The responses to illusory contours of neurons in cortex areas 17 and 18 of the cats

ZHOU Yifeng (周逸峰)[1,4], JIA Fan (贾 凡)[1], TAO Haiyang (陶海洋)[1] & SHOU Tiande (寿天德)[2,3]

1. Laboratory of Cognitive Science of CAS, Vision Research Laboratory, School of Life Sciences, University of Science and Technology of China, Hefei 230027, China;
2. Center for Brain Science Research and Liren Laboratory, School of Life Sciences, Fudan University, Shanghai 200433, China;
3. Laboratory of Visual Information Processing, Institute of Biophysics, Chinese Academy of Sciences, Beijing 100101, China;
4. Center for Brain and Mind Science, Chinese Academy of Sciences, Beijing 100101, China

Correspondence should be addressed to Zhou Yifeng (email: zhouy@ustc.edu.cn)

Received July 5, 2000

Abstract Responses to illusory contours (ICs) were sampled from neurons in cortical areas 17 and 18 of the anesthetized cats. For ICs sensitive cells, the differences of receptive field properties were compared when ICs and real contour stimuli were applied. Two hundred orientation or direction selective cells were studied. We find that about 42 percent of these cells were the ICs sensitive cells. Although their orientation or direction tuning curves to ICs bar and real bars were similar, the response modes (especially latency and time course) were different. The cells' responses to ICs were independent of the spatial phases of sinusoidal gratings, which composed the ICs. The cells' optimal spatial frequency to composing gratings the ICs was much higher than the one to moving gratings. Therefore, these cells really responded to the ICs rather than the line ends of composing gratings. For some kinds of velocity-tuning cells, the optimal velocity to moving ICs bar was much lower than the optimal velocity to moving bars. The present results demonstrate that some cells in areas 17 and 18 of cats have the ability to respond to ICs and have different response properties of the receptive fields to ICs and luminance boundaries via different neural mechanisms.

Keywords: cat, illusory contours (ICs), orientation selectivity, direction selectivity, receptive field.

Detecting the boundaries of different objects is a primary visual task. The perception of boundaries relies on many visual cues in addition to luminance. The amazing ability of humans to perceive a contour in the absence of luminance gradient is termed as illusory contours (ICs)[1]. The perception of ICs plays an important role in restoring the two-dimension figures on retina to three-dimension scene[2]. Recent computational theories suggest that the visual system can extract information about boundaries from different cues, such as color, motion, texture, perspective and shading regardless of whether luminance differences exist or not. Psychophysical studies indicate that boundary location is more precise when multiple visual cues are combined[3].

The neural mechanism of this important visual illusion is not clear yet. Electrophysiological studies indicate that in the visual cortex of cats and monkeys (including V1[4], V2[5,6], MT[7],

MST[8] and IT[9], etc.), some cells are able to respond to ICs. However, the difference between these cells' responses to real boundary and ICs needs more intensive investigations. Since the creative work of Hubel and Wiesel, neuroscientists have studied the receptive field properties of visual cortex cells for about 40 years, employing the stimulus such as light bars, spots and gratings. These important works make us understand the receptive field functional architecture of cells in visual cortex and neural mechanisms of information process in visual system better. But the classical theories can hardly interpret the cells' responses to ICs. Thus, the receptive field properties of these cells were analyzed in order to deepen the concept of the classical receptive field. The purpose of this study is to confirm the existence of ICs sensitive cells in cortex areas 17 and 18 of cats, to study the receptive field properties of the ICs cells, and to provide electrophysiological data for investigating the neural mechanism of ICs perception and establishing computational models.

