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Functional Synaptic Organization of Primary Visual Cortex Neurones in the Cat*

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Summary. The spontaneous and light evoked post-synaptic activity of cells of the primary visual cortex was investigated with intracellular and quasi-intracellular records. The resting membrane potential fluctuated mostly between 3—10 mV below the firing threshold owing to spontaneous EPSP- and IPSP-activity. Discharge activity was therefore low. Forms and amplitudes of the visible EPSP's showed a large variability, the frequency was 150—300/sec. Discrete IPSP's were between 0.5—3 mV and were less frequent than EPSP's (about 1:10). Their duration was only slightly longer than that of EPSP's. EPSP's and IPSP's could be elicited at on or off by appropriately positioned small light stimuli. During the initial reaction following a stimulus, single PSP's could be distinguished. Geniculate on-center- as well as off-center-afferents could lead to excitation or inhibition in different neurones. The receptive fields of cortical cells to monocular stimulation were analysed with averaged records. In each neurone 2—4 overlapping areas of on- or off-activation or -inhibition could be distinguished. Each of these activation or inhibition zones had the functional properties of a single geniculo-cortical on- or off-center fibre with their receptive field centers separated by 1—3°. The variety of functional organizations of the cortical neurones to monocular stimulation was explained by variable combinations of 2—4 converging geniculate on- or off-center fibres with either excitatory or inhibitory action and variable overlap of their receptive fields. This was tested in a simple computer model. — Most neurones with pronounced reactions to movement or with direction specific movement sensitivity (about half of the neurones investigated) had an excitatory contact with an off-center fibre, which seemed to be mainly responsible for the movement reaction. — The findings suggest that from each eye less than 5 geniculo-cortical afferent converging fibres have a major effect on the activity of one cortical cell. Inhibitory afferents may be indirect and relayed through another cortical pyramidal cell.

Key Words: Visual cortex — Intracellular recording — Receptive fields — Computer simulation

Introduction

Since the first recordings of unit activity in the visual cortex by Jung et al. (1952), a number of important contributions have been made to the functional organization

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of this area (BAUMGARTNER and HAKAS 1962; HUBEL and WIESEL 1962—1965; BURNS et al. 1962; JUNG 1961). These studies were restricted to extracellular records of unit activity and considered therefore only the "output" of visual cortex neurones under different stimulus conditions. Changes in the discharge rate served as criteria for activation, inhibition, on- or off-reaction. Schematizing models of the synaptic organization, i.e. the input into the cortical cells were developed mainly from the receptive field properties as derived indirectly from the discharge response to light shone into different parts of the neurones receptive field.

In the following paper an attempt is made to get more direct information on the synaptic input into visual cortex neurones by intracellular recording. Such an approach was complicated by the difficulty of getting long lasting satisfactory intracellular records of visual cortex neurones as pointed out by WATANABE et al. (1966). A few satisfactory intracellular records were obtained by FUSTER et al. (1965) in the visual cortex of rabbits, but in that study only diffuse light stimuli were used.

In part I, some characteristics of the spontaneous and light evoked post-synaptic potential will be shown. The analysis of this post-synaptic activity suggested that the visible PSP-activity was due to the afferent activity of only a few afferent fibres. In part II, the receptive fields of visual cortex neurones will be analysed. The functional organization of primary visual cortex neurones was in agreement with the conclusions of part I, i.e. the convergence of only a few specific afferent fibres with excitatory or inhibitory action on one cortical cell. Correspondingly, the reactions of cortical neurones could be simulated by a simple computer model.

Methods

The experiments were done on adult cats (operation in ether anesthesia; local anesthesia of operation wounds and pressure points; Flaxedil and arteficial respiration with CO_2-control during the recording; temperature control). The skull was removed over the visual areas of both sides and the dura over one side such that the posterior part of the lateral gyrus was exposed. Most recordings were done between 1 and 4 mm lateral from the midline and between 1 mm anterior and 4 mm posterior of the Horsley-Clark zero-ordinate. This includes area 17 and a strip of area 19 according to the histological classification of OTSUKA and HASSLER (1962).

Recording: Glass-micropipettes filled with 1.5 mol-potassium-citrate and a resistance between 25 and 60 MΩ were used. The electrode was connected to the amplifying and recording systems through a cathode follower (type Tönnies or Bak). During the experiment, the activity was recorded on tape and analysed after the experiment. A distinction between fibre and cell activity was not difficult because of the resting potential and the post-synaptic potentials. The injury activity during the impalement or at the end of the recording when the electrode was moved on, served as a further criterion for cells.

Spike histograms and slow potential averages were done with a CAT 1000. Averages of 10 consecutive stimuli at a time basis of 1000 and sometimes 2000 msec were used. They gave a clear picture of the post-synaptic slow potential changes. Occasional spikes may displace a few addresses of the CAT-average, but the baseline was still recognizable. A discrimination between polarizations due to lack of excitation or active inhibition could be done in connection with the original records.

Since the spontaneous discharge rate (HERZ et al. 1964) and the response patterns of cortical cells (HUBEL and WIESEL 1962) differ markedly from that of geniculate cells, it was mostly easy to discriminate between afferent and efferent subcortical fibre activity. The mapping of a few *geniculate fibres* below the cortical recording tract was a regular routine in order to get an idea of the distribution of the receptive field centers projecting into the cortical volume from which the cellular recordings were taken and to check the visual acuity.

Visual Stimulation: The animal was put in a Horsley-Clark frame which was arranged in such a way that the visual field was not affected by the fixation. In most experiments the exact position of the eye was tested with an ophthalmoscope and the projection of the optic disc on the screen was marked. The pupils were dilated with synephrine and/or atropine, the eyes covered with contact lenses of 0 or +1.5 dptr. Each eye could be illuminated separately. The animal faced a white tangent screen which was positioned 1 m from the eye. This screen was diffusely illuminated with about 3 Lux, and white light stimuli of different size, shape and intensity were projected onto it. Most stimulations were done with 30—50 Lux. At the end of each stimulation series one or two stimuli from the beginning of the series were repeated in order to check whether the eye had moved during a longer investigation (RODIECK et al. 1967). No marked displacements could be discovered.

Results

Part I: Post-Synaptic Potentials of Visual Cortex Cells

1. Recording of Cellular Activity

67 cortical cells and 31 geniculo-cortical fibres were fully investigated and recorded. About $^1/_3$ of the records were intracellular with resting potentials of 60—70 mV, spike potentials above 60 mV and spike durations below 1 msec. About $^2/_3$ of the records were of the "quasi-intracellular" type as defined by MCILWAIN and CREUTZFELDT (1967). These records were characterized by a DC-potential of 35—50 mV, by post-synaptic potentials between 1 and 5 mV and spike-potentials of 25—40 mV. Intracellular stimulation produced activation when the electrode tip was positive and inhibition if the tip was negative. The action potentials were monophasic positive and of short duration (1—3 msec), EPSP's were also positive, IPSP's negative. The apparent discharge threshold may change during a longer record by a few mV, but was as a rule stable over long recording periods (up to 2 h). — At the end of each record the electrode was moved 20—50 μ away from the recorded cell and the focal slow potential was checked in order to avoid contamination with field potentials of a larger cell population. It was found that extracellular field and cellular potentials differed by a factor of 10—100 in amplitude (see Fig. 14, stimulus 3e). Furthermore, the field potentials had "receptive field" properties like focal evoked potentials, i.e. always symmetrical in contrast to the mostly asymmetrical fields of cortical cells.

2. Spontaneous Post-Synaptic Activity of Visual Cortex Cells

The spontaneous post-synaptic activity of neurones in the visual cortex of non-anesthetized cats was characterized by irregular spike discharges at frequencies below 5/sec. The discharges may have appeared in short clusters consisting of 2—3 discharges separated by only a few msec. Only injured cells had higher spontaneous discharge rates. In good intracellular as well as in quasi-intracellular records single EPSP's and IPSP's could be distinguished. Prominent single EPSP's may have reached amplitudes of up to 3 mV, the smallest were below 0.5 mV. The larger EPSP's had durations between 8—15 msec, the smaller ones (below 1 mV) were always shorter than 5 msec. The rising times of EPSP's were between 1 and 5 msec, the decay times between 5 and 10 msec. Some of the larger EPSP's had rising times below 1 msec, while most of the medium and small EPSP's had almost symmetrical rising and decay times. The average rate of EPSP's was between 150 and 300/sec in different neurones during the resting state.

IPSP's were identified by the polarity and the time course (fast polarization of 2—5 msec and slower redepolarization time, see Fig. 1). Because of the continuous EPSP-activity superimposed, slow and smooth complete redepolarizations were practically never seen and the exact duration of IPSP's (as that of EPSP's for the same reasons) could not be determined, but durations between 5 and 10 msec maybe considered a realistic estimate. Short clusters of several IPSP's were occasionally

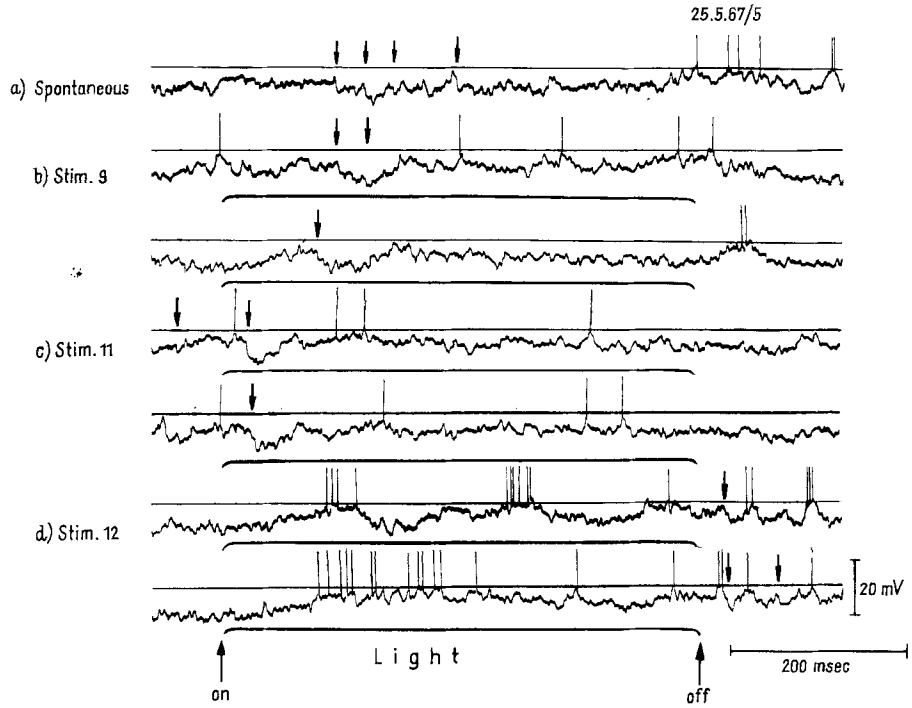

Fig. 1. *Intracellular record from a visual cortex neurone.* MP about 60 mV, AP 60 mV (not fully shown). Same neurone as Fig. 12 and 13. a: Spontaneous activity. b—d: Two examples of different stimuli according to the map of Fig. 12. This neurone showed many IPSP's (some of them indicated by arrow). Strong inhibitory on-response at stimulus 11, subthreshold initial on-activation at stimulus 9 followed by series of IPSP's. Slowly rising, "mixed" on-response at stimulus 12

observed leading to larger negative deflections of the membrane potential for 20—40 msec (see Fig. 1a). The amplitude of single IPSP's were between 0.5 and 3 mV. The number of identifiable spontaneous IPSP's was $^1/_{10}$ or less of that of EPSP's. Some cells showed more spontaneous IPSP's than others.

The membrane fluctutations due to this continuous bombardement with EPSP's and IPSP's were between 3 and 10 mV below the threshold potential.

