Evidence for Peak-shaped Gaze Fields in Area V6A: Implications for Sensorimotor Transformations in Reaching Tasks

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Abstract. The area V6A of the medial parieto-occipital cortex of the macaque is studied for gaze sensitivity. The reported experimental observations support the computational theory of the gain fields to produce a distributed representation of the real position of targets in head-centered coordinates. Although it was originally pointed out that the majority of the cells exhibit roughly linear gain fields [1] [2], we have verified that the peak-shaped gaze fields reported in this study are not in contrast with the gain field models developed in the theoretical neuroscience literature [3] [4]. Rather, the use of peak-shaped (e.g., non monotonic) gaze fields even improves the efficiency of the coding scheme by reducing the number of units that are necessary to encode the target position.

1 Introduction

When we want to reach for an object we must know its precise coordinates relative to the hand or to the body, and this notwithstanding the information extracted from the retinal images continuously changes with eye movements. To achieve representation invariance it is required that the eye position is integrated with retinal location of the target thus obtaining an information that does not change with respect to the eye position. In this way, the brain computes what it is usually called a coordinate transformation. Many neurophysiological studies of non-human primates have shown that the direction of gaze can modulate the gain of neuronal responses to visual stimuli [5] [1] [2], and also the ongoing activity [5] in parietal cortical areas, which are important for the performance of visually guided motor behaviors [5] [6] [1] [2]. The tuning of the visual and of the ongoing activity of lateral parietal cells is in most cases linear (but see [5]). These "gain fields" may be important for converting visual representations from retinotopic to head-centered coordinates [4] [3] [7] and the related transformations may be used for visuomotor performances. In this work we study the gaze-dependent modulations of the ongoing activity of V6A cells. In particular, we perform a quantitative analysis to investigate if the tuning of these gaze-related cells is linear or peak-shaped, and to assess how a model based on peak-shaped gaze modulations can show better performances in localizing targets in space.

2 Methods

Three juvenile monkeys (*Macaca Fascicularis*) weighing 3.1-3.8 kg were used in this study. Experiments were approved by the Bioethical Committee of the University of Bologna and were carried out in accordance with National laws on care and use of laboratory animals and with the European Communities Council Directive of 24th November 1986 (86/609/EEC), revised recently by the Council of Europe guidelines (Appendix A of Convention ETS 123: `http://conventions.coe.int/Treaty/EN/Treaties/PDF/123-Arev.pdf`).

The fixation task. Monkeys were trained to perform a fixation task here described: they were sat in a primate chair located in front of a milky tangent screen $80^\circ \times 80^\circ$ in extent, 57 cm apart from the eyes. The monkeys were trained to depress a lever when a 0.2° spot of light appeared on the screen and to release the lever after the changing of color of the spot of light. The spot of light was binocularly fixated by the monkeys in darkness. In order to test the possibility that gaze position influenced the activity of V6A neurons, animals were trained to fixate nine different positions on the screen, as shown in Fig. 1 (top): the center of the screen, in the animal's straight ahead direction, and other positions obtained by displacing the spot horizontally and/or vertically 20° from the center. As the animal's head was restrained, looking at different screen positions meant obtaining different eye positions in the orbit. Generally, nine different screen positions (in a 3×3 grid with 20° spacing and centred on the straight ahead direction) were tested in a pseudorandom sequence.

Surgical and recording procedures. After training completion, the head-restraint system and the recording chamber were surgically implanted in asepsis and under general anesthesia (sodium thiopenthal, 8 mg/kg/h, *i.v.*) following the procedures reported in [8]. Adequate measures were taken to minimize pain or discomfort. The recording chamber provided access to the cortex hidden into the parieto-occipital sulcus. Single neurons were extracellularly recorded from the anterior bank of the parieto-occipital sulcus using glass-coated metal microelectrodes with a tip impedance of 0.8-2 MΩ at 1 KHz. Action potentials were discriminated with a window discriminator (Bak Electronics, Mount Airy, MD, US). Recording procedures are similar to those reported in [8]. Briefly, spike times were sampled at 1 KHz, eye movements were simultaneously recorded using an infrared oculometer (Dr. Bouis, Karlsruhe, Germany) and sampled at 100 Hz. In both cases, eye position was controlled by an electronic window (5×5 degrees) centered on the fixation target. Behavioral events were recorded with a resolution of 1 ms. Procedures to reconstruct microelectrode penetrations and to assign recording sites to area V6A were as those described in [8] and in [9].