1 Materials and methods

1.1 Animal preparation

Twenty adult cats, weighing 1.6—4.0 kg, were initially anaesthetized with ketamine HCl (20 mg/kg). Procaine was given in all intended sites of surgical entry. After the intravenous and tracheal cannulae were inserted, cats were placed on the stereotaxic apparatus. Pupils were maximally dilated with atropine (1%), and appropriate contact lenses were used to protect the cornea. Neosynephrine (5%) was administered to retract the nictitating membranes. A mixture of urethane (20 mg/h/kg), gallamine triethiodide (10 mg/h/kg) and glucose (5%) was infused intravenously for maintaining paralysis and providing nutrition. Expired pCO_2 was maintained at approximately 4%. Heart rate (about 180—260 times/min) was monitored continuously to access the level of anesthesia.

1.2 Visual stimulus

Visual stimuli were generated on a Tektronix 608 display (Beaverton, USA) driven by a Picasso image synthesizer (Cambridge, USA). The Picasso was controlled by a computer through the CED system (Cambridge, England). The display's size is 12.9 cm × 10 cm with mean luminance of 19 cd/m^2 , and the background illuminance is 0.1 Lux. The position of display can be adjusted freely in three dimensions in order to make it centered at the recording cell's receptive field and keep the distance between the display and the cat's cornea to be 57 cm (so 1.0 cm on the display corresponding to 1.0 degree of visual angle). Visual stimulus was variable depending on different experimental purposes. The most stimuli used in our experiments are showed in fig. 1. The light bar in fig. 1(a) is usually 9.8° ×3° , and its moving velocity is 11 deg/s or using optimal size and velocity. Usually, the stimuli parameters of the ICs are the same as the light bars for convenience of comparison. The spatial phase, spatial frequency, orientation and contrast of the gratings composing the ICs in fig. 1(b) and 1(c) could be changed via a computer. For most cells,

the gratings' temporal frequency used was 1.0 Hz, and contrast was 0.8. Sometimes, the normal drifting sinusoidal gratings were also employed as visual stimulus. The gratings were generated in a circle whose diameter is 9° in visual angels with the temporal frequency of 2—4 Hz. The other parameters of grating are the same as the gratings composing the ICs. In order to minimize the incidental errors, responses to 20—50 cycles were added and averaged.

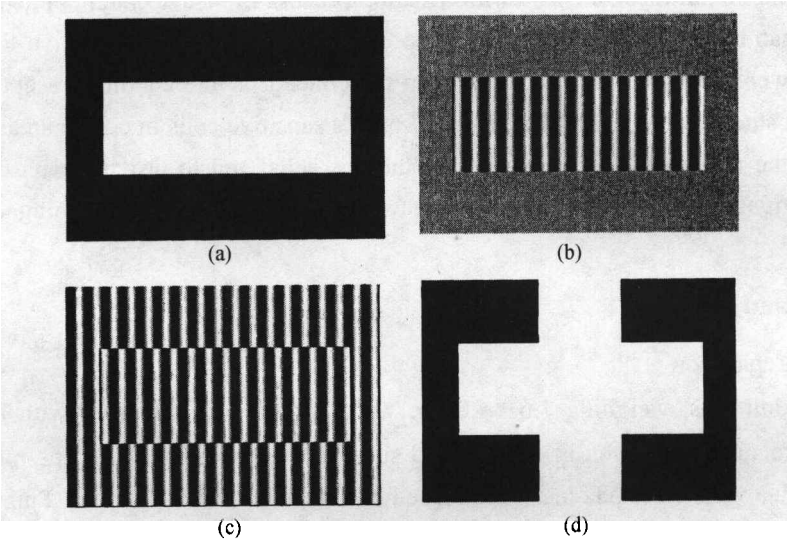

Fig. 1. The stimulus light bar (a) and ICs (b)—(d) were used in the experiments. Rectangles represent stimulus screen (12.9° × 10°), the black parts represent darkness, and white parts represent brightness. The direction of motion was always kept orthogonal to the long axis of the stimulus pattern. The stimulus pattern ((a)—(c)) is the same as Grosof and Shapley's[10].

