



Research paper

Interplay of orientation selectivity and the power of low- and high-gamma bands in the cat primary visual cortex



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HIGHLIGHTS

- The gamma-power is high for highly selective neurons in the low-gamma band.
- The gamma power is high for weakly selective neurons in the high-gamma band.
- The power in low-gamma band declines with decrease in OSI.
- The power in high-gamma band increases with decrease in OSI.
- The spike-width and OSI exhibit no relation with each other.

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ABSTRACT

Gamma oscillations are ubiquitous in brain and are believed to be inevitable for information processing in brain. Here, we report that distinct bands (low, 30–40 Hz and high gamma, 60–80 Hz) of stimulus-triggered gamma oscillations are systematically linked to the orientation selectivity index (OSI) of neurons in the cat primary visual cortex. The gamma-power is high for the highly selective neurons in the low-gamma band, whereas it is high for the broadly selective neurons in the high-gamma band. We suggest that the low-gamma band is principally implicated in feed-forward excitatory flow, whereas the high-gamma band governs the flow of this excitation.

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1. Introduction

Gamma oscillations are inevitable substrates of information processing in neural circuits [11,35], however, their role and exact mechanisms of origin are yet to be completely known [15,25]. Cell-assemblies typically reverberate in oscillatory cycles, wherein neurons synchronize their action potentials to encode the presence of the sensory stimulus within their receptive fields [16,33].

Stimulus selectivity is a fundamental property of a neuron which is indispensable for feature extraction. As a matter of fact, neurons in the primary visual cortex are orientation detectors, and thus

exhibit selectivity to a specific orientation when a series of random sine-wave drifting gratings is presented within their receptive field [19,20]. The selectivity of a neuron can be inferred by computing an orientation selectivity index (OSI) that is a measure of the sharpness of its tuning [1,28]. Recently, authors [36] have shown that orientation selectivity is modulated in the gamma phase — neurons exhibit high selectivity in the rising phase of the gamma cycle. Furthermore, in the latest investigation, we have also shown that in a recurrent network of primary visual neurons, low-gamma band (30–40 Hz) is associated to regular-spiking (RS) neurons and high-gamma band (60–80 Hz) is putatively linked to fast-spiking (FS) neurons [9]. However, to date, no evidence exists between the orientation selectivity of neurons and the gamma power.

To this aim, in the present investigation, we recorded neuronal ensembles in the primary visual cortex of anaesthetized cats, and thereafter systematically examined the relation between the orientation selectivity of neurons and the power of gamma bands.

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We report that the broadly tuned neurons with low OSI exhibit high power in the high-gamma band (60–80 Hz). On the other hand, sharply tuned neurons with high OSI display high power in the low-gamma band (30–40 Hz). From these results, we may conclude that within a distributive network of layer II/III neurons, the sharply tuned neurons interact in a feed-forward excitatory flow within the low-gamma band, wherein the excitatory flow is modulated by the broadly tuned neurons in the high-gamma band.

2. Methods

2.1. Ethical approval and animal surgery

Four adult animals (Cats) were prepared for electrophysiological recordings in the primary visual cortex (area 17, layer II/III). 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. Animals were supplied by the Division of Animal Resources of the University of Montreal. The experiments were conducted in accordance with the Guide for Care and Use of Laboratory Animals of the National Institutes of Health (USA).

Briefly, cats were premedicated with acepromazine maleate (Atravet, Wyeth-Ayerst, Guelph, ON, Canada; 1 mg/kg, intramuscular) and atropine sulphate (ATRO-SA, Rafter, Calgary, AB, Canada; 0.04 mg/kg, intramuscular). Thereafter, the animals were anaesthetized with ketamine hydrochloride (Rogarsetic, Pfizer, Kirkland, QC, Canada; 25 mg/kg, intramuscular). Then the cats were paralyzed with 40 mg and maintained with 10 mg/kg/h of gallamine triethiodide (Flaxedil, Sigma Chemical, St. Louis, MO, USA; intravenous) administered in 5% dextrose lactated Ringer's nutritive solution. General anesthesia was maintained with a mixture of N₂O/O₂ (70:30) supplemented with 0.5% isoflurane (AErrane, Baxter, Toronto, ON, Canada). Electrocardiogram, electroencephalogram, rectal temperature and end-tidal CO₂ partial pressure were monitored and kept in physiological ranges throughout the experiment. The pupils were dilated with atropine sulphate (1%, Isopto-Atropine; Alcon, Mississauga, Ontario, Canada). The nictitating membranes were retracted with phenylephrine hydrochloride (2.5%, Mydfrin, Alcon). The loci of the area centrales were inferred from the position of the blind spots which were focused and projected onto a translucent screen using an ophthalmoscope. After the experiment, the cats were euthanized with an intravenous dose (0.5 mL/kg) of Sodium Pentobarbital (CEVA, Sante Animale).