3. Post-Synaptic Reactions Elicited by Light Stimuli

Spots of light shone into appropriate parts of the receptive field of a neurone produced a variety of responses. "Pure" initial reactions to light "on" or "off" consisted of a series of EPSP's (Fig. 2b, 6a) or IPSP's (Fig. 1c, 3, 6a). The latencies

of these initial responses were between 30 and 40 msec, the frequencies of EPSP's between 80—200/sec, those of IPSP's between 50 and 150/sec and the peak of temporal summation was reached after 20—100 msec. These values depended on the stimulus position within the receptive field, the size and the intensity of the stimulus. The summation time of EPSP's to reach the firing threshold, i.e. the input-output delay, varied between 15 and 60 msec accordingly, giving spike latencies of 35—100 msec. Secondary activations or inhibitions had latencies of about 100

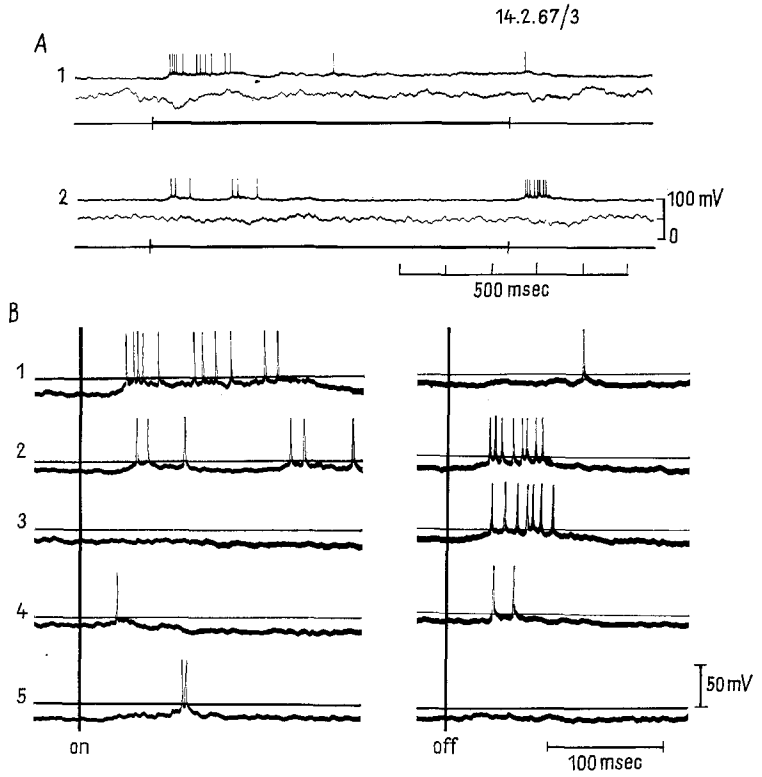

Fig. 2. *Intracellular recording from a visual cortex cell.* Same cell as in Fig. 10B, the numbers before each line refer to the stimulus map in Fig. 10B. MP 60 mV. A: Two examples of continuous recording. B: Magnification of the on- and off-responses. Note the small steady state depolarization in the continuous record of A, which is well recognized in the averaged record (Fig. 10B 1 and 2). Single, summating EPSP's can be recognized when the on-activation is small (B 5), but not if the depolarization is fast (B 2 on, off; B 3 off)

msec (Fig. 1a and b). The frequencies, latencies and durations of the initial PSP-responses corresponded to those of geniculo-cortical fibre activations under the same stimulus conditions (see Fig. 4).

The IPSP-responses did not necessarily lead into a hyperpolarization but often only reset the membrane-potential to the pre-stimulus level (Fig. 3 off). Some extremely slow depolarizing responses at light on suggested a mixed response, i.e. simultaneous activation of IPSP's and EPSP's or maybe even decrease of inhibition, i.e. disinhibition (Fig. 3 on).

The initial response was followed by a steady state de- or hyperpolarization which was often only recognizable in averaged records. A short secondary reaction of opposite polarity was often observed between the initial and steady state response. — It was practically impossible to trace one identified EPSP or IPSP throughout the initial as well as the steady state response. In the different cells and with appropriate stimulus location practically all combinations of initial on-excitation or -inhibition with off-excitation or -inhibition were seen in this study. The short latencies and the frequencies of the initial PSP's after light on or off can only be explained by the assumption, that geniculate on- and off-center units were able to produce EPSP's and IPSP's in the different cells. This does not preclude the possibility of intracortical relays for IPSP's (see discussion).

Input-Output Relation: The sometimes long input-output delays (15—60 msec) of cortical neurones due to long summation times or mixed initial excitatory and inhibitory reactions were already mentioned. The spike reactions of the cortical cells were generally low, except for the first 100—150 msec. Firing frequencies up to 100/sec were rarely seen during the steady state of an optimally located stimulus, they were mostly not above 20—30/sec. Initial discharge frequencies were generally not above 50 and 150/sec, but could sometimes reach up to 350/sec for 2 or 3 subsequent discharges.

The spike response did not only depend on the intensity of the PSP-response but also on changes of the spontaneous post-synaptic activity which sometimes may have been considerable and thus have given the false impression of a high response variability. Small excitatory reactions below or near threshold or inhibitions against a low spontaneous spike activity could often not be made visible with post-stimulus histograms, which only gave a vague impression of the actual subthreshold excitatory or inhibitory response. This could be made visible only with averaged analogue records.

Discussion of Part I

It is assumed that all the recordings used for this investigation were from pyramidal cells of the visual cortex, although a proof for this statement is lacking. The variety of forms and amplitudes of cortical PSP's must be related to several different mechanisms: dendritic location of the synapses at different distances from the soma; differences in the spatial dispersion and distribution of the synapses from the activated afferent fibres; different sizes of synapses. The factor of temporal dispersion of the miniature PSP's originating from single branches of one afferent fibre probably plays a more significant role for the PSP-shapes of cortical pyramidal cells than for that of motoneurones (BURKE 1967) because of the longitudinal extension of their apical dendrite and the climbing arrangement of afferent fibre contacts (COLONNIER 1966; GLOBUS and SCHEIBEL 1967; SZENTÁGOTHAI 1967).

The variable size and even form of single PSP's make it difficult to recognize the PSP's related to the same afferent fibre throughout a long record. The continuously varying membrane potential due to the convergence of several fibres on one neurone provides a variable driving potential and local interactions of PSP's originating in close vicinity must also be taken into account (RALL 1967).

In spite of this variability of shapes and amplitudes the frequency of PSP's allows a rough estimate of the number of afferent fibres causing the visible PSP's,

if the average firing frequency of the afferent fibres is known: The spontaneous frequency of EPSP's per second in our records was roughly between 150 and 300/sec, that of geniculate fibre discharges is around 15/sec and that of cortical neurones below 5/sec (HERZ et al. 1964 and this paper). If one would assume a purely geniculate input being responsible for the visible EPSP's 10—20 fibres, and in the case of purely intracortical input 30—50 intracortical fibres leading to visible EPSP's would be a maximal estimate. The relation between number of EPSP's and number of IPSP's appearing spontaneously was about 10:1. The order of magnitude of fibres leading to visible PSP's would then be between 10 and 100 per cell. The estimate is higher than the number of specific afferents derived from the receptive field analysis in the second part of this paper. As crude as these estimates necessarily are, the difference may indicate additional synapses with non-primary fibres.

The estimated number of synaptic contacts of cortical neurones is thus 1—3 orders of magnitude below the number of synapses known from histology, especially if it is realized that the spines do not represent all synapses. This divergence is partially explained by multiple synaptic contacts of each afferent fibre on each cortical pyramidal cell. Besides the "principal" input (mainly from specific afferents) leading to the visible PSP's, many more fibres may have synaptic contacts on smaller dendritic branches or only one or a few synapses per fibre. Their PSP's would only lead to small potential changes in the soma, which cannot be distinguished with an intrasomatic electrode. They may, however, have a considerable "modulating" effect on the subsynaptic membranes of the "principal" synapses.

The duration of the single IPSP's was between around 5—10 msec and their amplitude of the same range as that of single EPSP's. As one of the main criteria to identify IPSP's in this study was their sharp rise time, the question whether also IPSP's with slow rise times due to a distant dendritic localization might exist, cannot be answered. The findings differ from earlier statements on cortical IPSP's to have a principally long duration (time constant of decay around 70 msec), large amplitude (5—10 mV) and low driving frequency (up to around 10/sec) (see reviews by ECCLES 1964 and CREUTZFELDT et al. 1966). Such conclusions were derived from large IPSP's elicited by electrical stimulation of afferent pathways or the cortex itself, which resulted in synchronous activation of a large number of inhibitory pathways leading to a compound IPSP. But the present observations show, that IPSP's due to the discharge of a single fibre also appear as discrete potentials, principally not different from EPSP's except their polarity. This does not exclude a slightly longer conductivity change during IPSP's than during most EPSP's, which actually is suggested by the often long duration of the summated IPSP's elicited by a light stimulus (Fig. 3).

The longer latency of IPSP's after electrical stimulation of the afferent optic pathways had suggested an intracortical delay for IPSP's (WATANABE et al. 1966). In the present experiments the maximal frequencies of spontaneous IPSP's were lower than those of EPSP's, but after light stimuli IPSP-frequencies identical to the frequency of one geniculo-cortical fibre under comparable stimulus conditions were seen. An intracortical relay of IPSP's through inhibitory interneurones or other pyramidal cells and their recurrent collaterals is conceivable, but cannot be proved from these data.

The initial PSP-reactions of cortical cells show the typical characteristics of temporal summation. Due to the high "resting" membrane potential (5—10 mV above the firing threshold) and the relatively little effect of one single EPSP, a con-

siderable summation is needed in order to fire a cortical cell. This also explains the "sluggish" spike responses of cortical cells so well known to investigators in this field. The input-output relation between one excitatory afferent fibre and a cortical

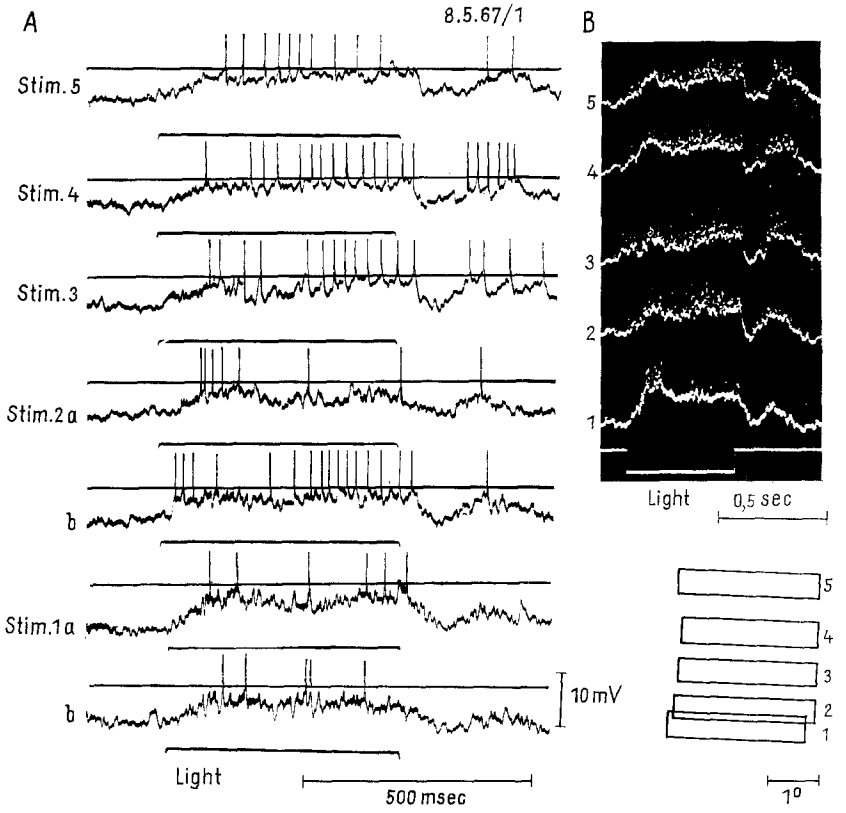

Fig. 3. *Intracellular record of a visual cortex neurone.* MP about 55 mV, AP about 55 mV (not fully shown). A: Original, B: averaged records (10 stimuli each). Stimulus map. Note "mixed" on response with slow depolarization. Inhibition at off with series of IPSP's, which do not lead to a "hyperpolarization" but only reset the MP (see averaged record). This repolarization is slower, if only few IPSP's are elicited (compare stimulus 2a and b). Spike discharges only slightly distort the averaged analogue record

cell can be described by a multiplicative transfer function with a factor between > 0 and < 1. This factor is variable within these limits due to the activity of other afferent fibres and is therefore only of academic interest.

