Cells in the anterior part of the inferotemporal cortex (anterior IT) respond to moderately complex stimulus features of object images. To study dependency of their responses on contrast polarity of stimulus images, we selected cells with optimal stimuli that were defined only by shape and not related to texture or color, and examined effects of reversing the contrast of the image or removing it except for edges between dark and bright parts of the image ("outlining"). The contrast reversal produced a reduction of the response to the optimal stimulus by >50\% in 60\% of tested cells; the outlining, in 70\%. When the two transformations were considered together, 94\% of the cells showed a reduction by >50\%. Effects of the transformations on shape selectivity were also studied by comparing responses to several different shapes each of whose contours were expressed in different ways. Statistically significant changes in relative effectiveness of the different shapes as a function of contour expression were observed in more than half of the cells. These results suggest that responses of individual cells in anterior IT carry information about contrast polarity as well as about shape.

The anterior part of the inferotemporal cortex (anterior IT) of the macaque monkey, which corresponds to cytoarchitectural area TE, stands at or near the final stage of the ventral visual pathway. This pathway is essential for object vision, because monkeys with bilateral lesions to anterior IT show severe and selective deficits in behavioral tasks that require visual discrimination or recognition of objects (Gross, 1973; Dean, 1976; Mishkin et al., 1985). Cells in anterior IT respond to complex stimulus features of object images (Gross et al., 1972; Desimone et al., 1984; Baylis et al., 1987; Tanaka et al., 1991; Fujita et al., 1992; Kobatake and Tanaka, 1994). The optimal feature varies from cell to cell: moderately complex shapes for some cells, combinations of a shape with color for some other cells, and combinations of a shape with texture for other cells. The subject of the present report is dependency of responses of anterior IT cells to shapes on the contrast polarity of stimulus images.

A characteristic of object vision is its invariance to changes in images caused by alterations in stimulus position, viewing distance, viewing angle, and illumination. As anterior IT is located at or near the final stage of the ventral visual pathway, it has been suggested that these invariant properties are realized in the responses of individual cells in anterior IT (Gross et al., 1972; Sato et al., 1980; Schwartz et al., 1983; Miyashita and Chang, 1988; Sáry et al., 1993). Gross et al. (1972) found in their pioneering work that anterior IT cells had large receptive fields across which a stimulus kept evoking responses. Schwartz et al. (1983) showed that some anterior IT cells did not change their selectivity for Fourier descriptor frequencies when the stimuli changed in position, size, and contrast polarity. Sáry et al. (1993) found that some anterior IT cells did not change their selectivity for shape when the attributes defining the contours of the shapes changed from luminance to motion or texture.

Perceptual invariance, however, is not a desirable characteristic under all circumstances when considering contours. While for outer contours of objects it may be advantageous if the representation of contours is independent of the attributes that define them, this is not always true for other contours, such as those created by depth structure of objects. Contrast polarity across these contours carries useful information for reconstruction of the depth structures. This is because shading is used to infer local surface orientation rela-

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tive to the direction of illumination, and therefore the contrast reversal may lead to a reversal in the reconstructed depth structure. To represent a feature containing depth structure, responses of cells have to be specific to contrast polarity.

We thus decided to examine dependency of responses of anterior IT cells on the contrast polarity across contours of stimulus images. We reversed the contrast polarity or removed the contrast except for edges between dark and bright parts of the stimulus image, and examined effects of these operations on responses of anterior IT cells. We call the latter operation “outlining,” because it is equivalent to taking outlines of the contour shape. The uniqueness of the present study is that the critical feature for the activation of individual cells was carefully determined and the effects of the contrast reversal and outlining were tested with the simplest stimuli that contained the critical feature (“optimal stimuli”). We have developed a method to identify the critical feature for individual cells: dozens of animal and plant models and junk objects were first presented to find the most effective 3D object stimulus, and the feature critical for the activation was then determined by reducing the complexity of the image of the object (Tanaka et al., 1991; Fujita et al., 1992; Kohatake and Tanaka, 1994). This procedure is important, because the contrast reversal and outlining differentially affected responses to the optimal stimulus and those to nonoptimal stimuli, as shown in this article.

Some of these results have been reported elsewhere in abstract form (Ito et al., 1993).

