Chapter 20
Aspect Ratio of the Receptive Field Makes a Major Contribution to the Bandwidth of Orientation Selectivity in Cat V1

Tao Xu, Ming Li, Ke Chen, Ling Wang and Hong-Mei Yan

Abstract Orientation selectivity is an emergent property of neurons in the primary visual cortex (V1). Orientation selectivity based on spike counts was quantified by bandwidth and circular variance (CV) of the orientation tuning curve. In this study, we studied bandwidth of the orientation tuning curve in cat V1 and its relationship to some physiological parameters. We used drifting sinusoidal grating to test the size of the length and width tunings for single neuron. We observed that simple cells have more elongated excitatory receptive field, while the complex cells have more squarer excitatory receptive field. Furthermore, we found that there was a stronger correlation between tuning width and aspect ratio than CV and aspect ratio. But there are notable differences in orientation selectivity between simple and complex cells. These findings suggest that the aspect ratio of the receptive field is a major factor that affects bandwidth.

Keywords Cat · Orientation selectivity · Tuning width · Circular variance · Primary visual cortex

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20.1 Introduction

Orientation tuning selectivity was estimated with two different quantitative measures: tuning width and circular variance (CV). The tuning width is a local measure of tuning around the preferred orientation [1], whereas CV is a global measure of the tuning curve [2, 3]. The data indicate that CV and bandwidth are not simply related. Besides peak, the shape of the tuning curve far from the preferred orientation has a strong influence on CV [1, 4]. It might be the cause that the diversity in CV is directly caused by the neural mechanisms that cause variation in bandwidth. But some studied report that the aspect ratio and number of receptive field subregions are major factors that affect the tuning width [5–7]. So one important question that whether or not there is a relationship between the aspect ratio of the classical receptive field (CRF) and bandwidth, and how much of an increase in aspect ratio do bandwidth mechanisms cause? This paper answers the question for the cat primal visual cortex.

20.2 Materials and Methods

20.2.1 Animal Preparation

This study was performed in strict accordance with the recommendations in the Guide for the Care and Use of Laboratory Animals from the National Institute of Health. The protocol was specifically approved by the Committee on the Ethics of Animal Experiments of the Shanghai Institute for Biological Sciences, Chinese Academy of Sciences (Permit Number: ER-SIBS-621001C).

Acute experiments were performed on 12 cats of both sexes. Detailed descriptions of procedures for animal surgery, anesthesia, and recording techniques can be found in previous studies [8, 9].

20.2.2 Single-Unit Recordings

Extracellular recordings were made from 175 neurons of the primary visual cortex of anesthetized cats. The methods of visual stimulation and single-cell recording are the same as those described by Song et al. [10] and Xu et al. [9]. Recordings were made mainly from layers 2/3 and 4.

20.2.3 Procedures

Each cell was stimulated monocularly via the dominant eye and characterized by measuring its response to conventional drifting sinusoidal grating. With this method, we measured basic attributes of the cell, including spatial and temporal frequency tuning, orientation tuning, and contrast response function, as well as area, length and width tuning curves. To obtain quantitative estimates of the length and width of a cell's excitatory response field, we measured the length and width summation curves and used standard procedures for fitting curves to the experimental data [11].

The cells were classified as "simple" if the first harmonic (F1) was greater than the mean firing rate (F0) of the response (F1/F0 ratio > 1) or "complex" if the F1/F0 ratio was < 1 [12].

20.2.4 Circular Variance and Tuning Width

The orientation tuning curves were fitted with the von Mises distribution:

$$R = R_0 + R_1 e^{k\left[\cos 2\left(\mathrm{Ori}-\mathrm{Ori}_p\right)-1\right]}. \tag{20.1}$$

where R represents the response of the cell as a function of orientation (Ori), and R_1, R_0, e, and k are free parameters [13]. We fit the raw data rather than the mean response at each orientation. The preferred orientation was defined as the peak of the fitted function (Orip). The tuning curve width at half-height (WHH) has been used previously [13]. WHH of the fitted function was used to describe the tuning width, which was calculated as follows:

$$\mathrm{WHH} = \arccos[(\ln 0.5 + k)/k]. \tag{20.2}$$

The CV was calculated from orientation tuning curves as follows. We measured the mean spike rates, r_k, in response to a grating drifting with angle k. The angles k spanned the range from 0 to 360° with equally spaced intervals [1, 14, 15]. From these data, the CV was defined as

$$\mathrm{CV} = 1 - \left|\frac{\sum_k \mathrm{e}^{i2\theta_k} r_k}{\sum_k r_k}\right|. \tag{20.3}$$

The CV ranges from 1 for a completely non-orientated (flat) curve to 0 for an exceptionally oriented (zero response at all orientations except the preferred one) curve.