Part II: Organization of Receptive Fields of Visual Cortex Neurones

The receptive fields of cortical neurones were analysed with spots of light shone into different parts of their receptive fields. Also lines were used for a fast screening of the receptive field and to find optimal stimulus conditions (HUBEL and WIESEL 1962). The intracellular responses recorded will be analysed and described in terms of excitatory or inhibitory input from single afferent geniculo-cortical on- and off-

center fibres (or their intracortical relays, see discussion). For this, some functional properties of geniculo-cortical on-center and off-center fibres will be remembered (s. HUBEL 1960; BAUMGARTNER and HAKAS 1962; RODIECK and STONE 1965).

1. The Afferent Input into the Cortex

The distribution of field centers of geniculate fibres entering a minute cortical area were distributed within 2—3° around the "field centers" of the cortical cells recorded from the same electrode tract. The receptive fields of the subcortically recorded geniculate fibres were extremely uniform, the diameters of field centers were between 0.5 and 3° (as determined with moving stimuli). Typical post-stimulus histograms of an off- (A) and an on-center fibre (B) at stimuli in different parts of the receptive field are shown in Fig. 4. The thin lines represent the actual stimu-

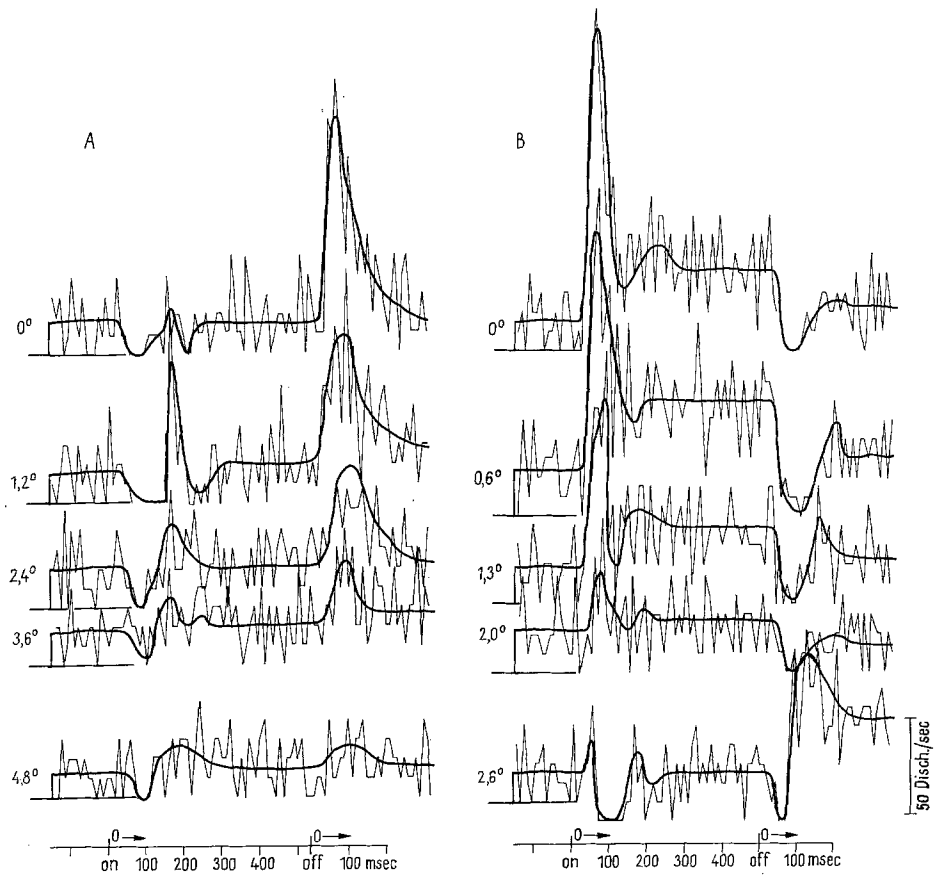

Fig. 4. *Post-stimulus histograms of a geniculo-cortical off-center (A) and on-center fibre (B).* Both fibres were recorded subcortically and their centers were in the central visual field. The stimuli (0.5° diameter) were placed at different distances from the field center (0°) as indicated. The *thin lines* are the averaged post-stimulus histograms from 10 stimuli each, the *thick lines* represent the calculated mean values of the prestimulus and steady state activity, the transient changes are smoothed out by hand. The bottom line at the beginning of each stimulus histogram represents zero, the single measurements are integrated discharge averages over 10 msec (see calibration)

lus histograms averaged over 10 stimuli, while the thick lines are smoothed curves drawn by hand. For simplicity the adaptation during the "steady state" was

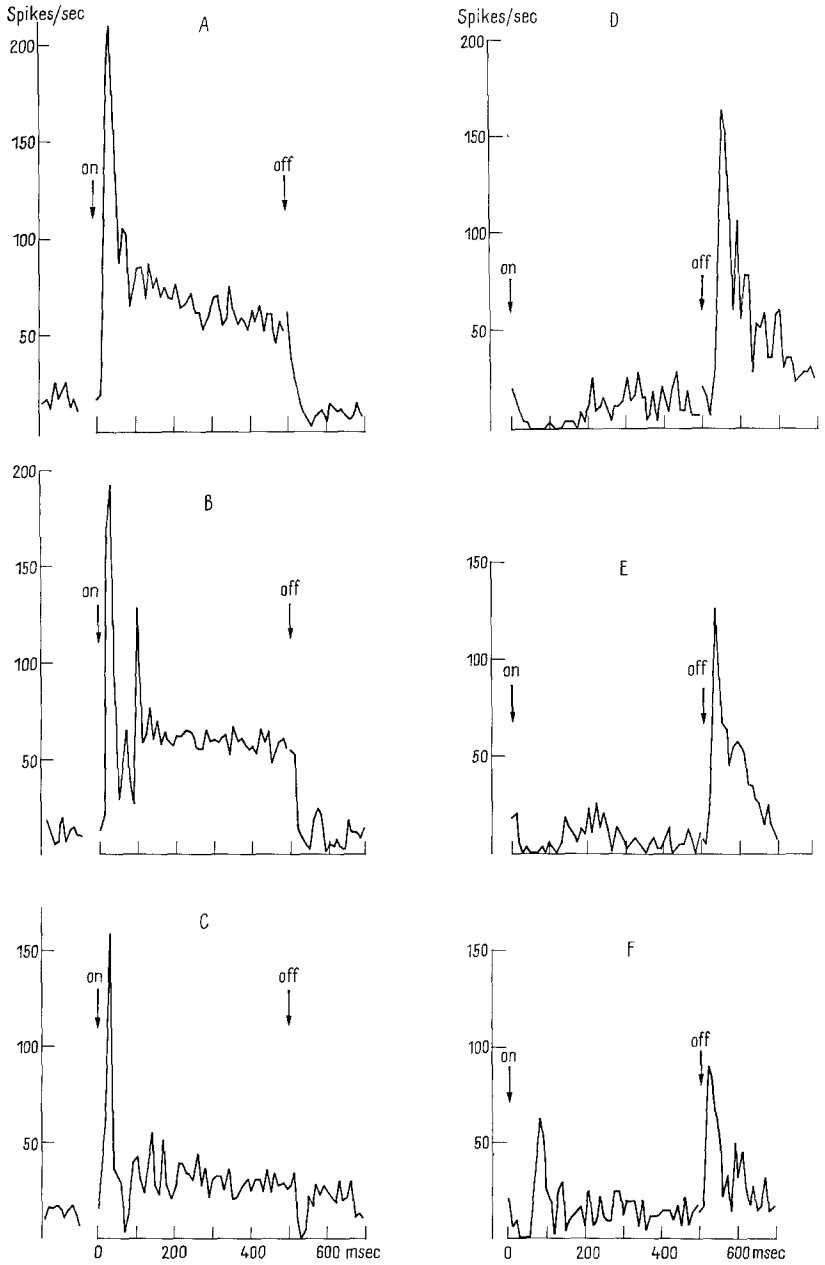

Fig. 5. *Averaged post-stimulus histograms of 6 on-center (A—C) and 4 off-center fibres (D—F) to stimuli of increasing diameter.* All fibres are from the central visual field and recorded subcortically. Stimulus diameter in A/D: 0.7—1.2° (according to the size of the individual field center). B/E: 3.5—4.5°, C/F: 11—14°. Post-stimulus histograms of the individual neurones were done like those in Fig. 6

omitted, and a horizontal line was drawn through the average of the steady state activity. The values of the thick lines were used for the computer simulations (see below). Some features of the PSTH's may be especially noted: The latency of the initial reaction after light on or off (inhibition or excitation respectively) does not change significantly with the stimulus localization, and only the intensity and duration diminishes with increasing distance from the receptive field center. Correspondingly the secondary reactions become stronger and appear earlier with increasing eccentricity, but the latency of the dominant periphery effect is always 20—30 msec longer than that of the primary center effect. Similar observations were mentioned for optic tract fibres by RODIECK and STONE (1965). Confirming earlier studies, no substantial asymmetries of the receptive fields of subcortically recorded geniculate receptive fields were seen. The effects of light bands crossing the field center were independent on the stimulus direction. It may be mentioned however, that light bands of 4—5° length and 0.3—0.5° width produced always stronger reactions than points of 0.5—1.0° diameter shone into the field center, and that the apparent center diameter becomes smaller if tested with lines instead of points. This is due to the simultaneous illumination of center and surround areas, if the line cuts the peripheral parts of the center.

Round spots of light of increasing diameter were investigated in order to get a rough idea of the effect of illumination of large receptive field areas (Fig. 5). Starting with a 0.5° spot, the primary on-reaction (activation in on-center neurones, inhibition in off-center neurones) increased with increasing stimulus diameters until the whole center was covered by the spot. At the same time the secondary effects (inhibition or excitation respectively) became stronger. But only if the stimulus was large enough to cover also the periphery of the receptive field, the secondary on-effect became strong enough to reduce the primary reaction and the steady state discharge significantly. Also at light off, the secondary reaction increased with increasing stimulus diameter. There was some variability of the effect of whole field illumination, but a complete suppression of the center reaction by large stimuli was not seen under the stimulus conditions, which were identical to those which were used for the cortical neurones. The minor reaction of cortical cells to diffuse light stimuli is therefore partly explained by the decrease of geniculate output as suggested by HUBEL (1963), but the apparent unreactiveness of many cortical cells to diffuse light must be sought in the functional organization of the cortical cells themselves.

