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MOVEMENT DETECTION PROPERTIES AND STRUCTURE OF STATIONARY RECEPTIVE FIELDS OF SINGLE NEURONS IN THE CAT EXTRASTRIATE AREA 21a

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Response patterns of single neurons in the extrastriate area 21a of the cat cortex to moving visual stimuli were studied, along with juxtaposition to the structure of their stationary receptive field. First, the precise mapping of stationary RFs was performed by flashing bright spots; then, moving visual stimuli of different shapes and sizes with two opposite contrasts were presented. We found that the majority of investigated neurons with a homogenous stationary RF organization demonstrate significant differences in their activity profiles depending on the size, shape, and contrast of the applied moving visual stimulus. The data obtained support a model in which the RF stationary structure undergoes specific dynamic changes due to simultaneous activation of the RF surround by the moving visual image; this provides more accurate incorporation of moving image information in movement detection.

Keywords: receptive field, stationary structure, moving visual stimuli, cortical extrastriate area 21a.

INTRODUCTION

Visually driven neurons in visually sensitive areas of the brain have receptive fields (RFs) with distinct static structures determined by the response patterns to presentation of stationary visual stimuli [1-3]. Generally, it is accepted that stationary spatial organization of a neuronal RF predetermines response patterns of the respective neuron to application of moving visual stimuli [4-6]. Since these pioneering observations, the properties of neurons capable of discriminating the direction of movement were subjected to numerous studies [7-11]. The property of neurons in the cat striate cortex to respond robustly to one direction of stimulus movement and decrease the activity (in some cases, up to complete inhibition) to the opposite direction (i.e., to generate direction-asymmetric responses) was attributed to the asymmetries in the spatial locations of the static *on* and *off* subregions within the RF. However, subsequent observations reported by various authors showed that, in some cases, the direction selectivity to moving light and dark bars may be independent of the spatial arrangement of these subregions within the RF [12-14].

Our study of neurons of the cat extrastriate area 21a suggests that there is no strict correlation between the RF stationary organization and that of the response patterns to moving visual stimuli. There exists a large diversity of neuronal activity profiles in response to the direction of particular stimulus motion that depend on the shape, size, and contrast of the stimulus used. In the experiments, an attempt was made to investigate in detail the precise stationary structure of the RFs of single neurons in area 21a and the response patterns to moving visual stimuli of neurons having a homogenous static structure of their RFs. Our observations allowed us to suggest that the static RF structure, as well as motion detection properties of a visually driven neuron, may undergo certain temporary modulations dependent on the contrasts, shapes, and sizes of applied visual stimuli; these modifications likely provide more complete and accurate processing of information in the detection of moving images through visual space.

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METHODS

The method used was described in detail in the preceding paper [11]. The cats were initially anaesthetized with alfa-chloralose (60 mg/kg, i. m.), the tracheostomy and cannulation of the femoral artery were performed. Throughout the experiment. anesthesia was maintained by additional doses of chloralose given i.v. (10-20 mg/kg per hour). The animal's head was fixed in a stereotaxic apparatus (Horsley-Clark, modified for visual research). A piece of bone (6 × 10 mm) was removed from the skull above the posterior suprasylvian cortex. The opening was covered with 3% agar in 0.9% NaCl solution, to prevent brain pulsations and provide visual control of electrode penetrations into the cortical area 21a. The immobility of the animal was achieved by i.m. injection of the myorelaxant Ditilin (diiodide dicholine ester of succinic acid, 7 mg/kg). Artificial respiration was administered at 19 min^{-1}, with the stroke volume of 20 ml/kg body mass. The body temperature was kept at 38°C with a heating pad. The pupils were dilated by topical application of 0.1% atropine solution, and corneas were protected from drying with zero-power contact lenses. Nictitating membranes were retracted by instilling Neosynephrine (1%) into the conjunctival sac. The arterial blood pressure was continuously monitored and stabilized at 90-100 mm Hg. The ECG and EEG were continuously monitored throughout the experiment.