Data analysis. V6A neural activity during the fixation task was quantified in the time epoch from 500 ms to 1500 ms after the lever depression (epoch FIX). During this epoch the animal was steadily fixating the spot of light on the screen. Gaze-related responses of single neurons were statistically assessed by comparing

the activities of the different gaze positions using a Kruskal-Wallis test (a non-parametric equivalent of one-way analysis of variance, $P < 0.05$). To quantify the selectivity of the recorded neurons we computed the preference index (PI). The PI, which takes into account the magnitude of the neuron response to each gaze position, was computed as defined by [11]:

$$\mathrm{PI} = \left(n - \frac{\sum_i r_i}{r_{pref}} \right) / (n-1) \tag{1}$$

where n is the number of positions, r_i is the activity for position i, and r_{pref} is the activity for the preferred position. The PI can range between 0 and 1. A value of 0 indicates the same magnitude of response for all positions, whereas a value of 1 indicates a preference for only one position. All the analyses were performed using custom scripts in MATLAB (Mathworks, Natick, MA, USA).

A full description of the methodology used can be found in [5].

3 Results

We recorded the activity of 215 neurons of area V6A in the medial parieto-occipital cortex of 3 Macaca Fascicularis. The animals looked at different positions (up to nine) on the screen they faced in complete darkness, while the activity of the studied cells was recorded during periods of steady fixation at these positions. We qualitatively tested whether the ongoing cell activity was modulated by eye position. 120 cells (56%) were modulated by eye position (gaze-related cells), whereas the remaining 95 were not (non-gaze-related cells). Out of the entire population, we quantified the activity of 99 cells (81 gaze-related and 18 non-gaze-related, Kruskal-Wallis test, $P < 0.05$) during the FIX epoch for further analyses below reported.

Planar tuning of gaze-related cells. Of 81 cells tuned by gaze direction in darkness, we tested whether the tuning can be considered planar or not on cells tested at least on 5 spatial positions (N=67). Out of these cells, only 18 (27%) turned out to be planarly tuned ($P < 0.05$). An example of a planar cell is showed in Fig. 1.

This cell fired vigorously when the animal looked leftwards, and the activity decreased progressively when the gaze of the monkey was directed in the central part of the screen and rightwards. The progressive decrease of the discharge was studied quantitatively finding the best plane fitting these data. This plane is represented in Fig. 1 (top right): the equation of this plane is $z = -1.17x + 0.025y + 79.29$ and the fit was excellent ($r^2 = 0.90782$, $P < 0.000783$). Out of the 18 cells whose planar fitting was statistically significant ($P < 0.05$), the fit was excellent only in 3 cells ($r^2 > 0.9$), very good only in 4 cells ($0.8 \leq r^2 < 0.9$), and good in 11 cell ($0.06 < r^2 < 0.8$). However, the behavior predominantly observed in our cell population was not planar, as shown in the example of Fig. 2.

The eye position field of this cell was clearly peak-shaped, with the peak of activity in the lower, central part of the animal's field of view. Of course,