2. Receptive Fields of Cortical Neurones

The cortical receptive fields described below are selected from 49 sufficiently explored cells. Excitations or inhibitions were related to the input activity of excitatory or inhibitory on- or off-center fibres if the latencies and receptive field characteristics corresponded to that of geniculate on- or off-center fibres. With this knowledge of the functional parameters of geniculate fibres in mind, it was mostly easy to decide whether a certain effect elicited by a spot of light was due to a center stimulation of an on-center fibre or a surround excitation of an off-center fibre or vice versa. As shown in part I, on- as well as off-center fibre activity may lead to EPSP's or IPSP's, and an on-activation at one stimulus does not necessarily imply active off-inhibition following the same stimulus or vice versa. In the following

description of the effects of localized light stimuli the words on-activation, on-inhibition, off-activation and off-inhibition will be used without implying a reverse effect of "off" or "on" respectively. — Furthermore, an excitatory or inhibitory

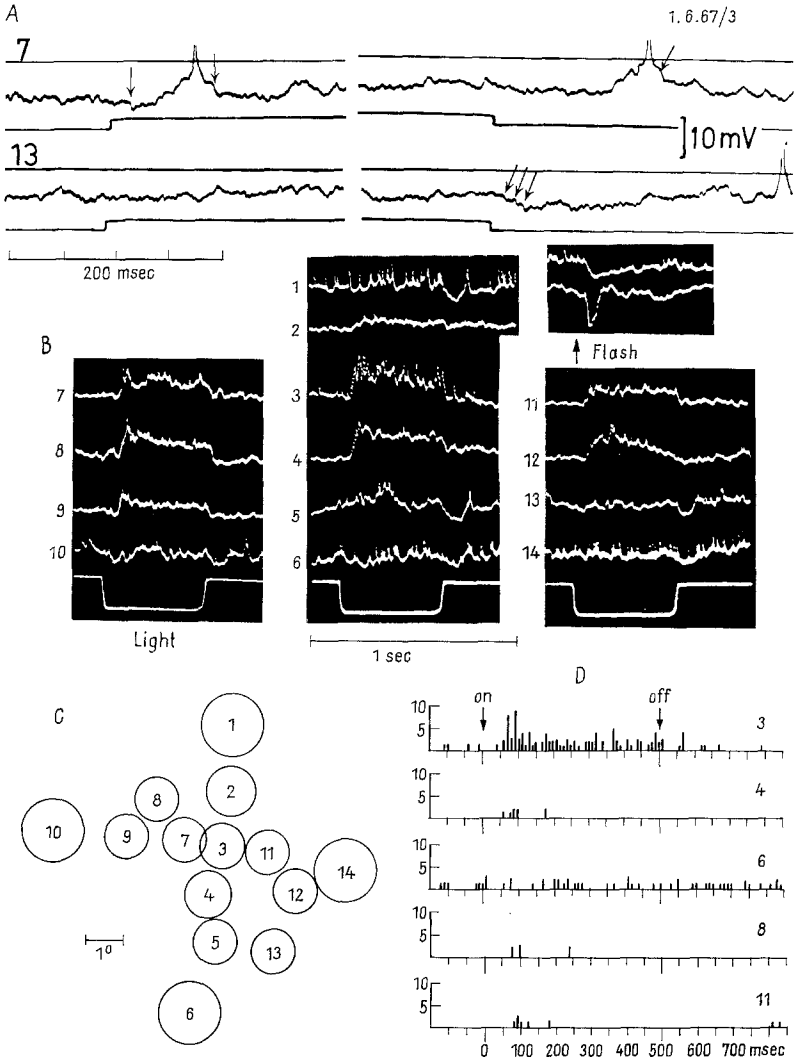

Fig. 6. *Receptive field analysis of a visual cortex neurone.* MP ca. 50 mV, broad action potential due to injury, amplitude 45 mV, constant firing level. A: Original records of reactions to stimulus 7 and 13. 200 msec cut out during the illumination period. Note the summating EPSP's after light on of stimulus 7, followed by some IPSP's and the early IPSP after on. After stimulus 13 off, a series of IPSP's is seen. Some of the IPSP's marked by arrow. B: Averaged analogue records of 10 responses each (CAT 1000, time basis 1 sec). The numbers correspond to the stimulus map in C. Upper right: Reaction to short electronic flash illuminating the screen diffusely (upper record cell, lower record EEG). D: Selection of some poststimulus histograms (see numbers). — The lines below the records in A and B are photocell recordings (light on: upward swing in A, downward in B). In D "on" and "off" are marked above the histograms, zero on the abscissa coincides with light on

area of a cortical neurone will be attributed to the activity of only one geniculate on- or off-center fibre, if its size and form as well as its functional organization (i.e. maximal effect in the geometrical center of one area) corresponds to that of a geniculate fibre. As there is mostly an overlap of such geniculate fibre fields, the additive effect of the two overlapping field compartments must be taken into account. It is thus possible, to explain the main characteristics of most cortical receptive field organizations shown in the following examples in terms of afferent activity from individual geniculate fibres. Further arguments in support of these interpretations of the observed effects are given in the discussion, where also the limitations of such an interpretation will be discussed. — The examples of cortical neurones explained in the following pages are put in an order of increasing complexity in the sense of increasingly complicated overlaps of several inputs.

The neurone of Fig. 6 mainly has one clearly defined on-activation area. — The original records in A are from stimulus 7 and 13. Stimulus 7 led to a series of EPSP's with a latency of 40 msec and an initial frequency of 120/sec leading to one spike (this was abnormally broad due to injury). This excitation was preceded by one single IPSP (latency 25 msec, arrow) resulting in a slight polarization in the averaged response (B). The excitation was followed by a few IPSP's which produced also a slight polarization in the average. A steady state depolarization was hardly recognizable in the original, but appeared well in the average. Stimulus 13 only led to a series of IPSP's at off (arrows), which had a frequency of 90/sec and produced a slight polarization in the average (latency 25 msec, duration 50—70 msec). Post-synaptic depolarization was produced by stimuli 3, 4, 7, 8, 9, 11 and 12, i.e. an area of about 3° in diameter. But a longer lasting suprathreshold reaction was elicited only by stimulus 3 (see histograms in D). Simultaneous stimulation of two points only resulted in a slightly stronger depolarization, which never reached the sum of the depolarizations (or spike discharges) produced by the two stimuli given alone. A bright electronic flash, on the other hand, led to a powerful inhibition (upper right record in B), masking the excitation.

The excitatory area of this neurone together with the initial frequency of the EPSP's elicited from this area suggests the conclusion that only one excitatory on-center fibre with its receptive field center near stimulus 3 was responsible for this excitation. The early appearance of the off-inhibition, which was strongest in 13 and 5, suggested a weak, maybe relayed inhibitory connection with one off-center fibre with its center near 5/13. The early inhibition which preceded the excitation mainly in stimuli 3, 7, 8, 9 and 10, suggests a weak inhibitory connection with another on-center fibre with its field center in about the same area.

The functional properties of other such neurones were relatively uniform and corresponded in principal to the circular fields described in some cortical neurones by BAUMGARTNER et al. (1965). The size of the excitatory centers were between 1° and 4°, inhibitory areas were often asymmetrical and always difficult to demonstrate with small spots of light. Light bands were not especially effective and moving stimuli produced only slightly stronger reactions, when the stimulus passed through the excitatory center. In our total sample we only found one neurone with an inhibitory center. This was extremely small (0.5° in diameter) and surrounded by a larger excitatory area.

Other neurones showed stronger inhibitory flanks, either on one or on both sides of the excitatory area. Fig. 7 shows an example of an almost bilateral symmetrical field: an excitatory on-center flanked by two fields with on-inhibition of short latency (20—25 msec). An off-inhibition of variable intensity was seen follow-

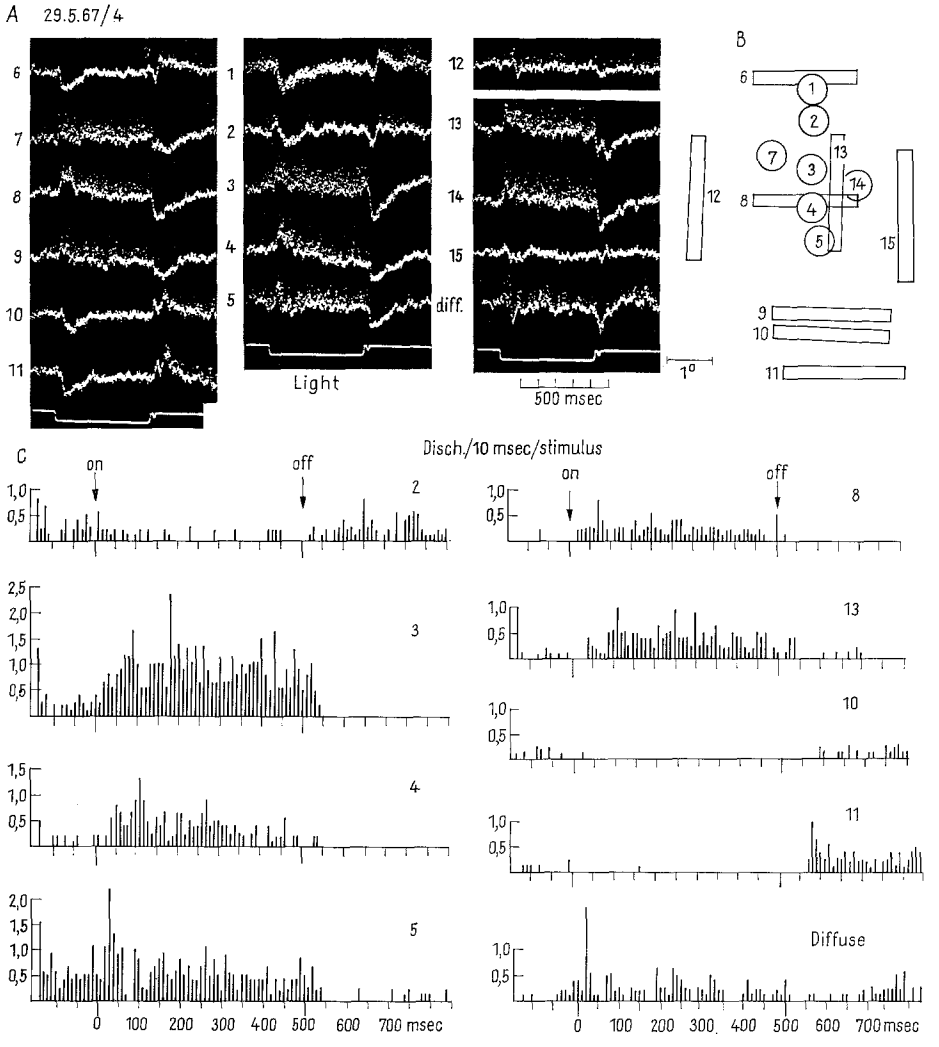

Fig. 7. *Receptive field analysis of a visual cortex neurone.* A: Averaged responses, B: Stimulus map, C: Selected post-stimulus histograms. Slight distortion of analogue baseline by spikes. (Compare simulation of this neurone in Fig. 15.) "diff.": Diffuse light stimulus

ing center stimuli (3, 4, 5). No inhibition could be induced by illumination of the two other flanks (12, 15). Short light bands in the center area produced slightly weaker reactions than the optimal point, but without striking directional preferences (13, 8). Only long light bands extending into the inhibitory areas showed certain directional preferences according to whether they covered the inhibitory

area or not. Moving stimuli were slightly but not strikingly more effective. A diffuse light stimulus ("diff." in Fig. 7A and B) led to a fairly strong but short initial excitation, followed by a sharp inhibition and a weak steady state activation, i.e. the expected result of simultaneous activation of the different afferents by a diffuse light stimulus. This field could be explained by an arrangement of affe-

