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FUNCTIONAL SYNCHRONY AND STIMULUS SELECTIVITY OF VISUAL CORTICAL UNITS: COMPARISON BETWEEN CATS AND MICE

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Abstract—In spite of the fact that the functional organization of primary visual cortices (V1) differs across species, the dynamic of orientation selectivity is highly structured within neuronal populations. In fact, neurons functionally connect each other in an organized Hebbian process, wherein their wiring and firing are intimately related. Moreover, neuronal ensembles have been suggested to be strongly implicated in sensory processing. Within these ensembles, neurons may be sharply or broadly tuned in relation to the stimulus. Therefore, it is important to determine the relationship between the response selectivity of neurons and their functional connectivity pattern across species. In the present investigation, we sought to compare the stimulus-evoked functional connectivity between the broadly tuned and the sharply tuned neurons in two species exhibiting different cortical organization for orientation selectivity: cats (columnar-organized) and mice (salt-and-pepper organization). In addition, we examined the distribution of connectivity weights within cell-assemblies in the visual cortex during visual adaptation. First, we report that the sharply tuned neurons exhibited higher synchrony index than the broadly tuned cells in the cat visual cortex. On the contrary, in mice, the broadly tuned cells displayed higher connectivity index. Second, a significant correlation was found between the connectivity strength and the difference of preferred orientations of neurons for both species. Finally, we observed a systematic adjustment of the connectivity weights within neuronal ensembles in mouse primary visual cortex similarly to the cat V1.

Key words: visual cortex, functional connectivity, cross-correlation, visual adaptation, orientation selectivity.

INTRODUCTION

In the sensory cortex, the precise synchronous firing between neurons occurring at millisecond-scales leads to the formation of functionally emergent neuronal ensembles. In fact, different types of neurons play distinct roles in stimulus coding. Depending on the organization of the selectivity of neurons for a specific feature, e.g. oriented stimuli in the primary visual cortex (V1), higher mammals exhibit a well-established columnar organization compared with rodents, wherein local neurons have differential selectivity for orientations (Harris and Mrsic-Flogel, 2013).

The complete understanding of how different neuronal classes perform computations between themselves still eludes us. As a matter of fact, in mouse V1, the broadly tuned neurons which fire strongly to a large spectrum of orientations, are classified as inhibitory interneurons (Hofer et al., 2011). However, Runyan et al. (2010) have reported a high selectivity for this class. Other authors have reported some differences between distinctly organized cortices. For instance, in the cat visual cortex (columnar organization), layer 2/3 interneurons are generally tuned sharply to orientation (Azouz et al., 1997; Cardin et al., 2007), whereas in rodents, interneurons exhibit weak selectivity (Niell and Stryker, 2008).

In the present paper, we examined the synchrony modulation of two distinctly selective neurons (broadly tuned and sharply tuned cells) in relation to orientation in both species. Indeed, synchronous firing between neurons is an essential characteristic within sensory systems (Alonso et al., 1996) as it could be implicated in stimulus discrimination (Samonds et al., 2003). We computed cross-correlations between the spike-trains of neurons with different orientation selectivity indices (OSIs) (Atallah et al., 2012). In addition, we investigated the effect of visual adaptation on the connectivity weight in mouse V1 and compared it with results observed in cats (Bachatene et al., 2015). We found that the sharply tuned cells were strongly connected in comparison with the broadly tuned neurons in the cat V1, whereas the opposite trend was disclosed in mice. Moreover, we observed an emergence of stable ensembles with maintained connectivity-strength (CS) following visual adaptation in mice, similarly to our recent work on cats (Bachatene et al., 2015). Our findings give new insights into visual coding and neuronal type dependence of synchronous events in cats and mice.

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Abbreviations: CS, connectivity strength; FR, firing rate; OSI, orientation selectivity index.

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EXPERIMENTAL PROCEDURES

Ethical approval

The experiments followed the guidelines of the Canadian Council on Animal Care and were approved by the Institutional Animal Care and Use Committee of the University of Montreal. This research was conducted in accordance with the Guide for Care and Use of Laboratory Animals of the National Institutes of Health (USA).

Anesthesia and surgery

For cat experiments, we performed electrophysiological recordings from supra-granular layers of the primary visual cortex of eight adult anesthetized animals of either sex (2.5–3.5 kg, age 12–24 months, Felis catus). Anesthesia was maintained by artificial ventilation with a mixture of N_2O/O_2 (70:30) complemented with 0.5% isoflurane (AErrane, Baxter, Toronto, ON, Canada). Basic parameters such as EEG, expired CO_2, temperature and heart rate were supervised during the experiments. Animals were euthanized with an intravenous injection of pentobarbital sodium (Somnotol, MTC Pharmaceuticals, Cambridge, ON, Canada; 100 mg kg^{-1}).