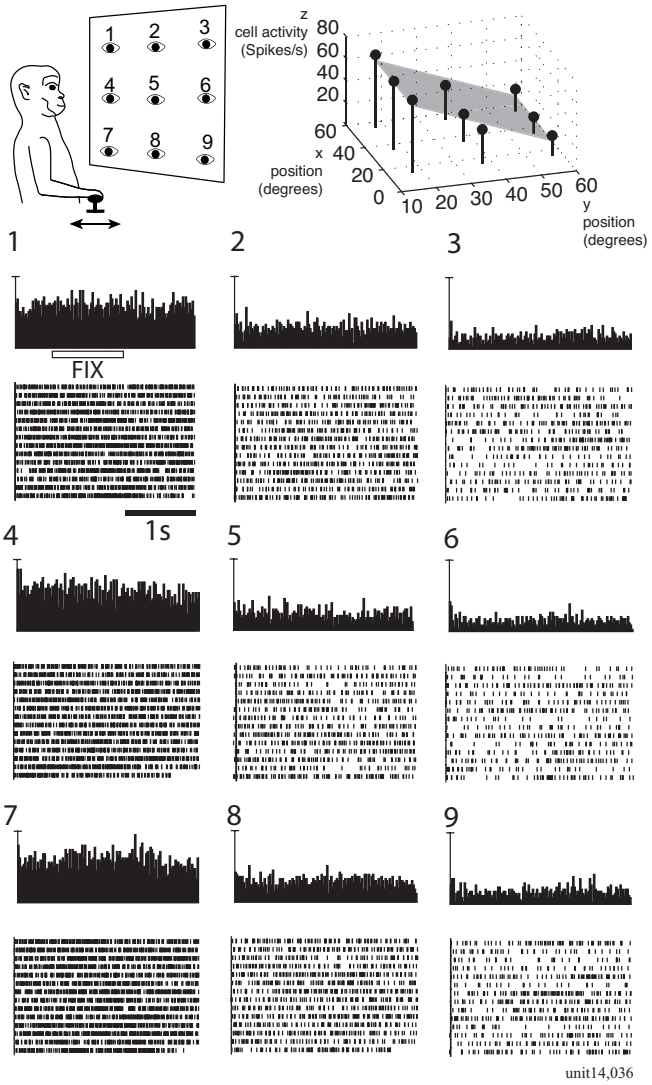

Fig. 1. Eye position-related activity of one V6A cell showing a planar tuning. Top left part: Scheme of the spatial positions (represented by eyes on the screen facing the animal silhouette) fixated by the monkey during the test. Top right part: the activity of the cell during epoch FIX (see Methods) is shown as bullets whose position in the z-axis is proportional to the firing rate. The plane that fits best the activity is also shown. Bottom part: The activity of the cell is shown as peristimulus time histograms, located in the spatial positions the animal looked during the test. Scale: 120 spikes/s per vertical division.

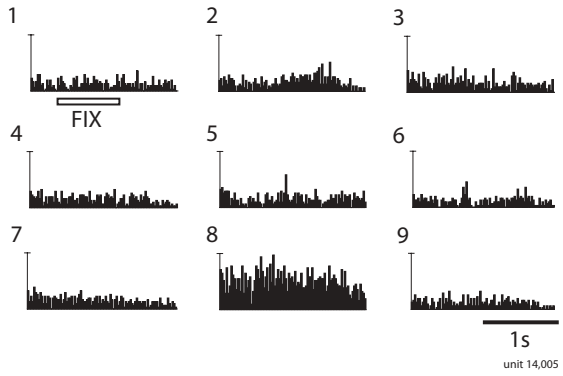

Fig. 2. Eye position-related activity of one V6A cell tested in nine gaze directions and showing a non-planar tuning. Scale: 110 spikes/s per vertical division. Other conventions as in Fig 1. It is evident a strong discharge only for the central position in the bottom row. Neurons peak-shaped as this one represent the 73% of V6A population.

the activity of this cell cannot be fitted on a plane (P = 0.55), but further investigations are needed to find the function that can fit best its tuning. Like the cell showed in Fig. 2, the majority (73%) of the cells of our population showed gaze modulations not fitting with a plane. This behavior also belongs to the examples reported in Fig. 3.

Amount of selectivity of gaze-related cells. To evaluate the amount of selectivity of the gaze-related cells, a preference index was computed (see Methods). Fig. 4(left) shows the distribution of this index of the gaze-related cells: 30/81 (37%) cells had a PI ≥ 0.5, but, despite the high percentage of cells statistically modulated by gaze direction, the majority of these cells (51/81, 63%) did not show a high amount of selectivity, as their PI was less than 0.5.

