

Functional Roles of Receptive Field Structures in the Perception of Orientation

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ABSTRACT

To investigate the cortical mechanisms underlying the determination of apparent tilt, including the tilt illusion, we developed and examined a V1 network model consisting of cortical neurons and phase-coupled oscillators for neural grouping. Grouping local orientations based on V1 colinear connections, the model showed quantitative agreement with psychophysically measured apparent tilt. Computational investigations on the functional roles of various receptive field structures suggest that even-phase receptive fields are crucial but not exclusive for the apparent orientation of a bar. Our results further suggest importance of the feedback of grouping information from complex cells, which are synchronized through colinear connections, to simple cells with specific phases.

Key words: Early Vision, Orientation, Psychophysics, Synchronization, Spatial Phase

1. Introduction

To determine the global orientation of a bar, the neural system has to group the local orientation signals extracted by neurons in the primary visual cortex (V1). If a bar junction exists, Gabor filters signal erroneous information around the intersection. Therefore, the global orientation of a bar will be misjudged, which is expected to be an origin of the tilt illusion. We investigate the cortical mechanisms underlying the neural grouping for the perception of apparent tilt, specifically in the tilt illusion.

It has been suggested that the horizontal connections exist among neurons in V1 superficial layers, most likely complex cells, as they form colinear connections [1], and that synchronization among them is responsible for contour saliency [9]. A similar colinear synchronization is expected to account for the neural grouping for the determination of global orientation. Given the colinear connections among complex cells, we examined recently what neural groups tend to be formed when a bar junction is shown [8]. We used a phase model as a simple and mathematically well-established mechanism to assess a tendency of grouping automatically. The results of simulations showed that the colinear synchronization realizes the exclusion of the intersection region, which agrees with grouping determined psychophysically. However, there was quantitative disagreement between the global orientations computed from the phase model and the apparent tilt measured psychophysically.

This disagreement between the model and apparent tilt might originate from that simple cells play somewhat more role than an equally weighted input to the grouping mechanism as is in that model. For instance, simple cells with even-phases and odd-phases might have different connections and roles for the determination of apparent tilt. It has been thought generally that even-phase simple-cells are responsible for the detection of bars, and odd-phase for the detection of edges [2]. Simple cells could be important for these detections, and complex cells could be crucial for texture processing [5] and context dependency [3]. We carried out simulations of a network model based on major properties of V1 including the colinear connections, in order to examine the functional roles of receptive field structures for the perception of global orientation of bars, specifically a role of simple and complex cells, and even- and odd-phase receptive fields of simple cells.

2. The Model

A schematic illustration of the model is shown in Figure 1, which consists of three major stages; a set of Gabor filters followed by half-wave rectification, estimation of local orientations by a winner-

take-all mechanism, and coupled neural-oscillators to assess tendency of grouping. We designed the model so that the entire input field covers $3.88^\circ \times 3.88^\circ$ in visual angle by 97×97 units. The first stage of the model consists of simple-cell-like units whose receptive field is given by a Gabor filter with a variety of orientation, spatial frequency and phase preferences. For the sake of computational simplicity, no temporal property of V1 neurons is taken into account, which maintains our focus on the spatial distribution of cellular activities. For each spatial position, there are 576 types of model cells: 36 types of optimal orientation with an increment of 5° , four types of optimal spatial frequency, 17, 10, 5, and 2.5 cpd, corresponding to multiples of 0.25, 0.5, 1.0 and 2.0 times the width of stimulus bars, and four types of spatial phase, 0, 90° , 180° , and 270° phases of the Gabor filters. The output of Gabor filters passes through half-wave rectification with thresholding to generate the output of simple-cell units.

The second stage of the model determines local orientation. We represent the local orientation by the *local peak orientation* as a simple and biologically plausible measure [5]. The local peak orientation is the optimal orientation of the unit that responds most strongly among those units located at the same spatial position, with various orientation and spatial frequency preferences. It has been reported that the bar orientation estimated from the local peak orientations is similar to that computed by taking vector summation [6]. The spatial-phase invariance of model complex-cells is established at this stage. It has been shown that this pooling by a winner-take-all mechanism reproduces the spatial nonlinearity of the receptive field [7].

