Encoding of Dynamic Visual Stimuli by Primate Area MT Neurons

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Abstract

Neural stimulus selectivity is thought to be optimized for the representation of real-world stimuli. Neural coding properties, therefore, may adapt to different environments. Here, we address the question if tuning curves depend on the statistics of visual stimuli. This is done by studying the directional tuning of macaque area MT neurons exposed to dynamic motion stimuli of two different direction progression statistics. Despite an apparent difference of tuning curves across stimulus conditions, our results support the view that the underlying encoding system is robust and subject to only restricted malleability by stimulus statistics.

Key words: directional tuning, stimulus statistics, area MT, reverse correlation

1 Introduction

Tuning properties in early visual cortex can be dynamic in several ways. Tuning curves can change within a few tens of milliseconds [1] and undergo substantial changes as the result of adaptation [2] over the course of hundreds of milliseconds to seconds. Since many properties of early visual cortex can be understood in terms of an evolutionary optimization for an efficient representation of natural scene statistics [3], tuning dynamics and adaptivity may be hypothesized to optimize representations within different stimulus contexts. If this is so, tuning properties ought to change with stimulus statistics.
In order to address this question, we designed a novel stimulus paradigm which mimics important aspects of natural scenes: subsequent stimulus states were

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determined both by a random component and a continuity requirement which dominates most of the motions we see. These stimuli were implemented as random walk trajectories in the motion direction domain, in which subsequent motion directions are correlated. Neural direction tuning obtained in this stimulus context was compared to tuning during stimulus sequences which only differed in the lack of any sequential correlations of motion directions.

2 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. Recordings were taken with Tungsten microelectrodes, signals amplified, filtered (350-5000 Hz), digitized (sampled at 25 kHz) and stored on computer disk for offline analysis.
Monkeys performed a fixation task, foveating a small white fixation spot ($0.13^\circ \times 0.13^\circ$) within a $3^\circ \times 3^\circ$ window, while 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. After appearance of the fixation spot on the otherwise dark monitor and after the monkey started foveating the fixation spot, stimuli appeared inside a circular aperture covering the classical receptive field of the neurons under investigation. Trials in which the monkeys broke fixation before the end of stimulus presentation were discarded. After each successfully completed trial the animals were rewarded with a drop of juice.
Visual stimuli consisted of random-dot surfaces undergoing translational motion. In both stimulus paradigms the single dot diameter was 0.2°, the dot density 2 dots per degree^2 visual angle, translation speed 7°/sec, dot lifetime was infinite, and motion coherence was 100%. Motion directions were updated at a rate of 50, 20 or 10 Hz. The length of individual motion sequences ranged from 3 to 5 seconds. In the first stimulus paradigm, an adoption of the approach in [1] to the motion direction domain [4], a stochastic sequence of motion directions was created (see Fig. 1 A and B for illustration). The sequence was generated by pseudo-randomly selecting a new direction out of a set ς of directions, sampled in steps of 30°. Selection from the set was done with replacement. The second stimulus paradigm also drew from ς, but the difference between two subsequent motion directions was now determined by

