

Encoding of Dynamic Visual Stimuli by Primate Area MT Neurons

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Abstract

Neural tuning properties are known to be adaptive on various time scales and are probably optimized to represent real-world stimuli. Here we study directional tuning in MT neurons in awake monkeys during presentation of motion stimuli with two different dynamical behaviors: a random sequence of movement directions and a random walk. Most MT neurons with significant direction tuning show characteristic tuning differences in the two stimulus conditions whereas neurons un-tuned in either condition do not significantly change their statistical properties. We suggest that MT neurons undergo a rapid adaptation to stimulus statistics, thus allowing for an optimal signal processing.

Key words: stimulus reconstruction, stimulus statistics, macaque, area MT

1 Introduction

Tuning properties in early visual cortex can be dynamic in several ways. First, tuning curves may change within a few tens of milliseconds [5], i.e. even during one brief fixation period. Second, tuning characteristics can undergo substantial changes as the result of adaptation [3] over the course of hundreds of milliseconds to seconds. Since many properties of early visual cortex can be

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understood in terms of an evolutionary optimization for an efficient representation of natural scene statistics [4], we assume that the dynamics of tuning properties can also be understood within this framework. We therefore ask: how general are dynamic tuning properties within different cortical areas of the visual system? How do they relate to the temporal dynamics of the stimuli which are to be encoded?

In order to address the latter question, we designed a novel stimulus paradigm which mimics important aspects of natural scenes: subsequent stimulus states are determined both by a random component and a continuity requirement which dominates most of the motions we see. This motion trajectory approach provides a means to identify relevant time scales for neural tuning changes by parametrically varying the degree of stimulus change.

In this paper we present results from motion sensitive macaque area MT. We employed two stimulus paradigms which critically differed in the statistics of the stimulus sequence. In the first paradigm subsequent motion directions were completely uncorrelated, while in the second paradigm, subsequent motion directions were similar. Reverse correlating the spike train with the stimulus sequence in the first paradigm revealed two patterns of short-term dynamics in MT directional tuning. A comparison of responses during the two different paradigms revealed a substantial dependency of neural tuning properties on the temporal statistics of the stimulus.

2 Methods

Experimental Methods

We conducted extracellular recordings in area MT in two male macaque monkeys (*Macaca mulatta*). Surgical procedures, single-unit recording and data acquisition were standard, in short: Prior to the experiments, the animals were surgically implanted with a head-holding device a recording cylinder, and a scleral search coil. Surgical, animal care, and experimental procedures conformed to the guidelines of the National Institutes of Health for the care and use of laboratory animals, the guidelines for the welfare of experimental animals issued by the Federal Government of Germany, and stipulations of local authorities.

We used Tungsten microelectrodes (World Precision Instruments), introduced to the cortex through a transdural guide tube positioned in a teflon grid inside the recording cylinder. The depth of the electrode in the brain was controlled by a hydraulic microdrive (Narishige Scientific Instrument Lab, Tokyo, Japan). Signals were amplified with conventional electrophysiological instrumentation (Multichannel Systems, Germany), filtered (350-5000 Hz), and displayed on an oscilloscope. Spike activity was digitized (sampled at 25 kHz) and stored on computer disk for offline analysis.

Monkeys performed a fixation task, while their gaze direction was monitored with the indirect scleral eye-coil method. Visual stimuli were presented on a CRT monitor at a distance of either 57 cm or 86 cm at 100 Hz or 85 Hz refresh rate, respectively. At the beginning of each trial, a small, white fixation spot (0.13×0.13 deg) appeared on the otherwise dark monitor. After the monkey started foveating the fixation spot, stimuli appeared inside a circular aperture, which was at least as large as the classical receptive field of the neurons under investigation, determined by a manual mapping procedure with gray bars. The animals were required to maintain fixation in a 3×3 deg window centered on the fixation point. Trials in which the monkeys broke fixation before the end of the stimulus presentation were discarded. After each successfully completed trial the animals were rewarded with a small amount of liquid.