1.3 Electrophysiological recording

Extracellular action potentials were recorded with the glass-coated tungsten microelectrodes. The impedance of the electrode was 5—50 MΩ. The recorded signals were amplified 500 or 1000 times and then input to the window discriminator. The discriminated signals were collected and stored in computer for analysis. Before physiological recording, the projection of the optic disks to a tangent screen was used to determine the position of the retinal area centralis. The distance from the tangent display to cornea was 114 cm (2 cm in tangent display corresponding 1 degree of visual angle). For every cell studied, receptive field (RF) was plotted on the tangent screen at first, then the distance between the projection of the center of RF and the projection position of area centralis was measured to determine the eccentricity of the cell. Cells were classified as simple or complex cells according to some properties of RFs, such as the size of RFs, the presence of distinct spatially offset On and Off flanks in the RFs, and the modulated responses to sinusoidal stimulus.

1.4 Data collection and analysis

Cells' responses to stimuli were performed on-line statistical analysis or stored in the computer for later analysis. The response amplitude to the drifting sinusoidal gratings was defined as

the amplitude of the fundamental Fourier component of post stimulus time histogram (PSTH). For the ICs or bars stimuli, the response amplitude was defined as the peak response of the smoothed PSTH. The orientation and direction selectivity was calculated for each cell using the circular statistic methods. Briefly, the responses of each cell to the different directions of the stimulus' motion were presented by a series of vectors. The lengths of the vectors represent the amplitude of the cell's responses and the directions of the vectors represent the moving direction of the stimulus. The vectors were added and divided by the sum of the absolute values of the vectors. The angle of the resultant vector is the optimal orientation or direction of the cell, while the length of the resultant vector is termed as the orientation or direction bias, which provides a quantitative measure of the orientation or direction selectivity. Because the range of orientation is 0 to 180 degrees, the angle of the orientation of the stimulus was multiplied by a factor of two. However, direction is cyclic as 360 degrees, therefore the actual direction of the stimulus was used to calculate the optimal direction of the cell. Orientation and direction bias ranged from 0 to 1. The cell prefers only one orientation or direction when the bias is 1. Generally, the cell is orientation or direction selective when the bias is bigger than 0.1[11].

2 Results

Our study was concentrated on the cells with orientation or direction selectivity, which is one of the cell's most important characteristics in boundary detection. For every cell studied, we determined the position and some properties of RF first. With a light bar as stimuli, the orientation/direction tuning curves of the cell were recorded to determine whether the cell is orientation or direction selective (bias > 0.1), and the cell's optimal orientation or direction. Then, the ICs bars in fig. 1(b) (the same size and velocity as light bars) were also used as stimuli, and the orientation/direction tuning curves were plotted again. To exclude the possibility that the ICs sensitive cells responded to the line ends of the gratings used to compose the ICs, the spatial phase tuning curves of the grating were measured. If phase index is smaller than 0.5 (phase index = (maximum response−minimum response)/(maximum response + minimum response)), it implies that the cell responded to extended contour of ICs rather than to individual line ends of gratings[10]. If the cell had orientation or direction selectivity for both ICs and bars stimuli and the optimal orientation or direction difference between the two stimuli was smaller than 5—10°, and the phase index was smaller than 0.5, the cell was classified as ICs sensitive cells accordingly[10,11]. Otherwise, the cell may respond to line ends and cannot be classified as ICs sensitive cells. Most cells had reliable responses to ICs and bars for more than one hour. To test the stability of our recording system, after all data had been collected we recorded the orientation and direction curves of light bars again to ensure that the tuning curves did not change significantly during the experiment.

2.1 Comparison of the responses to bars and different kinds of ICs

Two hundred orientation or direction selective cells (100 cells in cortical areas 17 and 18, respectively), whose eccentricities of receptive fields are within 15°, were studied quantitatively.

