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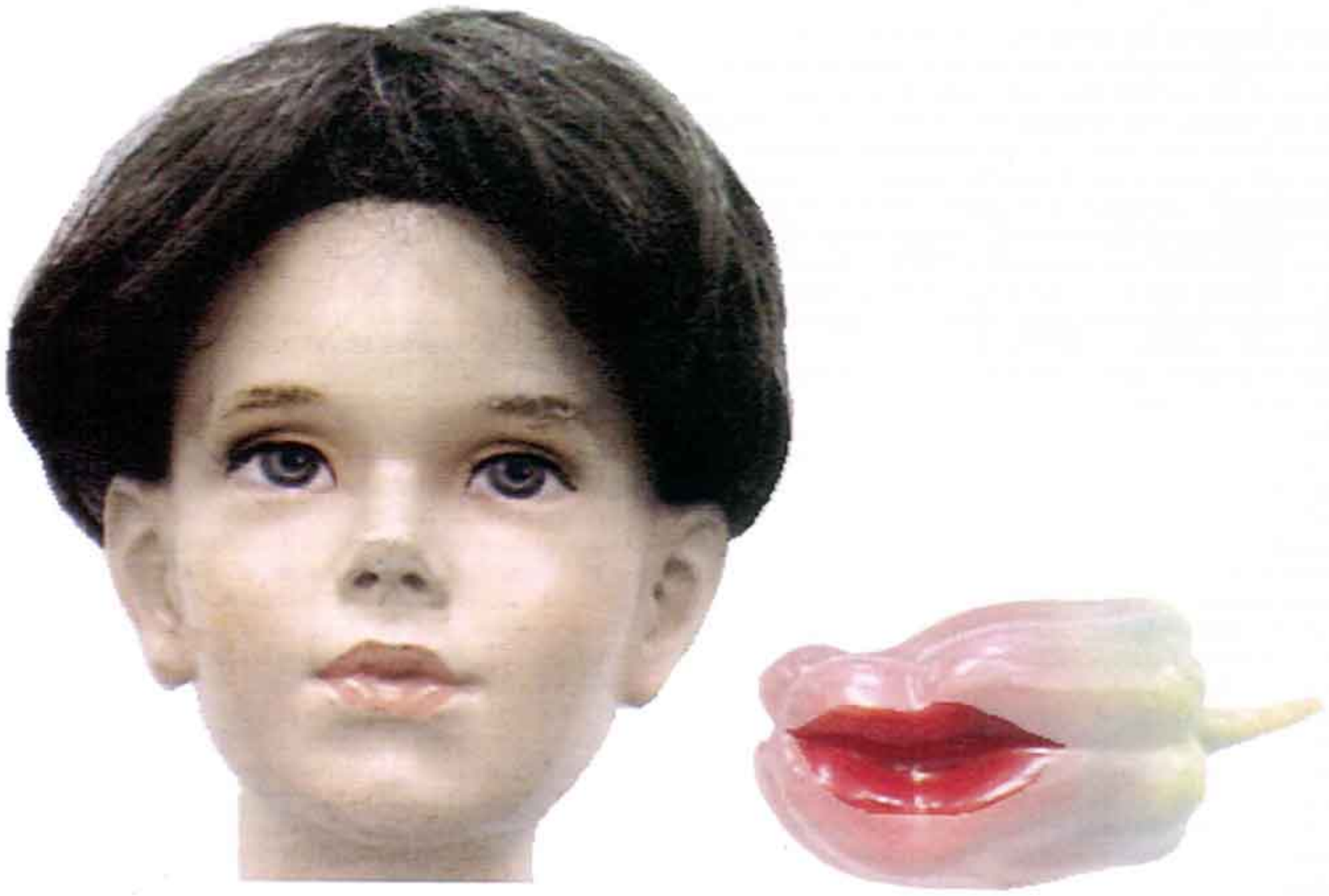

FEATURE RECOGNITION IN THE BRAIN

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Columns for visual features of objects in monkey inferotemporal cortex

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AT early stages of the mammalian visual cortex, neurons with similar stimulus selectivities are vertically arrayed through the thickness of the cortical sheet and clustered in patches or bands across the surface. This organization, referred to as a 'column', has been found with respect to one-dimensional stimulus parameters such as orientation of stimulus contours[1], eye dominance of visual inputs[1], and direction of stimulus motion[2]. It is unclear, however, whether information with extremely high dimensions, such as visual shape, is organized in a similar columnar fashion or in a different manner in the brain. Here we report that the anterior inferotemporal area of the monkey cortex, the final station of the visual cortical stream crucial for object recognition[3–8], consists of columns, each containing cells responsive to similar visual features of objects.