Materials and Methods

Preparation and Recording

General experimental procedures were similar to those described previously (Tanaka et al., 1991; Kohatake and Tanaka, 1994). Japanese monkeys (Macaca fuscata, 4.4–8.5 kg) were prepared for repeated recordings by initial aseptic surgeries. Under anesthesia with pentobarbital sodium (35 mg/kg, i.p., supplemented at 10 mg/kg when necessary), a brass block for head fixation was attached to the top of the skulls, two stainless steel screws for recordings of electroencephalogram (EEG) were implanted in the skull, the zygoma was partially removed, and the lateral surface of the skull was exposed and covered with resin for later recordings of cell responses.

Prior to the first session of recordings, the optics of the eyes was measured to select appropriate contact lenses. The curvature of the cornea was measured, and after a contact lens with appropriate curvature was placed on the cornea, the refractive power was measured to determine the power of the lens with which images at a distance of 57 cm from the cornea were focused on the retina. Photographs of the fundus were taken to determine the position of the fovea.

Recordings were made once a week on each monkey. A recording session began with induction of anesthesia with ketamine hydrochloride (10 mg/kg, i.m.). An endotracheal cannula was inserted through the tracheal opening, and a small hole was made in the resin-coated skull. Throughout the recording session, animals were immobilized with gallamine triethiodide (10 mg/kg, i.m., followed by 3 mg/kg/hr, i.m.) or pancuronium bromide (0.08 mg/kg, i.m., followed by 0.024 mg/kg/hr, i.m.) and the anesthesia was maintained by artificial ventilation with a mixture of N₂O and O₂ (70:30). The level of anesthesia was assessed by monitoring the electrocardiogram and EEG, and isoflurane was added to the gas mixture if necessary. Atropine sulfate (0.5 mg) was subcutaneously administered every 3 hr to reduce salivation.

Extracellular unit recordings were made from the dorsolateral portion of anterior IT (Tea and TEP; Turner et al., 1980; Iwai and Yukie, 1987) with glass-coated Elgiloy electrodes (2–5 MΩ at 1 kHz). The electrodes were advanced through a pinhole in the dura matter made by a needle with a shaft 0.6 mm in diameter. The exposed dura matter was covered with paraffin to prevent it from drying and to reduce movements of the brain caused by pulsation and respiration. The position of penetration was determined with reference to a point marked on the resin-coated skull. The data presented in this article were mostly recorded from four hemispheres (three right and one left) of three monkeys, but some data were collected from six additional monkeys that were prepared for other purposes.

Each recording session lasted 14–18 hr. The hole in the skull was filled with resin after the recording was finished. Within a few hours after the last injection of the muscle relaxant, spontaneous respiration resumed and became normal. The monkey was returned to its home cage after an injection of an antibiotic (Pentillin, Sankyo; 40 mg/kg, i.m.). Monkeys were regularly checked by a veterinarian and cared for in accordance with the Guiding Principles for the Care and Use of Animals in the Field of Physiological Science (Japanese Physiological Society).

Visual Stimulation and Procedure for Individual Cells

The pupils were dilated and the lenses relaxed by local application of 0.5% tropicamide, 0.5% phenylephrine. The corneas were covered with contact lenses of appropriate power with artificial pupils 3 mm in diameter. A television display (CM20-11, Shibasoku) was placed at a distance of 57 cm from the corneas. Several retinal landmarks, such as the intersection of blood vessels and the center of the optic disk, were projected onto the display by using a reversible retinoscope (Sanso), and the position of the fovea was determined geometrically by referring to the photographs of the fundus. The picture on the television display was 31 × 29 cm in size, and composed of 60 fields/sec with interlacing, and 512 × 480 pixels. The brightest white and darkest black (with room lights off) were 52.9 and 1.25 cd/m², respectively, as measured by a luminance meter (model 12A, Sanso). All the experiments were conducted with the room lights (fluorescent lamps) on.

After isolation of single-cell activity, we first deter-
Figure 1. The regions from which we recorded cell responses are indicated by the dotted areas on the lateral view (A) and a frontal section at the level indicated by the vertical line in A (B). The arrow indicates the direction of penetrations. sts, superior temporal sulcus; ios, inferior occipital sulcus; amts, anterior middle temporal sulcus; pts, posterior middle temporal sulcus.