Eight out of 18 cells whose tuning was planar had a PI less than 0.5. Ten cells showed a relatively high PI. The cell showed in Fig. 2, whose planar fitting was not significant, had a very high PI (PI=0.76) with respect to the entire population. Considering the entire population of the gaze-related cells, we asked whether one part of the space was predominantly represented in V6A. In other words, we tested whether there was an over-representation of spatial preferences with respect to the number of tested positions in each part of the space (χ^2 test, $P < 0.05$). The distributions of preferred gaze positions for our cell population are plotted in Fig. 4(right). As we recorded data in both hemispheres, the distribution of preferred positions is represented in the figure in terms of ipsi- and contralateral space parts and in upper, central and lower parts. No laterality effects were observed. Considering the distribution of preferred positions in each spatial sector, there was no skewing of preference in a sector of the space explored (χ^2 test, n.s. for both plots).

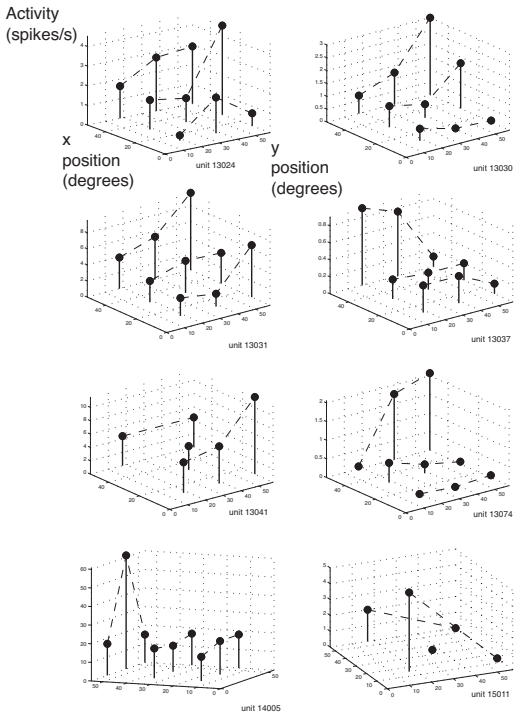

Fig. 3. Examples of non-planar tuned gaze-related cells. Other conventions as in Fig 1. Each graph represents the discharge of one cell in the different positions tested. The position of the bar represents the x and y eye position on the frontal plane. The height of the bar is proportional to the neuronal firing rate in the position. All these cells have an evident peak-shaped profile of activity. Dashed lines connect bars representing activities of the cell for spatial positions located on each row.

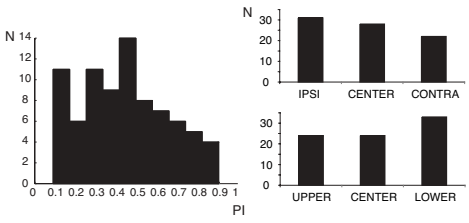

Fig. 4. Position selectivity of 81 gaze-related V6A cells, showed as (left) the distribution of preference index (PI, see Methods), and as (right) plot of the fixation locations at which V6A gaze-related cells show the peak of eye position-related activity. Results from different hemispheres are reported on the same plot. CONTRA and IPSI refer to spatial regions with respect to the hemisphere to which each neuron belongs. UPPER and LOWER refer to regions with respect to the animal. N= number of cells.

4 Functional implications

The reported experimental observations for area V6A described in Section 3 support the computational theory of the gain fields to produce a distributed representation of the real position of targets in head-centered coordinates. Although it was originally pointed out that the majority of the cells exhibit roughly linear spatial gain fields [1] [2], we have verified that the peak-shaped gaze fields reported in this study are not in contrast with the gain field models developed in the theoretical neuroscience literature [3] [4]. On the contrary, the use of peak-shaped (e.g., non monotonic) gaze fields even improves the efficiency of the coding scheme by reducing the number of units that are necessary to encode the target position. To analyze the effect of the gaze field on the representation capability of the neural population we refer to the model of Salinas and Abbott [3]. They consider to have a population of parietal neurons sensitive to a visual target positioned at retinal location x_{tgt} and characterized by a gain modulation by the gaze angle y_{gaze}. The output of the model is a population of motor neurons that, driven by the activity of the gain modulated cells through synaptic connections, are involved in the generation of the arm movement to reach the target. To this goal, the neurons must encode the target location in a body-centered reference frame. This implies that the retinal location of the target must be combined with the current eye position, to obtain a sensitivity to the sum $x_{tgt} + y_{gaze}$. For a gain modulated model neuron the response R^S can be described by:

