

SPATIAL SUMMATION PROCESSES IN THE RECEPTIVE FIELDS OF VISUALLY DRIVEN NEURONS OF THE CAT'S CORTICAL AREA 21A

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INTRODUCTION

The area 21 as a visually sensitive area of the cat's extrastriate cortex was first defined by Heath and Jones (15) on the basis of its morphology and cytoarchitectonics. Detailed investigations of the retinotopic organization and morphology of interconnections of area 21 with other brain structures have shown that area 21 consists of two distinct areas 21a and 21b (23, 30, 32, 33). More recent evidence has indicated, that the great majority of area 21a visually driven neurons are orientation sensitive (20, 31, 36, 38, 39). Furthermore, increasing evidence suggests that in addition to orientation selectivity, the neurons of area 21a are involved in the central processing of information concerning the shape perception of objects (8, 38). Earlier Xing and Gerstein (40, 41, 42) on the basis of modeling experiments, concluded that the central processing of sensory information was carried out by clusters of neurons that were organized in functional groups. The authors had emphasized that such groups were dynamic and could be changed by input stimuli. The latest findings presented by Warren et al. (37) have confirmed this interpretation. From this point of view, the fine spatial properties of area 21a neurons, become important as a basic neurophysiological substrate in the central processing of integration and differentiation of the visual information received by the neuron. Despite the great interest of researchers on the functional significance of cortical area 21a in the central processing of visual information, it has not been investigated in sufficient depth until now. Our earlier investigations concerning lateral geniculate neurons RF organization (13) have revealed well defined influence on the neuron activity from the surrounding visual field outside of the RF. Later, investigating RF organization of visually driven neurons in extrastriate area 21b Khachvankian et al. (17) had put forward a suggestion on the possible neurophysiological mechanisms of the complex

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RF organization depending on the activity of a neighbour neurons. And more recently Sharanbekian et al. (28) presented results of experiments conducted in area 21a, which have revealed substantial changes in the spatial substructure of the RF's at the increasing of applied stimulus size. Thus, it becomes evident, that complex spatial organization of individual RFs, as well their surrounding space need to be thoroughly investigated to approach understanding in central integrative processing of the visual information.

In this study we present the results of our experiments concerning spatial summation characteristics of area 21a neurons. We also made an attempt to elucidate the possible neurophysiological mechanisms of correlated group activity of neurons that govern the central integration of sensory information.

METHODS

Experiments were conducted on adult cats, weighing 2.5-3.5 kg. Cats were anesthetized with ether for initial surgery. The method used was described in detail earlier (13, 14). Tracheotomy and cannulation of femoral artery and a subsequent brain stem pretrigeminal transection (21, 43) were performed under deep ether anesthesia. To achieve the complete anesthetization of the animals it was supplemented with chloralose at (10 mg/kg per hour). The animal's head was fixed in a stereotaxic apparatus (Horsley-Clark type, modified for visual research). After trepanation, a window in the skull overlying posterior suprasylvian cortex was filled with 3% agar in 0.9% NaCl solution, which allows the visual control of electrode penetrations precisely to be done within the limits of cortical area 21a. All the operated areas were infiltrated with local anaesthetic Novocaine solution 0.2%. Intramuscular injection of the myorelaxant Dilitin (diiodide dicholine ester of succinic acid) 7 mg/kg immobilized the animal which was then maintained with artificial ventilation (19 strokes/mm, stroke volume 20 ml/kg body weight). Body temperature was kept at 37°-38° C with a heating pad. Pupils were dilated with a topical application of 0.1% Atropine solution and corneas were protected from drying with zero power contact lenses. Nictitating membranes were retracted by instillation of 1% Neosynephrine into the conjunctival sac. Additional spectacle lenses were used to achieve an optimal focusing of the eyes on the screen. Arterial blood pressure was continuously measured throughout the experiment and remained at 90/100 mm Hg. The heart activity and EEG were constantly monitored.

Single unit activity was recorded 23 h after the cessation of ether anesthesia. Tungsten microelectrodes covered with vinyl varnish, with a bare tip of 2-5 μ m were used. Single unit activity was recorded with conventional methods and analyzed with digital analyzer using the poststimulus time histograms mode with the bin width 920 ms. Averaging was achieved by repeating the same stimulus 16 times and summing the responses.

The receptive fields of neurons were plotted on a 90° white concave screen that could swing, thus covering 180° of the visual angle. It was situated in front of the animal at a distance of 1 m from the anterior nodal points of the cat's eyes. Positions of the "area centralis" on the screen were plotted as described by Bishop et al. (2).

Stimulation was performed by moving bright and dark spots and strips of different sizes with an angular velocity of 10°-30° deg/s, which was optimal for the most neurons of area 21a. The strip length was orthogonally oriented to the horizontal axes of neuron RFs in all experiments. The contrast for the bright and dark stimuli were held constant with contrast defined as $\frac{L_{max} - L_{min}}{L_{max} + L_{min}}$, where L_{max} and L_{min} are the maximum and minimum luminances respectively. Generally the luminance of the bright spots was 15 Lx against 2 Lx background; the dark spots had, conversely, 2 Lx luminance against 15 Lx of background. The reflexive index of the screen was 0.85 and, therefore, the ambient illumination was kept in the mesopic range. This helped to maintain a constant contrast sensitivity of the cells under investigation. The direction sensitivity index was defined as $DI = \frac{R_{90} - R_{270}}{R_{90} + R_{270}}$.

where R_{pr} – the response amplitude to preferred direction and R_{npr} the response amplitude to non-preferred direction. Both bright and dark spots were projected on the screen from the same projector system. The motion of the stimuli was achieved with a galvanometer system controlled by a trapezoidal waveform generator.

In some cases coagulation was performed at the successful recording points followed by a 10% formaline solution. The electrode track was reconstructed after the examination of 50 μm histological sections.