Of these cells, 84 cells (42%) were ICs sensitive cells. 91% of ICs sensitive cells were complex cells. In area 17, 31% of the recorded cells were ICs sensitive cells, and 90.3% of these ICs sensitive cells were complex cells. In area 18, 53% of recorded cells were ICs sensitive cells, and 92.5% of these ICs sensitive cells were complex cells. The maximum response amplitude and the orientation/direction bias of ICs sensitive cells to ICs were all significantly smaller than the light bars (the results of t-test are $P<0.001$, $P<0.02$ and $P<0.02$ respectively). The orientation and direction tuning curves shown in polar plot to the stimulus in fig. 1(a)—(c) of a complex cell are shown in fig. 2. Obviously, this cell has good responses to all the three kinds of stimuli.

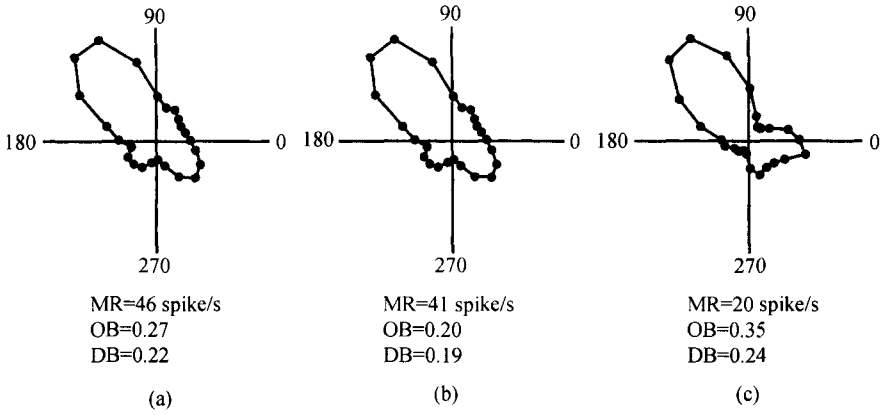

Fig. 2. The orientation/direction tuning curves of the ICs sensitive cells' responses to moving bar (a) and two kinds of ICs ((b), (c)). The visual patterns of fig. 1(a)—(c) are the stimuli used in (a), (b) and (c) of this figure, respectively. MR, Maximum response; OB, orientation bias; DB, direction bias.

If a cell responded to extended contour of ICs rather than to individual grating bar ends, this cell's response amplitude will not change with spatial phase shift of the composing gratings. In fig. 3(a), the spatial phase changing from 0° to 360° did not affect the response amplitude of this cell.

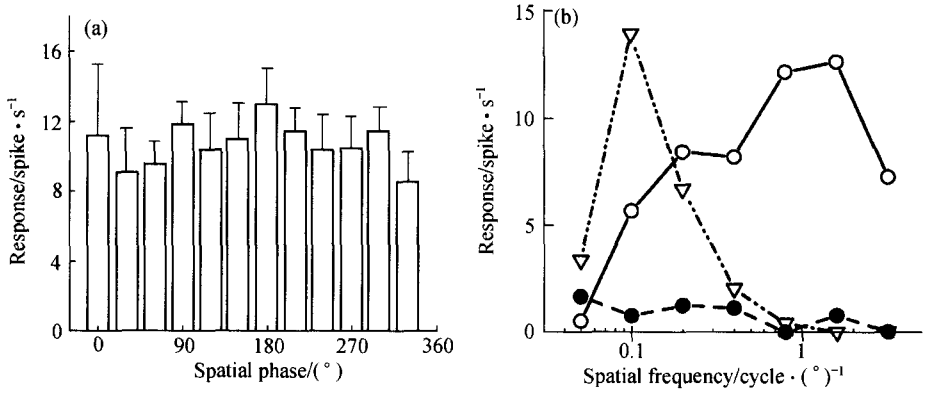

Fig. 3. The spatial phase curve to ICs (a) and the spatial frequency tuning curves (b) to the ICs in fig. 1(b) and the normal drifting sinusoidal gratings. The X-axis in fig. 3(a) represents the spatial phases of the sinusoidal gratings composing ICs. In fig. 3(b), the circles show the spatial frequency curve of gratings composing ICs. The orientation of the gratings is orthogonal to the preferred orientation of ICs. The curves of the black dots and hollow triangles show the spatial frequency curves of the drifting sinusoidal gratings, whose orientations are orthogonal and parallel to the preferred orientation of ICs, respectively.

