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21. Some nucleated cells may have been present but were not observed because of inadequate resolution, but we did observe a few small (~ 0.5 μm) red-autofluorescing nucleated cells (red autofluorescence usually indicates chlorophyll). These cells had no visible flagella and may be identical to the scaled prasinophyte alga of similar size described by P. W. Johnson and J. McN. Sieburth [J. Phycol. 18, 318 (1982)] that they found in abundance during warm months in nearby Narragansett Bay. This organism, a non-motile alga, is unlikely to be a bacteriovore, since motility is probably essential for a grazer; also, the chloroplast and nucleus seem to leave little room for digestive vacuoles. No heterotrophic eukaryotes could be found by transmission electron microscopy of glutaraldehyde- and OsO$_4$-preserved, 0.2- to 2.0-μm size fractions of coastal and open ocean samples (P. W. Johnson and J. McN. Seiburth, ibid.).
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27. We thank L. Moschella, T. Bell, and J. Mitchell for assistance with experiments, and S. Horrigan, S. Y. Newell, E. Sherr, and D. Comeau-Fuhrman for reviewing the manuscript. Supported by NSF grant OCE-8214488.

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Illusory Contours and Cortical Neuron Responses

Abstract. Figures in which human observers perceive "illusory contours" were found to evoke responses in cells of area 18 in the visual cortex of alert monkeys. The cells responded as if the contours were formed by real lines or edges. Modifications that weakened the perception of contours also reduced the neuronal responses. In contrast, cells in area 17 were apparently unable to "see" these contours.

A basic task in visual perception is to segregate the visual input into objects. Given a flat retinal image of a three-dimensional world, this is not trivial. An object boundary may be defined by a physical discontinuity in the image due to a difference in color or luminance between object and background, although any change in illumination, or a movement of the object or the observer, can change these conditions. Nevertheless, the contours of objects appear to be invariant. Contours may also be seen in the absence of discontinuity in the stimulus (1) (for example, Fig. 1, A, B, and D). These illusions (2, 3) show that perceived contours are the result of an image analysis performed in the brain. The nature of this process is not known, and different theories have been proposed (3,

4). We have examined the activity of cells in the visual cortex of monkeys during presentation of conventional stimuli producing contours by luminance gradients and of stimuli producing illusory contours. In area 18 we found responses that paralleled some of the perceptual phenomena. These responses could not be easily predicted from known receptive-field properties of cells in the visual cortex.

Rhesus monkeys (Macaca mulatta) were trained to perform a visual fixation task. To receive a reward they had to pull a lever when a fixation target appeared and to release it upon detecting a 90° turn of the target, which occurred after an unpredictable delay. The target consisted of two parallel short lines whose orientation could be resolved only

in foveal vision. It appeared in the center of a display at a viewing distance of 40 cm; the other stimuli were also presented on that display. For recording, the animal's head was fixed by means of a bolt implanted in the skull. Otherwise the animal was free to take a comfortable position in a boxlike primate chair. Single units were recorded with microelectrodes inserted through the intact dura throughout an experimental session.

Figure 2 shows three examples of neurons recorded in area 18. Neuron 1 responded to the lower right edge of a light bar (Fig. 2A). Its responses indicated precisely where, and in which orientation, a light-dark boundary appeared in the visual field: the response field measured 0.9° by 0.4° visual angle and was located 1.8° below the fixation point; only orientations between 46° and 101° produced a response (5). We then tested a stimulus in which a strip of 1.3°, covering the cell's response field, was blanked out, thus reducing the bar to a pair of notches (Fig. 2B). If one looks at such a stimulus with the notches moving back and forth together, one has the illusion of a light bar moving in front of two dark bars. The cell responded to this stimulus as it had to the edge of the bar, though less strongly. The response occurred at the same position, and the optimal orientation also remained the same.