RESULTS

A total of 108 visually responsive neurons were investigated in area 21a of the cat's cortex. A small population of neurons recorded along the border lines of area 21a, were not included in this report, to avoid any confusion with the neurons in neighboring visually sensitive areas (area 19 and PMLS). Of 108 neurons the spatial summation properties of 78 neurons were explored completely, using the whole set of light and dark visual stimuli. In this study mainly the qualitative characteristics of the patterns of single neuron responses to the different sizes of applied stimuli were determined. As a first step for each neuron under investigation the RF borders were defined and its precise localization in visual coordinate system was plotted by handheld dark stimulus. Then, using stationary flashing stimuli the RF dimensions of the same neuron were estimated using 1° - 2° light and dark spots. As a rule three different sizes of RF for the same neuron were observed, depending on the type of the stimulus used. In the majority of cases the smallest values of RF-s were observed when the dark stationary flashing spot was delivered. In the present study, the spatial dimensions of RF-s defined by handheld dark stimuli were chosen as basic RF size. Special attention was paid on the investigation of spatial summation processes in RFs of neurons with the specialized responses to the moving visual stimuli. About 32% of investigated neurons revealed direction sensitive properties. In Fig. 1 patterns of responses of a direction-selective neuron to the movement of dark (Fig. 1 A1-6) and light (Fig. 1 B1-6) stimuli of different shapes and sizes are presented. The RF's spatial dimensions were $12^\circ \times 18^\circ$, located in the close vicinity of "area centralis" in the contralateral upper quadrant of the visual field. As is seen from the figure the neuron responses to the moving dark and light spots (2°) and squares ($1^\circ \times 4^\circ$) are clear-cut direction sensitive, with the preferred direction from right to left (Fig. 1 A1,4, B1,4). However, dark and light spots of greater size (5°) and squares ($7^\circ \times 11^\circ$) elicit more discharges in the "null" direction thus direction sensitive index being decreased (Fig. 1 A2,5, B2,5). This fact may indicate on the existence of some spatial asymmetries in the substructure of the RF itself in respect to the sensitivity to the two opposite contrasts of applied stimuli. A moving dark and light spot of 25° in diameter, decreased the neuron discharges in the preferred direction, essentially transforming the overall pattern of the neuron response into a non-directional one (Fig. 1 A3, B3). Nearly the same changes were observed to the moving strips of 1° width, with the length covering the whole vertical meridian of the visual field (Fig. 1 A6, B6). Thus, evidently, the spatial surround of neuron's RF has rather inhibitory influence on neuron responses mainly in the preferred direction. Furthermore, it

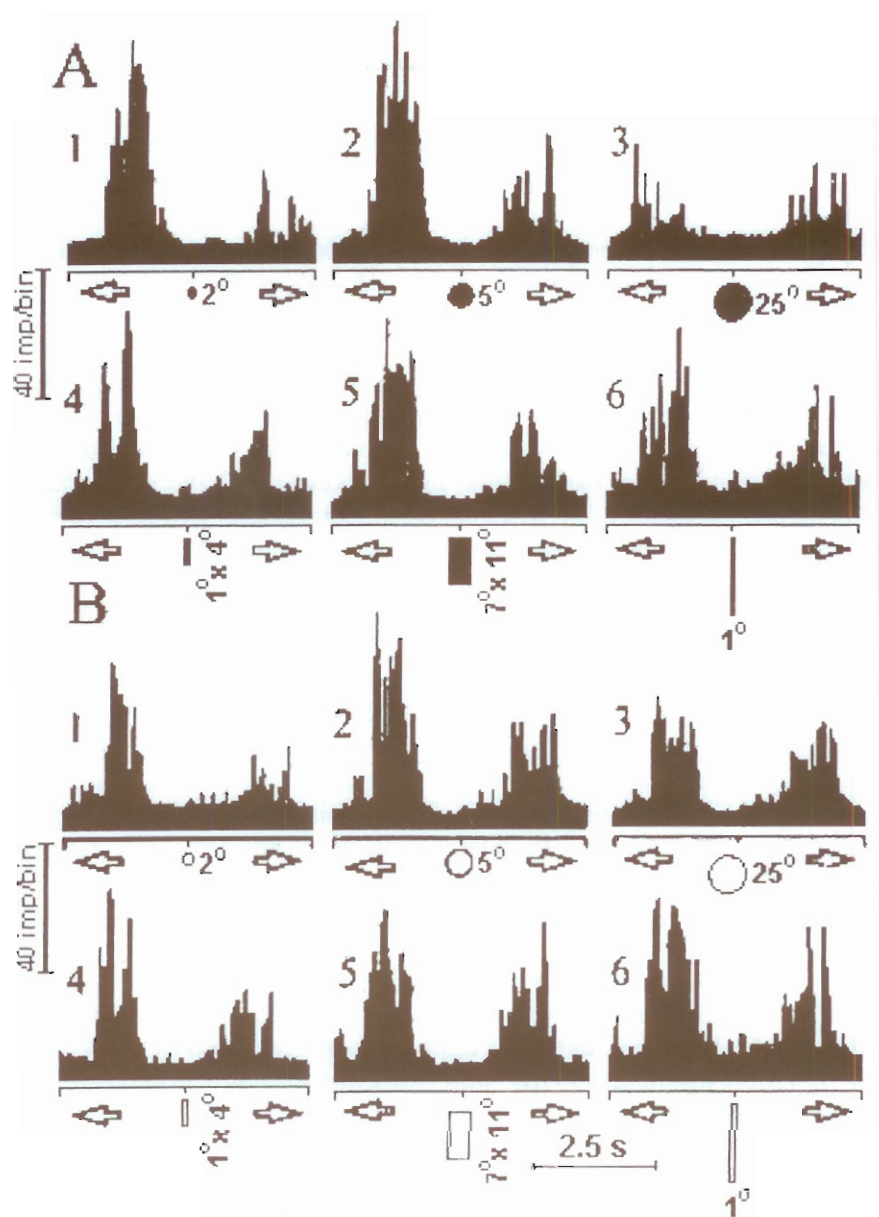


Fig. 1. - Responses of a directionally selective neuron in area 21a to the moving stimuli of different sizes.