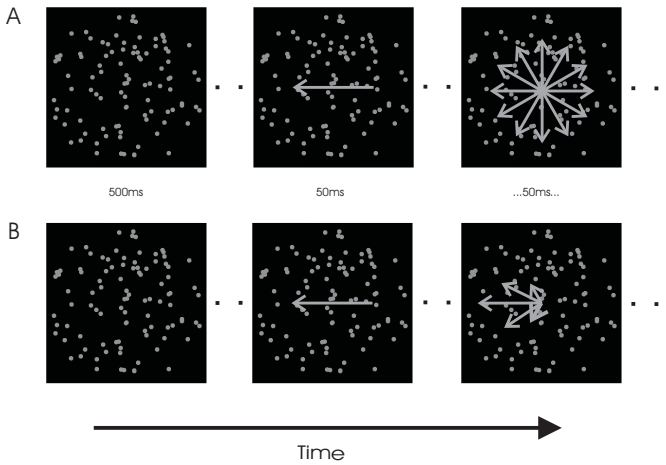

Fig. 1. Sketches of the two different stimulus paradigms. In both paradigms, a trial starts with a 500 ms period of static presentation of the random dot stimulus followed by a translational movement for 50 ms (here: leftward, indicated by the gray arrow). The only, but crucial difference between both types of stimulation is indicated for the third stimulation phase by the set of arrows, whose lengths indicate choice probabilities. While in the first, "*discontinuous*", stimulus paradigm consecutive motion directions are chosen randomly out of the set ς of directions with identical probabilities (**A**), in the second, "*continuous*", paradigm the consecutive directions are chosen from a Gaussian distribution centered on the current motion direction (**B**).

a Gaussian distribution with mean zero and standard deviation one, thus realizing a time-discrete random walk with fixed step size in direction space. The two stimulus paradigms will be referred to as *discontinuous* and *continuous*, respectively. Four different stimulus sequences have been generated, referred to as *trajectories*, with different starting directions (0°, 90°, 180°and 270°). Each stimulus sequence was repeatedly presented for 10 to 20 trials.
In order to assess the influence of stimulus statistics on neuronal responses we calculated estimates of tuning curves and optimal linear filters for the two stimulus paradigms. *Spike-Triggered-Averages* (STAs) were calculated for the discontinuous stimulation by reverse correlating the spike train with the stimulus sequence. As the discontinuous stimulus is uncorrelated, the STA closely approximates the optimal linear filter between stimulus and response. We defined the response *delay* of each neuron as the time difference between the occurrence of a spike and the maximum value of the time-dependent variance in the STA (see Fig. 2A). *Tuning curves* were then computed from responses within a time window centered at this delay. In order to limit the influence of preceding and subsequent motion directions on the response, we divided the analysis window into five partitions of equal length, weighting the firing rates within these partitions according to different distributions (the uniform distribution corresponds to the "standard" tuning curves). *Direction indices* were calculated as $DI = \frac{\text{optTK}-\text{orthTK}}{\text{optTK}+\text{orthTK}}$, where optTK (orthTK) indicates the tuning curve value at the (anti-)preferred direction.

3 Results

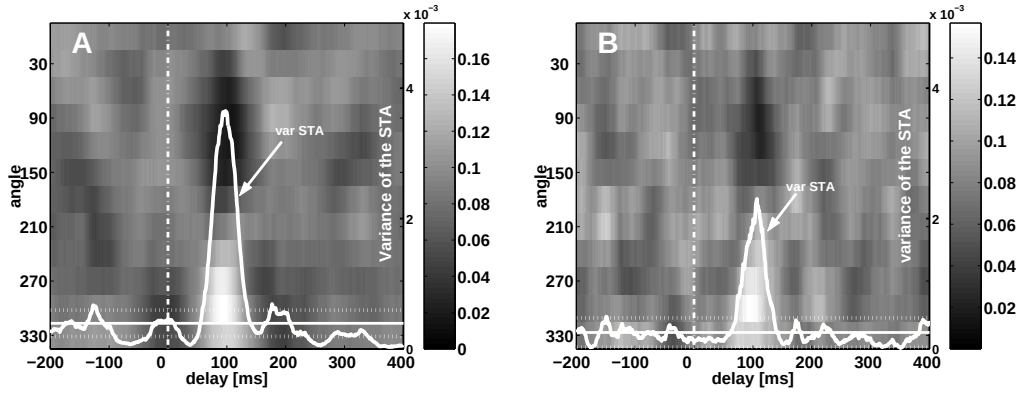

Fig. 2. Spike triggered averages for an exemplary MT cell, obtained during discontinuous stimulation. (**A**) was obtained with 50 ms motion intervals, (**B**) with 20 ms motion intervals. The abscissa denotes the time before a spike event, the left ordinate denotes stimulus motion direction. A column within the spike triggered average for a fixed time delay τ represents the probability distribution (grayscaled) for the stimulus present at that delay before a spike. The white line shows the variance of the STA. The solid horizontal lines depict mean variance of the STA in the interval 200 ms to 100 ms before a spike; dashed lines indicate the twofold standard deviation; the dashed-dotted vertical line indicates the spike timestamp. The cell shows a characteristic response latency of approx. 100 ms for both interval lengths.