Extracellular recordings of single unit activity were made by tungsten microelectrodes covered with vinyl varnish, with an exposed tip of 1-3 μm and impedance of 10-15 MΩ. Action potentials (APs) were conventionally amplified, triggered, and passed to a digital analyzer for on-line analysis and data storage, using the poststimulus time histogram (PSTH) mode. Averaging was achieved by repeating the stimulus 16 times.

The RF borders for each visually responsive cell were defined by hand-held stimuli and plotted on a semicircular perimeter screen placed in front of the cat's head at the distance of 1 m from the anterior nodal points of the cat's eyes. The optic discs and *area centralis* (AC) were plotted on the screen [15, 16], and the RF position within the visual field was referenced to the AC location. As a first step, the extent of RF borders was carefully tested by stationary flashing light spots (0.5°-l°) positioned consecutively side by side (test zones) within the hand-plotted area of the RF. Then, the horizontally moving visual stimuli (spots, bars, edges, and slits of different sizes and contrasts) were applied with a 20°/sec speed of the movement. The direction sensitivity index (DSI) was calculated from the histograms as follows: $(1 - R_{np}/R_p) \cdot 100$ where R_{np} and R_p are the numbers of spikes in the responses for the nonpreferred and preferred directions, respectively. An index of the contrast specificity (CSI) of a cell was derived from the following formula: $CSI = (\Sigma L / \Sigma L + \Sigma D) \cdot 100$, where L and D stand for the responses elicited by light and dark stimuli. An CSI value of 10 or less means that the cell responds almost exclusively to the light stimuli, while a value of 90 or more indicates a strong preference for the dark stimuli. A score of 50 about indicates for nearly equal response strengths to the light and dark stimuli [17].

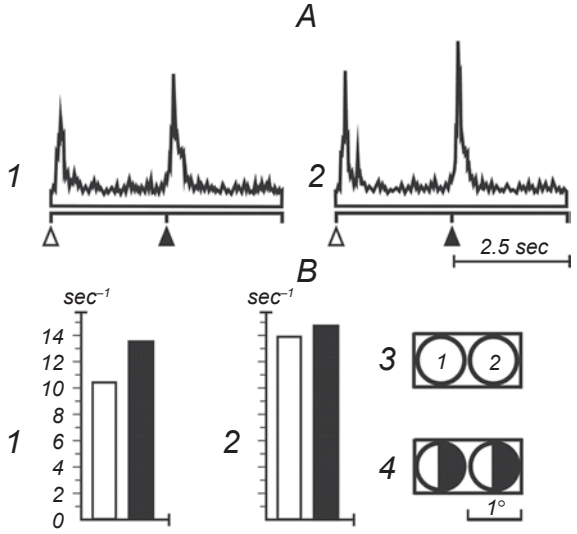
Values of the contrast for light and dark stimuli against the background were kept constant with the contrast defined as $(L_{max} - L_{min})/(L_{max} + L_{min})$, where L_{max} and L_{min} are the maximum and minimum luminances, respectively. The bright stimuli were 15-20 lx against a 2 lx background, while the dark stimuli were, conversely, 2 lx luminance against 15-20 lx of the background. The reflectivity index of the screen was 0.85; therefore, the ambient illumination was kept within the mesopic range. This helped us to maintain a constant contrast sensitivity of the cells during investigation.

In some cases, coagulation was performed at the successful recording points followed by a 10% formalin solution perfusion of the animal. The electrode track was reconstructed after examination of about 50-μm-thick histological sections.