2.2 Spatial frequency and velocity property

The spatial frequency tuning curves of a complex cell responding to the gratings composing ICs and normal drifting sinusoidal gratings are shown in fig. 3(b). The cell's responses to non-optimal orientation grating were very weak. For drifting gratings, the optimal spatial frequency at preferred orientation/direction was about 0.1 cycle/deg. However, for ICs (circle) it was about 2 cycle/deg, which was much higher than the optimal spatial frequency of the former, even exceeding the cut-off spatial frequency of the cell. In fig. 3(b), the cell's response to the ICs increased with the spatial frequency of the composing gratings and then decayed. This agreed with the result of psychophysiology study on the perception of ICs. The perception of ICs was enhanced with the elevating numbers of the lines composing ICs in a certain range. It suggested that the ICs sensitive cells' responses might play an important role in perception of ICs. These cells may participate in the high level process of ICs information.

According to the velocity tuning curves to moving bars, the cells can be classified as four types[12]: velocity low-pass, velocity broad-band, velocity high-pass and velocity tuned cells. The cells of the first two types do not have the ability to detect velocity, while the cells of the latter two types have. In our experiments, the velocity tuning curves to the moving bars and ICs of the cells of the first two types were similar (fig. 4(a), (b)). However, the optimal velocity tuning of ICs was much lower than the moving bars for the latter two types (fig. 4(c), (d)). This also agreed with the result of psychophysiology study on the perception of ICs. The high-speed moving bars can be discriminated by humans, but the high-speed ICs cannot. Once more, it suggested that these cells might be involved in the high level process of the ICs perception.

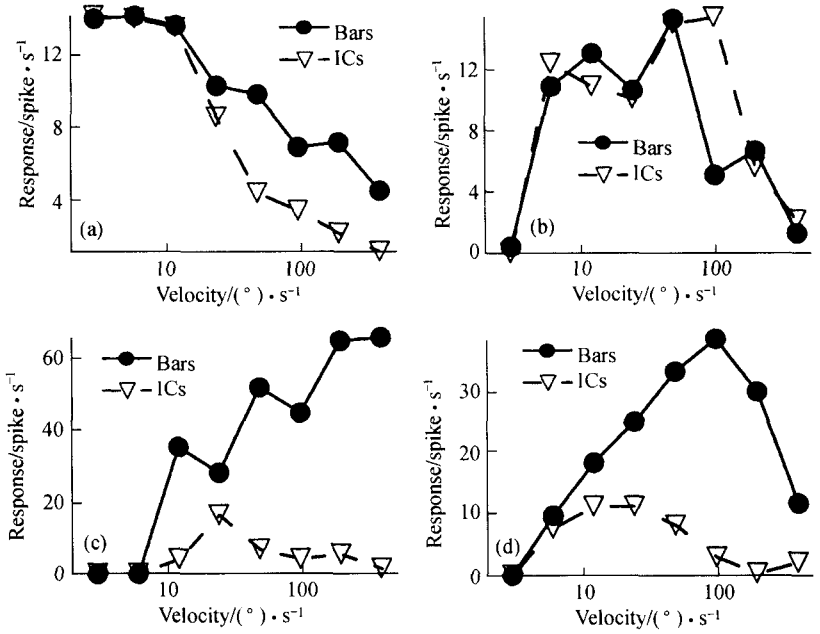

Fig. 4. The velocity tuning curves to moving bar and ICs of velocity low-pass (a), velocity broadband (b), velocity high-pass (c), velocity tuned (d) cells. The stimuli are the visual patterns in fig. 1(a) and (b).