A: Responses of the neuron to the moving dark stimuli of different shapes and sizes (1-6). B: Responses of the same neuron to the moving light stimuli of different shapes and sizes (1-6). The sizes and shapes of moving stimuli are indicated below the histograms. Arrows indicate the direction of stimulus motion. Explanations are the same for all the figures.

seems that influences from RF surroundings are somewhat differentiated, by inhibiting predominantly the excitatory synapses of the neuron at the preferred direction of motion, and conversely disinhibiting the neuron response in the null direction. The stationary organization of the RF, and properties of spatial summation at the stationary visual stimulation of the neuron presented in Fig. 1 were also investigated in detail. The RF was explored by light and dark stationary flashing spots positioned in the test-zones over the entire RF area (Fig. 2 D2). The results indicate that there exist

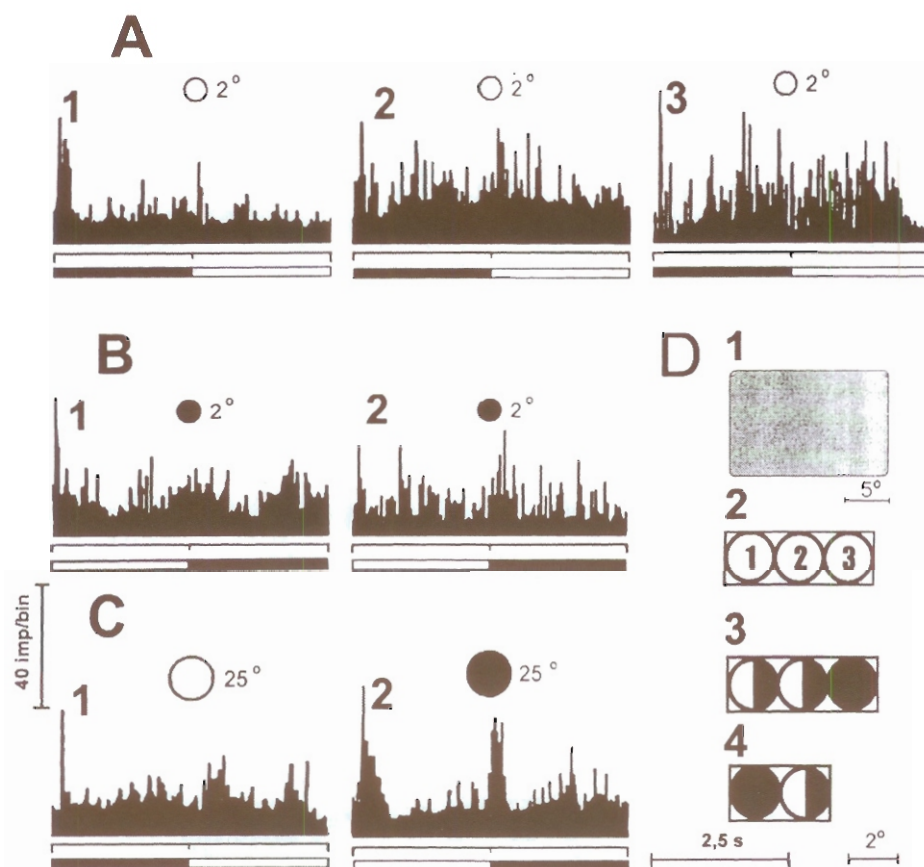


Fig. 2. - Stationary organization of the RF of the neuron presented on Fig. 1.

A: Responses of the neuron to the stationary flashing light spot (1-3) positioned in testzones of the RF (D 3). B: Responses of the same neuron to the stationary flashing dark spot (1-2) positioned in the testzones of the RF (D 3). C: Responses of the same neuron to the stationary flashing light (1) and dark (2) spots of 25° in diameter, positioned in the center of the RF. D: The size of the RF plotted by hand held dark stimulus (1), the testzones of the RF (2), RF estimated by light spot (3) and by dark spot (4). The black line under the histograms in A indicates OFF phase the light line ON phase of stationary flashing light spot. In B, the light line indicates ON phase, and the black line OFF phase of the flashing dark spot. Symbols in D 3, 4 indicate: ● OFF response, ○ ON-OFF response of the neuron. Explanations are the same for all the figures.

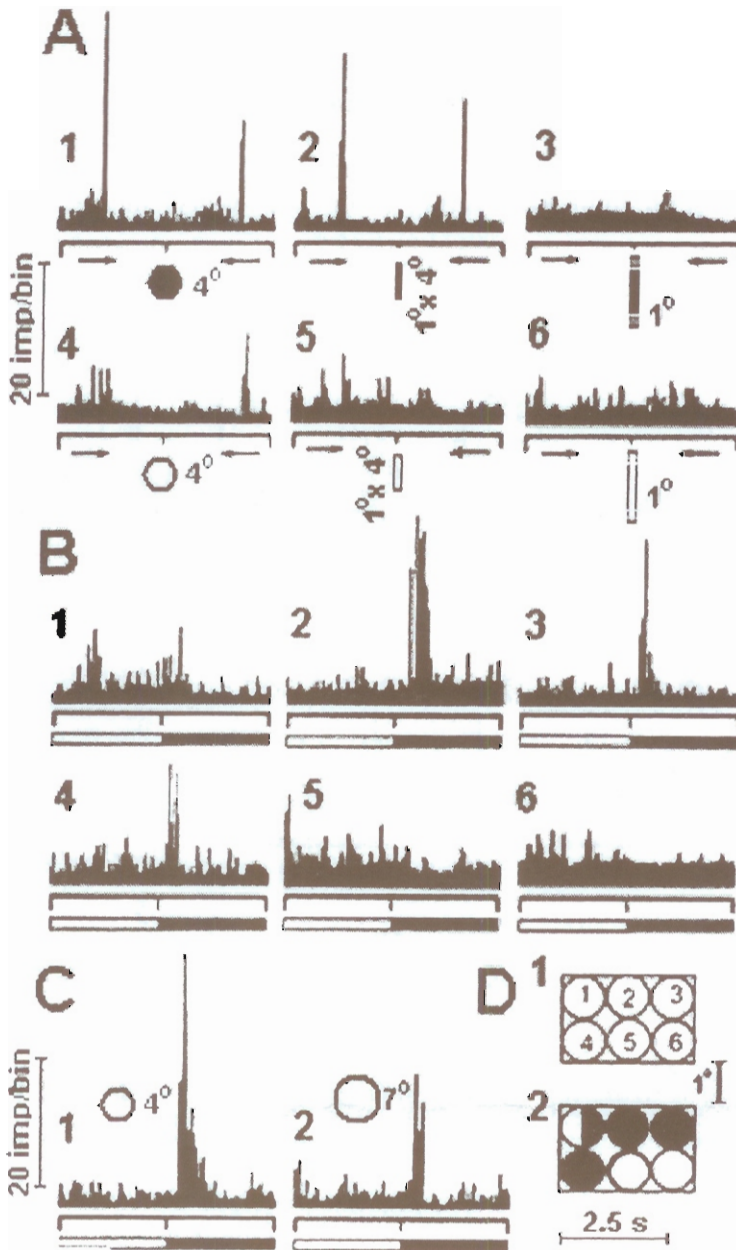


Fig. 3. - Response patterns of a dark sensitive neuron to the moving stimuli of different sizes.