The selectivity measures were calculated based on the mean spike rate of the neurons during the response to a visual stimulus. For simple cells, one could also define a similar measure with the first harmonic amplitude (F1) of the response. We

did not subtract the spontaneous rate of the responses from the visually driven responses before the calculation of CV and bandwidth. The statistical significance of the experimental data was evaluated using Student's t test.

20.3 Results

Here we present data collected from V1 of 12 cats, in which we completed quantitative tests and analysis of 175 single neurons at eccentricities within 10° of the visual axis. In our sample of cells, 60 were simple cells and 115 were complex cells.

20.3.1 WHH and CV in the V1 Population

There was a wide variation in orientation selectivity in cat V1 (Fig. 20.1). The white and black arrows indicate the median of WHH in simple (24.66° ± 15.13°) and complex cells (47.09° ± 29.01°), respectively. There was a significant difference ($p < 0.001$) between simple and complex cells in tuning width, which is in good agreement with previous findings about tuning width in cat V1 [16–18]. The results are also similar to observations in primary visual cortex of anesthetized and alert monkey [19, 20].

Considering the complete cell sample, there was a rather flat distribution over the entire CV range. The median CV of the simple cells was 0.23 ± 0.27, and the median of the complex cells was 0.54 ± 0.25. There was also a significant difference ($p < 0.001$) between simple and complex cells in CV, which is generally consistent with the results in anesthetized and alert monkey V1 [1, 20].

To better understand the relationship between CV and WHH measures, we constructed a scatter plot of CV versus WHH for our population of V1 neurons

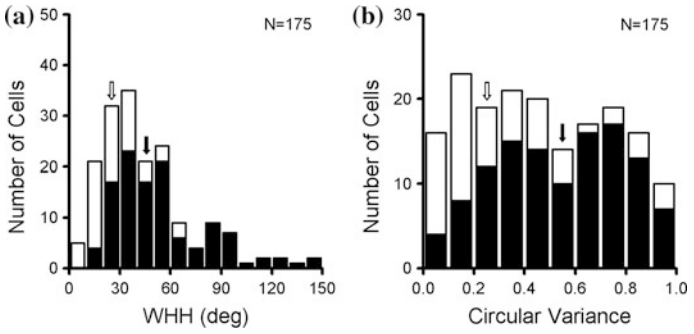

Fig. 20.1 Distribution of orientation selectivity in the V1 population. The white bars represent the simple cells and the black bars represent the complex neurons in V1