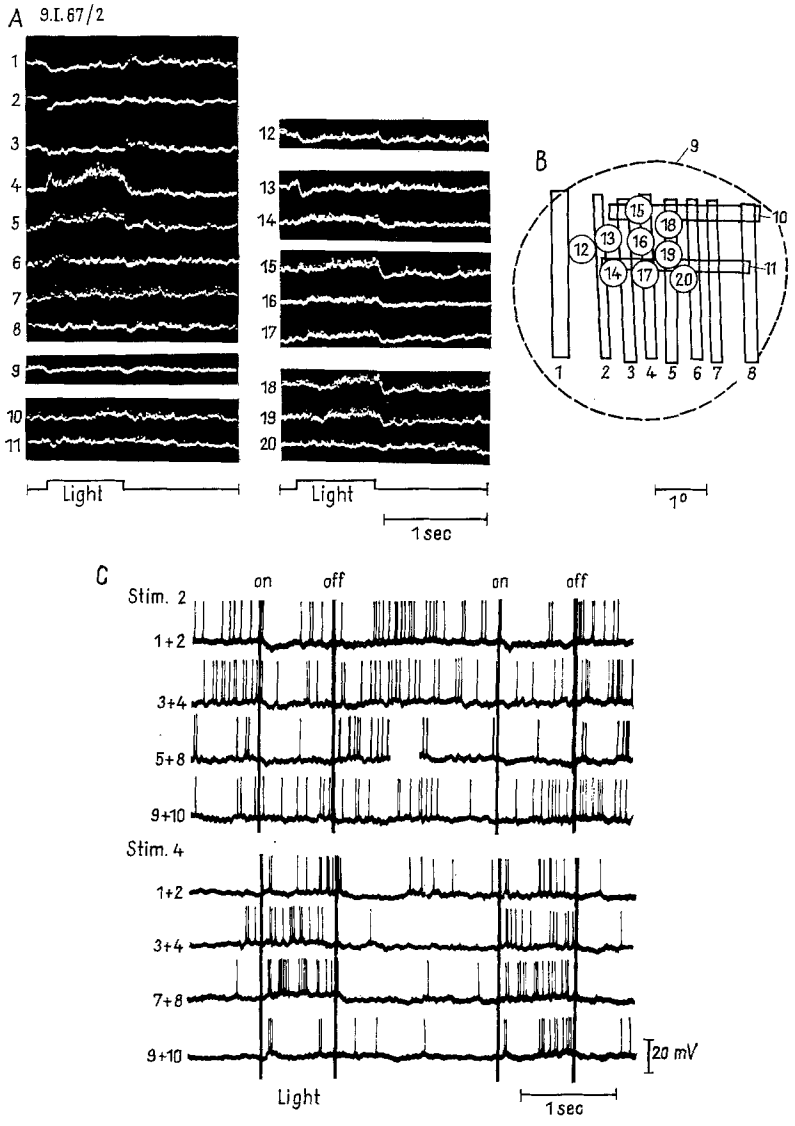

Fig. 8. *Averaged (A) and some original responses (C) of a visual cortex neurone.* Quasi-intracellular recording (DC-potential about 30 mV, AP 20 mV). Strong discharge reaction interrupted by secondary inhibition at stimulus 4 and 3. The original records of stimulus 4 (maximal excitation) and stimulus 2 show a slight adaptation to subsequent stimuli (numbers at left of records indicate sequential numbers of stimuli). Note the high variation of spontaneous spike activity. Explanation of receptive field see text

rent inputs assuming an excitatory on-center fibre with its center in 3, an inhibitory on-center neurone above 6 and one in 11 (see simulation in Fig. 15).

Figure 8 shows a neurone with an excitatory area and essentially only one inhibitory flank. The on-excitatory area was located around stimulus 15/16 (see also stimulus 4), the on-inhibitory area directly besides it (stimulus 12/13 and 1, 2, 3). In this neurone, light bands (stimulus 4 and 5) had a much stronger effect suggesting the convergence of at least two excitatory fibres lying closely together (near 15 and 17). Correspondingly, the direction of the light band was critical within an inclination of 10—20°. No summation in the inhibitory area could be shown. — A diffuse light stimulus (9) only led to a somewhat mitigated inhibition at on and off. The neurone was not especially movement sensitive. — The original records in Fig. 8C show the effect of the light stimuli on the spike discharges with a slight adaptation after a number of stimuli and varying "signal-noise" ratio according to the variable spontaneous activity. The record is "quasi-intracellular".

The principal properties of this receptive field suggests the convergence of two excitatory on-center fibres with centers along stimulus 4, and an inhibitory on-center input with its center near 13.

The main features of the neurone of Fig. 9 are an excitatory and an inhibitory on-area lying side by side. It reacted maximally to a black bar just below field 8. The exploration with spots of light showed a "powerful" inhibitory zone with its center at 2 and an excitatory zone with a center at 3. In addition, a weaker excitatory reaction at light on could be shown above the inhibitory area (1), which had a long latency and slow time course. The initial summation of inhibitory and excitatory influence at 3 resulted in a slower and steadily increasing excitation instead of the characteristic phasic-tonic reaction of geniculate fibres. Stimulation in 8 also led to an initial "mixed" response but with a stronger inhibition resulting in a slowly increasing polarization after the first brisk onset. The off-responses after the different stimuli can be understood as surround effects of the inhibitory (off-inhibition at 3) and the excitatory (off-excitation in 2) inputs. Simultaneous stimulation of both, the maximal on-excitatory and on-inhibitory zone (10+2) showed a dominating effect of the inhibitory area. Diffuse light had the same effect. Spatial summation within the excitatory zone did not go beyond that which could be attributed to the behavior of a geniculate on-center fibre (stimulus 4, 3, 10, 15; see also Fig. 5). Moving a white or black bar or spot between areas 8 and 10 had a strong effect on the discharge activity with a reversed directional effect of the black and white bands.

The receptive field of this neurone suggests the convergence of one excitatory on-center fibre with its field center in or just above 3 and one inhibitory on-center input with its center in 2. The slight and late on-excitation elicited by 1 could either be a weak late on-reaction due to surround stimulation of the on-center afference in 3 (see also Fig. 4), but might also suggest an additional, weak on-center input (possibly after a cortical relay).

The neurones described so far, did not show a specifically sensitive reaction to moving stimuli. But 22 out of the 45 neurones investigated with moving stimuli showed a marked *movement sensitivity* in one part of their receptive field. In most of them a preference or even exclusivity for one direction could be demonstrated. The movement sensitivity was principally the same for dark or light objects, and

the reaction could be elicited with small moving disks or with lines of a given inclination. We did not regularly search for the stimulus form which produced the maximal movement response. It was remarkable that in 18 out of the 22 movement

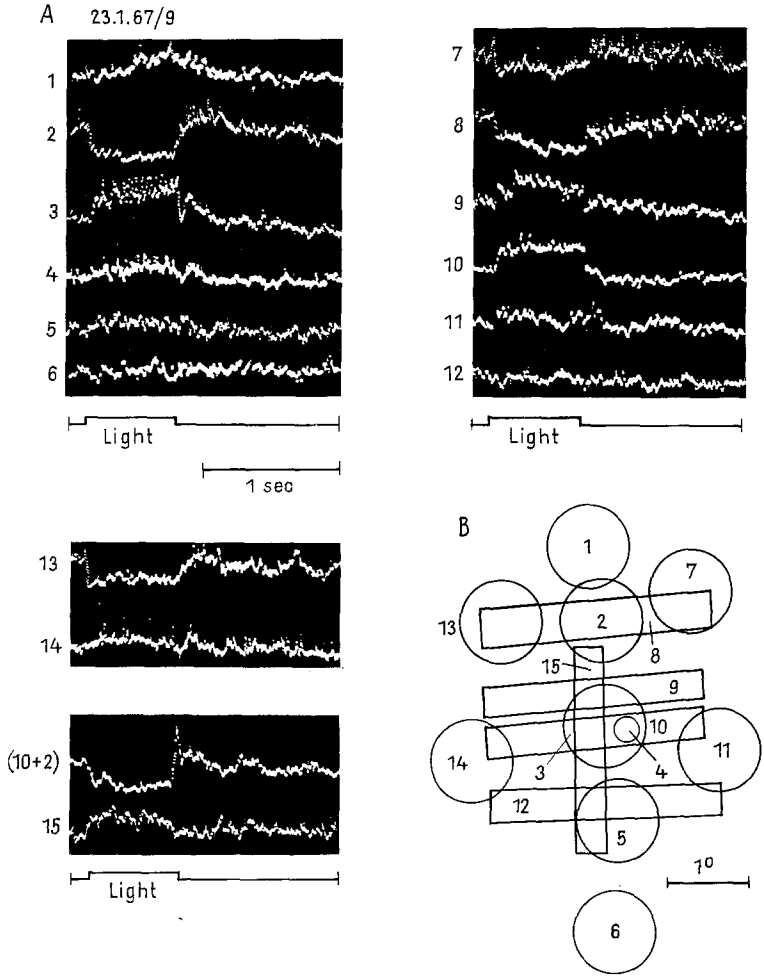

Fig. 9. *Receptive field analysis of a neurone in the visual cortex.* A: Averaged responses (CAT 1000, time base 2 sec). B: Stimulus map. Most effective stimulus was a black bar in location 8 (not shown). Further explanation see text

sensitive neurones an off-excitation area could be identified which coincided with the movement sensitive area. "Powerful" inhibitory areas were also only rarely seen in these neurones.

In Fig. 10 two neurones are shown, which illustrate this arrangement in spite of the somewhat uncomplete exploration with stationary stimuli. The neurone of Fig. 10 A is from the same experiment and penetration, only a few 100 μ away from that of Fig. 8. With stationary stimuli an off-activation area reaching from stimulus 2—5 and with its center above 9 was found. It had the same location as the on-excitation field of the neurone in Fig. 8. Stimulus 2 produced a slight polarization

at "on" without inhibitory potentials in the original record. It is thus due to lack of excitation (inhibition of the excitatory off-center fibre). Stimulus 6 and 7 led to a slight, phasic on-activation. This neurone was strongly excited by a moving stimulus (point or bar) between stimulus 2 and 7 (arrow). A movement from 7 to 2 or rectangular to this only produced a small increase of firing. The contrast (black or white moving stimulus) did not reverse this directional sensitivity, but the area of maximal movement sensitivity was further to the right for the light and further to the left for the dark band.

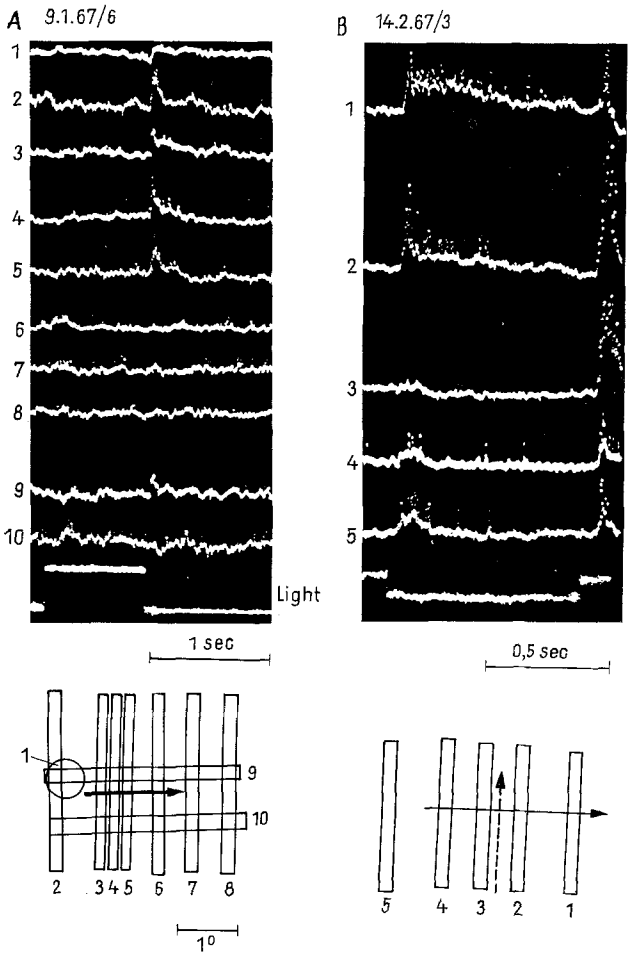

Fig. 10. *Receptive field properties of two movement sensitive neurones with direction preference.* A: Neurone from same experiment and same tract as neurone in Fig. 8. Note strong off-excitation after stimuli 2—5, on-inhibition at stimulus 2 and slight on-activation at stimulus 6. The arrow in the stimulus map indicates the area of movement sensitivity to a white bar and the most effective direction. Movement in the other direction had no effect. — B: Same neurone as Fig. 2. The slight negative dip at stimulus 3 "on" is not due to active inhibition (see Fig. 2). The continuous arrow indicates the direction of maximal movement response, movement in the direction of the interrupted arrow leads to less powerful excitation. The two other directions were uneffective

The reactions to stationary stimuli suggest for this neurone the connection with one excitatory off-center fibre (receptive field center between stimulus 2 and 3) and a less powerful connection with an excitatory on-center near stimulus 6. A light stimulus moving out of the activating off-center into the on-activation area as well as a dark stimulus moving through the off-center area would have a strong excitatory effect.

Figure 10 B shows a similar receptive field with stronger on-excitation. The central off-excitation area (stimulus 3) was flanked by two on-excitatory areas (stimulus 4/5 and 1/2, of which one (1/2) was more powerful than the other. Since no clear on-inhibition could be shown in the original records (see Fig. 2), the on-polarization at stimulus 3 must be explained by a decrease of excitation (inhibition of the excitatory off-center fibre). — Also this neurone showed a directional preference to black or white bars or dots moving in the area and direction indicated by the continuous arrow. An upwards moving stimulus in area 2—4 (dotted arrow) had a less pronounced excitatory effect while movements in the other directions did not produce a supra-threshold response. Diffuse light resulted in an on-off-activation.