For mice experiments, CD-1 strain adult mice aged from 9 to 11 weeks were anesthetized with intraperitoneal administration of 10% urethane (1.5 g/kg). It is to be mentioned that the definition of adulthood varies among several authors, for example: 90–100 days (Lehmann and Lowel, 2008), 70 days (Ruiz-Perera et al., 2015), 10 weeks (Leger et al., 2015) and 8 weeks (Tasic et al., 2016).

Subcutaneous injection of atropine sulfate (0.5 mg/kg) was administered to prevent the secretions inside the trachea. During the surgery, local anesthesia using lidocaine hydrochloride 2% (Xylocaine) was performed before the craniotomy. The level of anesthesia was monitored using pinch reflexes.

For visual stimulation and recording of the neural activity, the animals were moved to a stereotaxic apparatus. The animals' heads were secured in a head holder to prevent any movement. The skull and the dura mater (an area of 2.5 × 2.5 mm) over the visual cortex was dissected out.

Electrophysiology

Cats. Drifting sine-wave grating square patches (~2° to 5°) covering the excitatory RF (unidirectional movement) were generated using a VSG 2/5 graphic board (Cambridge Research Systems, Rochester, England) and displayed on a 21-inch monitor (Sony GDM-F520 Trinitron, Tokyo, Japan) placed 57 cm from the cat's eyes, with 1024 × 768 pixels, running at 100-Hz frame refresh. Optimal parameters were set to evoke maximal responses (contrast: 80%, mean luminance: 40 cd/m^2, spatial frequency: 0.1–0.5 cycles/deg, temporal frequency: 1.0–2.0 Hz). The signal from the microelectrodes (recording depth: 600 μm) was amplified and band-pass filtered (300 Hz–3 kHz). Nine orientations were randomly presented in blocks of 25 trials lasting 4.1 s each, with a random inter-trial interval (1.0–3.0 s). Single-unit spiking activity was isolated from the multi-unit activity using autocorrelograms, principal component analysis, spike wave-shapes and cluster separation.

Mice. A glass microelectrode filled with 0.9% NaCl was lowered in the primary visual cortex to record the spiking activity. Multi-unit and single-unit activities were recorded from superficial layers (100–300 μm). The signal was filtered within a range of 300 Hz–3 kHz. Multi-unit activity was recorded using data acquisition software (Spike 2, Cambridge Electronic Design, CED Limited, Cambridge, England). As for the cat experiments, single-unit spiking activity was isolated using autocorrelograms, principal component analysis, spike wave-shapes and cluster separation.

The stimuli covered ±30° horizontally and ±30° vertically of the mouse monocular field. The center of the monitor was positioned at about 45° azimuth 0° elevation. We used drifting full-contrast square sine wave gratings generated with a VRG Volante 34020 graphic board (Vision Research Graphics, New Hampshire, USA) and presented on a 21-inch monitor (60 Hz refresh rate, Mitsubishi FHS6115SLK Color Display Monitor, Tokyo, Japan) with 1024 × 6512 pixels placed 28.5 cm from the animal's eye. Optimal parameters were used in order to evoke the maximal firing; spatial frequency: 0.07 cycles/deg, velocity: 4 deg/s, temporal frequency: 2 Hz.

The presentation of stimuli, their duration and the inter-trial interval were similar to cats' experiments.

Visual adaptation for mice experiments

Once control orientation tuning curves were characterized, an adapting orientation was presented continuously for a period of 12 min (no recording during this time). Following this procedure, all the orientations were presented (post-adaptation) starting with the adapting orientation while the remaining orientations were recorded in a random order (Jeyabalaratnam et al., 2013).

Orientation tuning curves and OSI

After the isolation of single-unit activity of each neuron, the preferred orientations of all neurons were determined. Gaussian tuning curves were fitted from the raw data using the following equation:

$$y = y0 + \left(A \div \left(w \times \sqrt{\left(\frac{\pi}{2}\right)}\right)\right) \times e^{\left(-2\times\left(\frac{(x-xc)}{w}\right)^2\right)}$$

where $y0$ is the offset, xc is the center, w is the width and A represents the area.

Neurons were classified based on their stimulus selectivity. The OSI was calculated for every neuron as the difference between the firing rate (FR) at preferred and orthogonal orientations, as follows (Denman and Contreras, 2014):