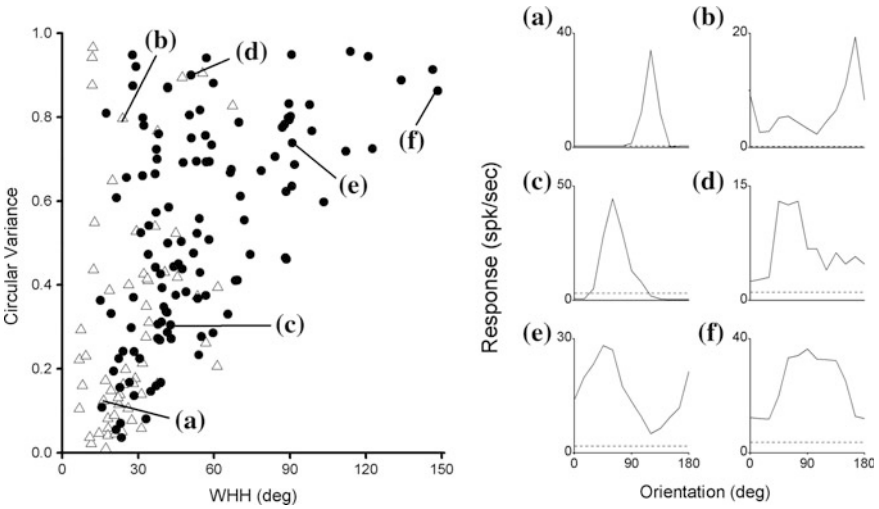

Fig. 20.2 Relationship between WHH and CV. *Left graph* Scatterplot of orientation WHH and CV for all neurons. *The open triangle* simple cells are scattered at bandwidth below 75°. *The filled circle* complex cells are scattered over the orientation width at half-height. In general, the CV increased with the orientation width at half-height. *a–f*, Examples of individual tuning curves in different locations of the scatterplot. The x-axis represents stimulus orientation, and its scale is the same for all cells, from 0 to 180°, as indicated in the bottom plots. The y-axis is the fire rate of the cell. *The dash line* indicates the spontaneous response of the cells

(Fig. 20.2). WHH and CV were strongly correlated in cat V1 neurons (simple cells: $r = 0.51$, $p < 0.001$; complex cells: $r = 0.58$, $p < 0.001$), which is consistent with the results in anesthetized and alert monkeys [1, 20]. In Fig. 20.2, orientation bandwidths of $0 \sim 75°$ are represented by the CV range from 0 to 1.0. Cells with bandwidths larger than 75° are mapped to values of CV between 0.5 and 1.0. However, often a single value of orientation bandwidth will be mapped to many different CV values.

To get an intuition for the differences between CV and bandwidth, it helps to inspect individual examples from Fig. 20.2. In this figure, the pairs a, b and c, d are examples of cells with similar bandwidth but quite different CV values. Examining the tuning curves, one sees that indeed the curves have similar shape around their peak. However, the responses near the orthogonal orientation are quite different. In both a and c, orthogonal stimulation produces a response very close to zero, whereas in b and d, orthogonal stimulation produces a significant response. This feature is picked up by the CV measure. Similarly, the pairs d, f and b, e are examples of cells with similar CV but quite different bandwidths. The cases in which the CV and bandwidth measures disagree illustrate how these two measures are indicating different aspects of orientation selectivity: bandwidth depends on the shape of the tuning curve around the peak, whereas CV weights responses at all orientations in its estimate of selectivity.

20.3.2 Comparison of WHH and CV with Aspect Ratio

The subregion aspect ratio of the feed-forward input is a major factor that affects the orientation selectivity of simple cells [6, 7, 21]. In our experiments, we observed that the aspect ratio (excitatory receptive field length/width ratio) is correlated with orientation selectivity in both simple and complex cells.

At this point, it is important to clarify how our receptive field measurements made with gratings relate to the detailed internal structure of the receptive fields of simple and complex cells. The response of a simple cell to a drifting sinusoidal grating reflects the net sum of stimulation of both the bright-excitatory and dark-excitatory subregions. Complex cells, on the other hand, respond to both bright and dark stimuli throughout their receptive fields [21].

As a measure of the size of a cell's receptive field, we adopted the extent of its excitatory summation area. We measured the effect of increasing first the length (parallel to the preferred orientation) and then the width (orthogonal to the preferred orientation) of a rectangular patch of grating of optimal spatial frequency and orientation. To obtain quantitative estimates of the length and width of a cell's excitatory receptive field (excitatory summation area), we used standard procedures for fitting curves to the experimental data [11].

For our sample of cells, the length and width of the excitatory summation areas ranged about from 0° to 15°. Some summation areas were relatively long and narrow, some were short and wide, while others were approximately symmetrical (see Fig. 20.3a). We plotted optimal width versus optimal length in Fig. 20.3a. For the population of cells, we can see that cells above the diagonal are mostly simple cells, which indicates that most simple cells have narrow, elongated excitatory receptive fields. Cells that lie along or near the diagonal in the plot are mostly