Visual stimuli consisted of random dots undergoing a constant translational movement in different directions. In the first stimulus paradigm, an adoption of the approach in [5] to the motion direction domain [1], a stochastic sequence of motion directions was created with direction transitions occurring every 50 ms or 100 ms. The sequence was generated by pseudo-randomly selecting a new direction out of a set ς of directions, sampled in steps of 30 deg. Each sequence was repeatedly presented for 10 to 20 trials for each cell. The second stimulus paradigm also draws from ς , but the difference between two subsequent motion directions was now determined by a Gaussian distribution, thus realizing a time-discrete random walk with fixed step size in direction space. Four different stimulus sequences have been generated, which we will refer to as *trajectories*, with different starting directions (0 deg, 90 deg, 180 deg and 270 deg). Each sequence was repeatedly presented for 10 to 20 trials analogical to the first approach.

Theoretical Methods

In order to assess the influence of stimulus dynamics on neuronal responses we calculated estimates of tuning curves and optimal linear filters for the two stimulus paradigms. *Tuning curves* were determined by discretizing the time in bins of 1 ms. The spike events were translated to firing rates by sliding a rectangular window function of width 20 ms along the spike train. Tuning curves were reconstructed from the mean of the firing rates $r(t_i)$ for a given stimulus value $s(t - \tau)$ for various time shifts τ between s and r . The latency τ between $s(t)$ and $r(t)$ was chosen to give the most pronounced tuning. The standard deviation of the tuning curve values were calculated as $\sigma = \frac{\sigma_s}{\sqrt{(p)}}$, where σ_s is the standard deviation of the single trial and p is the number of stimulus presentations of 50 ms or 100 ms. *Linear Filters* $L(x, t)$ were reconstructed with the reverse correlation method. This approach assumes a linear dependency between stimulus s and response r

$$r_{est}(t) = \int \int dx d\tau L(x, \tau) s(x, t - \tau). \quad (1)$$

As optimality constraint we used the minimum of the squared difference $\frac{1}{T} \int_0^T (r(t) - r_{est}(t))^2$ between the estimate $r_{est}(t)$ and the experimental response $r(t)$. $L(x, \tau)$ can be determined most easily under the minimal mean squared error constraint when the presented stimulus $s(x, t)$ is uncorrelated in time and the autocorrelation function of the stimulus is a Dirac delta function, $\langle s(x, t)s(x, t') \rangle = \delta(t - t')$. In this case the linear filter is proportional to the spike triggered average $T(x, \tau)$.

In the general case, if the stimulus sequence is not white gaussian noise, the fourier transform in both the spatial and temporal domain of the linear filter is given by

$$\tilde{L}(\omega_x, \omega_t) = \frac{\langle S(\omega_x, \omega_t)R(\omega_t) \rangle}{\langle S^*(\omega_x, \omega_t)S(\omega_x, \omega_t) \rangle} \quad (2)$$

where the brackets denote averages on trials [6]. $S(\omega_x, \omega_t)$ and $R(\omega_x, \omega_t)$ are the fourier transforms of $s(x, t)$ and $r(t)$

3 Results

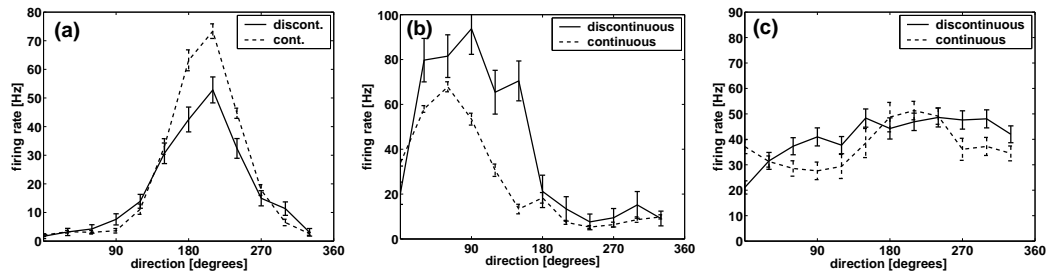


Fig. 1. Tuning curves of MT neurons assessed with two different stimulus paradigms for every neuron, plotted as mean firing rate [Hz] as a function of motion direction. Error bars denote standard deviations (see theoretical methods section) .

