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Bimodal modulation and continuous stimulation in optical imaging to map direction selectivity

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ABSTRACT

In the visual system, neurons with similar functional properties such as orientation and direction selectivity are clustered together to form modules. Optical imaging recordings in combination with episodic paradigms have been previously used to estimate direction selectivity, a fundamental property of visual neurons. The major drawback of the episodic approach is that the extraction of the signal from various forms of physiological noise is difficult, leading to a poor estimation of direction. Recent work, based on periodic stimulation and Fourier decomposition improved the extraction of periodic stimulus responses from noise and thus, reduced the recording time considerably. Given the success of this new paradigm in mapping orientation, the present study evaluated its reliability to measure direction selectivity in the visual cortex of anesthetized cats. Here, a model that exploits the harmonics of the Fourier decomposition is proposed where the first harmonic is related to direction responses, and the second to orientation. As expected, the first harmonic was absent when a static stimulus was presented. Contrarily, the first harmonic was present when moving stimuli were presented and the amplitude was greater with random dots kinematograms than with drifting gratings. The phase of the first harmonic showed a good agreement with direction preference measured by episodic paradigm. The ratio of the first/the second harmonic amplitude, related to a direction index, was weaker in fracture. It was also weaker in areas of the ventral pathway (areas 17 and 21a) where direction selectivity is known to be reduced. These results indicate that a periodic paradigm can be easily used to measure specific parameters in optical signals, particularly in situations when short acquisition periods are needed.

Introduction

It is well established that, in sensory systems, neurons with similar functional properties are clustered together to form modules. On the surface of the cortex, the selectivity of neurons changes gradually, forming cortical maps, such in the case of orientation in the primary visual cortex of cats and primates (Bonhoeffer and Grinvald, 1991; Frostig et al., 1990; Grinvald et al., 1986). In these maps, orientation selectivity of neurons changes steadily, forming domains that converge in singularities called “pinwheels”. A separate clustering of direction selectivity associated with orientation maps has also been revealed (Swindale et al., 1987; Tolhurst et al., 1981). This arrangement ultimately leads to the formation of direction selectivity maps. Along this spatial functional organization, iso-orientation columns are divided into columns of preference for opposite directions, orthogonal to the preferred orientation (Henry et al., 1974; Kim et al., 1999; Kisvarday et al., 2001; Ribot et al., 2008; Shmuel and Grinvald, 1996; Swindale et al., 2003).

The organization of direction selectivity was previously investigated by optical imaging of intrinsic signals (Kim et al., 1999; Kisvarday et al., 2001; Ribot et al., 2008; Shmuel and Grinvald, 1996; Swindale et al., 2003). In the first complete study (Shmuel and Grinvald, 1996), direction selectivity was calculated by the “vector sum”, a method generally used to compute orientation selectivity (Bonhoeffer and Grinvald, 1991, 1996; Grinvald et al., 1986; Kisvarday et al., 2001; Shmuel and Grinvald, 1996; Swindale, 1998). This approach is not ideal, particularly in regions of low selectivity because, in contrast to orientation, direction tuning is bimodal (Kisvarday et al., 2001; Swindale et al., 2003). Thus, when responses of opposite directions are close and the noise contribution significant, the vector sum does not provide a good estimate of direction preference and breaks the orthogonality between orientation and direction. To resolve this problem, Kisvarday et al. (2001) proposed to use the “vector maximum method” to evaluate direction selectivity. Yet, this alternative approach suffers from a low angular resolution and remains sensitive to noise (Swindale et al., 2003). A second alternative using the fit of

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the direction tuning by two Von Mises functions, was proposed (Swindale, 1998; Swindale et al., 2003). While this method answers the above concerns, it is however based on the analysis of data recorded in episodic paradigms (i.e. block design). The signal is therefore combined with physiological noise and long recording sessions are needed to increase the signal to noise ratio (by averaging the signal over multiple acquisitions). In some situations, averaging is nevertheless insufficient and additional processing, such as 2D-filtering (Fukuda et al., 2006; Ribot et al., 2006), PCA decomposition (Everson et al., 1997; Gabbay et al., 2000; Stetter et al., 2000; Yokoo et al., 2001), estimation of noise contributions by polynomial subtraction (Ribot et al., 2006) or local similarity minimization (Fekete et al., 2009), must be applied.

Separately, time-locked or periodic techniques have been proposed (Kalatsky and Stryker, 2003; Sornborger et al., 2003, 2005). In contrast to episodic paradigms, the periodic approach (i.e. continuous stimulation) combines different conditions by periodically changing the orientation of a stimulus (e.g. grating) and recovers the response by using amplitude and phase information at the stimulation frequency. Experiment duration is thus considerably reduced while more angular conditions are explored since an “infinite” number of orientations can theoretically be presented.

While the periodic method proved to be successful in measuring orientation selectivity in cats (Jha et al., 2005; Kalatsky and Stryker, 2003) and tree shrews (Zepeda et al., 2004), it has never been used to quantify direction selectivity, a fundamental property of visual neurons. In this work, a model-based periodic paradigm is studied for the first time to evaluate direction selectivity from multiple harmonics. A direction index, based on the first and second harmonic of the Fourier decomposition is proposed and tested with different visual stimuli in areas 17, 18 and 21a of the cat, and compared with episodic paradigms. As a demonstration of the exportability, the model is also applied to evaluate the monocular/binocular recipient zones in rodents' primary visual cortex. Part of this work has been previously published in abstract form (Vanni et al., 2007).