Figs. 2A and B show the spike triggered average of a typical cell and illustrates the procedure for delay estimation. When a spike of this cell occurred, it had, on average, most likely been preceded by a motion direction of about 300° approximately 100ms earlier. The least likely stimulus event preceding the spike was a motion direction of about 120° at about the same delay. The tuning behavior of the neuron depicted in Fig. 2 is shown in Fig. 3A. General activity and directional tuning differ in the two conditions. While activity levels did not vary systematically with stimulus statistics across the population of cells, directional tuning did. The histogram in Fig. 3B shows the distribution of directional indices for the whole population of 45 MT neurons. The two distributions' medians, *continuous* vs. *discontinuous*, differ significantly (paired Wilcoxon test: $p < 0.01$). Thus, when tuning curves in the two conditions are computed over the full width of one stimulus presentation window (here, 50 ms), directional tuning seems to be significantly more pronounced during random walk ("continuous") stimulation. However, this tuning difference between stimulus conditions depends on the choice of the analysis window (see Fig. 3C). With increasing emphasis on the window's core region, a continuous decline of the significance level for the difference between the direction indices is observed. What are the reasons for this effect? As the analysis window shrinks, tuning curves are constructed with fewer spikes and, thus, the accuracy of determining the directional index may degrade, obliterating real tuning differences. A second possibility, however, is that tuning can in fact be more