RESULTS

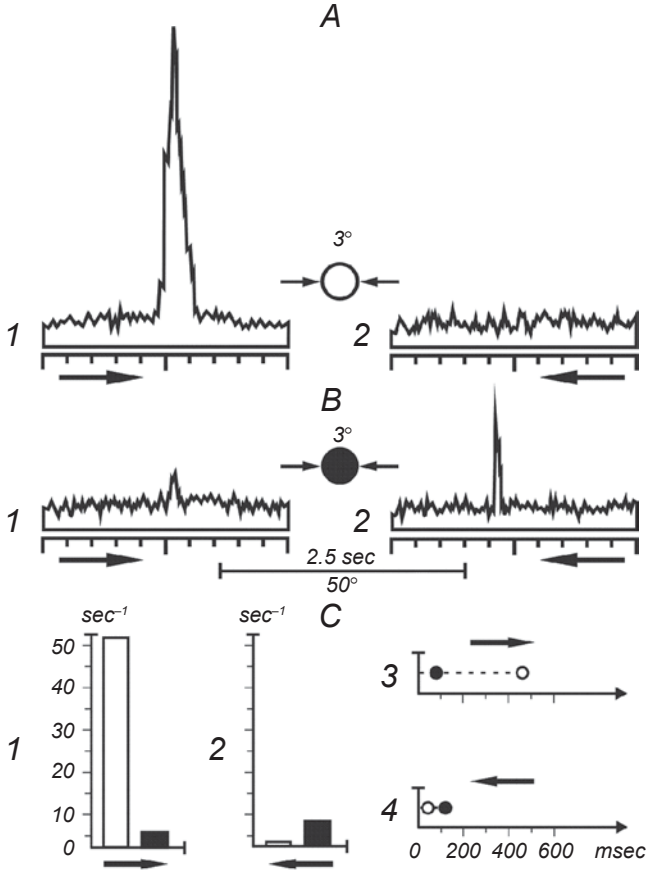
Response patterns of individual neurons evoked by moving visual stimuli were recorded in the extrastriate area 21a. Special attention was paid to the differences in response strength (number of evoked APs) and response duration related to the contrasts, sizes, shapes, and movement direction of the visual stimuli applied. Careful mapping and detailed exploration of the spatial RF structure was provided using a stationary flashing spot positioned consequently over the entire RF surface. This procedure enabled us to determine reliably the precise substructure of the RF spatial organization. In this study, the neurons with the homogenous stationary RF structure were selected to investigate, as a first step, the relationship between

the neuron's response pattern to moving stimuli and that of its stationary RF organization. Among 79 investigated neurons, 18 cells had homogenous RF stationary structures and responded with the same pattern to the stationary flashing light spot (*on*, *off*, or *on-off*) from every tested subfield within the RF surface. Seven neurons of 18 investigated had homogenous *on-off* static RFs. In Fig. 1, responses of a neuron of this group to stationary flashing light spot (1º) are shown. As can be seen from panels 1 and 2, the neuron responded from each spatial subfield of the RF to both light "*on*" and light "*off*" of the flashing light spot. Thus, the RF had a homogenous "*on-off*" structure, and it seemed predictable that stimulus contrast reversal will not lead to significant differences in the activity profiles of the neuron to moving bright or dark visual stimuli. However, when the cell was tested by moving stimuli of two opposite contrasts (i.e., bright and dark spots), the neuronal response profiles differed significantly from each other depending on the stimulus contrast used. The bright spot (3º) movement across the RF horizontal axis elicited a unidirectional (DSI = 100) response pattern with the preferred direction from left to right (Fig. 2A, 1,2). The reversal of the stimulus contrast to opposite one, on the other hand, led to a significant decrement of DSI (DSI = 28.5), with remarkable suppression of the response strength compared to that evoked by a bright moving stimulus (Fig. 2B, 1,2). This is clearly seen in Fig. 2C, 1,2, where these responses are juxtaposed quantitatively. Significant differences existed also in the duration of the responses evoked by moving a bright spot and its reversed contrast, a dark spot (Fig. 2C, 3,4). When the magnitudes of the moving visual stimuli were changed to 8º, which inevitably led to excitation of the RF surround for the bright, as well as for the dark, moving stimuli, the intensity of responses increased (Fig. 3A, 1,2, B, 1,2).