In general, illusory contours disappear when only part of the inducing configuration is viewed. When, for example, one of the disk sectors in Fig. 1A is occluded, not only the corner of the triangle disappears, but also the adjacent flanks. The Gestalt psychologists stated that the whole is greater than the sum of its parts. We found a similar effect in the neuronal responses. Neither half of the stimulus of Fig. 2B excited the unit (Fig. 2, C and D; E shows the spontaneous activity), whereas both together did (Fig. 2B). The exact width of the gap between the two halves was not critical for this effect. With 2° instead of 1.3°, the cell still responded, and 4.1, 0.8, and 0.7 spikes per cycle were obtained for the whole figure, the upper and lower halves, respectively. We have tested the influence of the gap width in several other cells; all gave gradually weaker responses when the gap was increased. The largest gap at which a response was still obtained was 4.4° in a cell whose center of response field was located 3° from the fixation point. It could be argued that these responses were due to stray light falling into the response field and moving along with the notches and that the light coming from only half the figure might just not reach the cell's threshold. However,

we have observed the same nonadditivity in the stimulus-response relationship at a sixfold stimulus intensity. Again, neither half of the stimulus alone produced a response. This result argues against a simple threshold explanation.

Small changes in configuration can have dramatic effects on the appearance of illusory contours. An example is the closing lines in Fig. 1C. A similar effect could be observed in the neuronal responses, as demonstrated by neuron 2. It responded well to a narrow bar (Fig. 2F) and also gave a regular response to the illusory bar stimulus bridging a gap of 2° (Fig. 2G). When the notches were closed by line segments 5 minutes of arc wide, the response was almost abolished (Fig. 2H). Nearly all cells that responded to the illusory bar stimulus showed this reduction; in some cells, lines as narrow as 2 minutes of arc had an effect. Again, the gap width was not critical; as long as the cell responded, closure reduced the response.

The responses so far seem to indicate the ability of the cortex to extrapolate lines to connect parts of the stimulus which might belong to the same object. The abutting gratings of Fig. 1D show an illusory contour which is not an extrapolation of the stimulus since it runs more-or-less perpendicular to the inducing lines. We have tested a contour that was straight and perpendicular to the lines. It could be moved back and forth along the lines, leaving the stimulus margin stationary. Responses were recorded for various orientations. Neuron 3, for example, responded to the illusory-contour stimulus better than to any of the conventional stimuli (Fig. 2I). Furthermore, the peak responses were obtained at virtually the same orientation for contour and bar. The curve of the illusory contour bends upward at both ends, indicating a second peak 90° from the optimum. This can be interpreted as a response to the inducing lines. Other cells showed only the peak related to the contour and thus were not activated by the gratings at all. When the cells also responded to the illusory bar stimulus, the optimal orientations were similar for both types of illusory contour.

To see the contour, a minimum number of lines are required; no contour is visible at the end of just one line, but it is usually perceived with four or more line ends. There was a similar threshold for the neuronal response (Fig. 2J). The density of lines, on the other hand, was not critical. Keeping the overall size of the stimulus constant, the responses were equal for line spacings of 12, 24, and 48 minutes of arc, and slightly less for 72

minutes of arc, but still stronger than the response to the bar.

There was a marked difference between striate and prestriate cortex (6). Of 70 cells tested in area 17, none showed responses related to the contour between abutting gratings (7), whereas about one-third (21 of 68) of the cells in area 18 did. Also, the results obtained with the other type of illusory contour (Fig. 2, B and G) were negative in area 17 (11 cells) but positive in 13 of 38 cells in area 18. (With this type of stimulus, the demonstration of the effect of closure (Fig. 2, G and H) was taken as a criterion.)

We were not able to relate responsiveness to illusory contour stimuli to the conventional classification of cells. With bars and edges, monotonic length-summation curves were usually obtained, but end-inhibition was also observed.

Responses of cells in area 18 that required appropriately positioned and oriented luminance gradients when conventional stimuli were used could often be evoked also by the corresponding illusory contour stimuli. In this area, one would be able to infer location and orientation of the various types of contours from the responses of single cells. In area 17, this would be possible only for

Fig. 1. Illusory contours. Such contours are perceived in A, B, and D, at sites where the stimulus is homogeneous. Small alterations in the stimulus can have dramatic effects on the appearance of these contours (C) (9).
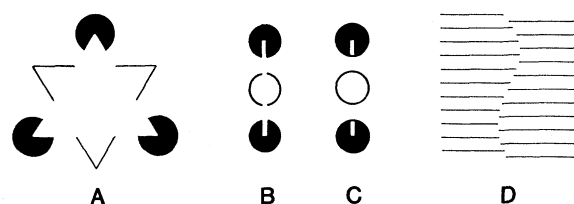