Most neurons in the anterior part of the inferotemporal cortex (IT) selectively respond to particular object features such as shape, or a particular combination of colour or texture with shape[9–12]. Anterior IT cells as a whole show a vast variety of preferred object features. If columnar organization exists, however, nearby cells should show a strong tendency to respond to similar features. We therefore first examined whether adjacent cells in the anterior IT respond to similar features or to distinct ones. We recorded extracellular action potentials from multiple cells with a single electrode, and activity of a single cell was isolated with a window discriminator. We determined the stimulus feature critical for activating this cell[12], and devised a set of stimuli including the optimal and suboptimal stimuli, and their modifications, as well as ineffective stimuli, for this cell. This set was used to examine the responses of an adjacent cell or multiple cells selected with another window.

Adjacent cells at most sites responded together to the same stimuli in the set. At 41 of 47 recording sites (87%), simultaneously recorded cells showed maximal or nearly maximal responses to the same stimulus. At nine of the 41 sites, adjacent cells behaved very similarly and no difference in stimulus preference was detected. At the other 32 sites, stimulus selectivities of adjacent cells were similar but differed in some aspects. At 21 of the 32 sites, neighbouring cells shared the most effective stimulus, but had a different selectivity to fine parameters. Two cells in Fig. 1, for example, responded to a vertical bar projecting from the top of a base, either a disk, a square or a horizontal bar (*a*, *b*, *e*). Components of the stimuli did not excite the cells (*c*, *d*). A small gap between the vertical bar and the base eliminated the responses (*f*). An '*L*-shape' or a 'mirrored *L*-shape' evoked no or weak responses in the two cells (*g*, *h*). Both cells thus required, for maximal activation, the two adjoining corners at the junction of the projection and the base. Changing the intersection angles at the junction, however, revealed a difference between them. Cell 1 responded best to right angles (*e*) and maintained 50–60% of the maximal activation to other angles (*i*, *j*), whereas cell 2 responded only to right angles. In the other 11 of the 32 cases, the most effective stimuli differed slightly between adjacent cells, although they responded well to both stimuli: for example, one cell responded most strongly to a horizontally striped triangle, whereas the other preferred a square filled with horizontal stripes. Finally, at the remaining six sites, stimuli that activated one cell did not excite the other cell(s) simultaneously recorded. Neurons with similar selectivities thus tend to cluster together within the anterior IT.

We assessed the spatial extent of this clustering by inserting electrodes either vertically or obliquely to the cortex. As in the simultaneous recording experiments, we first determined the critical stimulus feature for a neuron, and made a set of stimuli including optimal, suboptimal and ineffective stimuli for that cell. We then tested other cells sampled at 100 or 200 μm steps along the penetration with this same set.

In seven vertical penetrations where the angle between the electrode path and radial array of cells was 0–20°, the distance between the first recorded cell near the entry and the last recorded cell at the bottom ranged from 1.5 to 2.5 mm. Over a distance of 0.7–2.1 mm (mean ± s.d.; 1.3 ± 0.5 mm, $n = 7$) within this thickness, we consecutively obtained cells that responded well to stimuli which were identical or similar to the optimal stimulus for the first cell tested in each penetration. The clustering covered 79–86% of the estimated cortical thickness (distance between first and last cell) in five of the seven penetrations, and 43–54% in the other two penetrations. The results indicate that cells with similar selectivities span most of the cortical layers.

In the example shown in Fig. 2, the first cell we examined (arrow) needed three stimulus features for its activation: (1) horizontally elongated overall shape; (2) upper part darker than the lower; and (3) darkest in centre part. We devised a set of 24 stimuli, and tested other cells along this penetration. All but one cell recorded over a distance of 1.3 mm (80% of estimated thickness of grey matter) responded exclusively or maximally to stimuli with a half-dark, half-light pattern with the centre darkest. The darkest centre or a white ellipse alone did not evoke responses in any of the tested cells.

