VISUAL CORTICAL UNIT RESPONSES TO PHOTIC STIMULATION OF DIFFERENT ZONES OF THE RECEPTIVE FIELDS IN CATS

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In acute experiments on unanesthetized curarized cats the intensity functions, response thresholds, inhibition thresholds, and differential sensitivity of 96 neurons in the primary visual projection cortex were investigated by extracellular recording of unit activity during central and peripheral stimulation of their receptive fields. In darkness the neurons had wide threshold and above-threshold reliefs (3-30°). The threshold reliefs of the receptive fields of some cells were found to be V-shaped, whereas others were marked by alternation of zones of increased and reduced excitability. Sensitivity of both excitatory and inhibitory inputs of the receptive field as a rule was greatest in the center. Inhibitory inputs of different cortical neurons were much more standard and less sensitive to light, and they were mainly activated within the intermediate (mesoptic) range of brightnesses. During light adaptation the threshold contour of the receptive field narrows sharply, mainly because of the fall in sensitivity of its peripheral inputs. Compared with the lateral geniculate body and retina, the relative number of low-threshold elements, sensitivity in the system of inhibitory elements, and differential brightness sensitivity are greater in the cortex. The mechanisms of formation of receptive fields of cortical neurons and their modification during changes in the level of adaptation, and also the role of excitatory and inhibitory inputs of the cell in these effects are discussed.

INTRODUCTION

Dependence of a neuron response of the intensity of the afferent stimulus and, in particular, the threshold sensitivity of the neuron are among the most important characteristics on the basis of which the relative importance of excitatory and inhibitory inputs can be assessed in different parts of the receptive field (RF). Information on the microstructure of visual RF obtained as a result of threshold measurements is not distorted through the effects of scattering of light or an increase in the contrast between stimulus and background, features of particular importance during dark adaptation. Under these conditions the RF become wider and simpler in shape, but the acuity of the detector characteristics of the neurons falls [10, 11, 21, 23].

Thresholds of responses to light, i.e., the light sensitivity of neurons, at different levels of the visual system have been studied previously [3, 7, 8, 22]. However, these measurements were made only during diffuse illumination of the retina, and not during point photic stimulation. The main task of the present investigation was thus to study absolute and differential parts of RF of visual cortical neurons in dark-adapted cats.

EXPERIMENTAL METHOD

Acute experiments were carried out on 26 unanesthetized adult cats immobilized with tubocurarine. The animals were intubated and artificially ventilated; the rectal temperature was maintained at 37-38°C. The fixation points of the head, wound edges, and projection points of the semilunar ganglia were infiltrated with the long-acting local anesthetic Lidocaine.

A platform with detachable mechanical manipulator [4, 15] was fixed to the skull. Through a burr-hole (diameter under 1 mm) the dura was perforated with a pointed tube (diameter about 150 μ), inside which moved a glass microelectrode filled with 2 M NaCl solution (impedance 5-20 MΩ at a frequency of 1 kHz). Activity of single visual cortical units in area 17 was recorded extracellularly within the 150-4000 Hz band. Altogether 96 neurons were tested, more than half of them in detail.
tionally with the aid of neutral filters by 1 million times, i.e., to a relative intensity of -60 dB, if the 60 lx retina was determined. The second eye was covered with an opaque shield. During photopic light adaptation (10 lx on the screen) the center of RF, and the optimal size, orientation, direction, and velocity of movement of the photic stimulus were determined for each neuron. The experiment was then carried out in darkness 10-30 min after switching off the background illumination [25]. Local flashes of a round spot of light 1-2° in diameter, with a duration of 400 or 500 msec and a repetition frequency of 0.5-0.65 Hz were used as stimuli. The intensity of the spot of light on the screen (175 cm from the eye) was 60 lx, and it could be reduced fractionally with the aid of neutral filters by 1 million times, i.e., to a relative intensity of -60 dB, if the 60 lx level was taken to be 0 dB.

Poststimulus (PST) histograms with a bin width of 4 msec and an epoch of analysis of 1024 msec were constructed for 10-20 responses to flashes in the course of the experiment. Using the criterion of the mean number of spikes in a given interval of the PST histogram (200-400 msec) or using the "maximal mean" discharge frequency [7], calculated from the highest column of the PST histogram, a curve of response versus stimulus intensity ("strength curve") was plotted (Fig. 1a). From the projection of the point of intersection of the strength curve with the mean level of spontaneous activity on the abscissa the threshold intensity of light (Iₜ) for generation of a cell response in a given part of RF was determined: For the sake of brevity this will be called the threshold of the neuron. The minimal intensity after which the response was temporarily reduced as the brightness increased was taken to be the threshold level for development of inhibition of the neuron (the "threshold of inhibition" or Iₜ₈). Threshold reliefs of RF for the neuron in darkness and, in some cases, during light adaptation were plotted from measurements of Iₜ and Iₜ₈ in the center and at the periphery of RF.

EXPERIMENTAL RESULTS

The centers of RF for the tested neurons lay in the lower part of the field of vision between 10 and 15° from its center (Fig. 1b). During light adaptation they all had the typical characteristics of cortical RF (see [9, 10]) with well-marked detector properties. A feature of all cells tested during dark adaptation conditions was that the magnitude of the response and the frequency of the discharges were directly proportional to intensity (Figs. 1a and 2a-c). However, different neurons had a different threshold level, gradient, and range of their strength curve as well as a different degree of inhibitory disturbance of their steady course in the middle part of the range of intensities (Figs. 1a, 2c).

The distribution of all the tested neurons by threshold in the center of RF during dark adaptation was very wide: monomodally over more than 60 dB (Fig. 5a, 1). The essential point was that considerable differences in light sensitivity of the neurons were found within the same experiment, often in consecutive recordings. The maximum of the distribution in Fig. 5a, 1 falls at a relative intensity of -35 dB, but the maximum of the distribution of thresholds of the same cells at the periphery of their RF (Fig. 5a, 2) is shifted to -25 dB, i.e., by 10 dB toward the high-threshold region. Light sensitivity was thus ten times higher on average in the center of RF than at its periphery. The results of a more detailed analysis (Fig. 4a) also showed that thresholds in the center of RF for the majority of tested neurons were lower than at its periphery (points in the bottom right sector); this was particularly noticeable for the nearer periphery of RF, within 5° of the center (1). Differences in sensitivity of the center and the measurable part of the near periphery of RF for individual neurons amounted to 40-50 dB. As regards the more distant periphery of RF (Fig. 4c, 2) in more than two-thirds of cases studied the ratio of its threshold to the threshold at the center was the same as for the nearer periphery, but in one-third of the cases the far periphery of RF was more sensitive to light than the central zone (points in the top left sector).

Thresholds in the center of RF correlated negatively with their eccentricity, i.e., their distance from the center of fixation (Fig. 4a): As RF moved away from the center of the field of vision the mean thresholds of the neuron fell sharply. For instance, thresholds of cells with RF located near the center varied from -1 to -55 dB, whereas if the eccentricity of RF was 10°, they varied for different cells from -38 to -60 dB.

As already stated, the strength curves often (in 62% of cases in the center of RF and in 70% of cases at the periphery) rose unevenly because of the intervention of inhibition, delaying (Fig. 2a, b) or modifying this function in a certain part of the strength range (Figs. 1a and 2c). Thresholds of inhibition (Iₜ₈), measured from the beginning of this effect on the intensity scale (Fig. 1a) characterized the light sensitivity of the inhibitory