Figure 2. A cell for which contrast reversal reduced the response. A, The optimal stimulus of the cell was a black starlike shape with eight pointed protrusions (a). The cell did not respond to a black disk (b), a triangle (c), or a star with four protrusions (d). Both sharp inside corners and sharp tips were necessary for the maximal activation of the cell (e–h). The cell showed a moderately strong response to a star with 16 pointed protrusions (i). The response to the white star was significantly smaller than that to the optimal stimulus (k vs. l). The responses were averaged over 16 stimulus presentations. Horizontal bars indicate 1 sec period of stimulus presentation. Inset numbers show the response magnitude, which is normalized by the response to the optimal stimulus. A negative value indicates suppression below the spontaneous firing rate. Asterisks indicate responses that were significantly smaller than the maximal response (Kolmogorov-Smirnov test, *: p < 0.05; **: p < 0.001). B, The recording site (dot) and the receptive field of the cell.

mined the critical feature for the maximal activation of the cell. Dozens of 3D objects (see Kobatake and Tanaka, 1994, for the list of the objects) were presented, first directly and then through a CCD video camera (DXC-325 or 327, Sony) and a television display, to search for the most effective stimulus. The monkeys had no chance to see these 3D objects in their home cages. We determined the most effective view angle, position, size, and background color (black or white). The video image of the most effective stimulus was simplified step by step with the aid of a computer graphic system (600-M4, Nexus), and the critical feature was determined as the necessary and sufficient features for the maximal activation of the cell. The simplest image that contained the critical feature was designated as the optimal stimulus. Our analysis in this study was focused on cells selective for shape. If the critical feature contained some texture or color, we did not study the cell.

Then, effects of contrast reversal and of outlining were examined with the optimal stimulus. Outlines were drawn by white or black lines of one pixel (0.06°) thickness. Also, we prepared suboptimal stimulus by modifying the optimal stimulus, as well as ineffective stimuli for comparison. By analyzing responses to the contrast-reversed and outlined versions of these stimuli, we examined the effects of those transformations on shape selectivity.

The stimuli were presented to the eye contralateral to the recording site. Different stimuli being compared were always intermixed and presented 10 times in a cyclic order. They were presented for 1 sec with 2 sec blank intervals between trials. They moved along a circular path (without change in orientation) during the presentation time to avoid the sensory adaptation in paralyzed preparation. The radius of the circular translation was 0.58° or 0.29°. Period of the movement was 0.96 sec/cycle. The magnitude of responses was represented by the mean firing rate during the stimulus presentation minus the spontaneous firing rate for the 1 sec period just before the stimulus presentation. Considering response latency of each cell, the time window for the response was shifted within the range of 50–250 msec from the exact time of the stim-
ulus presentation so that the mean firing rate took the maximum value. Differences between two responses were analyzed by comparing two sets of ten individual responses with Kolmogorov-Smirnov test. The extent of the receptive field was determined by using the optimal stimulus. The borders were determined by the center of the stimulus.

**Histology**

After the final recording session was finished, several needles were inserted into the brain as reference by the same micromanipulator used for recordings. The monkey was deeply anesthetized with pentobarbital sodium and perfused intracardially. Recording sites were verified with 50 μm-thick Nissl-stained sections cut along the frontal plane.

**Results**

The effects of contrast reversal and of outlining (taking outlines of the contour shape) were examined in 58 cells recorded from the anterior IT. Their positions were distributed throughout nearly the entire posterior–anterior extent of anterior IT, but were limited to the lateral surface, lateral to the anterior middle temporal sulcus and ventral to the superior temporal sulcus (Fig. 1). This region includes both the lateral part of TEa and that of TEP (Turner et al., 1980; Iwai and Yukie, 1987). The 58 cells were selected by the following criteria from a larger sample of responsive cells. First, the critical feature for the maximal activation was successfully determined. Second, the critical feature was defined only by shape: cells that required color or texture were excluded from the present study. Finally, the critical feature was complex: a small population of cells that maximally responded to simple stimuli such as bars and disks with selectivity only for orientation, size, and contrast polarity of stimuli were also excluded. The receptive fields of the 58 cells were large (the square root of the area, 21.5 ± 16.0°) and included the fores, as reported previously for cells in anterior IT in general (Gross et al., 1969, 1972; Desimone and Gross, 1979; Tanaka et al., 1991).

**Figure 3.** Distribution of the degree of response reduction caused by contrast reversal. A ratio was calculated between the response to the stimulus made by reversing contrast of the optimal stimulus and that to the optimal stimulus. Hatched area indicates the cells in which the contrast reversal induced significant reduction in the response (Kolmogorov-Smirnov test, p < 0.05).