In another vertical penetration (Fig. 3), cells recorded over a distance of 2.1 mm (86% of estimated thickness of grey matter) responded only to stimuli with a gradual change of luminosity. Thus the preferred stimulus feature shared by vertical arrays of cells was not restricted to shapes, but could be other visual features of objects such as gradation.

Along tangential or oblique penetrations where the angle formed by the recording track and radial array of cells was 50–90°, cells with similar stimulus selectivity were localized within 0.2–0.7 mm (0.4 ± 0.2 mm, $n = 7$), a shorter distance than that obtained in vertical penetrations ($P < 0.001$, Student's *t*-test). This indicates that the clustering was vertically elongated in the direction of cortical depth and was patchy across the surface. Neurons immediately outside the cluster showed no response to stimuli that evoked maximal or substantial responses in the first tested cell. In six of the seven tangential penetrations, we found another cell or cluster of cells showing similar stimulus preferences after a gap of 0.4–1.0 mm. In three of the six recording tracks, there was a third cluster after a similar gap. Cells outside the clusters were visually responsive, and their preferred stimulus features were likely to be distinct from those activating the clusters, because some of them responded to stimuli in the test set which did not activate cells in the clusters or to some objects presented to the monkey.

Figure 4 shows an example in which a cluster of four single or multiple units localized within 0.2 mm and another cell 0.46 mm away responded to a combination of two different colours. Shape was not a critical factor, and we used rectangles of two colours in the test set. A component colour alone evoked no or weaker responses. Neither a combination of black and white nor equiluminant grey activated the cells. A cell outside the cluster responded to a star shape which did not activate the cells in the cluster.

The similarity of cells along a penetration was due to local clustering of cells responsive to overlapping object-features, not to ubiquity of this kind of cells in the IT. For example, apart