2.3 Responses to a special kind of ICs

Interestingly, we found that there were some cells sensitive to the specific ICs in fig. 1(d). Fig. 5(b) is the histogram of a complex cell's responses to this stimulus. When the cell's receptive field shown as ellipses was stimulated by the left half or the right half of this stimulus respectively, no clear response was found. However, the same cell responded remarkably when stimulated with the whole ICs pattern. This means that the cell could detect the existence of this special kind of ICs. Fig. 5(a) is this cell's responses to the left half, the right half and the whole of the light bars. Totally, we recorded five cells sensitive to this kind of ICs only in area 18.

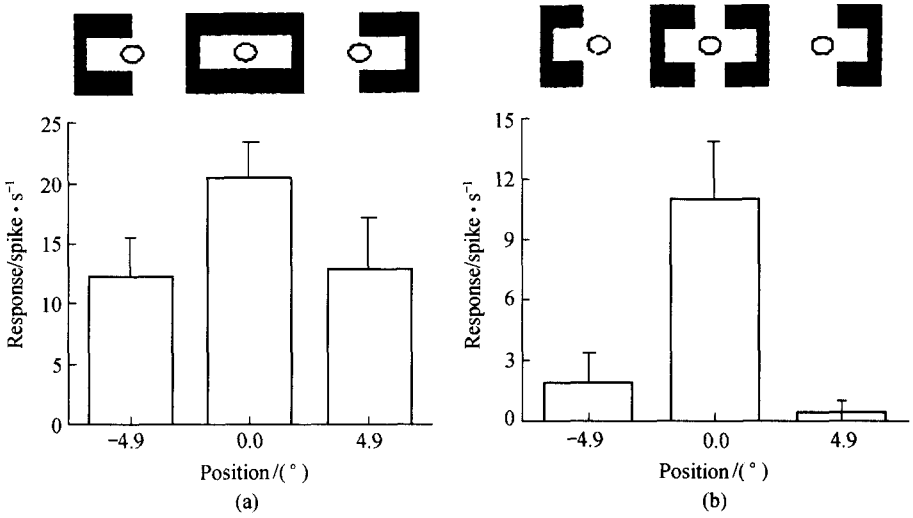

Fig. 5. The response amplitudes to a moving bar (a) and a specific IC (b). The patterns above the columns are the stimuli used. The ellipses represent the RFs of the cell. The stimuli were moving vertically. The left and right columns represent the cell's responses to the left and right half of the stimulus pattern, respectively, while the middle columns represent the responses to the whole stimulus pattern.

2.4 Response modes and properties of RF

The response modes of the ICs sensitive cells were also obviously different to the two kinds of stimuli, especially in latency and time course. Fig. 6(a), (c) and 6(b), (d) are the PSTHs of a cell to real light bars and ICs in fig. 1(b), respectively. The latency of responses to ICs longer than bars suggested that the cell needed a longer time to process this relatively complex neural analysis for ICs information.

Fig. 6(c) and 6(d) are another cell's responses to the different stimuli. Their response modes were obviously different. Because ICs were lack of luminance gradient, there was no difference between the responses induced by the two illusory edges for no light or dark edge existed. However, the responses induced by the light bars changed with the different stimulated spatial location of on, off and on/off regions within RF, and the amplitude of responses to dark and light edges could not be equal. In fig. 6(c), there are two peaks distinct by 190 ms in the PSTH of the cell's response to the light bars. These two peaks represent the on and off responses respectively, while in fig. 6(d), only one broader peak with a longer latency was observed.