**Figure 4.** A cell that responded despite contrast reversal of the stimulus. A, The cell selectively responded to a combination of a disk and a bar projecting from it toward the lower left (a). The cell was selective for orientation of the optimal shape (b–d). Although the two components could be separated (e), each component alone did not activate the cell (f, g). The cell did not respond to a long bar (h), ellipses (i, j), or figures with multiple protrusions (k–l). The response to the optimal shape brighter than the background was as large as that to the optimal shape darker than the background (p vs al). B, The recording site (↓↓) and the receptive field of the cell.

**Figure 5.** Effects of outlining. A, Responses of the cell shown in Figure 2. The cell did not respond to outline versions of the stimulus. B, Responses of cell shown in Figure 4. Although the outline figures evoked responses, they were significantly smaller than the responses to the solid figures (35% and 44%, p < 0.01).
Kobatake and Tanaka, 1994). The effects of contrast reversal and of outlining were examined with the simplest stimuli that contained the critical feature (the term “optimal stimuli” is used to indicate these simplest stimuli in this article).

**Effects of Contrast Reversal**

Responses of the majority of the cells were sensitive to changes in the contrast polarity of stimulus image. A reversal of contrast of the optimal stimulus reduced the response by more than 50%. Figure 2 shows an example. The optimal stimulus of the cell was a starlike shape with eight pointed protrusions and darker than the background. The stimulus with the same shape but with brighter-than-background contrast polarity evoked only a nonsignificant response, much weaker (24%) than the response to the optimal stimulus. Two-thirds of the tested cells responded more strongly to features darker than the background, and the remaining cells responded more strongly to features lighter than the background.

To quantify the effects of the contrast reversal, a ratio of the magnitude was calculated between the response to the optimal stimulus and the response to its contrast reversal version (reversal/optimal). Sixty percent of the cells showed ratios smaller than 0.5, and most of them (52% of the total cells) smaller than 0.3 (Fig. 3). The change caused by the contrast reversal was statistically significant in most of them (hatched area in Fig. 3; *p < 0.05*). Thus, the majority of anterior IT cells preferentially respond to a particular contrast polarity when tested with optimal stimuli.

Figure 3 also shows the presence of other cells that tolerated the contrast reversal. We show an example of this group in Figure 4. The optimal stimulus of the cell was determined as a combination of a disk and a bar projecting toward the lower left. Although the optimal stimulus was determined to be darker than the background, the same shape with reversed contrast evoked a comparably strong response.

**Effects of Outlining**

Responses of the majority of the cells required luminosity contrast between the inside and the outside of contours (solid figures). The operation of “outlining”
that removed the contrast except for contour lines reduced the response to the optimal shape by more than 50%. The two cells that have been introduced in Figures 2 and 4 showed such a property (Fig. 5). The cell that responded to the starlike shape was not activated by the outline versions of the shape either in white lines or in black lines (Fig. 5A). The cell that responded to the combination of a disk and a bar showed some responses to both outlines drawn in white or black, but the responses were significantly smaller than those to the solid figures (35% and 44%, p < 0.01; Fig. 5B).

There were a few cells for which the optimal stimulus was identified as a shape drawn by lines (see Fig. 7). Figure 6 shows a typical example. The optimal shape of the cell was a black circle. The cell did not respond to black or white solid disks. The response decreased, as the width of contour line increased. There was no response to circles drawn by white line.

As in the examples shown in Figures 5 and 6, we always tested four versions of the optimal shape: (1) white solid, (2) black solid, (3) outline drawn in white, and (4) outline drawn in black. The preference to the solid versus outline versions was evaluated by comparing the larger of the responses to two solid versions and that of the responses to two outline versions and calculating the ratio between the two values. The smaller value was divided by the larger value.

The distribution of the ratio is shown in Figure 7. Seventy percent of the cells showed ratios smaller than 0.5, which means that their responses were biased or specific to either the solid or the outline version. Most of them preferred the solid version (open areas in Fig. 7), and three cells the outline versions (crosshatched areas).