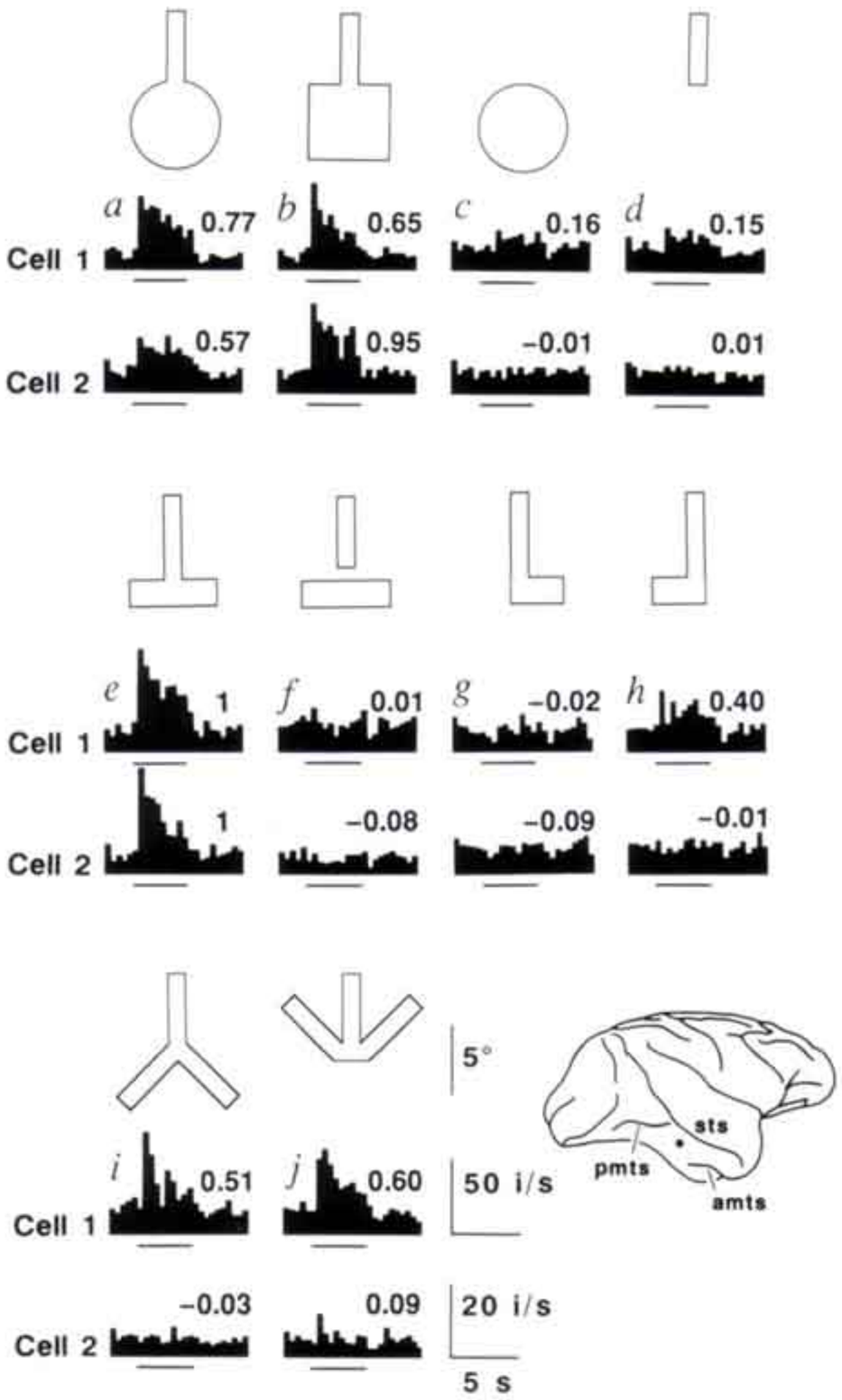

FIG. 1 Two adjacent cells in anterior IT showing similar, but not identical, stimulus selectivity. The recording site is shown on the lateral view of the cortex. amts, pmts, Anterior and posterior middle temporal sulcus; sts, superior temporal sulcus. Stimuli were white solid shapes on black background. Impulse histograms below each visual stimulus were averaged over 10 stimulus presentations. Horizontal lines indicate 4-s periods of stimulus presentation. Numbers show response magnitude relative to the maximal response. Negative values indicate suppression below the ongoing firing rate. Both cells responded to two adjoining corners at the junction of a base and a vertical projection, but had different selectivity to intersection angles.

METHODS. General experimental procedures were similar to those in ref. 12. Recordings were made in area TEd[23] of six monkeys (*Macaca fuscata*) prepared for repeated recordings[12]. In recording experiments, a small hole was made in the skull for electrode insertion under initial anaesthesia with ketamine followed by isofluorane. During the recording, the monkey was immobilized, and anaesthesia was maintained with a mixture of N_2O and O_2. Electrocardiogram helped us to judge anaesthetic depth, and sodium pentobarbital was supplemented when necessary. Extracellular activity was recorded simultaneously from multiple cells with single electrodes. Responses of one cell isolated from multiunit activity were tested with a set of hand-held stimuli (see ref. 12) for effective stimuli survey. An image of the most effective object was taken with a video camera and stored on a computer. Stimuli were moved with a small amplitude (up to 1.2°) around the centre of the predetermined receptive field on a TV monitor. With a computer graphics system, we simplified the effective stimuli step by step to determine stimulus features essential to cell activation. We first changed the image from full colour to monochrome. If the monochromatic image was as effective as the original one, we did not pursue the cell's selectivity to colour. If the original image was better, we examined colour selectivity of the cell. We next removed texture, gradual luminosity change, and highlight from the image one by one to determine whether any of these features was essential. If not, we modified the image to a regular geometrical figure; for example contours of an apple were changed into a disk with a projecting bar. If the cell's response survived this transformation, we then determined the critical aspect of the figure by modifying shapes of components or overall configuration or by decomposing the image into components. Throughout these procedures, impulse histograms were generated for the isolated cell and for a nearby cell or multiple unit, which were selected by a second window discriminator. Electrolytic lesions were made at some recording sites to reconstruct electrode tracks, and were later verified in Nissl-stained sections.