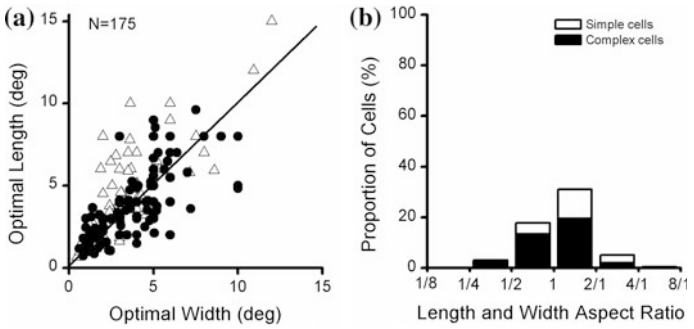

Fig. 20.3 Comparison of the length and width of excitatory receptive fields of the population of simple and complex cells. **a** Summary of the relationship between optimal length (L_{opt}) and optimal width (W_{opt}) is shown as a scatterplot. *Open triangle* simple cells, *filled circle* complex cells. *Diagonal line* indicates the cells have the same degree of Lopt and Wopt. **b** Distribution of the preferred grating aspect ratio (L_{opt}/W_{opt}) among 175 V1 neurons. *White columns* indicate simple cells and *black columns* indicate complex cells

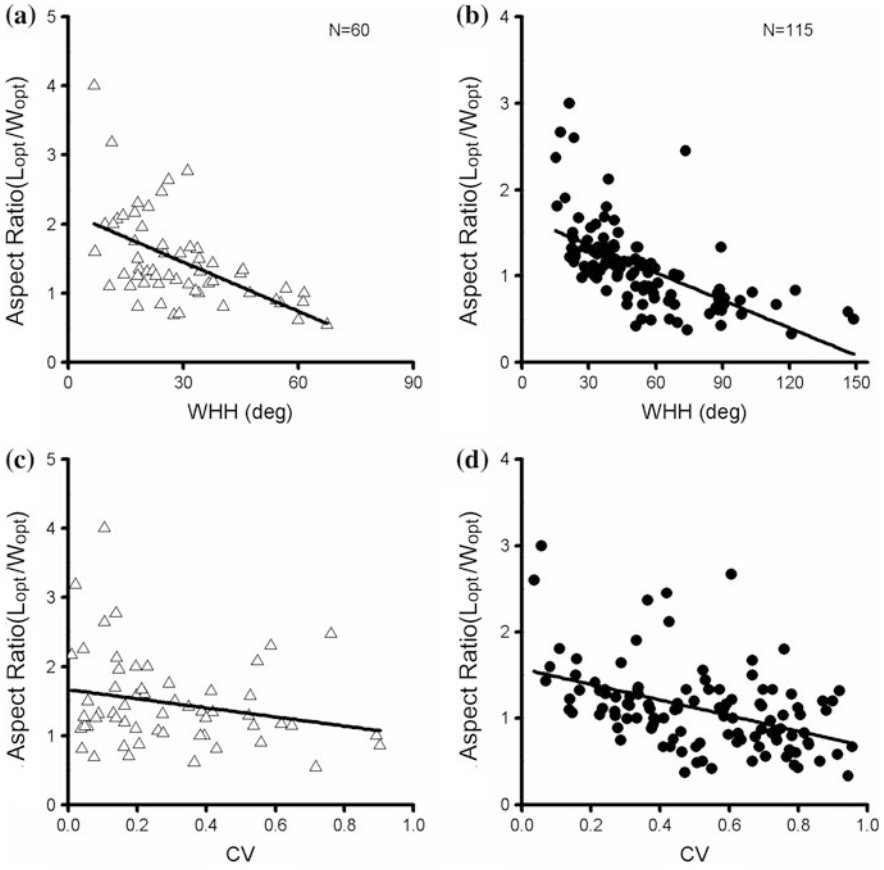

Fig. 20.4 Relationship between orientation selectivity and aspect ratio of the L_{opt}/W_{opt} of V1 cells. *Open triangle* simple cells, *filled circle* complex cells. **a** The relationship between WHH and the aspect ratio of the simple cells. **b** The relationship between WHH and aspect ratio of the complex cells. **c** The relationship between CV and aspect ratio in simple cells. **d** The relationship between CV and aspect ratio in complex cells. The CV and aspect ratio have weaker negative correlations than WHH and aspect ratio in simple cells and complex cells

complex cells, which illustrates that most complex cells have symmetrical excitatory receptive fields.

