

distinguish critically between nuclear genes and extra-nuclear entities.

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Stereoscopic Vision in Macaque Monkey

Random-dot stereoscopic patterns have been used to provide behavioural evidence of stereoscopic vision in macaque monkeys. Cells sensitive to binocular depth have been found in area 18 of the macaque monkey cortex.

Cells sensitive to Binocular Depth in Area 18 of the Macaque Monkey Cortex

Barlow, Blakemore and Pettigrew¹, and Nikara, Bishop and Pettigrew², have described a group of cells in the cat visual cortex that responds selectively to horizontally disparate stimulation of the two retinas. It seems very likely that such cells play an important part in stereoscopic depth perception. We wished to determine whether similar cells were present in the monkey cortex, especially in view of Bough's behavioural demonstration of stereoscopic depth perception in the monkey (page 42).

In fifteen macaque monkeys we have examined binocular interaction in 547 cells of area 18, a topographically ordered region anterior to area 17 (the striate cortex). Parallel anatomical studies show that there is an ordered projection from area 17 to area 18 on the same side; there is no evidence for any direct input to 18 from the lateral geniculate body^{3,4}.

Recordings were made simultaneously from an extra-cellular electrode in each hemisphere⁵. The main recording electrode was inserted into area 18, either in the posterior bank of the lunate sulcus or in the annectant gyrus, which is buried in the lunate sulcus. An adjustable prism in front of the left eye allowed the relative directions of gaze of the two eyes to be varied. Eye movements were almost completely prevented by the use of intravenous curare and gallamine². The second electrode monitored the eye positions and detected any residual movements. A binocular unit was recorded in area 17 and kept, if possible, for the duration of the experiment. The receptive fields in the two eyes were mapped out on a projection screen 1.5 m away. The field positions were checked each time a new unit was studied with the main recording electrode; eye movements could thus be detected and corrected for immediately.

About half (57 per cent) of the cells in area 18 react to simultaneous stimulation of the two eyes in a manner similar to the complex and hypercomplex cells of area 17. We term these "ordinary cells of area 18". Most ordinary cells respond actively to either eye stimulated by itself, and the responses of the two separate eyes are usually about equal. Receptive fields of these cells are in anatomically corresponding parts of the two retinas. There is often moderate summation when the two eyes are stimulated together, and the relative positioning of stimuli within the two fields is generally not critical for a cell to show maximum response.

Forty-three per cent of cells in 18 show more specialized properties. We term these "binocular depth cells". There

are several distinct types of binocular depth cells; we describe here only the most common. In these, stimulation of either eye separately gives no response or only weak responses, whereas appropriate stimulation of the two eyes together results in very brisk responses. Some of these cells respond best with the two eyes lined up so that exactly corresponding retinal regions are stimulated simultaneously; in others there is a disparity in the positions of the two receptive fields. The displacement of the field in one eye, relative to the field in the other, is usually at right angles to the receptive field orientation. Vertically oriented fields are thus horizontally displaced, whereas with oblique fields there is a vertical component to the disparity as well. In binocular stimulation, when the position of one eye (or the prism setting) is varied along a line at right angles to the orientation of the optimal stimulus (the receptive field orientation), the response rises from zero or some low value to a maximum and then falls off over a range that is usually very small compared with the dimensions of the receptive field. Variation in position along a line parallel to the orientation of the optimal stimulus gives a much more gradual rise and fall in response. Because of this, the responses of cells with obliquely oriented fields also peak sharply when the prism placement is purely horizontal, giving nearly maximal responses (Fig. 1). Binocular depth cells with receptive fields oriented within 15° of the horizontal are much less common than one would expect in a random distribution, and their responses have not yet been adequately analysed.

The frequency with which one encounters binocular depth cells varies in a systematic way in area 18. Just in front of the 17-18 border and 10-15 mm lateral to the midsagittal plane (representing the vertical midline, 3°-4° below the fovea), most cells are "ordinary"; many of these have fields straddling the vertical midline. As one proceeds forwards and down into the lunate sulcus, and then up over the buried annectant gyrus, the retinal representation moves out from the midline. At the same time, the proportion of binocular depth cells increases to more than 50 per cent. As an electrode traverses the cortex, sequences of cells that are all ordinary, or all of the binocular depth type, are recorded; neighbouring binocular depth cells often have the same horizontal disparity, though varying in orientation. This suggests an organization in which cells representing a given stereoscopic depth relative to the surface of fixation are grouped together, and segregated from cells that are not particularly concerned with depth. These groupings may have the form of columns that extend from surfact to white matter. There is probably also an independent