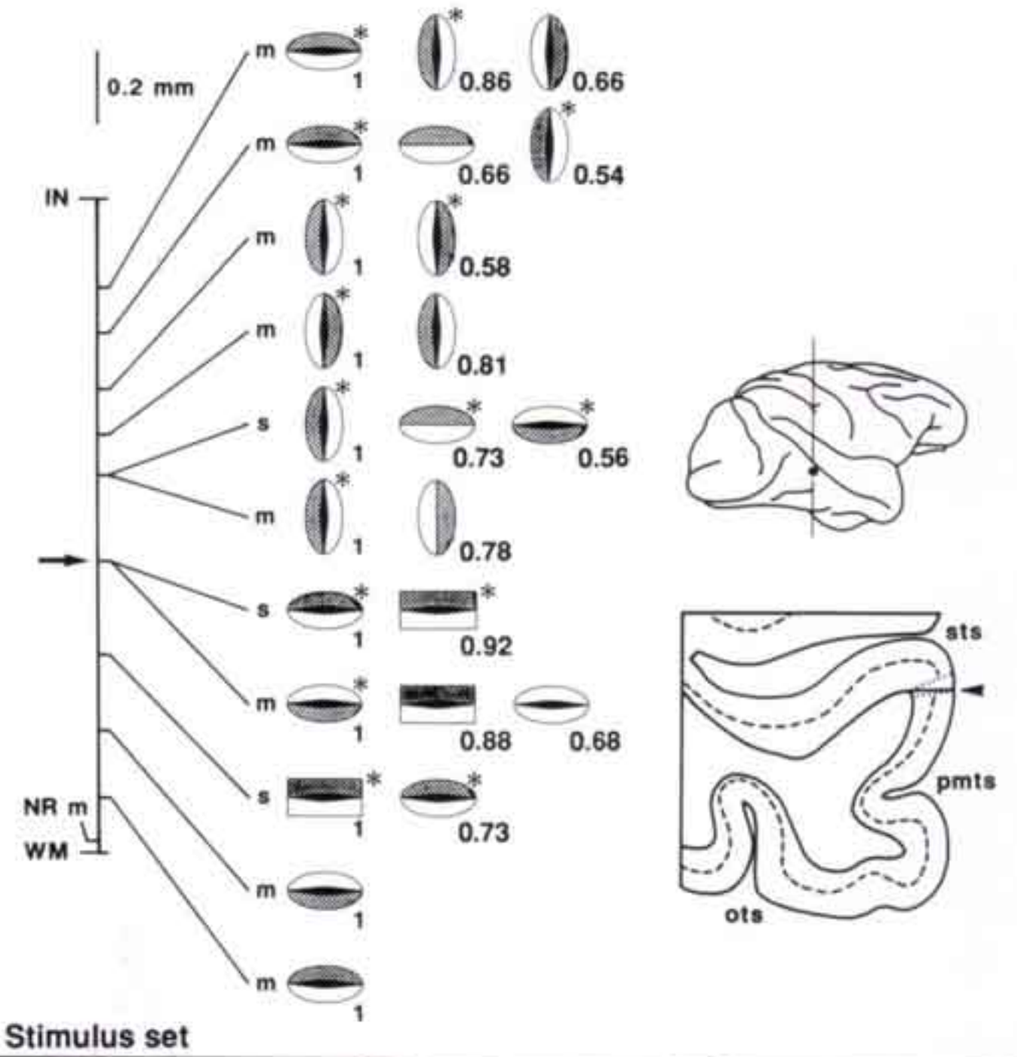

FIG. 2 Response profiles of 12 IT cells or multiple units recorded in a penetration directed vertically to the cortex. Location of the penetration is shown on the lateral view of the brain. The penetration is reconstructed on a coronal section through the IT (arrow head; ots, occipitotemporal sulcus). Dashed line indicates layer 4. Dotted lines indicate radial array of cells from which the penetration deviated by 10° at layer 4. A schematic drawing of the recording track (left) shows recording depths (IN, site where first neuron was recorded in this penetration; WM, entry into white matter). The first cell examined, seventh from the top (arrow), responded most strongly to the lips of a face among several tens of three-dimensional objects presented to the monkey. An extensive test revealed that the stimulus feature critical for activation was horizontally elongated shape with an upper half-dark, lower half-light pattern with the centre darkest. Neither colour nor contour shape of the lips was essential to activation. We then devised a set of 24 stimuli which included effective stimuli for this cell and their modifications (bottom), and tested other cells distributed throughout the grey matter in this penetration (s, single cell recording; m, multiple cell recording). Effective stimuli are shown to right of corresponding recording sites in order of the most to least effective stimuli, for statistically significant responses greater than 50% of the maximal response of each cell. None of the other stimuli in the stimulus set evoked significant responses in these cells. Responses were averaged over 10 stimulus presentations, and were considered significant when firing rate during stimulus presentation differed from the ongoing discharge rate just before presentation (Kolmogorov–Smirnov test; $^*P < 0.01$; no mark $P < 0.05$). Numbers show response magnitude relative to the maximal response for each cell. All but one cell recorded over a distance of 1.3 mm responded only or maximally to stimuli with a half-dark, half-light pattern with the centre darkest. One multiple unit near the white matter did not respond to any of the stimuli in the set (NR).