The third stage of the model determines the groups of cells that correspond to each of two bars. A phase model governed by Kuramoto's equation [4] is employed for the grouping process. We designed the model so that units fire periodically and the temporal phase of each unit indicates the timing of cellular firing. It is assumed that cells are grouped together if the timing of firing is synchronized. Although it is doubtful that neurons *in vivo* are actually governed by this equation,

the phase model is a simple and suitable model to employ here because our specific aim is to examine what neural groups are formed given the colinear connections and the local orientations deduced from X-shaped stimuli that produce illusory tilt.

Synchronization will be established if coupling between two units is strong. The coupling coefficient is determined depending on three measures: (1) co-circularity, (2) relative difference in local orientation, and (3) spatial distance. The product of the three measures gives the overall coupling coefficient, which realizes the preference to colinearity [9, 8]. In most cases, starting from randomized phases, the synchronization reached a stable state after 10 to 20 cycles of iterations. The last part of the stage computes the global orientation of bars by taking the ensemble average of the local peak orientations among the synchronized cells.

3. Spatial Distribution of Effective Neuronal Responses --- Simulation Results

We examined the spatial distribution of neuronal responses effective for the perception of the global orientation of bars, with specific interests in differences among simple and complex cells, and even- and odd-phase receptive fields.

A. Spatial Distribution of Local Orientations

We carried out simulations of the model to estimate the local orientations when an X-shaped stimulus is presented. The retinotopic distribution of local peak orientations computed by the complex-cell units are shown in Figure 2 (A). The responding complex-cell units are distributed retinotopically for a wide range, almost twice the width of actual bars, because complex-cells lack the spatial localization of orientation information. It is uncertain whether all complex cells hold necessary and meaningful information for the determination of bar orientations. To clarify the effects from the complex cells outside the bar region, we extracted the responses within the extent of the vertical bar from Figure 2 (A), and showed in (B). Figure 2 (C) shows the local orientations of the synchronized units that correspond to a vertical bar. The next stage of the model computes

the global orientation by taking the ensemble average of these synchronized units. Complex-cell-unit responses are determined by pooling four types of simple-cell-units with different spatial phases. We computed the local orientations that is determined by pooling only even-phase units (Figure 2 (D)), and 0° -phase units (E). We can observe that the responses outside the bar extent originate mostly from odd-phase units, and that strong tilt effects originate from even-phase units, particularly 0° -phase units. For further quantitative analysis, we computed the global orientation of a vertical bar by selectively pooling units with distinct phase type.

B. Complex-Cell Responses Inside the Bar Region

We computed the global orientation of a vertical bar by taking the ensemble average of the local peak orientations among synchronized units corresponding to the vertical bar. Disregarding the responses of complex-cell-units whose receptive field center is located outside the bar region, we also evaluated the global orientation from the synchronized units located inside the bar region. The difference between these two would clarify the significance of the responses of complex cells located inside or outside the bar region. Note that the responses outside the bar extent originate mostly from odd-phase units. The computed global orientations for various X-shaped stimuli are shown in Figure 3. For comparison, we re-plotted the apparent tilt measured in corresponding psychophysical experiments [8]. The amount of global orientation computed from inside the bar extent is greater than that incorporates outside the bar extent, and closer to the apparent tilt psychophysically measured.

Psychophysical experiments have shown interesting characteristics in multiple-gray X-shaped stimuli; apparent tilt is independent of segmentation but dependent on contrast as shown in Figure 4(A). It is important to confirm that the model reproduces the major human response characteristics, segmentation independence and contrast dependence, as well as the amount of apparent tilt. We computed global orientation of the vertical bar in multiple-gray stimuli from the responses of synchronized complex cells as shown in Figure 4(B). The model reproduces

segmentation independence and contrast dependence. Stimuli consisting of a variety of contrasts evoke various activities in V1-cell-units, which further deduce various local peak orientations. Therefore, even if the grouping is similar, the resultant apparent tilt is different. On the other hand, the segmentation-dependent difference in the activities is not large enough to alter the apparent tilt.

The above results indicate that the orientation information, carried by the complex cells whose receptive-field center is located within the bar extent, is crucial for the tilt illusion. This is natural in the sense that local orientation apart from a bar is less significant than that close to or placed on a bar. However, the complex cells whose receptive-field centers are apart from but closed to a bar are likely to respond to the bar, since complex cells hold the invariance to spatial phase. Given that a complex cell consists of a pooling of simple cells with various spatial phases [7], the responses of complex cells positioned outside a bar originate from simple cells whose receptive field has an odd-phase or anti-phase of a bar. Therefore, the results suggest that even-phase simple cells play a crucial role in the tilt illusion and the perception of global orientation of a bar. In the next section, we examine further a role of even-phase receptive fields, and a plausible cortical mechanism for a phase-specific operation in grouping.