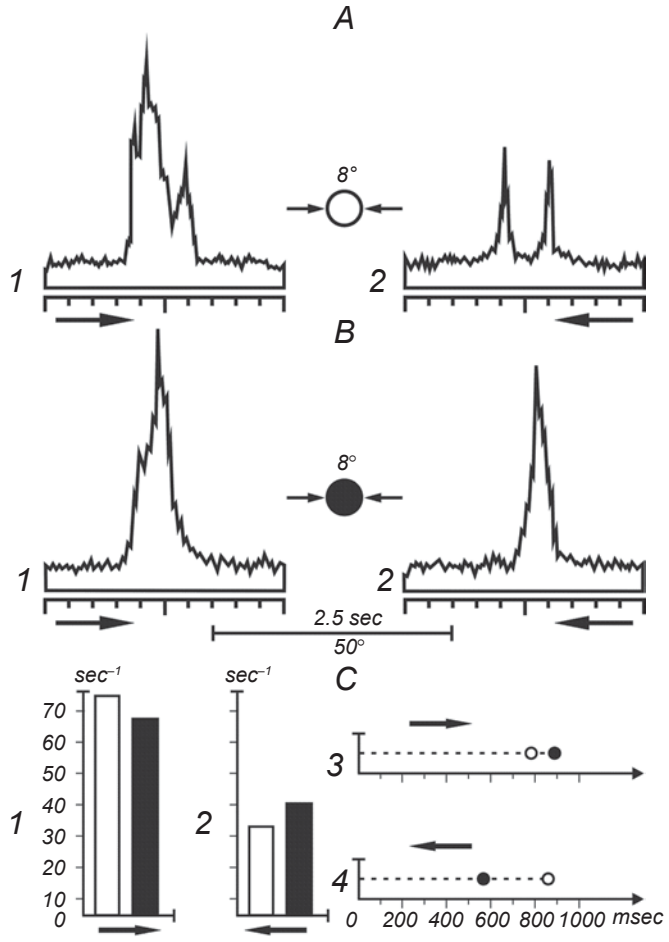
F i g. 1. Averaged responses of a neuron in extrastriate are 21a to the stationary flashing bright spot. A1, 2) Poststimulus time histograms (PSTHs) of responses of the neuron to the stationary bright spot (1°) positioned in the test fields of RF. B1, 2) Frequencies (sec^{-1}) number of evoked discharges(proportional to the number of spikes) at flash-*on* (open columns) and flash-*off* (field columns). B3, 4) Positions of test fields (3) and functional organization of the RF (4). Open symbols indicate in A the "*on*" phase of the stationary flashing spot, filled ones indicate the *off* phase, and half-filled symbols in B 4 indicate the *on-off* pattern of the response.

P и с. 1. Усереднені відповіді нейрона екстрастріатної зони 21а на пред'явлення стаціонарних яскравих плям, що спалахують.