Figure 8 shows an example of the smaller group of cells (30%) that showed comparably strong responses to both solid and outline versions of the optimal stimuli. The optimal stimulus of the cell was determined as a combination of a rounded body and a rounded projection from the body (a shape like a fat mushroom). The figure had to be darker than the background. Although the response was highly selective for the shape and for the contrast polarity, there was a good response to the optimal shape drawn by white lines. The response to this white outline version was as strong (92%) as the response to the black solid version of the optimal shape. There was no response to the outline drawn in black.

No correlation was found between the ratio for the contrast reversal (x-axis in Fig. 9) and the ratio for the

Figure 9. Relationship between the response reduction by the contrast reversal (ordinate) and that by the solid-outline transformation (abscissa).
solid-outline transformation (y-axis; $\gamma = 0.26, p > 0.20$). This means that selectivity for the contrast polarity of a cell was independent of its specificity to solid or outline versions.

To test whether there were cells that responded to their optimal shape despite either transformation, we calculated another index, which is the ratio between the maximal and minimal responses among the responses to the four contour versions. A ratio of 1 means that the cell responded to the four stimuli with equal magnitude. As shown in Figure 10, the maximum ratio was 0.58, and most cells (94%) showed ratios smaller than 0.5.

We failed to find a systematic change of the ratio for the contrast reversal (upper) and that for the solid-outline transformation (lower) along the anteroposterior coordinate of the penetration in which the cell was recorded (Fig. 11). There was no correlation between these ratios and the cell’s position along the anteroposterior coordinate (contrast reversal: $\gamma = 0.08, p > 0.20$; solid-outline transformation: $\gamma = 0.05, p > 0.20$).

Changes in the Selectivity for Stimulus Shape

In this section, we describe the effects of the contrast reversal and solid-outline transformation on the selectivity of cells for the stimulus shape. We combined several suboptimal and ineffective shapes with the optimal shape to get a set of three to six shapes, and made four contour versions for all of them. This full set of stimuli was intermixed and presented. The data for this part are based on 19 cells that showed significant responses to more than two contour versions.

Twelve of the 19 cells (63%) showed significant changes in selectivity for shape as the stimulus images were transformed. The changes were induced by contrast reversal in 11 cells, and by outlining in the remaining one cell. Figure 12 exemplifies such changes for the cell shown in Figure 2. The optimal stimulus was a black starlike shape with eight pointed protrusions. The cell also responded to a black figure with eight protrusions of constant width, but the response was smaller than the response to the optimal stimulus (56%, $p < 0.01$). This selectivity for shape was not preserved in responses to the white solid shapes. The white figure with protrusions of constant width evoked a response significantly stronger than the response to the white solid version of the optimal shape ($p < 0.01$). The responses to the shape with pointed protrusions were different between the black and white versions ($p < 0.01$), but the responses to the shape with protrusions of constant width were not significantly different.

Figure 13 shows another example of a cell that showed significant changes in selectivity for shape. The optimal stimulus of the cell was a black, vertically elongated ellipse, whereas a black, horizontally elongated ellipse also evoked a good response, which was numerically but not significantly smaller than the response to the vertically elongated ellipse (77% and $p > 0.05$). Disks or rectangles evoked no or significantly smaller responses. Although this selectivity for shape was preserved in responses to the outline versions, different selectivity was shown for the white solid versions of stimuli. The response to the white, horizontally elongated ellipse was significantly stronger than the response to the white, vertically elongated ellipse ($p < 0.01$).

Discussion

Responses of most cells in anterior IT were reduced by the two kinds of luminosity contrast transformations of the optimal stimulus, namely, contrast reversal...
Figure 12. A cell in which the selectivity for stimulus shape changed by contrast reversal of stimulus images. A, Among the black solid figures, the starlike shape with eight pointed protrusions evoked a response significantly larger than the responses to the other shapes (a vs b–d; p < 0.01). The white solid figure with protrusions of constant width, however, evoked a response significantly larger than the response to the white solid star with pointed protrusions and others (f vs a, p < 0.01). The responses to the shape with pointed protrusions were different between the black and white versions (a vs e; p < 0.01), but the responses to the shape with protrusions of constant width were not significantly different (b vs f). Asterisks indicate responses that were significantly smaller than the maximal response in each contour expression (a vs b–d; f vs a, g, h, **, p < 0.01). B, Response magnitude normalized by that of the maximal response is plotted. The recording site and the receptive field of this cell are shown in Figure 2B.

and outlining. The contrast reversal produced a reduction by >50% in 60% of anterior IT cells, and the outlining in 70% of the cells. When the two transformations were considered together, 94% of the cells showed a reduction by >50%. We conclude that responses of anterior IT cells carry information about contrast polarity as well as that about shape.