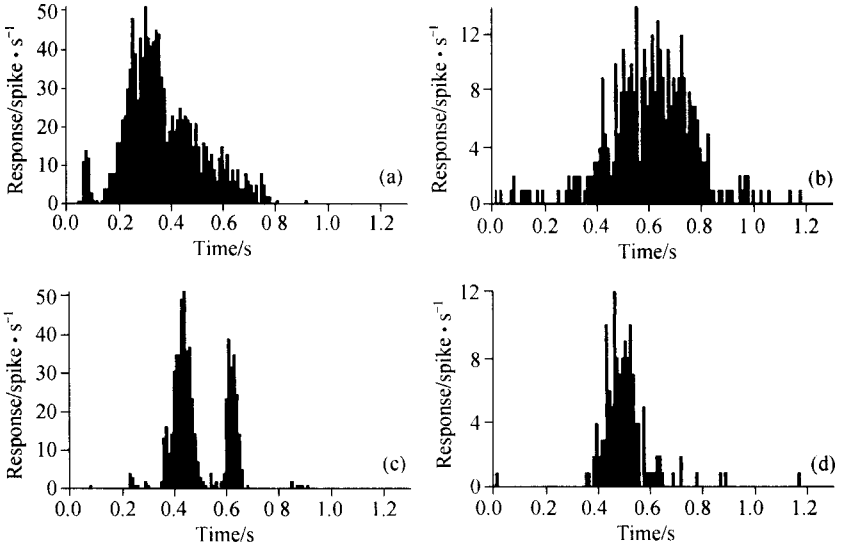

Fig. 6. The PSTHs of two cells' responses to moving real bars ((a), (c)) and moving ICs bars ((b), (d)). The peak in (a) occurred at about 0.3 s, while the peak in (b) occurred at about 0.6 s. The difference in the latency is obvious. (c), (d) are PSTHs from another cell. There are two peaks occurring at 0.4 and 0.6 s (c), while there is only one peak in (d) at about 0.5 s. The stimuli used in (a) and (c) are the same as fig. 1(a) and the stimulus used in (b) and (d) is the same as fig. 1(b).

3 Discussions

The present results demonstrate that some cells in cortex areas 17 and 18 of the cats have the ability in responding to at least one kind of ICs. The amplitude of the cells' responses to ICs is independent with the spatial phase of the composing gratings. Because the optimal spatial frequency of the composing gratings is higher than the cut-off spatial frequency of real gratings, these cells responded to extended edges of ICs rather than the line ends of the composing gratings. The response modes to ICs and bars are also different. The findings of the cells that are sensitive to ICs in fig. 1(d) give another evidence of the existence of ICs sensitive cells in area 18. The lesion experiments in the cat [13] have shown that the lesion of areas 17 and 18 will severely affect the detection of ICs irreversibly. However, the lesions of the cortex other than areas 17 and 18 did not eliminate, but only weakened the ability of ICs response. All these suggest that the ICs detection originated from areas 17 and 18.

A century has passed since the formal recognition of ICs by Schumman[14]. Recently, by employing ICs and luminance boundaries to investigate human's detection ability to ICs, Westheimer et al.[15] found that the discriminating ability of orientation was weaker for ICs than for luminance boundaries. Here we show that it is also true in the responses of a large proportion of cortical cells in areas 17 and 18 of the cats.

The selective responses of cortical cells to ICs orientation and direction suggest that these cells can perform relatively complex analyses of edge lack of local luminance differences. It is likely that such analyses take more time. Unlike light bars, ICs have no leading or tailing edges

and no difference in the luminance within and outside of the receptive field. The present results suggest that the RFs of the same cell can respond differently to the ICs and the luminance edges implying the two different neural mechanisms of the perception of ICs and real boundary.