A: Responses of the neuron to the moving dark spot (1) and dark strips (2,3) and light spot (4) and light strips (5,6) along the horizontal axis of RF. B: Responses of the neuron to the 1° stationary flashing spot (1-6), placed respectively in testzones of RF (D1). C: Responses of the neuron to stationary flashing 4° light spot (1) and 7° light spot (2) located in the geometrical center of RF. D 2: qualitative characteristics of the RF, schematically.

certain differences between RF sizes, depending on the type of the visual stimulus used during measurements. The size of the RF was the largest, when plotted by handheld dark stimuli (Fig. 2 D1). The smallest RF dimensions were estimated by a stationary flashing dark spot (Fig. 2 B1,2, D4). The RF size measured by flashing light spot was between the two mentioned above (Fig. 2 A1-3, D3). Thus three different values for RF sizes were obtained due to the application of different types of visual stimuli. A stationary light and dark spots nearly twice as large (25°) as the RF itself were also delivered. The patterns of neuron responses are presented on Fig. 2 C1, 2. As is seen from the figure, no inhibitory influence on the neuron activity was observed. Thus, our previous observation on the lack of suppressing effects from the RF surround, when stationary visual stimuli are used, was confirmed.

A group of neurons (9 neurons of 78) in area 21a, revealed high sensitivity to dark moving visual stimuli exhibiting weak or no responses to moving light stimuli, ("dark sensitive" neurons). Responses to moving spots and strips of a neuron, belonging to this group are presented in Fig. 3. Moving dark spot (4°) and dark strip ($1^\circ \times 4^\circ$) elicited well defined responses of the neuron with slight tendency to the direction sensitivity (Fig. 3 A1,2), whereas the light spot and light strip of the same sizes respectively evoked weak or no response of the cell (Fig. 3 A4,5). The RF of this neuron was rectangular $3^\circ \times 3^\circ$ in size. To the movement of the long dark strip of 1° width, with the length covering the whole visual field and oriented orthogonally to the horizontal axis of the RF, the neuron reacts with almost complete inhibition of the discharges (Fig. 3 A3). There was no response of the cell to the contrast reversal of the stimulus either (Fig. 3 A6). Thus, it appears, that even neurons with a high specialization, as dark-sensitive neurons are, essentially modulate their activity, when the visual space outside of the RF is involved into the action. The stationary spatial organization of the RF, of the neuron presented in Fig. 3, was investigated in detail by a flashing light spot (1°). As shown in the Fig. 3 B1-6, it is a heterogeneous RF with ON, OFF and ON-OFF responses from different test-zones of the RF (Fig. 3 D1,2). It is interesting that stationary light spot of 4° in size evokes pure OFF optimal response of the cell (Fig. 3 C1) without an ON component, but the light spot of 7° in size (Fig. 3 C2) evokes weaker OFF response of the neuron with a small ON component compared with the previous one. Thus, the inhibitory influence of the RF surround is evident.

Some neurons (7 of 78 investigated) revealed changes in the spatial substructure within the limits of their RE's, depending on the gradual increase of the moving stimulus sizes. Responses of one such neuron are presented in Fig. 4. The RF of this neuron plotted by handheld dark stimulus was of $4^\circ \times 6^\circ$ magnitude. As is seen from the figure, a dark spot (3°), and dark strips ($1^\circ \times 2^\circ$ and $2^\circ \times 4^\circ$), moving within the limits of the RF, evoke nondirectional responses of the neuron showing only one discharge peak in the center of the RF (Fig. 4 A1-3). Increasing the length of the dark strip to 7° , when it covers the close surround of the RF by 1.50° to its upper and lower borders, doesn't change much the response pattern of the neuron (Fig. 4 A4). But when the strip is 10° long expanding about 6° into RF's surround (Fig. 4 A5) two distinct discharge centers appeared in the RF. The movement of the longer dark strip although suppresses

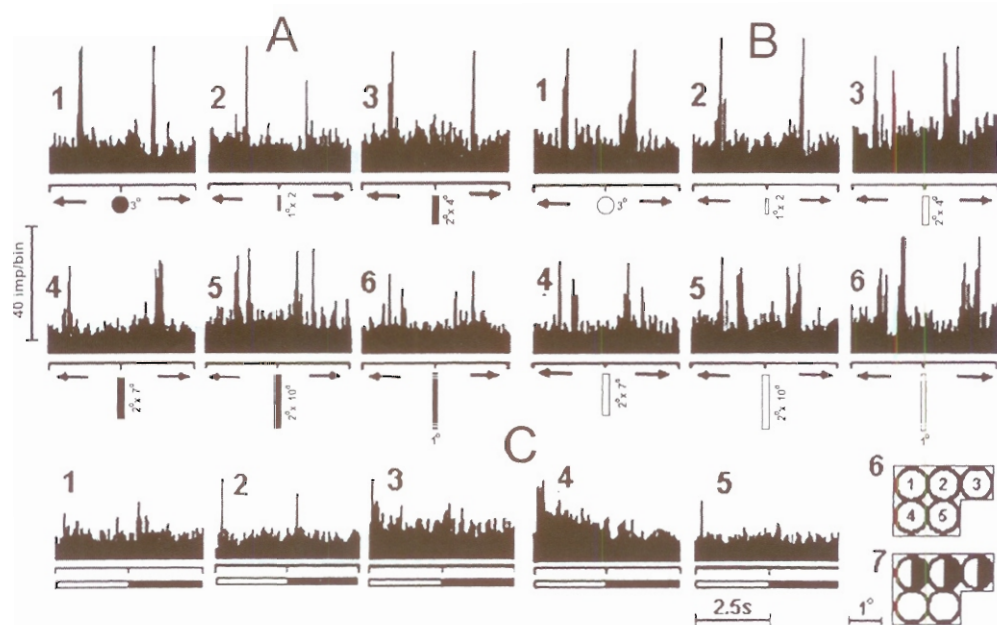


Fig. 4. - The displacement of the RF's discharge center depending of the size of moving stimuli.