C. Even-Phase Simple-Cell Responses within the Region Determined by the Synchronization

In this section, for the ensemble average of local peak orientations to compute global orientation, we take the responses of the even-phases (0° and 180°) or 0° -phase simple-cell units located within a spatial extent of the group determined by the synchronization of complex-cell units. This mechanism is equivalent to considering feedback from the complex cells, synchronized through colinear connections, to simple cells with specific phases. Since the inclusion of both odd- and even-phase simple-cell responses is equivalent to the utilization of complex-cell responses, the contribution of odd-phase simple cells can also be easily induced from this simulation. The results will give a clue as to the roles of simple and complex cells, as well as even- and odd-phase receptive fields, in the perception of global orientation.

The computed global orientation of the vertical bar in X-shaped stimuli is overlaid in Figure 3. The amount of the global orientation computed from even-phases is similar to the apparent tilt psychophysically measured, and that from the previous model that takes into account the complex cell responses within the bar extent. This result also suggests that the simple cells with an even-phase receptive-field account largely for the tilt illusion compared with those with odd-phase. The amount computed from 0°-phase simple-cell units is almost twice that of the models with multiple phases. This overestimation of apparent tilt suggests that the responses of the cells with phases other than the optimal one for the bar are not disregarded for the perception of global orientation. We also computed global orientation of the vertical bar in multiple-gray X-shaped stimuli, and confirmed that the models with even-phases and 0°-phase reproduce the major characteristics of human responses, namely contrast dependence and segmentation independence, as shown in Figure 4(C) and (D), respectively.

4. Conclusions

We propose that receptive-field structures, specifically spatial phase preference, have different functional roles in the perception of global orientation including the tilt illusion. Our computational investigations indicate that even-phase receptive fields are crucial but not exclusive for the apparent orientation of a bar. This further suggests the importance of the feedback of grouping information from the complex cells, which are synchronized through colinear connections, to simple cells with specific phases.

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Figure Captions

Figure 1. An illustration of the model. The first stage consists of a set of Gabor filters followed by half-wave rectification. The second stage estimates local orientations by determining the strongest unit among others. The last stage computes the global orientation of a bar by taking the ensemble average of local orientations within the group determined by the phase model.

Figure 2. The retinotopic distributions of computed local peak orientations. The tilt of a needle indicates the local peak orientation at the position. The responses less than a threshold are not shown here. Each panel shows the result of specific pooling of units as indicated in the panel.

Figure 3. The computed global orientations for stimuli consisting of two bars with identical contrast. Open circles indicate human responses psychophysically measured [8].

Figure 4. The estimated global orientations for stimuli consisting of two bars with different contrasts. The configurations of the stimuli are indicated in inset. For example, insets (A) and (B) have identical segmentation but different contrast.