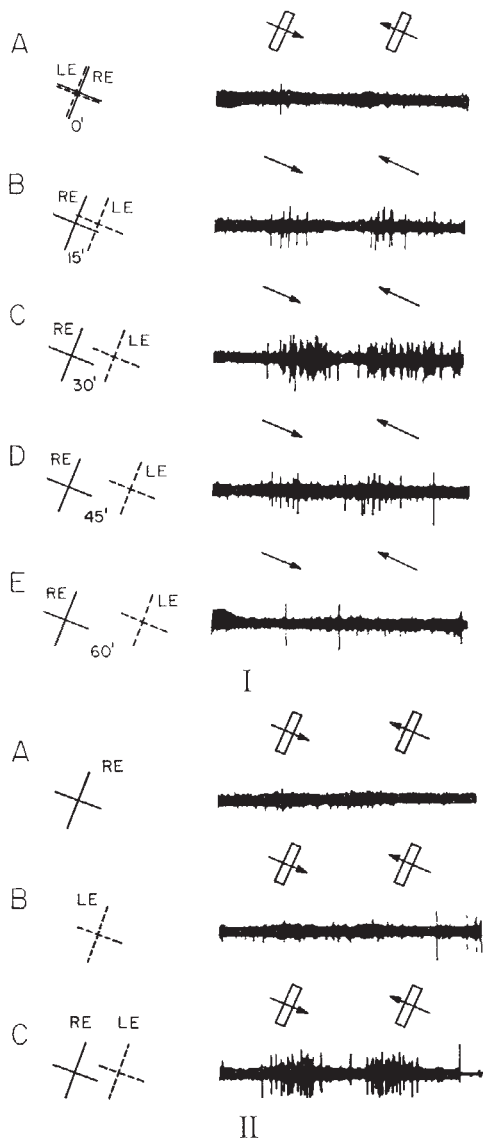


Fig. 1. Responses of a cell recorded from area 18 in right hemisphere 12 mm lateral to the midline, on the anterior tip of the lunule sulcus about 3 mm in front of the 17-18 boundary. Cell was in layer 6. It responded best to a slit 1° long and 0.125° wide, oriented 20° clockwise from the vertical. The receptive field was approximately 1° by 0.75° in size, and in the right eye was situated 1.75° below and 1° to the left of the fovea. In the left eye it was displaced, relative to this, 0.5° to the right and slightly downwards. I: Both eyes stimulated together in anatomically corresponding regions (A). In B-E, position of stimulus to left eye was horizontally displaced to the right on the screen in steps of 15 min of arc. Maximum responses were obtained with a displacement of 30 min. (Displacement was produced by shifting direction of gaze of left eye to the left, with a prism.) Duration of each sweep was 4 s. II: A, Left eye, stimulated alone; B, right eye, stimulated alone; C, both eyes, stimulus to left eye shifted 30 min to the right. Projection screen was 1.5 m away from the monkey. With eyes fixed on the screen, maximum response to a long object moved in front of the animal occurred when the object was 0.5 m in front of the screen. For eyes fixed at infinity this would be equivalent to a stimulus about 3 m from the animal.

system of columns containing areas of similar receptive field orientation as is found in area 17 (ref. 6). Sequences of cells with the same receptive field orientation are rather brief, suggesting that the orientation columns are very narrow compared with the depth columns.

We have also studied hundreds of cells in area 17, but have found no convincing examples of binocular depth cells. In this respect the monkey seems to differ from the cat^{1,2}. Possible differences between binocular depth cells in cat area 17 and monkey area 18 are the failure of most depth cells in the monkey to respond to stimulation of

either eye alone, and the linking, in the monkey, of vertical disparity to receptive field orientation.

Area 18 in the monkey seems, therefore, to have at least two independent functions, that of linking the two visual half fields across the vertical midline (as in the cat⁵), and the elaboration of stereoscopic depth mechanisms. The parts of 18 near the vertical meridian representation have both functions, whereas more peripheral areas probably lack the first.

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Stereoscopic Vision in the Macaque Monkey: a Behavioural Demonstration

STEREOPSIS is the sensation of relative visual depth that results from the neural integration of dissimilarities in the images seen by the two eyes. These dissimilarities arise because an object in front of or behind a surface of reference determined by the fixation of the two eyes produces images that fall on non-corresponding points in the two retinas. As a distinct attribute of human vision, stereopsis has been studied extensively for many years¹. Julesz has recently developed random-dot stereoscopic patterns which minimize monocular and familiarity cues to depth perception². Such patterns have enabled the psychophysical basis of human stereopsis to be defined more precisely³⁻⁷. These patterns also seemed to be well suited for the investigation of stereopsis in animals by behavioural methods. In this study, random-dot patterns were combined with standard operant conditioning procedures to determine whether or not macaque monkeys have stereoscopic vision.

The subjects, two young stump-tail monkeys (*Macaca arctoides*), were restrained in a standard primate chair modified for operant conditioning. A flat square response key was mounted in front of the animal below the line of vision. Two overhead projectors cast the visual stimuli onto an aluminium screen 1.6 m away. Sets of oppositely polarized circular polarizers, mounted on the projectors and on goggles worn by the monkey, made it possible to confine stimuli to separate eyes. Because the use of goggles made it necessary to restrain the monkey from touching its face, a liquid reward was delivered through a solenoid valve and a conveniently located water pipe. Automated programming and recording equipment operated the apparatus.

The monkeys were taught to perform visual discriminations on a simple operant schedule involving a random but predetermined sequence of two different stimuli. One of the two stimuli to be discriminated, the "positive" stimulus, was presented for 20 s, during which ten presses of the key was defined as a correct response and fewer presses an incorrect response. The other stimulus of the pair, the "negative" stimulus, was also presented for at least 20 s, during which five or more presses were defined