$$R^S = f(|x_{tgt} - a|)g(|y_{gaze} - b|) \tag{2}$$

where f is the the receptive field profile of the sensory neuron, a is the preferred retinal target location, g is the function that represents the gain field and b is the preferred gaze direction. By using a Hebbian learning algorithm, [3] determined the strength of the synaptic weights w of the afferent sensory neurons, which drive the response R^M of a motor neuron as function of $x_{tgt} + y_{gaze}$:

$$R^M = F(x_{tgt} + y_{gaze}). \tag{3}$$

For the sensory neurons a Gaussian tuning curve is adopted, while the gaze direction modulation is modeled by clipped linear functions that cannot increase beyond a maximum value M. From Eq. 2 the response of a sensory neuron R_i^S, sensitive to a retinal target location a_i and a gaze direction b_i, is given by:

$$R_i^S = e^{\left(-\frac{|x_{tgt}-a_i|^2}{2\sigma^2}\right)}[m(y_{gaze} - b_i) + M]_+^M \tag{4}$$

where $[\cdot]_+^M$ means that the linear function g is clipped and bounded between 0 and M, and m represents the slope of this function. The population of sensory neurons, each with their preferred a_i and b_i, drives the activity of the motor neurons through synaptic coupling:

$$R_j^M = \sum_i w_{ij} R_i^S \tag{5}$$

where w_{ij} is the weight between the sensory neuron i and the motor neuron j. In their original paper [3], the authors state that the gain modulation mechanism, which is responsible of the sensori-motor transformation, does not require restrictive assumptions on the average tuning curves. Indeed, the functions g's may be obtained by averaging operations that combine tuning curves with very different characteristics in similar preferred gaze locations. Furthermore, when the model specifically considers linear gain curves, it postulates bounds on the cell's response and adopts clipped linear functions that cannot increase beyond a certain value. The combined use of pairs of cells with mirror gain modulation tuning curves yields *de facto* a peak-shaped functions to characterize the gaze direction effect. With reference to the Salinas and Abbott's model, we have compared the results obtained by using peak-shaped gaze fields in the modulations, explicitly. Specifically, we implemented the model by substituting the clipped functions with simple peaked functions directly obtainable by linear combination. To focus on the effects of the gaze field modulation function, instead of learning the synaptic weights, we used pre-wired fixed synaptic connection kernels modeled by Difference of Gaussians. Fig. 5 shows the resulting population response of the motor cells for three different gaze angles. For a fixed number of cells in the population, we compared the target localization capability when one uses clipped linear or peak-shaped gaze fields. Increasing the number of cells of the sensory population neurons the model yields correct target localizations, independently of the gaze field function we adopt. Though, when the number of cells approaches a small critical value (in our simulations 20), the accuracy of target localization is worse if clipped linear functions are used. A further analysis pointed out a linear relationship between the sharpness of the gaze field and the localization of the target in head-centered coordinates (see Fig. 6).

5 Conclusions

The work of Andersen and Zipser [2] suggested that the tuning of the visual and of the ongoing activity of lateral parietal cells is in most cases linear, even if the interaction between visual information and information about the position of the eyes in the orbit may be more complex. On the other side, the work of Galletti [5] in the medial parieto-occipital cortex suggested that in most cases the gain field is not linear, as in this region of the brain there are peak-shaped tuning curves to gaze direction. The analysis of the data conducted in this work on one region of the medial parieto-occipital cortex (V6A) pointed out the presence of a large number of cells with such characteristics. From a computational point of view, the analysis of gain modulation with peaked-shaped functions evidenced advantages in terms of the efficacy and efficiency of the representation of the target location, when a limited number of units are considered.