METHODS. For vertical penetrations, electrodes were inserted into the brain from the side at right angles to midsagittal plane with or without a downward tilt (5 or 20°). In two of nine such penetrations we made, electrodes traversed in the bank of the superior temporal sulcus or of the anterior middle temporal sulcus, and the data were excluded from the analyses.

from the penetration shown in Fig. 3, only one penetration made in another monkey, among our whole sample of 86 penetrations in six monkeys, contained cells responding to a gradual luminosity change. This penetration was also made vertically to the cortex, and stimuli with a gradual luminosity change activated nine cells recorded over 85% of the cortical thickness. The cells shown in Figs 2 and 4 are the only ones in our sample that had the critical stimulus features shown there.

We conclude that anterior IT neurons selective for similar object-features are aligned normal to the cortical surface across most, if not all, cortical layers. Previous studies have shown clustering of cells with similar response properties in the IT[12,13], a cortex in the superior temporal sulcus[14,15], and the medial superior temporal cortex[16]. But evidence for columnar organization is fragmentary, or analysis of neuronal stimulus selectivity is insufficient in these studies. Our results provide, to our knowledge, the first evidence for the existence of functional columns in a higher association cortex, and together with results in lower sensory cortices of various modalities[1,2,17,18], support the notion that columnar organization is a basic feature of the cerebral neocortex[19–21].

Although neurons in an IT column responded to similar stimuli, optimal stimulus and tuning properties differed among constituent cells, even between adjacent ones. This has a computational implication. Any useful representation system for object recognition should satisfy two conflicting conditions: ability to reflect the degree of similarity between two shapes in their descriptions and sensitivity to small differences between the two[22]. Our results imply that activation of a column may encode an extracted object feature common to two similar shapes, whereas activity of individual cells may be useful for signalling subtle differences between them.

The surface area of the anterior IT dorsal to the anterior medial temporal sulcus (TEd[23]), from which our recordings were made, is $330 \pm 76\ mm^2$ ($n = 4$; our unpublished observation). Cells with similar selectivity were localized in clusters of 0.4 mm width on average. If we take a square of this width ($0.16\ mm^2$) as the area of an individual column, this gives us 2,000 as a rough estimate of the number of columns in this area. The number of distinct object features represented in this area