Fig. 2. Responses of neurons in area 18 of the monkey visual cortex to edges, bars, and stimuli producing illusory contours. The stimuli (insets) (10) were moved back and forth across the receptive fields (neuron 1, 1° at 1 Hz; neurons 2 and 3, 2° at 1 Hz). Each was presented 8 (I), 16 (J), or 24 (A to H) times; blocks of eight repetitions were alternated in pseudorandom order. For neurons 1 and 2, the response fields (the regions in the visual field where the neurons could be activated by a bar or edge) are represented by ellipses, and the fixation point is marked by crosses in A and F; the responses are represented by rows of dots; mean numbers of spikes per stimulus cycle are indicated on the right. Neuron 1, which responded to the lower right edge of the light bar (A), was activated also when only the illusory contour passed over its response field (B). Either half of the stimulus failed to evoke a response (C and D); (E) spontaneous activity. Neuron 2 responded to a narrow bar (F) and, less strongly, to the illusory bar stimulus (G). When the ends of the "bar" were intersected by thin lines, however, the response was nearly abolished (H). In neuron 3, the border between two abutting gratings elicited a strong response. The orientation tuning curves show corresponding peaks for bar and illusory contour (I). When the lines inducing the contour were reduced in number to less than three, the response disappeared (J); compare the lines above the curve (the actual stimuli were centered over the response field). The lines were 1 minute of arc wide and spaced 48 minutes apart.
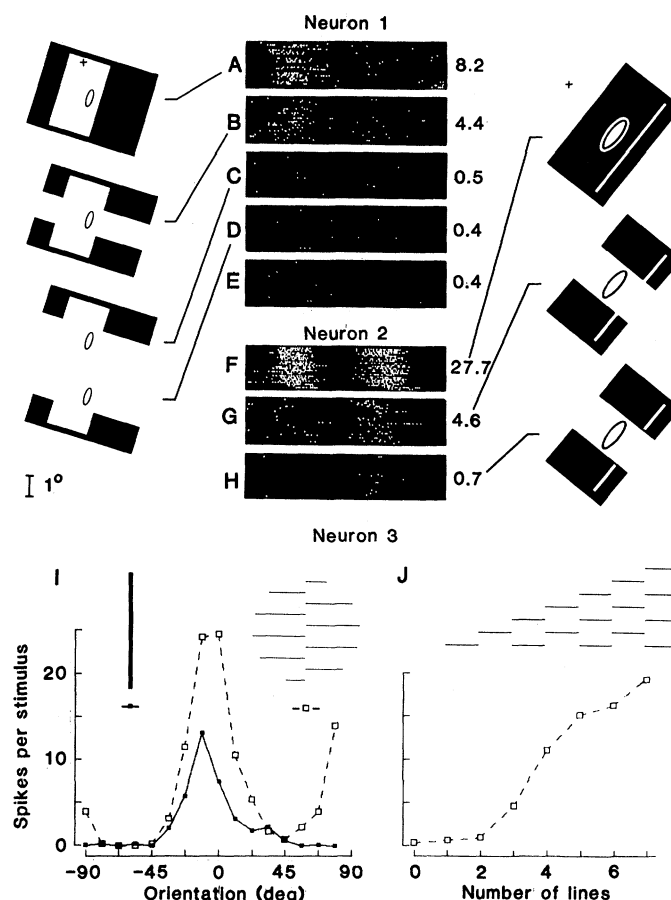
edge or line type contours produced by luminance or color differences. Responses in area 18 showed several other parallels to perception, such as the relation between the responses to a figure and to its parts and the dramatic effect of small elements added to the figure.

Gregory (4) formulated an antithesis between physiological and cognitive explanations of illusory contour effects. According to his cognitive approach, the contours are perceived because an illusory object is "postulated" as a perceptual hypothesis to account for the sensory data. The explanation suggested by the present experiment is physiological, but it differs from the one stated in Gregory's antithesis (and criticized by him) that "feature detector cells of the striate cortex are activated by the disk sectors [scilicet of the Kanizsa triangle] . . . to give the appearance of continuous lines, though only their ends are given by stimulation" (4, p. 51). Our results do not support this idea. With stimulus configurations like those of B or G in Fig. 2, cells in area 17 did not respond, some of them not even when the gap was narrowed so that the ends of the bar entered the response field. The responses in area 18 on the other hand cannot be interpreted simply as suboptimal excitation due to partial stimulation of the response field, since they can be evoked by stimuli well outside that field and are affected by small changes in configuration that are negligible in terms of luminous flux. Also the responses to stimuli with lines perpendicular to the cell's preferred orientation reveal an unexpected new receptive field property. The way widely separated picture elements contribute to a response resembles the function of logical gates. The important elements in our stimuli seem to be corners on opposite sides of the response field (Fig. 2, B and G) and line ends arranged in a row (Fig. 2, I and J). Line ends and corners are in fact emphasized in certain signals of area 17 (8), and a number of such signals might converge on neurons of area 18. Corners and line ends play a role in the formation of contours because these picture elements are frequently produced by interposition of objects, that is, when an object partially occludes others. Thus, several such elements aligned in a row are likely to mark an object boundary.