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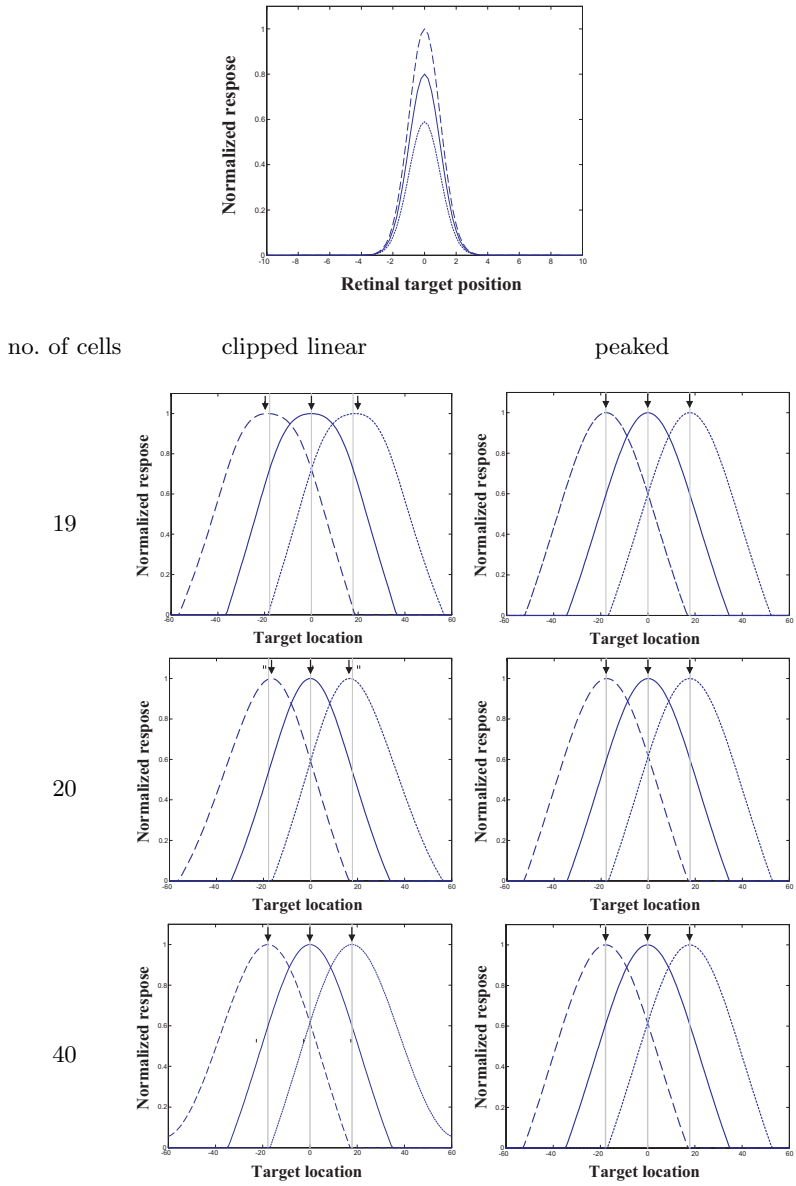

Fig. 5. Comparative behavior of the model. (Top) Gain modulation of the sensory cell. The three curves correspond to different gaze directions: 0° (solid line), -23° (long-dashed line), and 23° (dotted line). (Bottom) Outputs of the motor neuron population when the population of sensory neurons is characterized by different number of cells and different gaze field modulation functions (see text). The population activity peaks shift when the gaze angle changes, thus coding the absolute spatial location of the target. The arrows emphasize the discrepancy between the estimated target location and the real one indicated by the reference vertical lines.

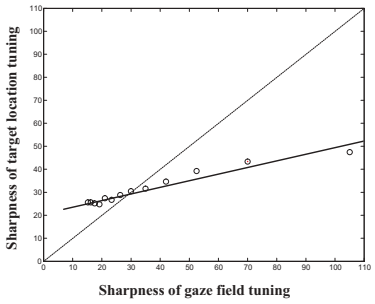

Fig. 6. Relationship between the sharpness of the gaze field and the sharpness of the target localization in head-centered coordinates.

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