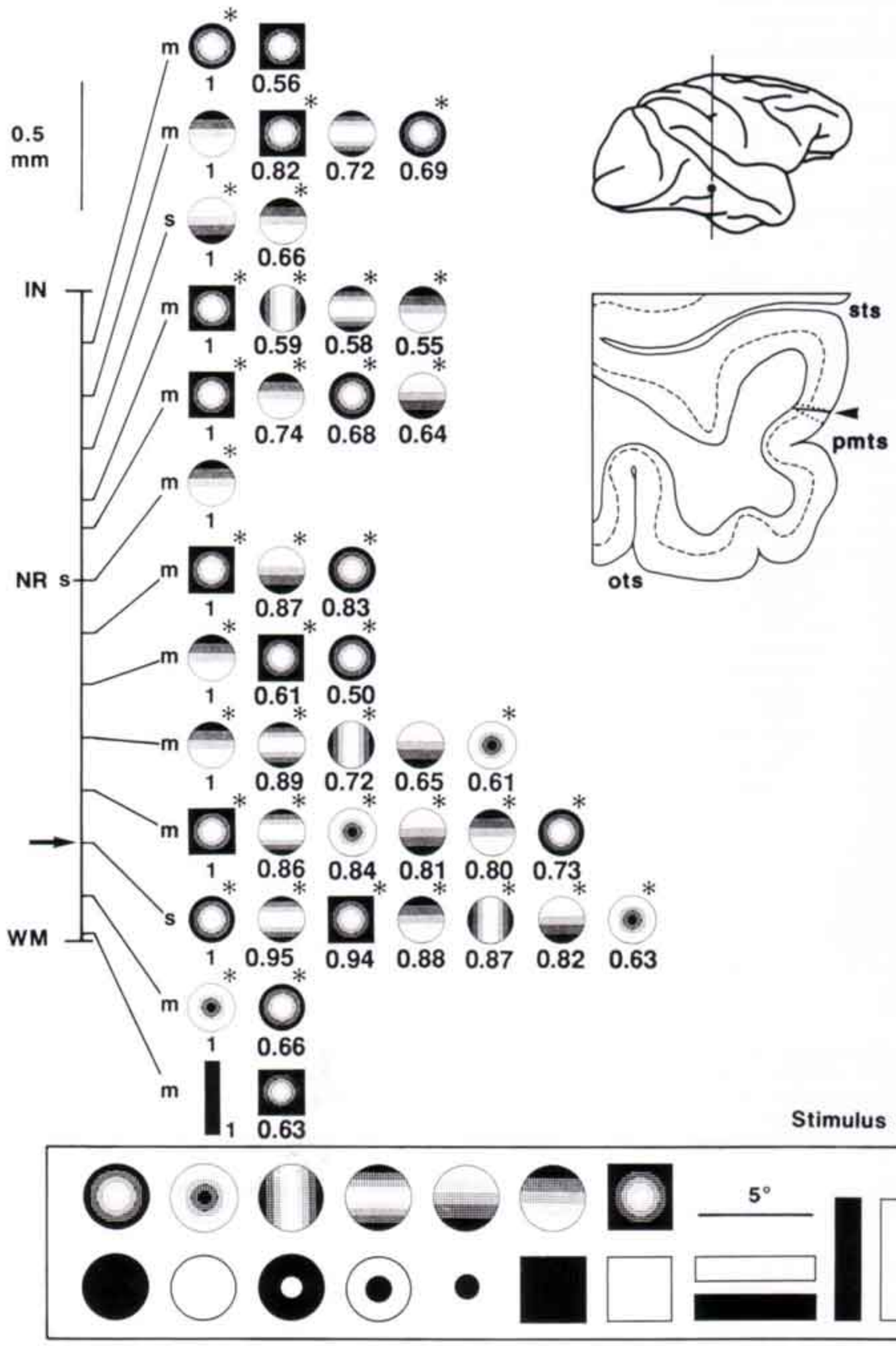

FIG. 3 Response profiles of 14 anterior IT cells recorded in a vertical penetration to the cortical surface. The angle between the penetration and radial arrangement of cells was 20° at layer 4. The stimulus feature essential for activation was first determined for the third cell from the bottom in the figure (arrow). Other neurons in this penetration were tested with a set of 18 stimuli (bottom) which included the optimal, suboptimal and ineffective stimuli for the first examined cell. Although actual stimulus figures presented to the monkey had 256 grey levels, they are shown only with 5 grey levels for clarity. All cells except two responded only to stimuli with a gradual change of luminosity. Two exceptions were one cell near the white matter which preferred a black vertical bar over a square with a gradation, and the other recorded in the middle of the penetration (indicated as NR), which showed responses to a gradation stimulus (upper row, fifth from left, in the set) in 5 of 10 presentations, but the response did not reach a significant level.

