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Brain Research

Research Report

Frequency-band signatures of visual responses to naturalistic input in ferret primary visual cortex during free viewing

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ARTICLE INFO

Article history:
Accepted 6 December 2014
Available online 12 December 2014

Keywords:
Primary visual cortex
Naturalistic visual stimulation
Ferret
Cortical oscillation
Free viewing
Local field potential

ABSTRACT

Neuronal firing responses in visual cortex reflect the statistics of visual input and emerge from the interaction with endogenous network dynamics. Artificial visual stimuli presented to animals in which the network dynamics were constrained by anesthetic agents or trained behavioral tasks have provided fundamental understanding of how individual neurons in primary visual cortex respond to input. In contrast, very little is known about the mesoscale network dynamics and their relationship to microscopic spiking activity in the awake animal during free viewing of naturalistic visual input. To address this gap in knowledge, we recorded local field potential (LFP) and multiunit activity (MUA) simultaneously in all layers of primary visual cortex (V1) of awake, freely viewing ferrets presented with naturalistic visual input (nature movie clips). We found that naturalistic visual stimuli modulated the entire oscillation spectrum; low frequency oscillations were mostly suppressed whereas higher frequency oscillations were enhanced. In average across all cortical layers, stimulus-induced change in delta and alpha power negatively correlated with the MUA responses, whereas sensory-evoked increases in gamma power positively correlated with MUA responses. The time-course of the band-limited power in these frequency bands provided evidence for a model in which naturalistic visual input switched V1 between two distinct, endogenously present activity states defined by the power of low (delta, alpha) and high (gamma) frequency oscillatory activity. Therefore, the two mesoscale activity states delineated in this study may define the degree of engagement of the circuit with the processing of sensory input.

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http://dx.doi.org/10.1016/j.brainres.2014.12.016
0006-8993/

1. Introduction

Encoding of sensory stimuli in cortex represents the process of transforming external physical signals into neuronal activity patterns that reduce the redundancy of the sensory input (Barlow, 1961; Simoncelli and Olshausen, 2001b). In primary visual cortex (V1), the responses of individual neurons and networks of neurons to synthetic visual stimuli measured by changes in action-potential firing are well characterized (Hubel and Wiesel, 1959; but see Olshausen and Field, 2005). These "artificial" stimuli have been optimized to elicit neuronal spiking responses as a function of basic input properties such as orientation, contrast, and spatial frequency. Recently, it has been proposed that synthetic stimuli modulate neuronal activity differently than naturalistic visual stimuli (Felsen and Dan, 2005; Smyth et al., 2003b) due to the different image statistics of synthetic laboratory stimuli and real-world visual input (Simoncelli and Olshausen, 2001b). Specifically, naturalistic stimuli exhibit a characteristic $1/f$ to $1/f^2$ power distribution as a function of spatial frequency f (Ruderman and Bialek, 1994; Simoncelli and Olshausen, 2001a; Tolhurst et al., 1992; van der Schaaf and van Hateren, 1996). Studies that employed naturalistic images and movie segments to investigate neuronal responses have revealed sparse coding in V1 (e.g. Baddeley et al., 1997; Froudarakis et al., 2014; Haider et al., 2010; Vinje and Gallant, 2000; Weliky et al., 2003; Willmore et al., 2011) that facilitated decoding, maximized coding capacity, and was driven by higher-order statistics of the stimulus. In addition, sensory-evoked activity has been recognized to closely relate to the ongoing spontaneous activity (Berkes et al., 2011; Luczak et al., 2013; Scholvinck et al., 2011; Tsodyks et al., 1999). For example, the structure of spontaneous network dynamics was only modestly altered by naturalistic visual input as determined by similarity in correlation structure of spiking activity (Fiser et al., 2004). Sparse coding of naturalistic visual input was demonstrated to be state-dependent such that the quiet waking animal employed a less sparse code than the alert animal (Froudarakis et al., 2014). In general, visual responses depend on overall state (Bennett et al., 2013; Niell and Stryker, 2010; Polack et al., 2013). Also, in theoretical models, overall state-defining fluctuations explain response distributions (Goris et al., 2014). Together, these results point towards a model of sensory processing of naturalistic input in which visual responses (1) are sparse and reliable, and (2) emerge from the modulation of ongoing endogenous network dynamics that depend on overall behavioral state. Yet, a limited number of studies have considered the local field potential (LFP) dynamics of naturalistic vision in the awake animal (Brunet et al., 2013; Ito et al., 2011; Kayser et al., 2003; Whittingstall and Logothetis, 2009) and very little is known about the temporal structure of mesoscale network dynamics in V1 across cortical layers measured by the LFP and its relationship to the microscale spiking activity in the awake, freely viewing animal.