A: Responses of the neuron to the moving dark spot (1) and strips of different sizes (2-6). B: Responses of the same neuron to the moving light spot (1) and strips of different sizes (2-6). C: Responses of the same neuron to the flashing light spot 1° (1-5) positioned in the test zones of RF (6), functional structure of the RF (7).

sed the neuron response in general also revealed two discharge peaks (Fig. 4 A6). When this same neuron was tested by the light stimuli (Fig. 4 B1-6) the split of the discharge center into two, already occurred at the stimulus size spatially well fitted to that of the RF sizes (Fig. 4 B3). Further lengthening of the moving stimulus doesn't change the pattern of the neuron responses (Fig. 4 B4-6). This fact clearly indicates, that the spatial summation processes may affect the spatial organization inside the RF limits, effectively changing its characteristics. It is interesting, to note that the long strip of 1° width, moving orthogonally to the horizontal axis of the RF doesn't change the distance between the discharge peaks, which shows, that the split of the discharge center isn't a result of the leading and trailing edges of applied stimuli (Fig. 4 A6, B6). The investigation of the stationary organization of this neuron's RF has shown very weak responses to stationary stimulation, revealing rather heterogeneous RF structure with ON and ON-OFF responses (Fig. 4 C1-7).

In Fig. 5A, the response patterns of another neuron in area 21a to different sizes of moving spots and strips across its RF, are presented. The RF size of this neuron is $6^\circ \times 8^\circ$, with the long axis in the horizontal direction. The patterns of neuron responses undergo qualitative, as well as quantitative changes depending on the size and contrasts of the applied visual stimulus (Fig. 5 A1-8). A moving dark spot (2°), crossing only the central region of the RF, evoked a clearcut direction-nonsensitive

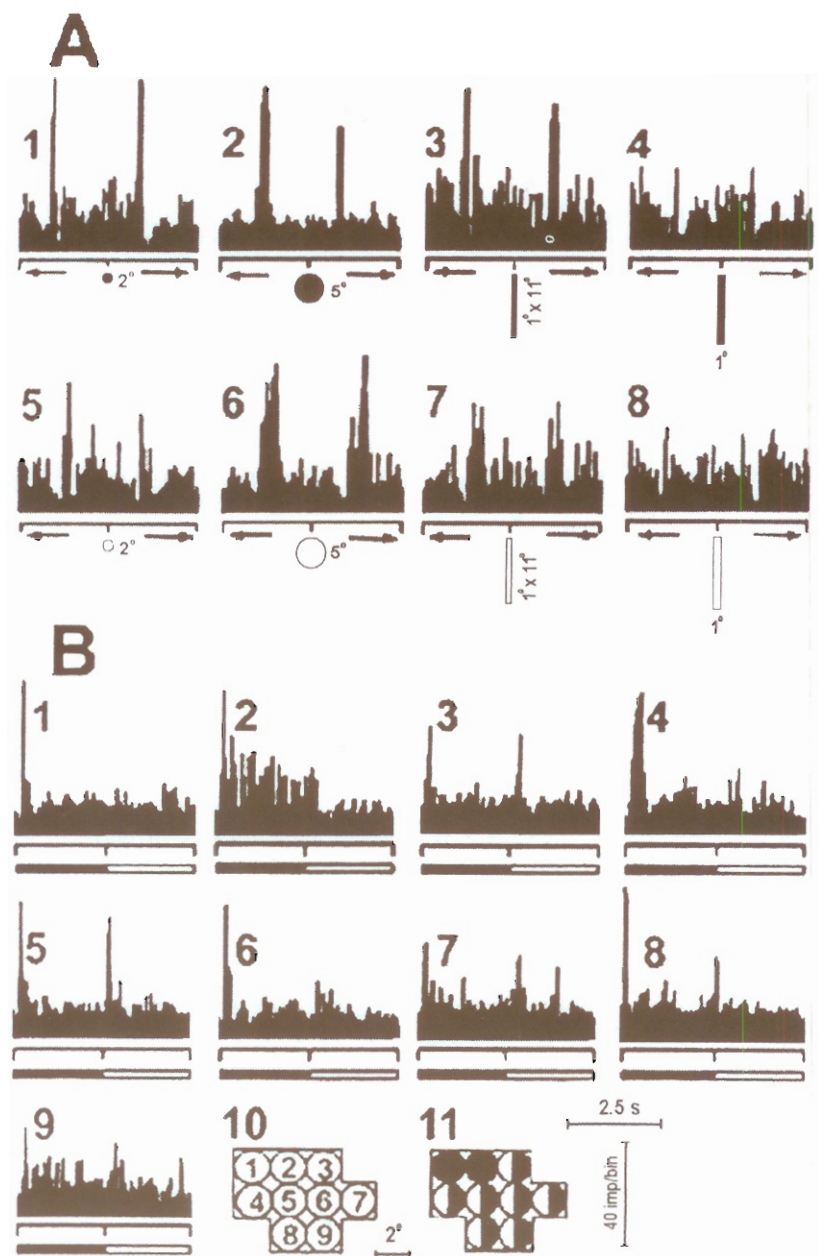


Fig. 5. - Responses of area 21a neuron to the moving dark and light stimuli of different sizes and stationary organization of its receptive field.

