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Evoked responses to visual patterns in area 17 of the rhesus monkey

The mechanism of production of 'constancy' remains one of the most fundamental unanswered problems in visual psychophysiology: How is it that an object appears invariant when the retinal image of the object can vary in size, orientation and position? This report is one of several[4,5] in which techniques are developed and some initial data are brought to bear on the problem.

In the present study the question was asked whether differences in the patterns of electrical recordings made from aggregates of neurons in the striate cortex of monkeys in any way reflects the differences in the patterns of external luminous cues. To this end, 12 small bipolar macroelectrodes (each made up of two 300 μ nichrome wires held together by a vinyl polymer, their cut ends staggered 3 mm apart) were implanted in each lateral occipital cortex of 7 monkeys. The electrodes were inserted under direct visual guidance so that the longer tips ended in the region of junction between gray and white matter while the shorter tips rested on the cortic. l surface. The columnar organization of the cortex seems to make it preferable to record within a column rather than across columns. All electrodes were found, histologically, to be in or near the projection of the fovea in area 17.

For the purposes of the experiment, a monkey was placed in a restraining chair (with head and eyes free to move) set into a darkened enclosure at one end of which was a translucent screen. During a 'trial' either a circle or vertical stripes, equated for area, were displayed by a modified Kodak Carousel projector on the screen. Each such 'trial' consisted of fifty 0.01 msec duration flashes presented at 1/sec. The monkey had no task to perform and no special effort was made to capture his attention. Most monkeys, bored at being in the dark, welcomed the flashing stimulus and looked at it. When, however, the monkey's head was observed to be turned away from the screen for a prolonged period, or when he was observed to have his eyes closed, the 'trial' was interrupted and begun again later. A record of the electrical activity obtained during a trial from the cortical implants was made after adequate amplification on Ampex FM 1/4 in. tape. A synchronizing pulse was also recorded from the flashing unit on the tape. Four of these recordings were monitored on a computer for average transients (CAT) from which a paper write-out of the 'average' of the potentials evoked was performed by an X–Y plotter.

Visual inspection of these plots showed that 8 out of 84 placements gave records from which one could decide which display pattern (circle or vertical stripes) had been in effect during the 'trial'; no correlation could be found between active sites and their position in area 17.

Once such differential activity had been identified to occur in an electrode, no marked change was observed to take place over trials, or even over days of testing.

In order to determine quantitatively the differences upon which this decision depended, the following system of data analysis was instituted. The activity following each flash over a period of 500 msec was digitized, averaged, and displayed on an oscilloscope by using an appropriately programmed PDP-8 Computer system. A different program was then used which allowed a vertical line to be positioned at each inflection point of the displayed wave pattern; these lines then served as break points for data analysis. The amplitude values of the segment of the wave between two break points were then averaged and stored. By this device the relative amplitudes of comparable segments of different waves could be statistically analyzed. Thus, *e.g.*, the third segments of 6 waveforms obtained under the condition 'circle' could be compared with the third segments of 6 waveforms obtained under the condition 'vertical stripes'.

Fig. 1a shows 3 averaged waveforms evoked by circle; Fig. 1b shows the averaged waveforms evoked by vertical stripes in the same electrode. Fig. 2 shows the activity recorded from another electrode under these two conditions. Visual inspection suggests that the waveforms recorded in Fig. 1 are different from each other and that those in Fig. 2 are not. Statistical analysis confirms this impression. A t-test of the difference of the fourth segment alone shows these amplitudes to be different at the 0.01 % level of confidence. This would seem to indicate that this component is related to units or processes activated by some properties of the striped stimulus. No such differences exist between the amplitudes of the waveforms shown in Fig. 2.

The results obtained demonstrate differences in electrocortical responses evoked by differences in the external stimulus pattern. These differences were obtained from monkeys whose heads and eyes were unrestrained and who were given no obvious fixation point. Thus, the data suggest that such differences can be obtained relatively independently of the retinal locus excited by the stimulus pattern. It would also appear that, while the activity of a great majority of cells is modified by the stimulus, only a small proportion of the units is optimally activated by the non-overlapping characteristics of the stimuli.

These results are in agreement with those obtained in man by Spehlmann[3] and John[1]. The data of the present experiments differ from, and extend, these other ob-

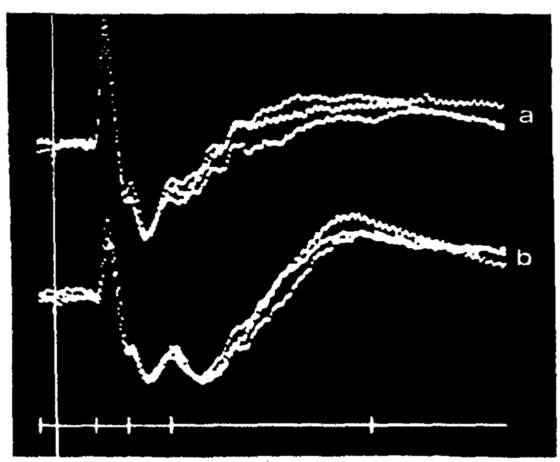

Fig. 1. From top to bottom: (a) three averaged waveforms obtained when the circle was flashed (50 responses each) are shown superimposed; (b) three averaged waveforms, obtained when the stripes were flashed. The vertical marker shows when the stimulus was presented; on the horizontal marker the breakpoints are shown. Statistical analysis shows that the greatest and most significant difference between the two waveforms is in component No. 4, as was also apparent from visual inspection.

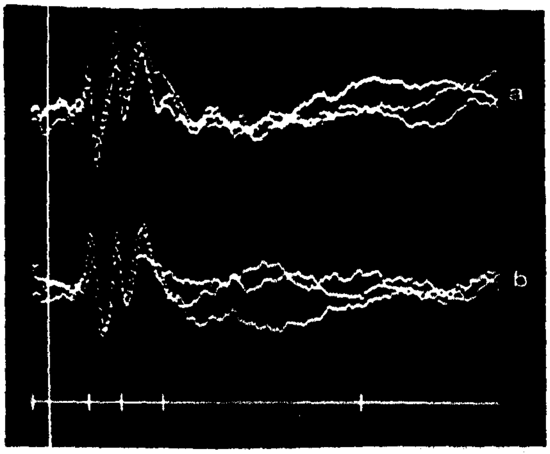

Fig. 2. Same as Fig. 1 but from a different electrode placement. There is no statistical or apparent difference in the waveform components.

servations in one important respect, however. In man, the use of gross scalp recording led to the supposition that the entire occipital cortex showed the differential response to stimulation. The data from the present experiments accomplished with discrete cortical implants show rather that the differential response is restricted to scattered cell aggregates within the striate area. That the great majority of the electrodes should not show any difference is understandable on the basis that it is more likely to place electrodes in a part of the brain that has nothing to do with the situation examined than the reverse. These results suggest that a good deal of processing of visual input has already occurred by the time the recorded activity is generated. This suggestion is further supported by data presented in a separate communication[2].

In summary, bipolar transcortical electrodes implanted in the visual cortex (area 17) of 7 rhesus monkeys were used to record the activity produced by visual patterns flashed on a screen for 0.01 msec once every second. Two patterns consisting of a circle and vertical stripes equated for area and total luminous flux were used. Fifty responses were averaged and the resultant waveforms were broken down into their components. Statistical analysis shows significant differences in some of these components at some discrete cortical sites.

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