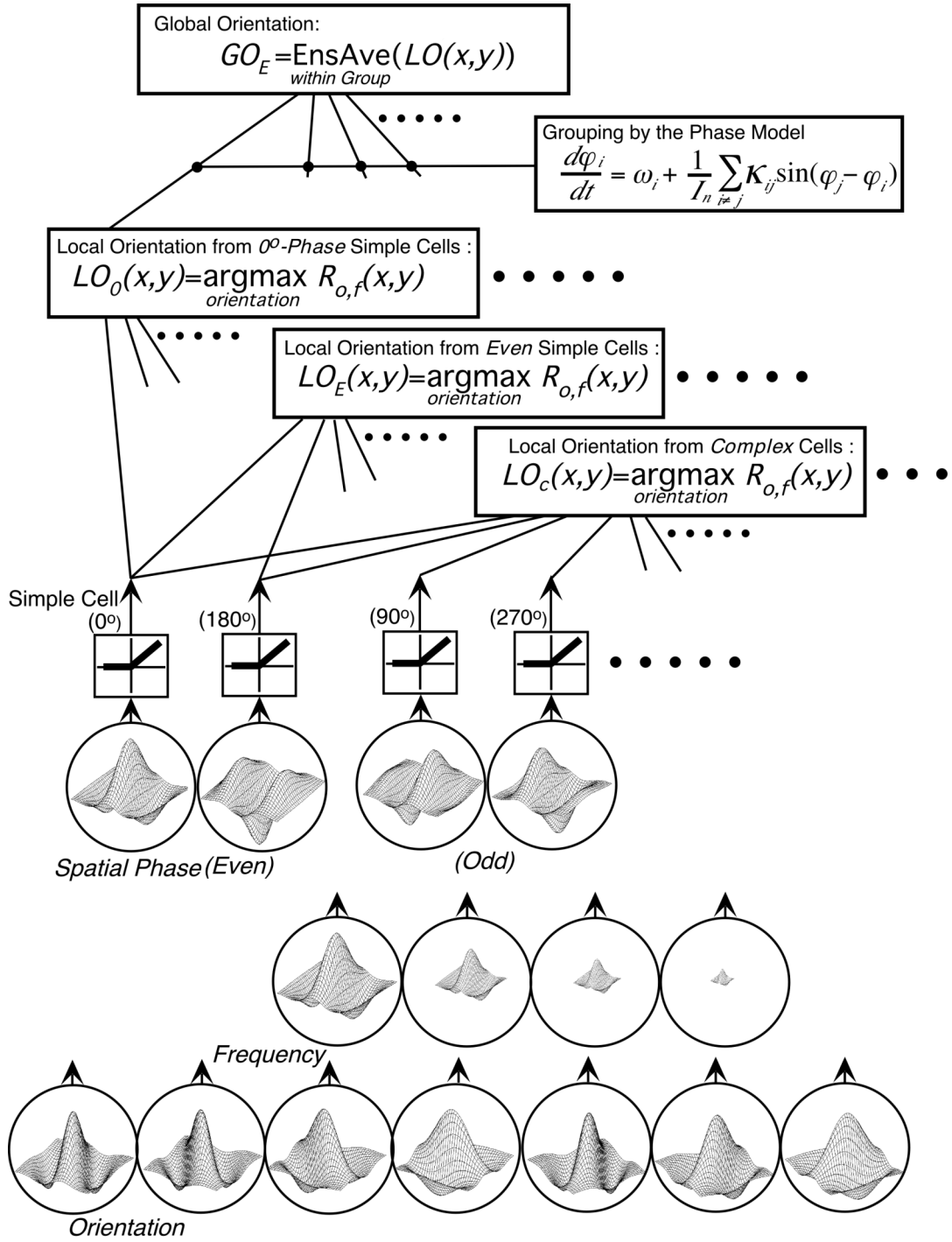


Figure 1

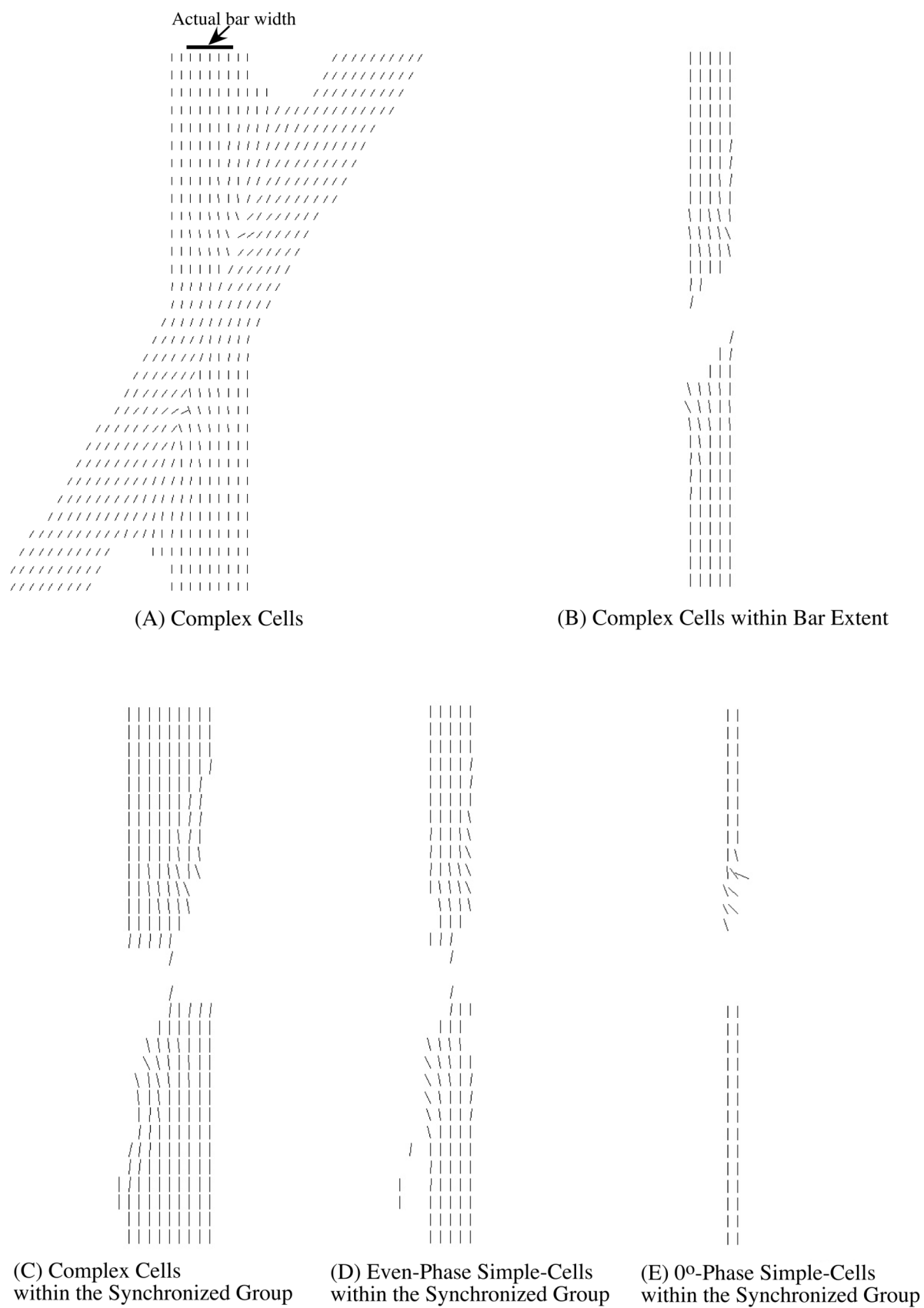


Figure 2