Activity of MT neurons was recorded in response to both stimulus paradigms: discontinuous (random sequence) and continuous (random walk) jumps in the direction domain. The latency of 80 ms for tuning curve reconstruction was almost optimal for all neurons. The behavior of three typical kinds of cells is shown by example in fig.1. Typically, weakly tuned cells (fig.1c) responded at similar firing rates to both stimulation types. Instead, almost all neurons with distinct directional tuning (fig.1a) exhibited a dependence of their general activity level on stimulus statistics. Such multiplicative scaling of tuning properties could take both possible directions, response enhancement and suppression: in fig.1a the maximum firing rate increased strongly from 48.3Hz to 74.0Hz for the random walk stimulation, while for the cell shown in fig.1b the maximum firing rate decreased from 93.8Hz to 67.7Hz (values obtained by

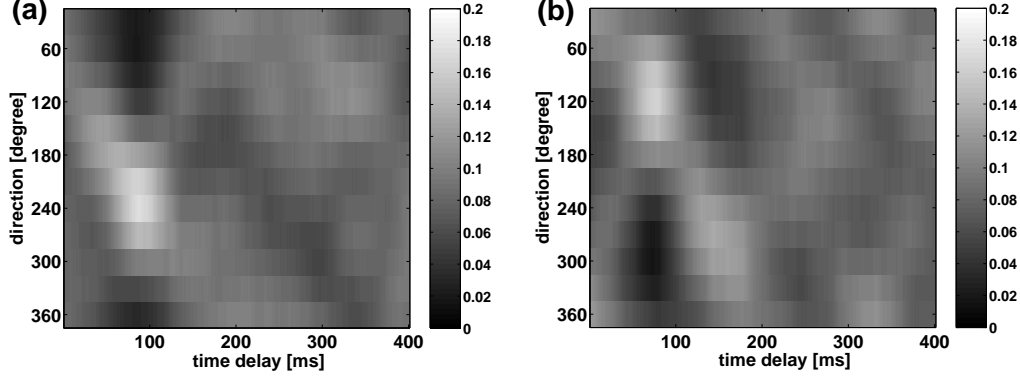


Fig. 2. Representative response profiles of MTneurons in response to white noise stimuli in the motion direction domain. Linear filters have been reconstructed for cells whose tuning curves are shown in figs. 1a and 1b. The time axis denotes the time before a spike event. The cells show a distinctive continuous shift of orientation selectivity in time.

Gaussian fits to the curves). Thus, *ceteris paribus*, the stimulus statistic altered neural response magnitude to an extent which renders simple predictions of responsiveness between stimulus paradigms practically impossible. Furthermore, changes in tuning width have been found, again going in both directions: in example 1a, tuning width at half height decreases from 48.2 degrees during random walk stimulation to 39.4 degrees. The neuron in fig.1b, again, showed the opposite behavior increasing tuning width from 56.0 to 45.9 degrees.

As shown in fig.2 the temporal characteristics of the neuronal response cannot be captured by the tuningcurves. A column for a fixed time delay τ represents the probability distribution (grayscaled) for the stimulus present at the given τ before a spike. The neurons exhibit a continuous shift of preferred direction, e.g. in fig.2b from 350 degrees ($\tau = 180\text{ms}$) to 120 degrees ($\tau = 80\text{ms}$). The dependency of tuning curves in figs.1a,b on the stimulus paradigm may be due to the time dependency of the preferred direction. When the trajectory used in the random walk stimulus is favorable for the directional-temporal receptive field of a cell, the maximum of the tuning curve will increase in comparison to the discontinuous random direction stimulation. If the trajectory is not favorable, the reverse effect of decreased neuronal peak activity may be seen. Hence, reconstruction of stimulus trajectories may be affected by the trajectory itself used for the extraction of the neuronal response properties.

4 Discussion

We have presented results from a novel approach to the study of visual tuning dynamics and stimulus statistics. Depending on the stimulus statistics of otherwise physically identical stimuli neurons in macaque area MT can undergo substantial changes of both their directional selectivity and sharpness

of directional tuning width. The change in the sequence of stimulus statistics, furthermore, results in a profound perceptual change: an object moving along a motion trajectory is perceived, while only random motion can be seen during stimulation with the discontinuous stimulus paradigm. Thus, our future research will have to differentiate whether changes of tuning properties can be explained by a potentially pure bottom-up adaptation process or is influenced by top-down factors as well.

The stimulus trajectory approach, we believe, is of significance for studying sensory system coding at least two reasons. First, it allows mimicking many aspects of real world motion patterns in a parametric way. Second, it allows for an elucidation of population codes within the visual domain in a way directly comparable to those used for studying the motor system [2]. Thus, it will eventually be possible to directly compare sensory and motor population codes.

Acknowledgements This work has been supported by SFB517, B7, of the German Science Foundation (DFG).

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