The reactions of this neurone suggest the convergence of one excitatory on-center fibre (center near stimulus 1), one excitatory off-center fibre (center near 2),

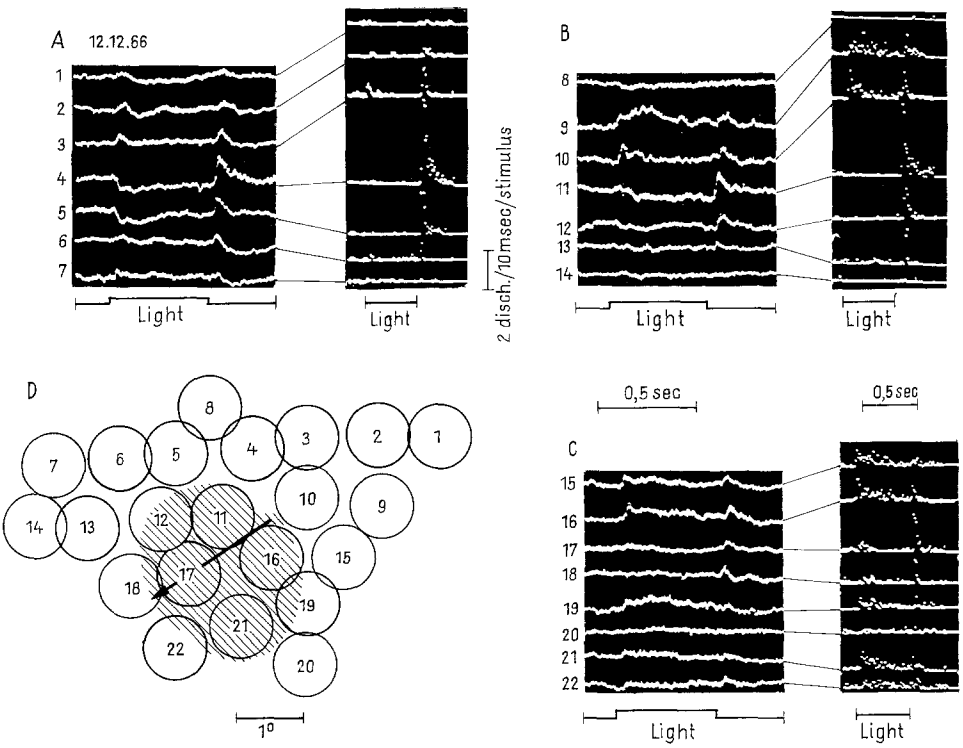

Fig. 11. *Mapping of the receptive field of a movement sensitive neurone.* A—C: Analogue records (left columns) and post-stimulus histograms (right columns). D: Stimulus map. Movement within the shaded area and in the indicated direction (arrow) elicited a strong excitation. Compare simulation in Fig. 16

and one excitatory on-center fibre (center near 5) with a less powerful connection. The on-activation (depolarization) at stimulus 5 consisted in the original record (Fig. 2B, 5) of a series of EPSP's with a rate of 120/sec, which corresponds to the initial frequency of a geniculate fibre.

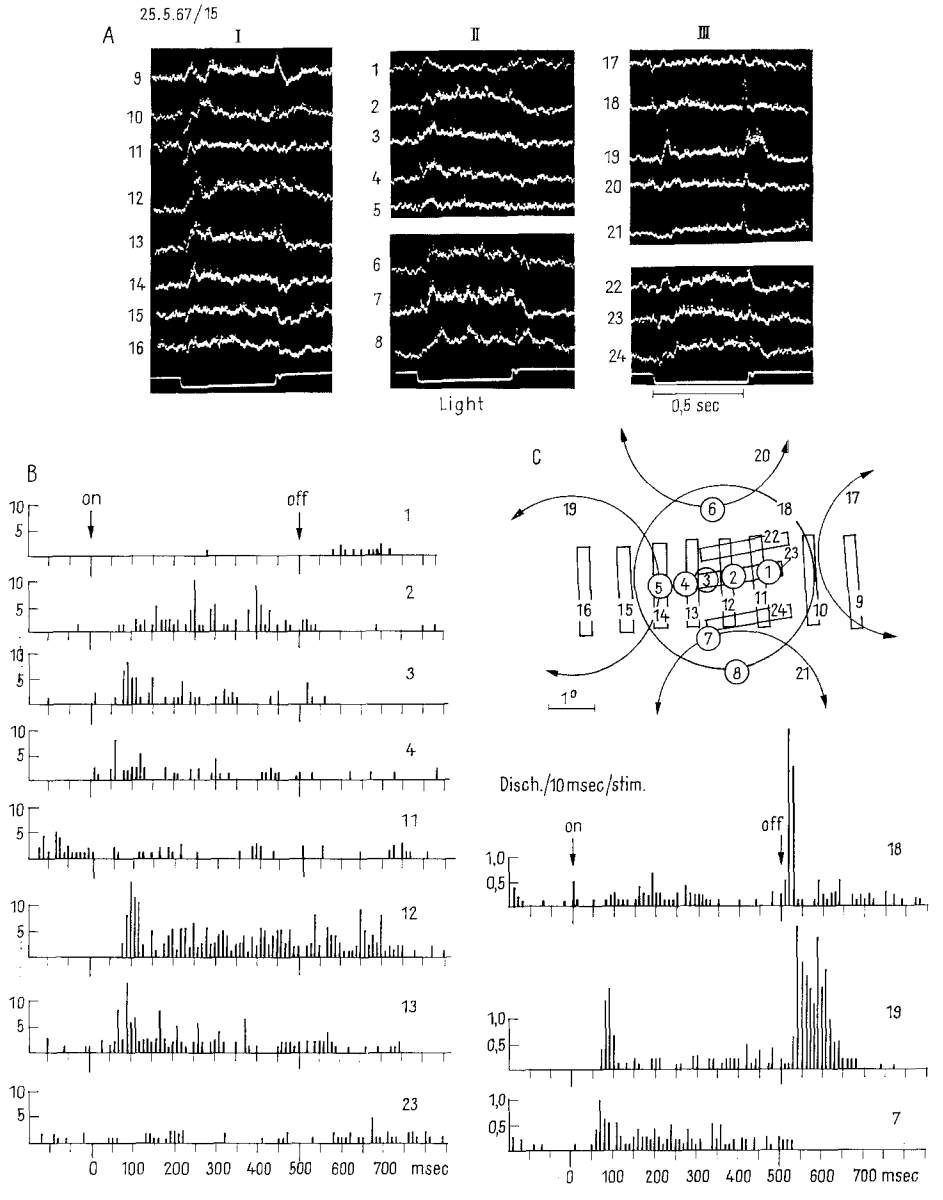

Fig. 12. *Receptive field of a movement sensitive neurone with directional preference.* Same neurone as Fig. 1 and 13. A: Analogue averaged records, B: Post-stimulus histograms, C: Stimulus map (the large round stimuli 17, 19, 20, 21 are not fully drawn). This neurone showed a strong and long lasting reaction to stimuli moving between 11 and 14 from right to left, while in the reverse direction only short discharge bursts were elicited (see Fig. 13)

The neurone of Fig. 11 was also highly sensitive to an object moving in the direction and area indicated. The analysis with stationary stimuli showed three main input characteristics: one area with a strong on-inhibition having its maximum near stimulus 4 and 5 and extending to 11/12 and 8, one with on-excitation (center at about 9) and one with off-excitation (center in 11 and extending over a relatively wide area: 4, 5, 10, 11, 12, 16, 17, 18). Accordingly, a convergence of three afferent inputs can be assumed: an excitatory on-center fibre with its center in about 10, one inhibitory on-center neurone with its center in 4 and one excitatory off-center fibre with its center in about 11. A computer simulation of the behavior of this neurone based on these assumptions will be shown below (Fig. 16).

In some neurones a powerful on-inhibitory zone was responsible for the directionality effect of a moving stimulus. In the neurone of Fig. 12 (see original records of some stimuli in Fig. 1), the excitatory responses were maximal to stimuli 12, 13, 6 and 7. Inhibitory on-responses were elicited from areas 10 and 11, and a less powerful excitatory on-response, interrupted by a strong secondary inhibition from area 9. Large stimuli given to the center of the receptive field (stimulus 18) and in the periphery (19, 20, 21) produced a short initial on-inhibition followed by a slight or no increase in firing rate during the stimulus, but a strong off-excitation. This was interrupted by a subsequent off-inhibition in stimuli 18, 20 and 21, but

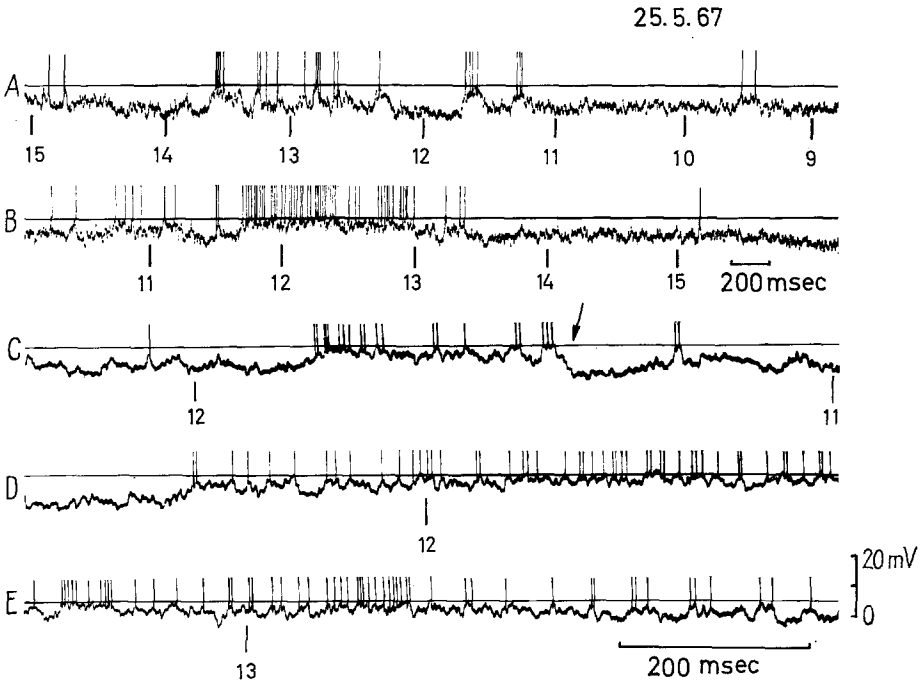

Fig. 13. *Original records of the movement reactions of the neurone of Fig. 12.* A thin line (0.3°) was moved between stimuli 9—16 according to the map of Fig. 12. The numbers below the records indicate approximately the location through which the stimulus passed. A and C: Movement from left to right, B and D/E: movement from right to left. Slow record in A and B, fast record in C—E, but different movements. D—E: Continuous record. Note series of IPSP's in C (arrow) interrupting the response

not in 19. Stimulus 17 only resulted in a short on-inhibition. Diffuse light had about the same effect as stimulus 18. — This receptive field could be explained and simulated in spite of its complexity by the convergence of two excitatory on-center fibres (centers between 12 and 13), an inhibitory on-center fibre (center between 10 and 11), and an excitatory off-center fibre (center roughly at the lower left of the stimulus map).