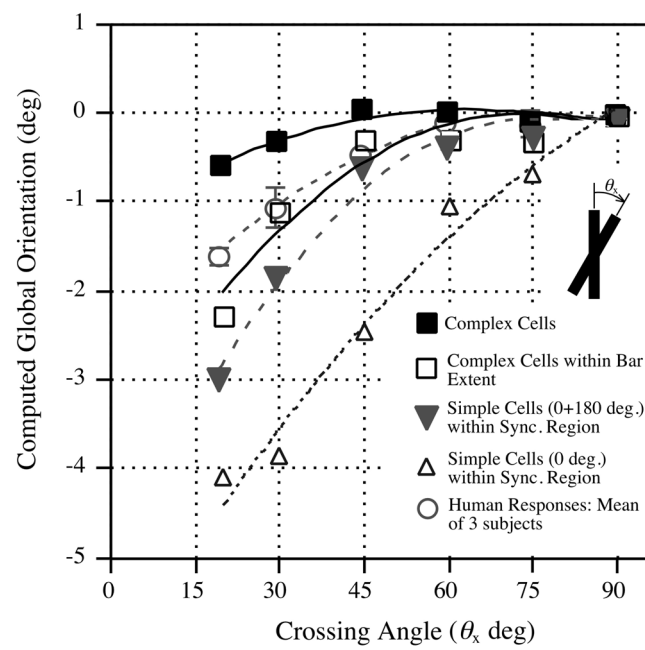
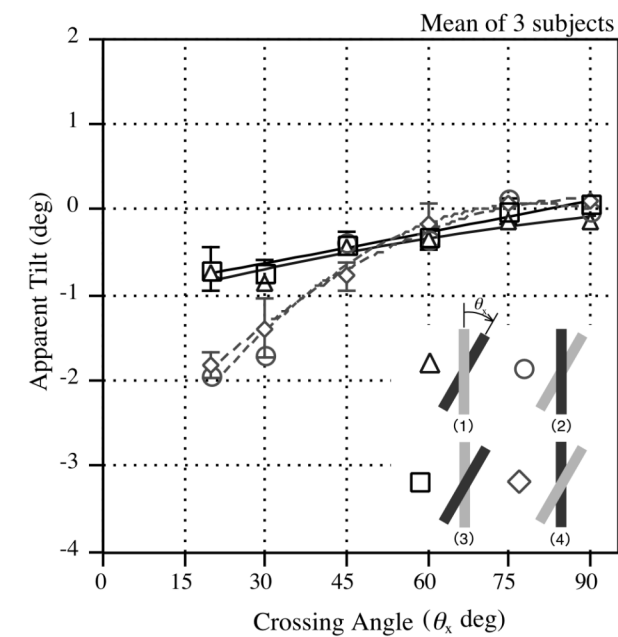
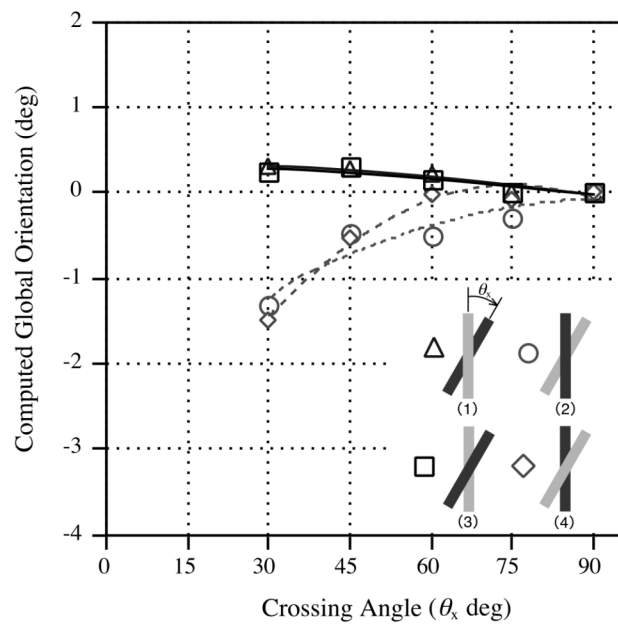