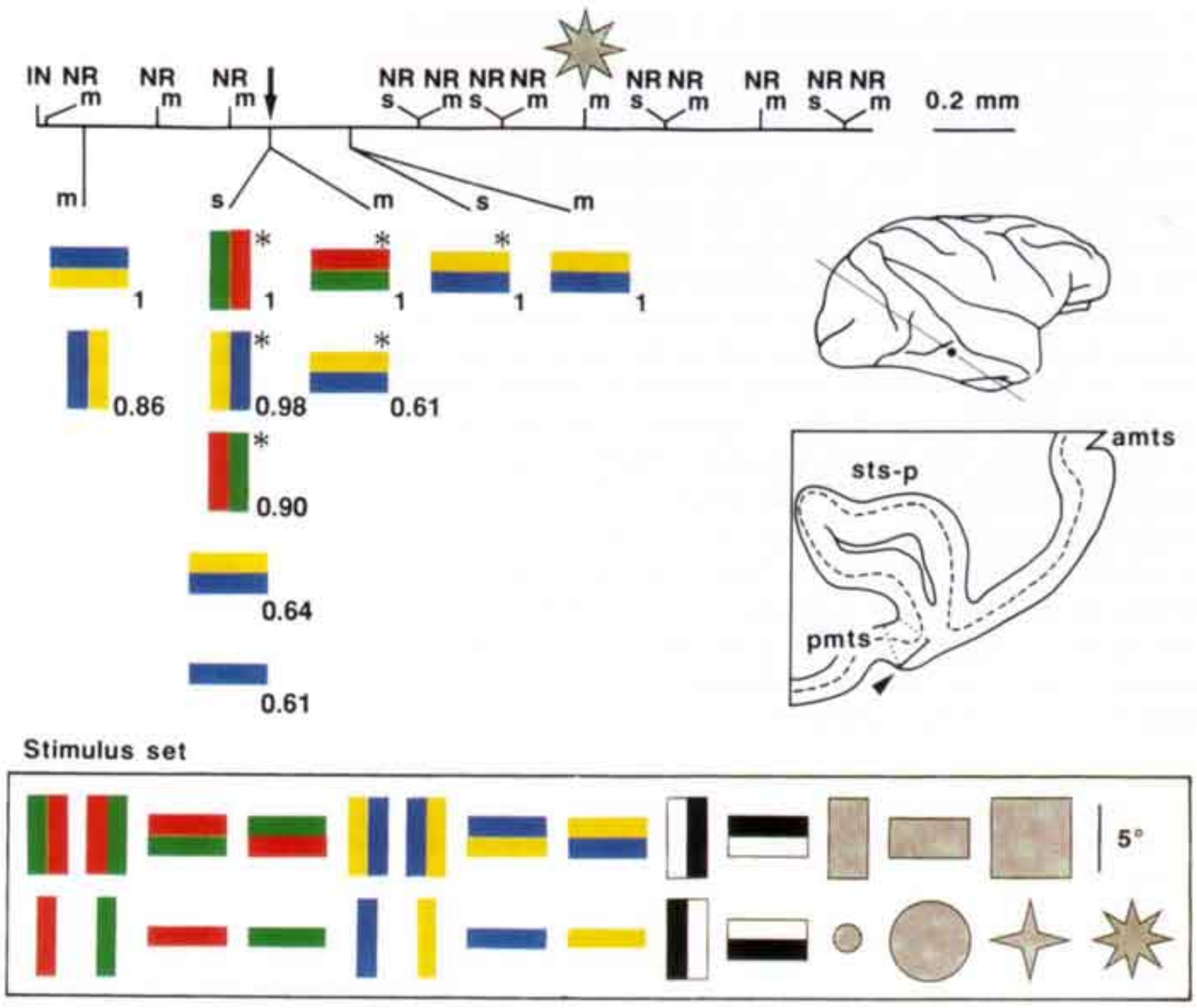

FIG. 4 Response profiles of 18 cells or multiple units obtained over a distance of 2 mm in a penetration directed tangentially to the cortical surface in the anterior IT. The entry site of the electrode penetration was immediately anterior to the posterior middle temporal sulcus. The recording track traversed radial arrangement of cells at an angle of 70–90°, indicating that the penetration ran almost tangential to the cortex (inset, sts-p, a pocket in the superior temporal sulcus). The stimulus feature critical for activation was first determined for a single cell marked with an arrow, then the stimulus set (27 stimuli shown at bottom) was devised to test other cells along this recording track. Four different colours (red, green, blue, yellow) and grey were equiluminant. A cluster of four cells and one multiple unit 0.46 mm away responded only or maximally to a combination of two colours. Twelve other cells or multiple units did not respond to any stimulus in the test set (indicated as NR). One cell 0.58 mm away from the cluster responded to a star shape with eight protrusions.
METHODS. For oblique or tangential penetrations, electrodes were directed anteriorly into the brain from the side at an angle of 45° to midsagittal plane and downwards by 27–30° (see inset).

would be smaller than this number because we observed multiple clusters of cells with similar selectivities along tangential penetrations. Studies on this limited number of distinct object features common to vertical arrays of cells may help us to understand what the 'basis functions' are in the neural coding of object images. □

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