2.2. Visual stimulation, electrophysiological recording, and single-unit selection

The stimulation was done in a monocular fashion. The multi-unit receptive fields (RF) were mapped as the minimum response field [6] by using an ophthalmoscope after clearly detectable neuronal activity had been obtained. These preliminary tests disclosed the qualitative properties such as dimensions, velocity-preference, orientation, and directional selectivity of neurons. A VSG 2/5 graphic board (Cambridge Research Systems, Rochester, England) was used to generate visual stimuli. Visual stimuli were 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. The blank screen was gray (~35 cd/m²). Contrast was set at 80%. Mean luminance was 40 cd/m². Optimal spatial and temporal frequencies were set at 0.24 cycles/deg and a range of 1.0–2.0 Hz, respectively, where V1 neurons are known to be driven maximally by sine-wave drifting gratings [5]. Each drifting grating was presented in blocks of 25 trials (the duration of each

4.1 s) with varying inter-stimulus (1–3 s) intervals during which no stimulus was presented. Hence, the presentation of a stimulus lasted 180 s, with all the trials and inter-stimulus intervals. Multi-unit activity in the primary visual cortex was recorded by a tungsten multi-electrode (Frederick Haer & Co, Matrix Electrode; the multi-electrode had four columns, and each column had one row). The recordings were performed at locations 410 or 820 μm apart. The excitatory RFs were located centrally within a 15° radius from the fovea. Fourteen recordings (28 sites) were done across all cats either in the left or the right hemisphere. Recordings were performed in the supragranular layers (cortical depth < 1000 μm; mean = 650 μm). The signal from the microelectrodes was amplified, band-pass filtered (300 Hz–3 kHz), digitized and recorded with a 0.05 ms temporal resolution (Spike2, CED, Cambridge, England). Spike sorting from the multi-unit signals was done. Neurons were discriminated on the basis of three criteria: 1) the spike-waveform difference 2) principal component analysis (PCA) showing well dissociated clusters 3) and auto-correlograms (ACG) showing no events (indicative of the refractory period of neuron) at the central point [7,10,14].

2.3. Orientation tuning and OSI (Orientation Selectivity Index) computation

Once single cells had been sorted out offline from multi-unit spike trains accumulated during data acquisition, orientation tuning curves of cells were obtained from raw data and fitted with the von Mises function [31].

$$M(\theta) = A \cdot e^{b(\cos(\theta-c))} + d \quad (1)$$

where, A is the value of the function at the preferred orientation 'c', and 'b' is the width parameter. An additional parameter 'd' represents the spontaneous firing rate of the cell. $M(\theta)$ is the firing rate of the neuron at orientation, 'θ'. This allowed us to determine the preferred orientation of every cell. An orientation selectivity index (OSI) was calculated to ensure the tuning of neurons. It was measured using the fitted tuning curves by dividing the firing rate at the baseline (orthogonal orientations) by the firing rate at the preferred orientation, and subtracting the result from one [3,23,27]. The closer the OSI is to one, the stronger the orientation selectivity.

2.4. Perievent spectrogram analysis

The analysis was performed with NEUROEXPLORER 4 (Nex Technologies). For each selected variable, this analysis results in multiple spectrograms that start at the specified time after the occurrence of each reference event (stimulus onset). These spectrograms are then averaged over all of the reference events. An optimal or a near optimal orientation for the neurons was chosen to generate the spectrograms. The power spectra were calculated by the use of 512 frequencies between 1 and 120 Hz, smoothed with a Gaussian kernel with a bin-width of 3. The analysis window lasted 4 s (1 s before the stimulus and 3 s after the stimulus onset). The sliding window (shift) was set at 20 ms (i.e. 200 shifts for the window of analysis). The power spectrum was calculated for the specified number (number of shifts) of windows. For a time-stamped variable, the rate histogram was calculated and copied into a signal array. The parameters were used as follows:

$$\text{Histogram start} = \text{start} + \text{shift} \times (\text{window number} - 1)$$

$$\text{Bin} = 1 / (2 \times \text{maximum frequency})$$

$$\text{Number of Bins} = 2 \times \text{Number of Frequency Values}$$

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