A: Responses to the moving dark (1-4) and light (5-8) spots and strips along the horizontal axis of the RF. B: 1-9 responses of the same neuron to the stationary flashing light spot of (1°) positioned in test zones of RF (10). 11 - qualitative characteristics of RF stationary organization presented schematically.

response to two opposite directions of motion (Fig. 5 A1). But the moving dark spot of 5° in size, being still within the limits of RF, evoked a response with a slight tendency of directionality with a preferred direction from right to left (Fig. 5 A2). A dark strip ($1^\circ \times 11^\circ$) moving across the RF, again evoked direction nonsensitive response of the neuron (Fig. 5 A3). When the moving dark strip of 1° width, with the length covering the whole vertical meridian of the visual field was administered to the same neuron a clear-cut suppression of the cell discharges occurred (Fig. 5 A4). Movement of the light spot (2°), in contrary to the dark one, evoked a response with tendency to the direction-sensitivity (preferred direction from right to left) (Fig. 5 A5), whereas 5° light spot as well as the strip of $1 \times 11^\circ$ in size evoked directionally-nonsensitive responses (Fig. 5 A6, 7). However, the moving light strip of 1° width, substantially longer than the width of the RF, suppressed the neuron discharges almost completely (Fig. 5 A8) as was the case with the dark stimulus (Fig. 5 A4). The majority of investigated neurons (64 of 78), have shown such characteristics of changes of the response patterns. Thus, it becomes evident, that the movement of visual stimuli, long enough to stimulate the visual space surrounding the RF in far distant from it, generally reveals inhibitory influences on the discharges of the neuron regardless of the contrast of the applied visual stimuli. The stationary spatial organization of the RF of the neuron presented in Fig. 5A was investigated by a flashing light spot (2°) positioned in the test-zones of the RF (Fig. 5 B10). As seen in Fig. 5 B1-9, the RF of the neuron consists mainly of ON-OFF and OFF subregions irregularly distributed over the entire RF area (Fig. 5 B11). On the basis of such stationary substructure of the RF it is rather difficult to explain the differences in response patterns of the neuron to moving visual stimuli presented on Fig. 5 A1-8.

In Fig. 6 the patterns of responses of another visually driven neuron in area 21a to moving stimuli are presented. The RF of this neuron was $5^\circ \times 7^\circ$ in size with the long axes oriented horizontally. This neuron too, didn't show any reduction of discharges when the moving stimulus covered only the central region and the close surround of RF (Fig. 6 A 1,2,4,5). However, when the stimulus size was increased and it expanded beyond RF's limits the neuron response became suppressed, with clear-cut inhibitory zones around the discharge center of the RF and the contrast reversal didn't have any influence on this effect (Fig. 6 A3, 6). In Fig. 6 B2, 3 the first and second halves of the response to the moving long light strip (Fig. 6 B1) are presented using different time domain. The neuron suppressed its spontaneous discharges almost completely when the long strip entered the RF, and suppression of the spontaneous activity occurred before and after the crossing by the strip the discharge center of the RF (Fig. 6 B2,3). This fact clearly shows, that significant inhibitory influences are arising far beyond the limits of the RF. The spatial stationary organization of this RF, tested by 1° flashing light spot, shows homogenous ON-OFF structure (Fig. 6 C1-3), and the dimensions of the RF estimated by flashing light spot differed of that plotted by hand-held dark stimulus, being $1^\circ \times 3^\circ$ in size (Fig. 6 C 4,5).

The results of experiments presented in this study definitely indicate the presence of certain asymmetries in the spatial substructure of RFs of area 21a neurons. Thus

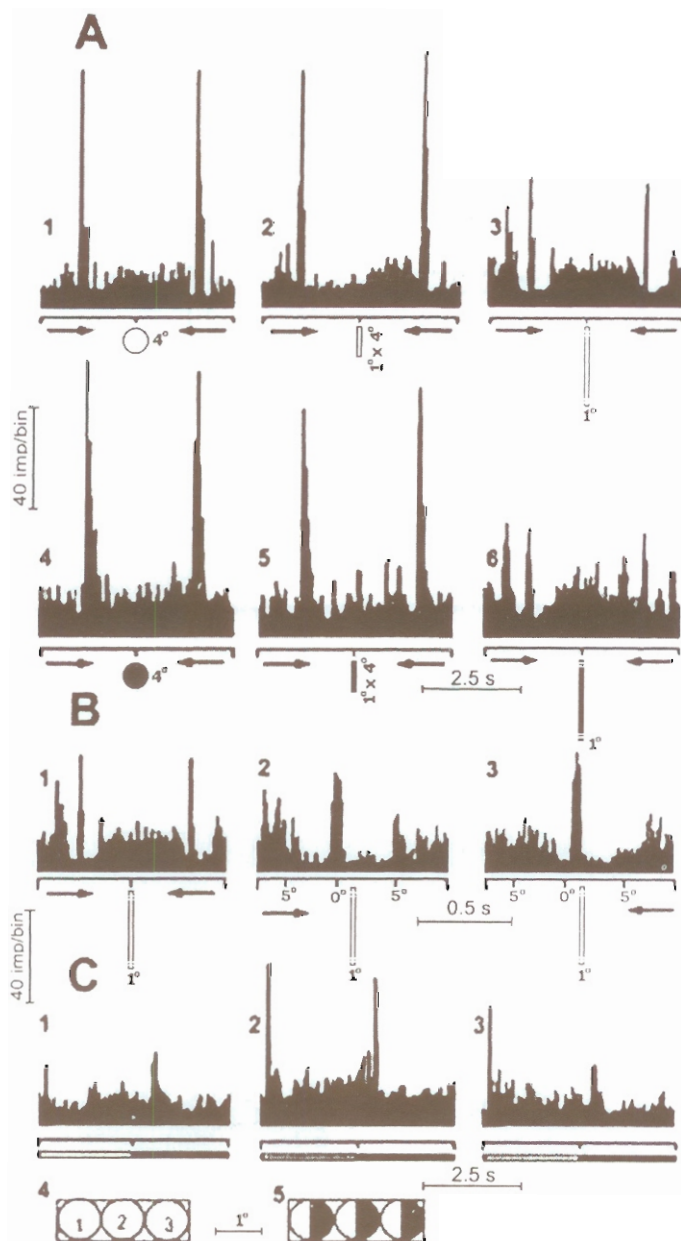


Fig. 6. - The inhibition of the neuron spontaneous activity evoked by the excitation of the RF surrounding.

A: Responses of the neuron to the moving light (1) and dark (4) spots 5° in size, and light (2,3) and dark (5,6) strips of different sizes (indicated below the histograms). B: 1 responses of the same neuron to the moving slit of 1° width and the length covering the whole vertical meridian of visual coordinates (1), the first (2) and the second (3) halves of the response in 1s. time domain. The inhibition of spontaneous activity around the discharge center is evident. C: Responses of the same neuron to stationary flashing light spot 2° in diameter (1-3) positioned in the testzones (4) of the RF, stationary organization of the RF schematically (5).