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3. For a review see G. Kanizsa, Organization in Vision. Essays on Gestalt Perception (Praeger, New York, 1979).
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6. Most of the cells assigned to area 18 were recorded in the posterior bank of the lunate sulcus. The cortical area was judged also from physiological criteria such as the presence of the typical activity of layer IVc in area 17 [G. F. Poggio, R. W. Doty, Jr., W. H. Talbot, J. Neurophysiol. 40, 1369 (1977)] and the topography of receptive fields; it has been confirmed histologically for part of the data. A few cells recorded near the 17-18 border were not counted.
7. The orientation tuning curves obtained with the illusory contour stimulus in area 17 typically showed a single peak corresponding to the orientation of the grating lines.
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9. Part A and D are reproduced from figures 4.2 and 12.12 in (3); parts B and C are figures 1, C and D, in A. T. Smith and R. Over [Percept. Psychophys. 20, 305 (1976)].
10. To simplify the figure, stimuli have been reproduced in reversed contrast; the parts shown in black were actually lighter than the background (about 2.5 versus 1 foot lambert). To avoid confusion, the text has been made consistent with the figure.

Treatment of a 12-Hour Shift of Sleep Schedule with Benzodiazepines

Abstract. Normal sleepers underwent sleep recordings and daytime tests of sleep tendency, performance, and mood while being shifted 180° in their sleep-wake schedule. After two baseline 24-hour periods, subjects postponed sleep until noon. For the next three 24-hour periods, they were in bed from 1200 to 2000 and received triazolam, flurazepam, or placebo at bedtime in parallel groups. Placebo subjects showed significant sleep loss after the shift. Active medication reversed this sleep loss. Despite good sleep, flurazepam subjects appeared most impaired of the three groups on objective assessments of waking function; triazolam subjects were least impaired.

Many people are familiar with the insomnia, disturbed mood, and reduced daytime alertness that often accompany rapid travel across time zones ("jet-lag") or sudden changes in sleep schedule (for example, shift work). Laboratory studies have documented impairments of sleep and performance that accompany such alterations in sleep-wake schedule (1). In particular, Weitzman et al. (2) shifted the bedtime of normal subjects 12 hours by having them stay awake for a single night. Sleep at the shifted time in bed was disturbed, and function during the nocturnal waking hours was judged impaired. The results were interpreted as the effect of attempting to sleep and to be awake in opposition to the underlying circadian rhythm. The same group carried out a related study (3). After a sudden 12-hour phase shift of scheduled time in bed, subjects were given a widely prescribed hypnotic (30 mg of flurazepam) at bedtime. Sleep time and continuity significantly improved; the quality of subsequent wakefulness, however, was not improved. This result was interpreted as evidence that the underlying circadian rhythm of sleep and wakefulness is more important in facilitating daytime alertness than the total amount of sleep one has had recently.

Flurazepam has a long-lived active metabolite (4). More recent studies have shown that bedtime ingestion of flurazepam is followed by daytime sedation and performance decrements even in the absence of a shift in the sleep-wake schedule (5, 6). Thus, the impaired wakefulness following treated sleep may have been a carry-over of the sedative effect of the drug rather than a circadian effect. Elsewhere, we have suggested that if a hypnotic drug were free of carry-over into the next day, daytime functioning should improve as a result of better sleep (6).

The difficulties in assessing daytime function with any of the myriad available performance tests have been evaluated in recent reviews (7) and will not be considered here. The multiple sleep latency test (MSLT) (8) may be useful as a primary measure of improved daytime functioning in hypnotic efficacy studies because (i) it is a direct measure of an electroencephalographic (EEG) state associated with reduced alertness and (ii) it seems relatively unaffected by practice, learning, or fluctuating motivation. This