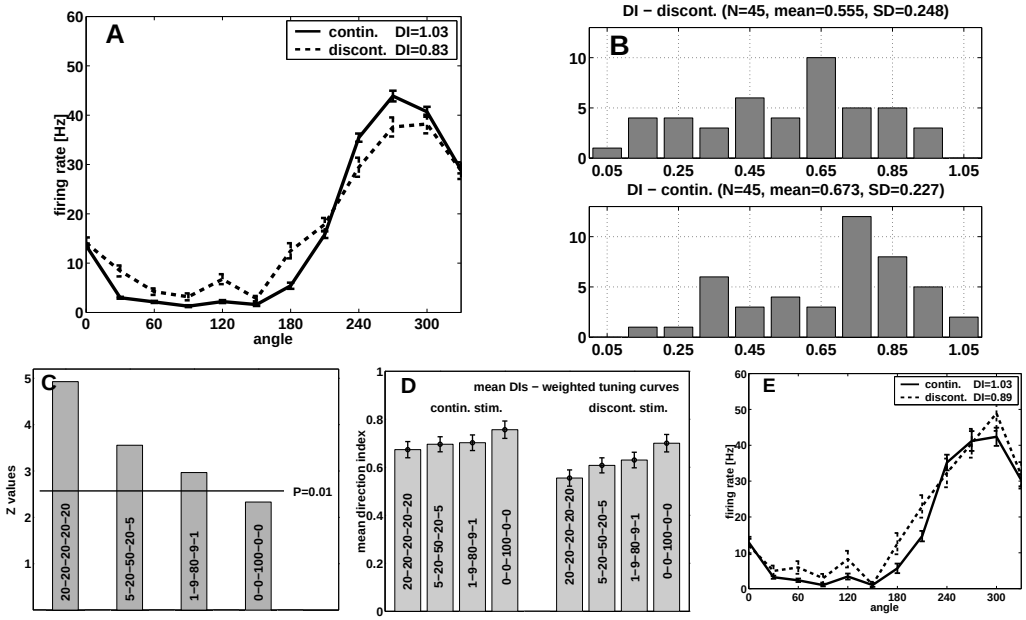

Fig. 3. Emphasis of different partitions of analysis windows is crucial for the obtained tuning curves. (**A**) Tuning curves of the neuron in Fig. 2 for both stimulation paradigms, obtained with an analysis window of 50 ms (full stimulus presentation window) and taking into account the cells response latency, obtained with STAs (see Fig. 2). Solid line: continuous stimulation. Dotted line: discontinuous stimulation. Note that the continuous stimulation paradigm provides the sharper tuning curve. (**B**) Distribution of direction indices (DI) for all recorded neurons (n=45) and both stimulus paradigms. The mean DI obtained with the discontinuous paradigm (upper panel) is significantly lower ($p < 0.01$, paired Wilcoxon test, see also Fig. 3C) than the mean DI obtained with the continuous paradigm (lower panel), indicating that tuning sharpness is reduced in the latter condition. DIs were obtained by using the full analysis window of 50 ms. (**C**) Significance of the difference between the mean DIs obtained with the two paradigms (ordinate) depends on the different weighting of the partitions of the 50 ms-analysis-windows (abscissa). The 50 ms-windows were divided in 5 parts of 10 ms. The numbers within the bars indicate the weighting of each of the windows partitions (see methods for details). With higher weighting of the central region, the significance level decreases, indicating that the tuning curves obtained with the two paradigms assimilate to each other. (**D**) Mean DIs of the population (ordinate) depend on the weighting of the windows partitions as done in (C) (abscissa). With higher weighting of the inner partitions, DIs increase both in the continuous as in the discontinuous paradigm, indicating sharper tuning curves. Note that the increase is stronger in case of the discontinuous stimulation, meaning that the differences between both paradigms decrease. (**E**) Tuning curves of the neuron in Fig. 2 for both stimulation paradigms, obtained with an analysis window of 10 ms, which is located in the center of the 50 ms presentation window, whereas the other partitions are discarded. Note the similarity of tuning curves in comparison to Fig. 3A.

accurately determined with temporally restricted analysis windows, thereby minimizing the influence of responses to preceding or subsequent stimuli. Our

data support the latter scenario. As is shown in Fig. 3D directional tuning improves during temporal focussing of the analysis window. This improvement is more pronounced for directional tuning during discontinuous than during continuous stimulation, thereby reducing the difference in directional tuning between the two conditions. This is illustrated in Fig. 3E for the example neuron, whose tuning curves are more similar when computed over a 10 ms than when computed over the full 50 ms (Fig. 3A) window.

4 Discussion

We have studied the malleability of neural tuning by stimulus statistics using as a model system directionally selective neurons from macaque area MT. When exposed to direction trajectories from two different statistics, neural tuning seems to be sharper during continuous stimulation. This effect can have two explanations. First, stimulus statistics genuinely alters the tuning properties of neurons in area MT. In the continuous stimulus paradigm, i. e., the random walk in movement direction, motion direction changes less abruptly than in the discontinuous stimulus paradigm and may better reflect physical motion we see in our natural environment. Neurons in MT may therefore adapt better to this stimulus statistics, resulting in tuning curves that are more selective. Second, since neurons in MT integrate stimuli over time, as shown for example in Fig. 2, a response at any point in time may result from the influence of more than a single stimulus. Due to the continuity constraint subsequent stimuli tend to be similar in case of continuous stimulation, but not in case of discontinuous stimulation. Therefore, sharper tuning can be expected during continuous stimulation - not as a result of a genuine change of tuning characteristics, but as the result of a direct effect of stimulus statistics on the analysis procedure. The evidence from area MT presented here lends support to the latter explanation. Directional filter properties of MT neurons appear robust and may not adapt to the different stimulus statistics used in our experiment. Since prolonged presentation of a single motion direction has been found to induce substantial adaptation [5] and does constitute an important characteristic of stimulus statistics, future research will need to identify the precise stimulus patterns to which the information processing system adapts and to which it does not. Our finding provides some constraints on the time-scale of such conditions and, furthermore, demonstrates that neural tuning curves obtained with a random stimulus sequence can be directly used to predict responses in quite different stimulus contexts.

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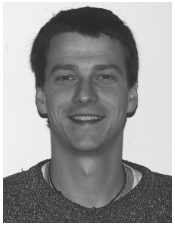

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