Quantitatively, we found that the preferred grating aspect ratio (optimal length/optimal width ratio) is significantly different ($p < 0.001$) between simple (mean = 1.48, SD = ±0.66) and complex (mean = 1.10, SD = ±0.49) cells. Figure 20.4b shows the distribution of the preferred grating aspect ratio of simple and complex cells. For simple cells, most often the optimal length was larger than the optimal width; for complex cells, the optimal length was mostly almost identical to the optimal width.

Next, we evaluated the correlation between preferred grating aspect ratio and orientation selectivity of simple and complex cells. Figure 20.4a, b shows that there are strong negative correlations between aspect ratio and WHH in simple cells ($r = -0.54$, $P < 0.001$, Fig. 20.4a) and complex cells ($r = -0.61$, $P < 0.001$, Fig. 20.4b). The relationships between CV and aspect ratio in simple and complex cells are shown in Fig. 20.4c, d. In that plot, much less covariation of the two measures can be observed than between WHH and aspect ratio. There is a moderate negative correlation between aspect ratio and CV in complex cells ($r = -0.44$, $P < 0.001$, Fig. 20.4d), and there is almost no correlation between aspect ratio and CV in simple cells ($r = -0.23$, $P = 0.09$, Fig. 20.4c).

20.4 Discussion

The result of this work is the wide diversity of orientation selectivity in the population of cat V1 neurons, which is similar with the observation of Ringch et al. [1] in anesthetized macaque V1 neurons. Furthermore, we displayed that the diversity of CV is greater than WHH mainly in the sample of simple cells (see Figs. 20.1 and 20.2). The orientation of WHH is similar in simple cells, while diversity in complex cells. However, the orientation CV is diversity both in simple and complex cells.

Figure 20.3b shows that most simple cells have the elongated excitatory receptive fields, while the geometry shape of the complex cells is diverse. Perhaps, it can explain why orientation WHH is similar in simple cells, while diversity in complex cells.

The factors that control WHH are likely to be different from those that determine CV. Figure 20.4 shows that there is stronger negative correlation between aspect ratio and WHH, whereas there is a weaker negative correlation between aspect ratio and CV. Thus, the diversity of the relative heights of the plateau and peak would strongly influence the diversity of CV, whereas the shape differences of the excitatory receptive fields might affect the variability of WHH.

A previous study reported that the suppression far from the peak could account for the low values of CV [1]. In the present study, we showed that the cortico-cortical suppression could also contribute to narrowing the WHH.

We found that the orientation selectivity of simple cells is significantly higher than that of complex cells (see Figs. 20.1 and 20.2). Previous studies have reported that simple cells have narrower tuning width than complex cells in cat V1 [16–18]. The feed-forward model makes an important prediction regarding the strong relationship between the tuning width and the aspect ratio of a simple cell's subfield [21]. More critically, Jones and Palmer [6] measured orientation tuning in cells whose receptive fields they mapped and found a strong relationship between tuning width and receptive field shape. As predicated, the higher the aspect ratio of the subfield, the sharper was the orientation tuning. The aspect ratio found in this study differs from the subregion's aspect ratio of simple cells in the primary model [6]. It is similar to the aspect ratio reported in studies of tree shrews [22, 23]. Although the

circuits responsible for generating aspect ratio would be different, the fundamental mechanism may be the same. Thus, whether orientation selectivity emerges at the first cortical synapses or beyond, an orientation selectivity bias in geometry is likely to be the common initiating event [22].

In Fig. 20.4a, b, we found that there are strong negative correlations both in simple cells and complex cells between aspect ratio and WHH. Figure 20.4a quantitatively shows that the aspect ratio is significantly different between simple and complex cells. Perhaps, this is the reason why simple cells have narrower tuning widths than complex cells.

The results of this study may lend further understanding to the mechanisms of orientation selectivity. These findings suggest that the aspect ratio of the receptive field is a major factor that affects bandwidth. Perhaps, at least in cat V1, the orientation selectivity of simple cells mainly relies on feed-forward models, whereas the orientation selectivity of complex cells relies on lateral inhibitory to refine selectivity relative to a weak bias provided by feed-forward input (cortico-cortical excitatory interactions).

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