Electrophysiological data are not of satisfactory explanation of the perceptive phenomenon of ICs. The existence of a large number of the cells signaling ICs (about one third of cells in area 17 and more than half of cells in area 18) raises the question why the system puts so much effort into analyzing these contours. It can hardly create an illusion. As mentioned at the beginning of this paper, detection of ICs is a key problem of understanding images. It seems, as result of evolution, the circuitry of areas 17 and 18 can detect ICs at an early stage of visual processing. Among a lot of computational models about the detection of boundary, the parallel processing model supposed by Peterhans et al.[16] and the nonlinear interaction model by Victor et al.[17] are corresponding to the electrophysiological data of ours. In the parallel processing model, the ICs sensitive cortical cells receive two parallel inputs, one from classical simple or complex cells that respond to contrast borders, the other from end-stopped cells that are sensitive to terminations of the lines and edges. Both inputs are integrated in the ICs sensitive cells. This means that a coincidence of terminations can be equivalent to contrast. In the nonlinear interaction model, many nonlinear subunits, which are parallel to the cell's optimal orientation/direction or without orientation/direction selectivity, send their inputs to the ICs sensitive cells. These nonlinear subunits may directly or indirectly originate from the nonlinear cells in LGN, and interact with cortical cells via the long-range horizontal connections in cortex to produce the perception of ICs.

In conclusion, the perception of ICs should not be simply regarded as an artifact of visual process. Rather, their generation is likely to be as a result of basic visual information processing and originates from areas 17 and 18 of the cortex.

Acknowledgements This work was supported by the National Natural Science Foundation of China (Grant No. 39893340-03) and the Chinese Academy of Sciences.

References

1. Brigner, W. L., Callagher, M. B., Subjective contour: apparent depth or simultaneous brightness contrast? Percept. Mot. Skills, 1974, 38: 1047.
2. Grossberg, S., Cortical dynamics of three-dimensional figure-ground perception of two-dimensional pictures, Psychological Reviews, 1997, 104: 618.
3. Rivest, J., Cavanagh, P., Localizing contours defined by more than one attribute, Vision Research, 1996, 36: 53.
4. Redies, C., Crook, J. M., Creutzfeldt, O. D., Neuronal responses to borders with and without luminance gradients in cat visual cortex and dorsal lateral geniculate nucleus, Experimental Brain Research, 1986, 61: 469.
5. von der Heydt, R., Peterhans, R., Baumgartner, G., Illusory contours and cortical neuron responses, Science, 1984, 224: 1260.
6. Peterhans, E., von der Heydt, R., Mechanisms of contour perception in monkey visual cortex (II)—— Contour bridging gaps, J. Neuroscience, 1989, 9: 1749.
7. Albright, T. D., Form-cue invariant motion processing in primate visual cortex, Science, 1992, 225: 1141.
8. Geesaman, B. J., Adersen, R. A., The analysis of complex motion patterns by form/cue invariant MSTd neurons, J. Neuroscience, 1996, 16: 4716.
9. Sary, G., Vogels, R., Orban, G. A., Cue-invariant shape selectivity of macaque inferior temporal neurons, Science, 1993,

260: 995.

10. Grosof, D. H., Shapley, R. M., Hawken, M. J., Macaque V1 neurons can signal 'illusory' contours, Nature, 1993, 365: 550.
11. Leventhal, A. G., Wang, Y. C., Schmolesky, M. T. et al., Neural correlates of boundary perception, Visual Neuroscience, 1998, 15: 1107.
12. Orban, G. A., Kennedy, H., Mares, H., Response to movement of neurons in area 17 and area 18 of the cat: Velocity sensitivity, J. Neurophysiology, 1981, 6: 1043.
13. De Weerd, P., Sprague, J. M., Vandenbussche, E. et al., Two stages in visual texture segregation: a lesion study in the cat, J. Neuroscience, 1994, 14: 929.
14. Schumman, F., Beitrage zur analyse der gesichtaswahrnehmungen, Zeitschrift Für Psychologie, 1900, 23: 1.
15. Westheimer, G., Li, W., Classifying illusory contours: Edges defined by "pacman" and monocular tokens, J. Neurophysiology, 1997, 77: 731.
16. Peterhans, E., von der Heydt, R., Subjective contours bridging the gap between psychophysics and physiology, TINS, 1991, 14: 112.
17. Victor, J. D., Conte, M. M., Spatial organization of nonlinear interactions in form perception, Vision Research, 1991, 31: 1457.