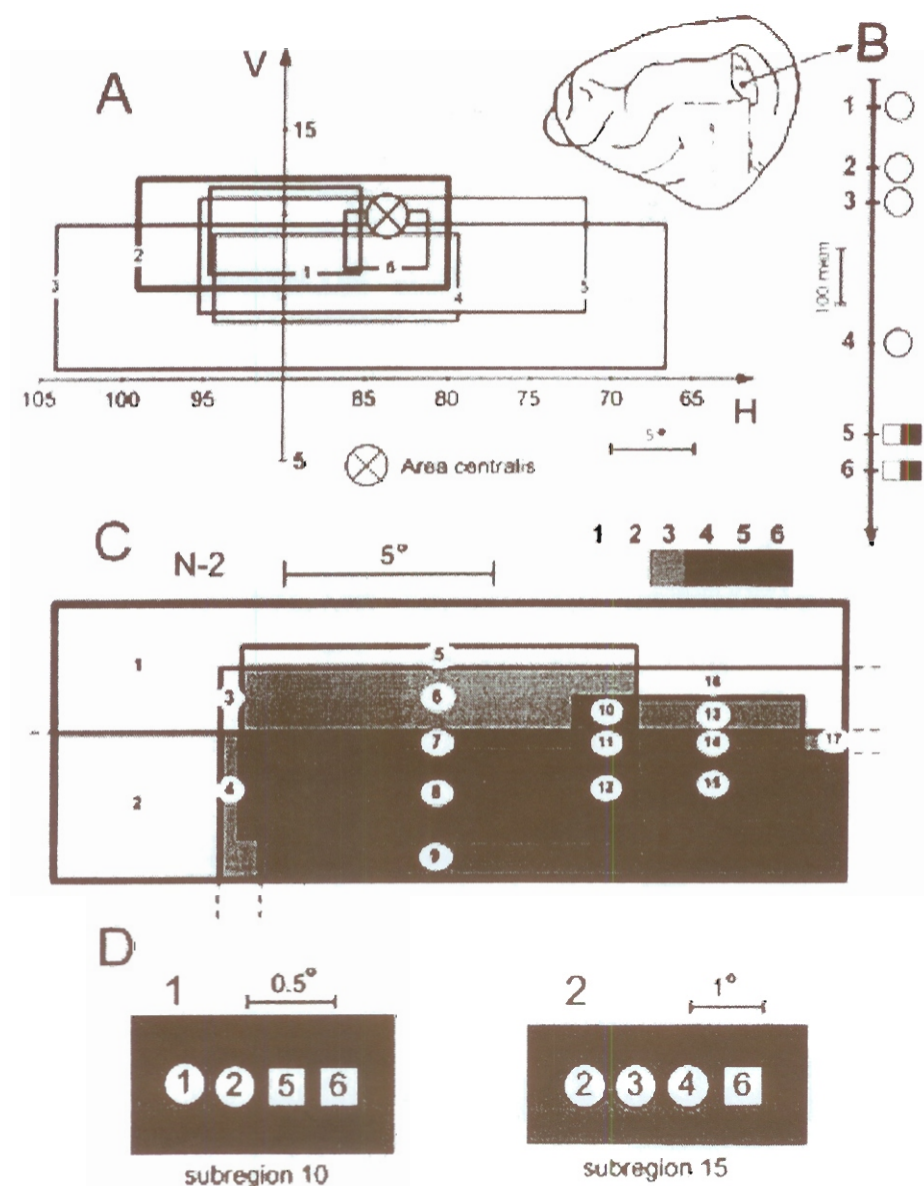


Fig. 7. - The spatial superposition of RFs of six neurons in area 21a recorded in the same penetration of the microelectrode.

A: Spatial localization of RF's in visual coordinate system, B: Microelectrode penetration track. On the left the numbers indicate the recorded neurons, on the right the symbols indicate qualitative characteristics of recorded neurons correspondingly - $\bigcirc$ - directional sensitive ON response, $\blacksquare$ - directionally non sensitive ON-OFF response. C: Distribution of the density of spatial superpositions of different RFs over the N2 RF (bold line). D: 1,2 the detailed qualitative organization of subregion 10 and 15. The numbers in circles and squares indicate the consecutive neurons in the electrode penetration shown on B. V-vertical meridian, H-horizontal meridian of the visual coordinate system.

the issue of further investigations becomes to be the problem concerning the neurophysiological substrate available to provide the reorganization of RF's substructure at certain environmental circumstances. Thus the next series of experiments were devoted to the problem of finding out any patterns in the spatial arrangement of the neurons RFs in close neighborhood of the neuron under investigation. We investigated the columnar organization in area 21a by recording the activity of consecutive neurons in the same penetration of the microelectrode. Each neuron's RF borders and its position in respect to the "area centralis" in the visual coordinate system were plotted carefully. In addition, the qualitative characteristics of recorded neurons were defined by stationary and moving visual stimuli. Afterwards the map of multiple superimposed RFs of the investigated neurons was made all over the visual field. On Fig. 7 the localization's of RFs of six neurons, recorded in the same electrode penetration (Fig. 7B) are presented. As is seen from the figure there exist a great degree of spatial superposition of the individual RF areas (Fig. 7A). In Fig. 7C the number of superimposed RFs spatial distribution over the individual neuron's RF is presented. It becomes obvious, based on the presented data, that any single RF has its own set of superimposed sub-regions, which are spatially asymmetrically distributed. Thus each sub-region of RF differs from the other sub-region of the same RF by different densities of the overlapped RFs. We called it the "density factor". Taking into account this aspect of RF structure, we couldn't find two RFs in area 21a to be similar to each other. Even in those cases, when the "density factor" in different sub-regions of the RF is the same, when examining in detail, it has been revealed, that as a rule each subregion is composed of RFs of different types of neurons with their different qualitative properties. As shown in Fig. 7D 1,2, the sub-region 10 (Fig. 7 D1) is composed of RFs of two directionally sensitive and two directionally non-sensitive neurons, whereas the subregion 15 (Fig. 7 D2) is composed of three directionally sensitive and one directionally non-sensitive neuron. Thus, a moving visual stimulus when crossing RF area depending on its dimensions evidently would be able to activate subsequently the neurons with different qualitative and quantitative characteristics of discharges. As a result of integration and spatial summation of all these influences on the neuron under investigation, the final response of the cell could be modulated, respectively conditioned by the parameters of applied visual stimuli.