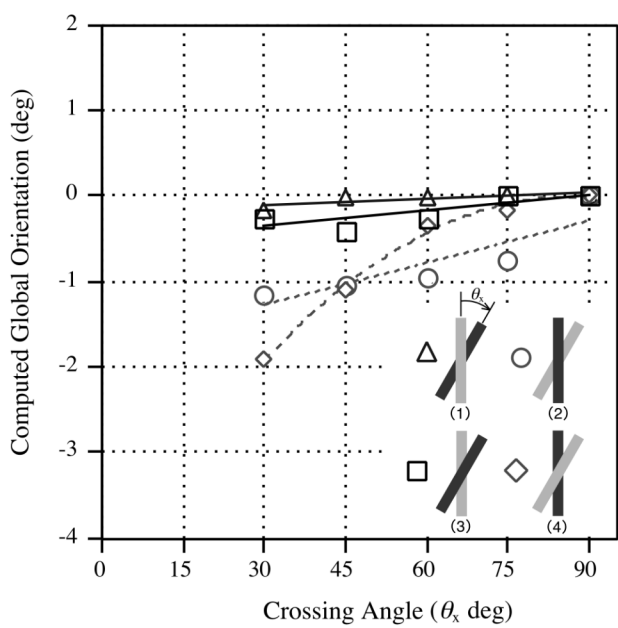
Figure 3



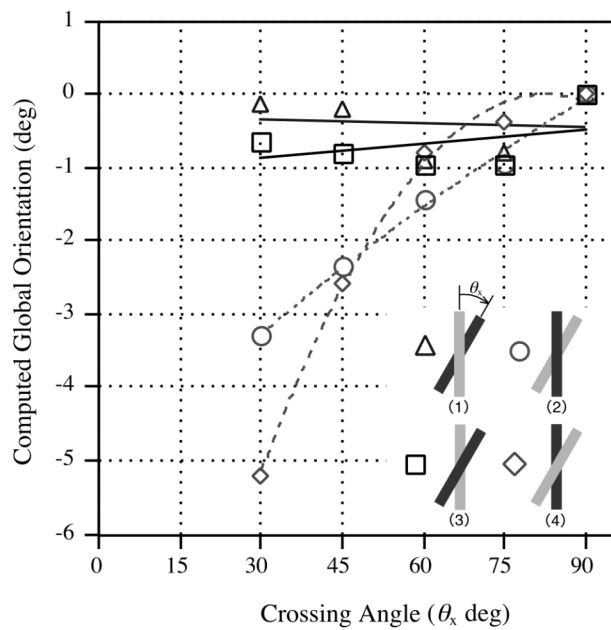
(A) Psychophysics



(B) Complex Cells



(C) Even Phases



(D) 0° Phase

Figure 4