It was also found that the selectivity for shape is not necessarily preserved over the transformations of images. Statistically significant changes in the relative effectiveness of different shapes were observed in 65% of the tested cells. Because the number of shapes tested in each contour expression was limited (three to seven), this proportion must be an underestimate.

Figure 13. Another example of the cells in which the selectivity for stimulus shape was changed by contrast reversal. A, The optimal stimulus was determined as a black, vertically elongated ellipse (a), while a black, horizontally elongated ellipse evoked a response that was numerically but not significantly smaller than the response to the optimal shape (c; p > 0.05). The cell did not respond to black disks or black rectangles. Among the white solid figures, the horizontal ellipse evoked a response significantly larger than that to the vertical ellipse (f vs e, p < 0.01). Asterisks indicate responses that were significantly smaller than the maximal response in each contour expression (a vs b–d; f vs e, g, h; i vs j–l, m vs n–p; *, p < 0.01; **, p < 0.05). B, The normalized responses for different contour expressions. C, The recording site and the receptive field of the cell.
This result means that the information about shape is not independent from information about contrast polarity in responses of anterior IT cells.

These results are presented for the first time in this article, and are consistent with previous results. One of us has previously reported that responses of anterior IT cells were selective for the contrast polarity of contours of the optimal shape, but a systematic and quantitative study was not performed (Tanaka et al., 1991). Schwartz et al. (1983) found that three of the four anterior IT cells they tested preferred the same frequency of Fourier descriptors for both black and white figures, but they did not describe what proportion of cells responded to Fourier descriptor patterns of both contrast polarities. Finally, Säry et al. (1993) found that some cells showed similar selectivity for shape despite the attributes (luminosity, texture, or motion) that defined the contours. However, only 28% of cells showed responses to the contours expressed by the three kinds of attributes. We understand that the other 72% of cells responded only to some of the contours. As for cells with selective responses to faces, clustered in the depth of superior temporal sulcus (Bruce et al., 1981; Perrett et al., 1982), there have been two conflicting results: Perrett et al. (1984) reported that the contrast reversal of face images reduced the responses, whereas Rolls and Baylis (1986) reported a considerable invariance of the responses to the contrast reversal.

The function of the information about contrast polarity in anterior IT may be discussed in relation to "shape from shadow" (Cavanagh and Leclerc, 1989; Cavanagh, 1991). The internal depth structure of objects, such as the nose and lips in a face, causes shadow, highlight, and gradation of luminosity in the image. Whether a particular part of the object image becomes shaded or highlighted is determined by the relative angle between the orientation of the local surface and the direction of illuminating light. Based on this relationship, the visual system can reconstruct the depth structure of the object from the pattern of highlight and shading with assumption on direction of light source. If anterior IT cells are involved in representation of features including depth structure, their responses should carry information about contrast in addition to information about shape, which was partially proved in this study. Only the contribution of the contrast polarity was examined in this study; that of gradual changes in luminosity, which may give more precise information about the depth structure, remains to be examined. We have recently found quite a few anterior IT cells for which luminosity gradient is contained in the critical features (an example is shown in Fig. 3 of Fujita et al., 1992).

This discussion may seem to conflict with the fact that schematic line drawings are very effective for specifying objects. However, we should be careful in relating such line drawings to contours in raw images. Raw images have additional contours other than those drawn in the line drawings; there are "cast shadows" caused by occlusion of lights by the other, separate parts of the object. Contours of the cast shadows should be eliminated to obtain full line drawings. Also, in raw images, some of the contours drawn in line drawings are obscured by shadows. Because of these, the fact that line drawings are informative does not necessarily mean that contours without contrast polarity should be abstracted from the raw images for the purpose of object recognition. Processes of recognizing the schematic line drawings may be different from those of recognizing raw images.

Although we failed to sample "perfect cells" that showed comparably strong responses to all the four contrast versions of the optimal shape, responses of some cells tolerated either the contrast reversal or the solid-outline transformation. The contrast across the outer contours of objects varies depending on the surface quality and illumination conditions of the background, and the perception is largely invariant for changes in contrast of such contours. This invariance of perception may be established by integrating activities of different groups of cells invariant for different types of transformations.

Notes
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