The reaction to a moving spot or band of light showed a strong directional preference for stimuli moving from right to left (Fig. 13a, d—e). A stimulus moving in the reverse direction only produced a minor spike reaction when moving through

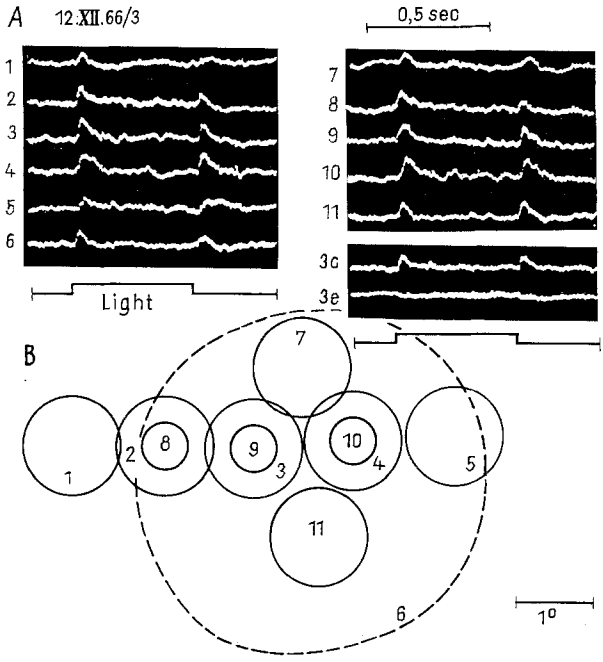

Fig. 14. *Neurone with on-off-excitation from all parts of its receptive field.* Quasi-intracellular record, only little spike activity and occasional single spike reaction to on or off. Stimulus 3 was the first in the series, record 3c was taken about 20 min after 3, and 3e after movement of the electrode by about 50 μ from the cell. Note slight decrease of the amplitude of the reaction in 3c, mainly due to slight injury to the cell. The extracellular field potential (3e) is much smaller than the cellular potential and of reversed amplitude

the excitatory field (13), but a barrage of IPSP's interrupted this excitation when the stimulus entered the inhibitory area between 11 and 12 (Fig. 13, a and c).

The receptive fields of the cortical neurones shown so far had thus all in common: 1—3 principal areas whose illumination produced an activation or inhibition at on or off. The centers of these areas were separated by 1—3°. The sizes of the different areas were of the same order as those of individual geniculo-cortical fibres and overlapped. The total receptive fields of cortical neurones as determined by the post-synaptic polarization or depolarization were therefore all above 4—5°. If only the output of the cells (spike discharges) would be used for determination of the receptive field, smaller fields resulted.

A few cells were recorded which only showed phasic, but identical, either polarizing or depolarizing reactions to light on *and* off. The receptive fields of these neurones were uniform and large (3—6°) and only slight quantitative differences could be found between different parts of the field (CREUTZFELDT and ITO 1967). Figure 14 shows one example of a neurone with a phasic on-off-excitation. The extracellular record (3e) shows that the recorded reaction was not due to a field potential. The input into such cells was difficult to analyse. The spontaneous and light induced discharge frequency was low. They were mainly found in superficial parts (50—200 μ) of the cortex.

3. Computer Simulation of the Functional Organization of Cortical Neurones

In order to test the interpretation made throughout the foregoing section of cortical receptive fields in terms of afferent excitatory or inhibitory inputs from only a few geniculate fibres a simple computer simulation was done. Smoothed post-stimulus histograms of geniculo-cortical on-center and off-center fibres like those in Fig. 4. were stored in an IBM 1130. The histograms were collected during the cortical mapping experiments using 0.5° spots of light, under identical stimulus conditions as for the cortical neurones. The activity was integrated over periods of 10 msec. The points in the map were separated by 0.5 or 1°, but any intermediate point down to steps of 0.1° distances could be interpolated. The field centers could be located on any point within an area of $10 \times 10°$ and the histogram maps of up to 15 neurones could be placed within that area. The fibre discharges

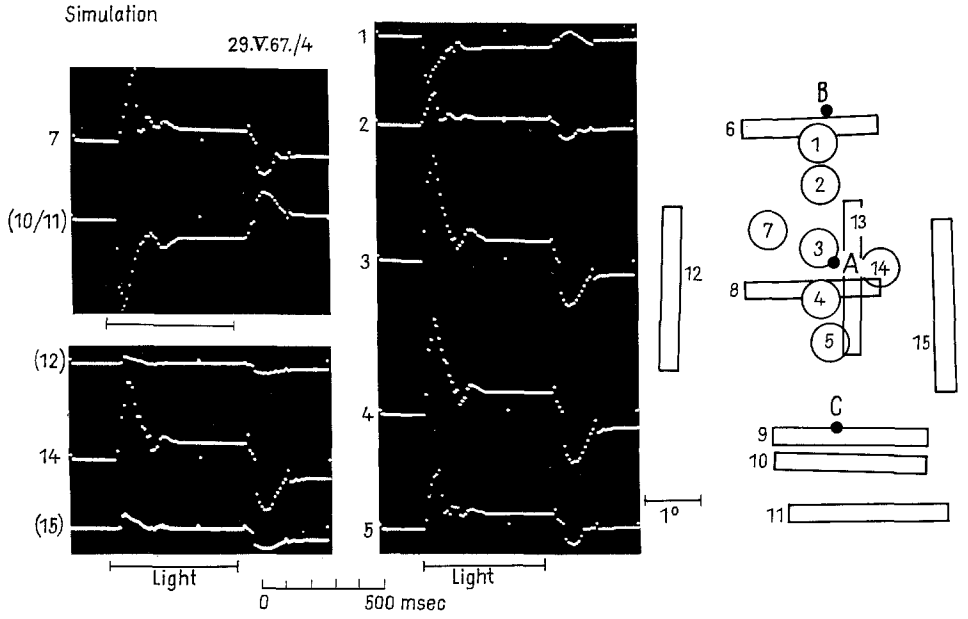

Fig. 15. *Simulation of the neurone of Fig. 7.* In the map are shown the receptive field centers of the assumed afferents. A: on-center fibre with excitatory effect (factor 1.0). B and C: on-center fibres with slightly mitigated inhibitory effect (factor —0.8). Line stimuli could not be simulated, instead points of 0.5° diameter were given into the middle of the line locations (stimulus numbers in brackets). Further explanations see text

could either produce excitatory responses (EPSP) or inhibitory responses (IPSP) by giving it a positive or negative weighting factor between 0.1 and 1.0 ("power"). Once the input fibres with their excitatory or inhibitory "power" were located in the receptive area, the parameters were fixed throughout the "Experiment". "Stimuli" of 0.5 diameter could be placed anywhere within the $10° \cdot 10°$-receptive area and the response of the cell was the sum of spike discharges converging from different input fibres, following the formula:

$$MP = \sum_{i=1}^{n} w_i \cdot d_i$$

(MP = the resulting "membrane potential"; w = weighting factor, which was positive to simulate EPSP's and negative for IPSP's; d = number of discharges per 10 msec).

It is clear that this model contains a number of simplifications: identical size of field centers of geniculate neurones; identical duration and integration times of

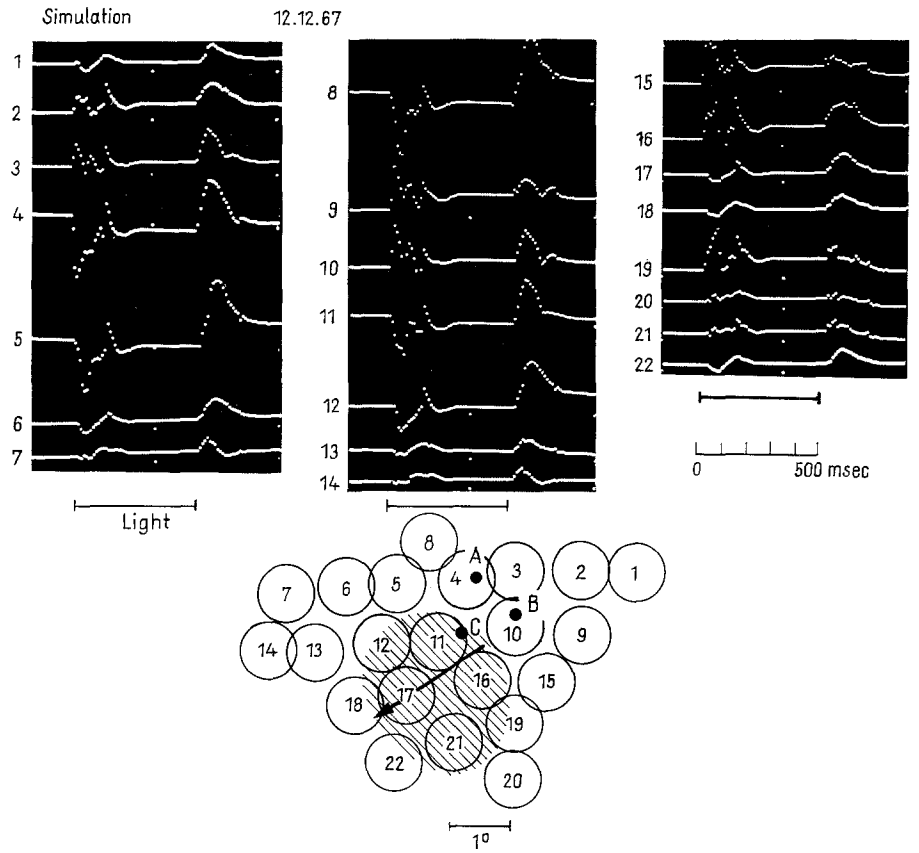

Fig. 16. *Computer simulation of the neurone of Fig. 11.* The receptive field centers of the assumed geniculo-cortical afferents are drawn into the stimulus map. A: geniculate on-center fibre with an inhibitory effect (factor —1.0), B: on-center fibre with excitatory effect (factor +1.0), C: off-center fibre with excitatory effect (factor —1.0). Movement could not be simulated. Further explanations see text

PSP's; no interaction between PSP's. Furthermore, the maximal depolarization of the cell was not limited by the firing threshold as in a real neurone. Therefore, some of the simulated depolarizing reactions were more similar to the post-stimulus spike histograms of the cells than to the analogue records. But in spite of these limitations the model was suited to test quickly and in a semi-quantitative manner the assumption of simple temporal summation of direct inputs from geniculate fibres, made throughout the analysis of receptive fields in section II.

Figure 15 shows the simulation of the neurone of Fig. 7 assuming a convergence of one excitatory (A) and two inhibitory on-center fibres (B and C) with the location of their receptive field center as shown in the stimulus map. Since only the reactions of geniculate fibres to points of light were available in the program, line stimuli could not be tested, so that stimuli 10, 11, 12 and 15 had to be simulated by points which were located in the middle of the lines. The reactions of the model only differ in minor quantitative aspects from those of the original records: initial excitatory on-responses were slightly exaggerated and the reaction to stimulus 3 and 4 differed slightly from each other in the original records but not in the model.

Figure 16 shows a simulation of the neurone of Fig. 11. Here, the original analysis had suggested inhibitory input from one on-center fibre (A), excitatory input from another on-center fibre (B) and excitatory input from an off-center fibre (C). The reactions of the model correspond well to that of the original, especially to the post-stimulus histograms. Only stimulus 8 was different. During the real experiment, this stimulus was the last of the series after the neurone was injured and almost unreactive. It is therefore most probable, that the reaction in the original record only gave a qualitative impression, while the simulated response was more realistic.

In such a way the main response characteristics of all neurones investigated could be simulated by using only 2—4 input fibres. In most cases, it was necessary to reduce the inhibitory inputs by giving them a factor between —0.5 to —1.0 and the areas of the simulated inhibitory inputs may have differed slightly from the originals. The initial excitatory responses of on- or off-center neurones at light on or off were often relatively higher than those of the averaged responses. This was, as mentioned above, mainly due to the unlimited "depolarization" of the model.

Discussion of Part II

Most of the receptive fields described in this analysis may be called "simple" according to the definition of HUBEL and WIESEL (1962), although some cells also had "complex" properties. But we want to avoid a definite classification in this paper since it is known, that often a long exploration is necessary in order to make a definite decision. This time was mostly not available. The essential functional properties of the fields of these neurones could be explained satisfactorily by the convergence of only a few (2—4) afferent fibres. The variety of forms of receptive fields resulted from the variable combinations of on- and off-center fibres with either excitatory or inhibitory action on the cell and by the variable localization of the field centers of the converging fibres in relation to each other (1—3°). The arrangement of overlapping fields of the converging fibres makes it geometrically easy to understand, that bars of light in a certain position may often be the optimal stimuli.