Given the recent description of different activity states characterized by the relative presence or absence of slow rhythmic activity in the cortical LFP of awake animals (Harris and Thiele, 2011; Poulet and Petersen, 2008), we here asked (1) how naturalistic visual input modulated the mesoscale V1 activity structure during free viewing in the awake animal, and (2) how the mesoscale activity structure related to the microscopic spiking response. We used the well-known trial-to-trial variability of sensory responses (Tolhurst et al., 1983) as a tool to answer these questions and thereby fill a key gap in our understanding of how sensory input interacts with ongoing network dynamics in the awake animal. In this study, we used the ferret animal model due to its well-studied visual system (Law et al., 1988) and columnar architecture of V1 (Chapman and Stryker, 1993). We presented full-field nature movie clips to awake, head-fixed ferrets and determined the rhythmic architecture of the LFP before and during visual stimulation (corresponding to spontaneous and sensory-evoked activity) and how these mesoscale network dynamics related to the multiunit spiking response elicited by the visual stimulus as a function of cortical layer.

2. Results

Little is known about the mesoscale network dynamics in V1 of awake animals in absence of experimental constraints such as anesthesia or reward-driven attentional processes that define cortical state by shaping the overall network dynamics. In order to characterize how naturalistic visual input modulates local network activity in the freely-viewing animal, we presented fullfield ($58 \times 33^\circ$ visual field) movie clips displaying nature scenes to awake, head-fixed ferrets. The presentation of the movie clips was interleaved with periods of no visual stimulation (spontaneous activity). The visual stimuli exhibited the characteristic $1/f$ to $1/f^2$ spatial frequency structure of naturalistic stimuli (Fig. 1A, left), which is comparable to the spectra of a point-of-view naturalistic visual stimulus (Fig. 1A, left middle). Traditionally used synthetic visual stimuli (checkerboard noise pattern, luminance grating) exhibited characteristically different spectra (Fig. 1A, right middle, right). The animals were acclimated to restraint but did not receive any other behavioral training and the recording sessions did not include any reward contingencies. We verified that the animals were awake during the entirety of the recording sessions by reviewing infrared videography for open eyes and minor movements. Local field potential (LFP) and multiunit activity (MUA) were recorded with multichannel depth probes in V1 ($N=3$ animals). Raw LFP traces revealed strikingly different network dynamics for periods of spontaneous activity and visual stimulation (Fig. 1B). Prominent high amplitude, low frequency oscillations often occurred during periods of spontaneous network activity; this slow rhythmic activity was typically suppressed for the duration of the visual stimulus. Full-field naturalistic visual input therefore altered overall mesoscale activity in structure in V1, with the most obvious difference present in the low frequencies. Spectral analysis averaged across trials ($N=578$) and cortical depth revealed that visual stimulation modulated the power in the entire spectrum included in the analysis (Fig. 2A, 0.5–40 Hz, change in power determined by subtraction of spectra during and before visual stimulation). In particular, power at low frequencies (with the exception of a narrow peak around 6 Hz) was lower during visual stimulation and power at higher frequencies was enhanced with a cross-over frequency of suppression and enhancement around 18 Hz. We mapped this broadband modulation of oscillatory activity onto the standard frequency bands as determined by the percent of total power for any given frequency band. This provided a measure of the relative presence of oscillations in difference frequency bands (El Boustani et al., 2009). When comparing