Methods

Model

In this section, notations are introduced for the standard periodic stacking method by including the canonical HRF previously developed (Vanni et al., submitted for publication). The model assumes that measurements are taken with a camera positioned over the cortex to image a zone where activation patterns are expected (Bonhoeffer and Grinvald, 1996). The cortex is illuminated by light at a wavelength for which hemoglobin dominates the absorption (Dunn et al., 2005). The images are recorded continuously to form a dynamical image $I(t)$. Since only one wavelength is used in this work, it is assumed that a combination of deoxyhemoglobin (HbR) and oxyhemoglobin (HbO) is measured. For a point in the cortical image, $\{ij\}$, the measured attenuation can be modeled as the sum of a physiological signal and the response to the stimuli, i.e.

$$I_{ij}(t) = \alpha_{ij}\mathrm{HRF}_{ij}(t) * R_{ij}\{s(t)\} + b_{ij}(t) + e_{ij}(t), \tag{1}$$

where e_{ij} represents the acquisition noise (e.g. generated by the camera), b_{ij}, the physiological signals, namely respiration, cardiac pulsations and vasomotion, and $s(t)$, the stimulation vector defined as $s(t) = 1$ when the stimulation is on, zero otherwise. The specificity of the neuronal response is described by a functional, R_{ij}, describing the normalized response of the neuron to the given stimulus with a response strength α_{ij}, and $\mathrm{HRF}_{ij}(t)$ is the hemodynamic response function which convolves the stimuli. It is understood here that the HRF represents the response to a combination of oxy- and deoxy-hemoglobin depending on the illumination wavelength.

In previous work, hemodynamic measurements associated with the above model were used to study the response shape (e.g. the width of the neuronal response in a retinotopic paradigm). This work is extended here by considering a bi-modal stimulation paradigm. Consider the following: a stimulus moving in a direction that continuously rotates at frequency ω_1. If this stimulus is a sinewave grating, with its orientation orthogonal to its direction, the orientation and direction selectivity of neurons can be modeled by a response function taking the form

$$R_{ij}\{s_1(t) + s_2(t)\} = \alpha_{ij}^{(1)} R_{ij}^{G}\{s_1(t)\} + \alpha_{ij}^{(2)} R_{ij}^{G}\left\{s_1\left(t - \frac{\pi}{\omega_1}\right)\right\}. \tag{2}$$

In this formula, the direction selectivity is encoded in the response amplitudes, α_{ij}, which are associated with preferred directions. If both $\alpha_{ij}^{(1)}$ and $\alpha_{ij}^{(2)}$ are equal, neither direction can be distinguished from the other and only the orientation response will be measured. If only one $\alpha_{ij}^{(a)}$ is non-zero, then the direction component dominates the response. This is apparent when taking the Fourier transform of the above expression,

$$R_{ij}\{s_1 + s_2\}(\omega) = R_{ij}^{G}\{s_1\}(\omega)\left(\alpha_{ij}^{(1)} + \alpha_{ij}^{(2)} \mathrm{e}^{-i\frac{\pi}{\omega_1}\omega}\right) \tag{3}$$

where, for simplicity, the function R_{ij}^{G} assumed to be described by a periodic Gaussian centered on the preferred orientation at that location in the cortex, i.e.

$$R_{ij}^{G}\{s\}(\omega) = \mathrm{e}^{-\omega^2\sigma^2/2} S_{ij}\{s\}(\omega) \tag{4}$$

and S_{ij} the periodic Dirac response. These Gaussian functions are introduced to model the tuning widths of the underlying neurons. It can be observed that the Fourier transform of (2) will exhibit two peaks, one at ω_1 and one at $\omega_2 = 2\omega_1$, each having a distinct interpretation in terms of orientation and direction. Consider two special cases. First, if both $\alpha_{ij}^{(a)}$ are equal, (3) will be zero at $\omega = \omega_1$ while non-zero at the second harmonic, $\omega = 2\omega_1$. This is the orientation response where the phase can be associated with the preferred orientation. On the other hand, if one $\alpha_{ij}^{(a)}$ is zero, then the first harmonic will have a non-zero response and the phase will correspond to the direction selectivity. Thus, in view of the above model, the amplitude and phase of the responses located at those two peaks can be related to direction selectivity. In fact, it is possible to develop measures that are independent of the contrast or the strength of the response. For example, a quantity of interest, introduced by Swindale et al. (2003) is the direction index, here referred to as periodic direction index (PDI) because of the nature of the stimulation (i.e. in contrast to the episodic direction index (EDI)):

$$\mathrm{PDI}_{ij} = \frac{\left(\alpha_{ij}^{(1)} - \alpha_{ij}^{(2)}\right)}{\left(\alpha_{ij}^{(1)} + \alpha_{ij}^{(2)}\right)} \tag{5}$$

It measures the direction selectivity of a group of neurons at a given location. Combining (3) and (1), and assuming physiological signal and noise are much lower than the signal at the stimulation frequency, it can be shown that

$$\left|\frac{I_{ij}(\omega_1)}{I_{ij}(2\omega_1)}\right| = \left|\frac{\left(\alpha_{ij}^{(1)} - \alpha_{ij}^{(2)}\right)}{\left(\alpha_{ij}^{(1)} + \alpha_{ij}^{(2)}\right)}\right| \left|\frac{\mathrm{HRF}(\omega_1)}{\mathrm{HRF}(2\omega_1)}\right| \mathrm{e}^{\frac{3}{2}\omega_1\sigma_{ij}^2} = \mathrm{PDI}_{ij} K_{ij}(\omega_1) = \mathrm{PDI}' \tag{6}$$

where σ_{ij} describes the temporal width at that stimulation frequency of the modeled Gaussian response of the neurons to orientation and $\mathrm{HRF}(\omega)$ is the Fourier transform of the HRF. Thus, the remaining factor $K_{ij}(\omega_1)$ depends on both the HRF and σ_{ij} and may vary spatially.