DISCUSSION

The results of experiments presented in this study have shown that area 21a visually driven neurons reveal well defined changes in response patterns to different sizes of applied visual stimuli moving across their RFs. To have precise and complete investigation of spatial properties of neurons it was necessary to get the values of RF sizes for each neuron under investigation and its correct position within the visual coordinates system. According to the presented data, the RF sizes varied substantially depending of the type of visual stimulus used in the measurements. As a rule, the

largest values were obtained by handheld dark stimuli. In the majority of cases, the RFs defined by flashing light spots were smaller than the RFs plotted by handheld stimuli. The smallest values for RFs dimensions were acquired by the dark flashing spots. Thus, we confirmed the previous observations made on primary visual cortex and area 18 of the cats and primates, according to which the size of the visual RF depends on the type of visual stimulus used at measurements, (11, 26, 31). The results of our experiments allowed to conclude that the inhibitory influence from outside of the RFs when stationary visual stimuli were used, in contrary to the moving ones, is absent or very weak in area 21a neurons of the cortex. It is interesting that in subcortical midbrain structures there were no such observations, although the main flow of visual afferent information to area 21a neurons comes from these brain structures (12). However, this problem needs further more detailed investigation.

The presented data agreed well with the earlier observations of Dec et al. (6) on the existence of spatially distinct sub-regions having different response profiles in the RFs of visually-driven superior colliculus neurons. According to our data, at spatial summation processes, certain changes were taking place in the substructure of the RF within its limits. For instance the gradual increase of the sizes of moving visual stimulus, probably due to the involvement of the additional sub-regions of the RF, results in the displacement and sometimes the splitting of the discharge center of the RF into two. Changing the width of the stimulus did not change the distance between two discharge peaks, which means, that the splitting wasn't a result of stimulus width. It is interesting, that this phenomenon depends to some degree on the contrast of applied stimuli, the light stimuli usually having lower thresholds.

McIlwain (18, 19) was the first to observe a phenomenon, called "the periphery effect" when the modulation of neuron responses occurred at the excitation of spatially remote of RFs visual field. Our data indicate that, the well-known "endstop" effect described earlier in primary visual cortex (3, 7, 22, 26, 34, 35, 37) also exists in extrastriate area 21a.

We also demonstrate that the surround space of the visual field close to the borders of RF, in the majority of observed cases has mainly the facilitatory effect on neuron discharges, evoked by the excitation of its proper RF. But this facilitatory surround is variable for each neuron. We suggest that the facilitation results because of the activation of neurons in close neighborhood to the RF of the neuron under investigation, and probably having spatial overlap with the latter. Our results show that the great majority of investigated neurons as a rule decrease essentially the number of their optimal response discharges, when the stimulus strip was elongated far outside of the RF. Thus the excitation of neurons with RFs situated spatially far from the RF of the investigated neuron, as a rule reveal inhibitory influences. Nevertheless, in some cases, especially that of specialized neurons, this surround influence could be quite differentiated, as the blockade of excitatory input in the preferred direction and disinhibition in the null direction in directionally selective neurons. The question is, what neurophysiological mechanism provides this differentiation. At the beginning of 70's, Blakemore a. Tobin (3) investigating the columnar organization of orientation-sensitive neurons in visual cortex, had put forward a sug-

gestion, that the fine orientation tuning properties of these detector neurons were the result of complex activity of neighboring columns. Moreover, the authors came to the conclusion, that such coordinated integrated activity of a group of neurons could be a universal form of organization, governing other sensory structures of the brain. A series of recent investigations confirm this concept in relation to the primary visual cortex (1, 4, 5, 9, 10, 24, 27, 29). Thus, from this point of view, the neurophysiological substrate providing the complex regulation of coordinated activity of a group of neurons is the major problem to be solved. We think, that the main neurophysiological substrate, on the base of which becomes available such fine processing of visual sensory information is the spatial overlap (superposition) of neuron RFs in the visual space. The results of our investigations conducted by the method of sequential recordings of single neurons in the same penetration of the microelectrode in area 21a of the cortex with precise definition of sizes and localizations of their RFs, as well as their qualitative characteristics, show, that the RF of any single neuron is not a simple structure. It consists of multiple (sometimes more than 10) spatially distinct sub-regions with different density of overlapping RFs (density factor) of neighboring neurons. Due to such an organization, the qualitative properties of a single neuron undergo an integration processing according to the degree of their spatially overlapped areas and their geometrical position in the RF of the investigated neuron. As a result, any moving visual stimulus, is available to excite sequentially along its path the distinct subregions of the RF having different "density factors" and different qualitative properties, as well as the quantitative and temporal influences (25). Thus, we suggest, that depending of the angular sizes of the visual stimulus a number of neurons become activated almost synchronously, which may result in the modulation of the final response pattern of the neuron both qualitatively, and quantitatively. The probability of the existence of morphological interconnections between neighboring neurons is quite high. As Hensch and Stryker (16) have indicated, intracortical inhibitory circuits shape the geometry of incoming thalamic arbors, and therefore the cortical columns. The probability of mutual interactions among simultaneously activated neighboring neurons, undoubtedly become to be very high, which may result in differentiated, integration processing of the visual information. A suggestion is put forward that specific spatial summation processes determine the final output pattern of a group of neurons, which than integrates into the sensory map of the detected event defining ultimate perception.

SUMMARY

The spatial summation in receptive fields (RF) of single neurons in cat's extrastriate area 21a was investigated as a basic neurophysiological substrate for central integration processing of visual information. The results showed that the majority of investigated neurons changed their response patterns with gradual increase of applied stimulus size. In approximately 82% of cases the suppression of neuron discharges was observed when the length of the moving strip exceeded that of the RF. In some neu-

rons the increased size of the moving stimulus leads to the changes in the RF sub-structure. Receptive fields of neurons recorded at the same microelectrode penetration depth showed a great variety of RF superpositions distributed in a spatially asymmetric manner. As a result, every single RF consists of multiple sub-regions within the RF, differing from each other by the number of superimposed RF-s (density factor). We suggest that such complex spatial organization of the RF provides the neurophysiological basis for central integration processing of the visual information.

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