The conclusion that single fibres and not pools of neurones produced the circumscribed inhibitory or excitatory post-synaptic reactions, is based on 1) the field properties of the different effects and 2) the frequency of the summating EPSP's or IPSP's at light on or off (see page 328). The results of the computer simulation further supported this conclusion, and certain quantitative differences between the original and the simulated records in some neurones were due to the limitations of the model mentioned on p. 347. Unfortunately, neither the field analysis nor the simulation experiments answer clearly to the question, whether the inhibitory input is direct or relayed through other cortical neurones. The difficulty to simulate some inhibitory fields may suggest an intracortical relay, but the frequency of initial IPSP's seen in some neurones also leaves the possibility that they originated from geniculo-cortical fibres. Considering the long input-output latency of cortical neurones (see p. 328) and the mostly weak, phasic spike response to non-optimal stimuli, a marked synaptic input from intracortical relay cells should be characterized by these characteristics. It is remarkable that we hardly ever saw marked post-synaptic effects which unequivocally suggested the origin from another cortical cell. This might indicate, that such effects were too small to be recognized with our analysis.

An estimate of the number of specific geniculo-cortical fibres, which produce a major effect on the post-synaptic membrane of cortical cells would come to a figure of 2—4 from one eye. Since we only investigated the input from the "dominant" eye, it is not sure whether about the same number of geniculate fibres comes from each eye. Assuming this to be the case, the total number of specific afferents converging on one cortical neurone would be still between 5 and below 10. The physiological action, functional significance and organization of the many thousands of non-specific synapses (including transcallosal, intracortical and thalamic) per cell has yet to be analysed. Until now, only the mass action of such inputs after electrical stimulation has been demonstrated.

The lack of systematic organization of cortical cells (in contrast to LGN or retinal cells) and the relatively low number of afferent convergence may lead to some speculations on the "Bauplan" of thalamo-cortical connections. The variety of combinations of afferent convergence suggests a random composition of afferents on each cell. If one assumes, that the number of afferent fibres per cell would be limited during the development, a cortical pyramidal cell would only "accept" a few afferents, which would then establish a large number of synapses on that cell without leaving space for other competing fibres.

The higher sensitivity of cortical neurones to moving stimuli (BURNS et al. 1962) and the preference of about half of the neurones to movements in certain directions (HUBEL and WIESEL 1962; BAUMGARTNER et al. 1964) is a consequence of the organization of the afferent input. It is remarkable, that the main characteristic of the movement sensitive neurones was an excitatory input from an off-center fibre. Direction sensitivity was either due to a combination of excitatory on- and off-center areas laying side by side or — less frequently in our sample — due to neighbouring excitatory and powerful inhibitory on-areas.

As far as can be concluded from the limited number of cells recorded during each electrode penetration through the cortex, the receptive area of neurones within one electrode tract covered about the same area. This corresponds to a similar arrangement in the somato-sensory cortex (MOUNTCASTLE 1961) and HUBEL

and Wiesel's (1962) observations on the columnar organization in the visual cortex. It is in agreement with recent histological findings derived from Golgi studies (Colonnier 1966; Globus and Scheibel 1967). On the other hand, the combination of excitatory and inhibitory on- or off-fibre convergence and thus the actual field organization could vary considerably even between two neighbouring cells. — The distribution of receptive field centers of geniculate fibres entering a minute area of the cortex also agrees with anatomical data. The somewhat wider distribution of receptive field centers of geniculo-cortical fibres picked up in one minute area at the grey-white border (3—6°) as compared to the narrower center separation of fibres converging on single cells (1—3°) in our experiments is explained by the frequently oblique course and sometimes wide horizontal intracortical extension of geniculate fibres (O'Leary and Bishop 1937; Ramon y Cajal 1923; Sholl 1955).

Conclusions

Some general comments may be made about the functional meaning of the synaptic arrangement of cortical neurones. Owing to the variable interactions of different afferents on cortical cells, the cats primary visual cortex does not seem to be designed for an analysis of brightness of large areas as has been pointed out by Hubel and Wiesel (1962). Also in our study, only a few neurones reacted with a lasting excitation to diffuse light and most neurones were difficult to classify as "on" or "off" according to their reactions to diffuse light. A distinct on- and off-system still separate in cortical cells as suggested by some findings (Baumgartner and Hakas 1962; Jung 1961) may be present in some neurones, but the majority of cortical neurones cannot distinguish a dark spot or bar in one part of their receptive field from a spot or bar of light in another part. Various combinations of inputs explain the maximal reactions of cells to certain "optimal" stimulus shapes. But the wide variety of stimuli able to influence any given cortical cell, the great variability of connections and therefore receptive field configurations make it difficult to conceive of an organization, in which one given cell is designed to "recognize" a certain pattern and to convey this information to the next neurone or group of neurones. At a first glance the functional organization of receptive fields and the reactivity of cortical neurones may suggest to the investigator a decoding mechanism with separate, well defined functions of different groups of cells (as e.g. "line detectors", "movement detectors" or "directionality detectors"). However, the actual variety of functional organizations would be difficult to force into such a scheme. A model designed in this manner might be useful for some very limited pattern recognition programs of computers (and may be even used in some "lower" centers or organism), but biologically it would reduce the available information "seen" by the eye considerably. All one can say is that the great variety of connections of cortical neurones enable the cortex as a whole, to receive a wide range of aspects from any stimulus or combination of stimuli. Because of the variety of cortical field organizations we feel uncertain as to what the cortex as a whole "reads" with this variety of input arrangements. In trying to understand the functional design of the visual cortex its control functions for the behavior should first be taken into account. In this respect the control of eye movements and their feedback control can be considered one major function of the visual

cortex. Electrical stimulation of the primary visual cortex leads to coordinated eye movements dependent on the place of stimulation (STRASCHILL and SUKIMURA, unpublished observations). It also may be significant that of all the stimulus patterns with a specially effective action on cortical cells of cats, the moving stimuli are known to play a significant role also in the cats behavior (LEYHAUSEN 1956). Therefore, the high sensitivity of many neurones in the cats cortex to moving stimuli due to excitatory connections with off-center fibres may be related in some restricted way to behavior. Since at least in area 17 the movement sensitivity is always restricted to a limited part of each neurones receptive field, the reaction elicited by the movement thus also carries a spatial information.

When this manuscript was finished, a paper of BARLOW et al. (1967) appeared which describes the effects of binocular stimulation on cortical neurones. Their findings of a variable disparity of the binocular inputs agree with our own observations which emphasized the variations of afferent monocular input and the variable distances of field centers of converging fibres in the different cortical neurones. — BARLOW et al. also mention the fact, that stimulation of one part of a receptive area of a cortical neurone may "veto" the reaction to another stimulus. The demonstration of inhibitory areas in the receptive fields of cortical neurones is the synaptic basis for this observation.

References

BARLOW, H.B., C. BLAKEMORE and J.D. PETTIGREW: The neural mechanism of binocular depth discrimination. J. Physiol. (Lond.) **193**, 327—342 (1967).

BAUMGARTNER, G., u. P. HAKAS: Neurophysiologie des simultanen Helligkeitskontrastes. Pflügers Arch. ges. Physiol. **274**, 489—510 (1962).

—, J.L. BROWN and A. SCHULZ: Visual motion detection in the cat. Science **146**, 1070—1071 (1964).

— — — Responses of single units of the cat visual system to rectangular stimulus patterns. J. Neurophysiol. **28**, 1—18 (1965).

BURKE, R.E.: Composite nature of the monosynaptic excitatory postsynaptic potential. J. Neurophysiol. **30**, 1114—1137 (1967).

BURNS, B.O., W. HERON and R. PITCHARD: Physiological excitation of visual cortex in cat's unanaesthetized isolated forebrain. J. Neurophysiol. **25**, 165—181 (1962).

COLONNIER, M.: The structural design of the neo-cortex. In: Brain and Conscious Experience, pp. 1—23. Ed. by J.C. ECCLES. Berlin-Heidelberg-New York: Springer 1966.

CREUTZFELDT, O., and M. ITO: Inhibition in the visual cortex. In: Inhibition in the nervous system, pp. 343—349. Ed. by K. v. EULER. Oxford and New York: Pergamon Press 1968.

—, H.D. LUX and S. WATANABE: Electrophysiology of cortical nerve cells. In: The Thalamus, pp. 209—235. Ed. by D. PURPURA and M.D. YAHR. New York and London: Columbia University Press 1966.

ECCLES, J.C.: The physiology of synapses. Berlin-Göttingen-Heidelberg: Springer 1964.

FUSTER, J.M., O.D. CREUTZFELDT and M. STRASCHILL: Intracellular recording of neuronal activity in the visual system. Z. vergl. Physiol. **49**, 605—622 (1965).

GLOBUS, A., and A.B. SCHEIBEL: Synaptic loci on visual cortical neurones. I. The specific afferent radiation. Exp. Neurol. **18**, 116—131 (1967a).

HERZ, A., O. CREUTZFELDT u. J.M. FUSTER: Statistische Eigenschaften der Neuronenaktivität im ascendierenden visuellen System. Kybernetik **2**, 61—71 (1964).

HUBEL, D.H.: Integrative processes in central visual pathways of the cat. J. Opt. Soc. America **53**, 58—66 (1963).

HUBEL, D., and T.N. WIESEL: Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. J. Physiol. (Lond.) **160**, 106—154 (1962).

— — Shape and arrangement of columns in cat's striate cortex. J. Physiol. (Lond.) **165**, 559—568 (1963).

— — Receptive fields and functional architecture in two non-striate visual areas (18 and 19) of the cat. J. Neurophysiol. **28**, 229—289 (1965).

JUNG, R., R. v. BAUMGARTEN u. G. BAUMGARTNER: Mikroableitungen von einzelnen Nervenzellen im optischen Cortex: Die lichtaktivierten B-Neurone. Arch. Psychiat. Nervenkr. **189**, 521—539 (1952).

— Neuronal integration in the visual cortex and its significance for visual information. In: Sensory communication, pp. 627—674. Ed. by W. ROSENBLITH. New York-London: Wiley & Sons and M.I.T. Press 1961.

LEYHAUSEN, P.: Das Verhalten der Katzen (Felidae). Handb. d. Zool. **10**, (21) 1—34 (1956).

MCILWAIN, J.T., and O.D. CREUTZFELDT: Microelectrode study of synaptic excitation and inhibition in the lateral geniculate nucleus of the cat. J. Neurophysiol. **30**, 1—21 (1967).

MOUNTCASTLE, V.B.: Modality and topographic properties of single neurones of cat's somatic sensory cortex. J. Neurophysiol. **20**, 408—434 (1957).

O'LEARY, J.T., and G.H. BISHOP: The optically excitable cortex of the rabbit. J. comp. Neurol. **68**, 423—478 (1937).

OTSUKA, R., u. R. HASSLER: Über Aufbau und Gliederung der corticalen Sehsphäre der Katze. Arch. Psychiat. Nervenkr. **203**, 212—234 (1962).

RALL, W.: Distinguishing theoretical synaptic potentials computed for different soma-dendritic distributions of synaptic input. J. Neurophysiol. **30**, 1138—1168 (1967).

RAMÓN Y CAJAL, S.: Studien über die Sehrinde der Katze. J. Psychol. Neurol. (Lpz.) **29**, 161—181 (1923).

RODIECK, R.W., J.D. PETTIGREW, P.O. BISHOP and T. NIKARA: Residual eye movements in receptive field studies of paralysed cats. Vision Res. **7**, 107—110 (1967).

—, and J. STONE: Analysis of receptive fields of cat retinal ganglion cells. J. Neurophysiol. **28**, 833—849 (1965).

SHOLL, D.A.: The organization of the visual cortex in the cat. J. Anat. **89**, 33—46 (1955).

SZENTÁGOTHAI, J.: The anatomy of complex integrative units in the nervous system. In: Results in neuroanatomy, neurochemistry, neuropharmacology and neurophysiology, pp. 9—45. Ed. by K. LISSAK. Budapest: Akademiai Kiado 1967.

WATANABE, S., M. KONISHI and O. CREUTZFELDT: Postsynaptic potentials in the cat's visual cortex following electrical stimulation of afferent pathways. Exp. Brain Res. **1**, 272—283 (1966).

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