of one square and the appearance of another. On average, responses to 660 stimulus positions were acquired for