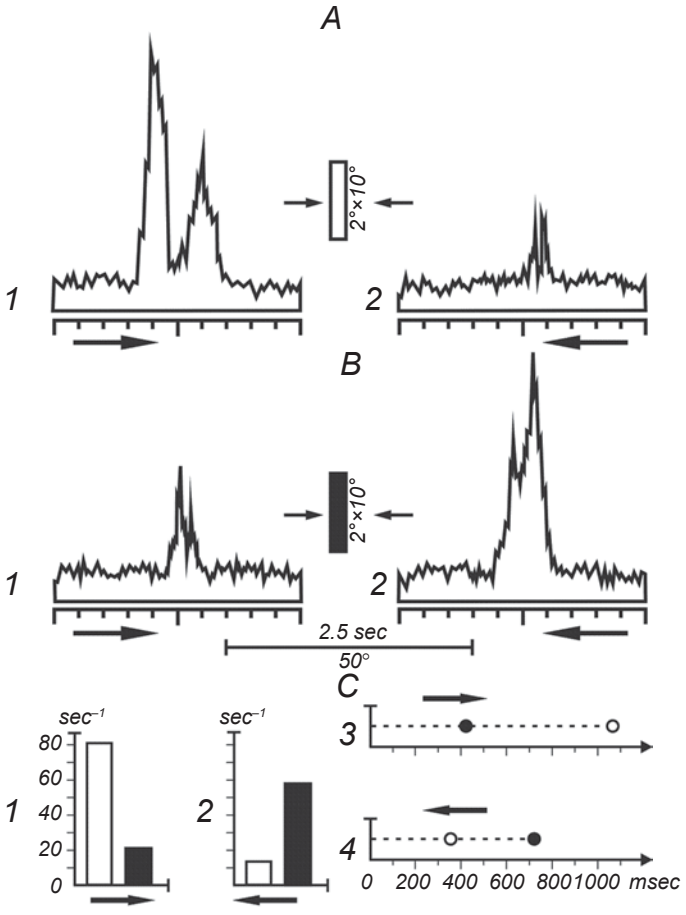
F i g. 2. Response patterns of the neuron to moving visual stimuli of two opposite contrasts. A1, 2) PSTHs of neuronal responses to the bright spot (3°) moving across the horizontal axis of the RF. B1, 2) PSTHs of the neuronal responses to the moving dark spot. C1, 2) Spike frequency (sec^{-1}) in the neuronal responses evoked by the moving bright (open columns) and dark (filled columns) spots. C3, 4) Durations of the response measured for bright and dark moving stimuli. Arrows indicate the direction of stimulus motion. Open and filled symbols indicate bright and dark stimuli, respectively. Other explanations are analogous to those for Fig. 1.

P и с. 2. Профілі відповідей нейрона на пред'явлення рухливих візуальних стимулів з двома протилежними контрастами.



F i g. 3. Profiles of neuronal responses to moving bright and dark spots of the 8° magnitude. Designations are analogous to those for Fig. 2.

Р и с. 3. Профілі відповідей нейрона на пред'явлення рухливих яскравих та темних стимулів розміром 8°.

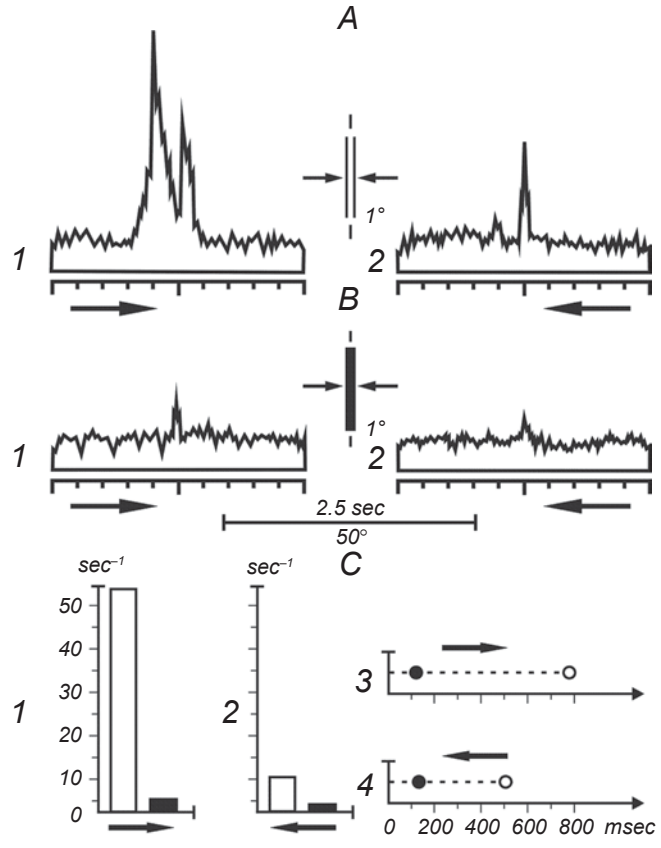


F i g. 4. Profiles of neuronal responses to moving bright and dark rectangles. Designations are analogous to those for Figs. 2 and 3.

Р и с. 4. Профілі відповідей нейрона на пред'явлення рухливих яскравих та темних прямокутників.

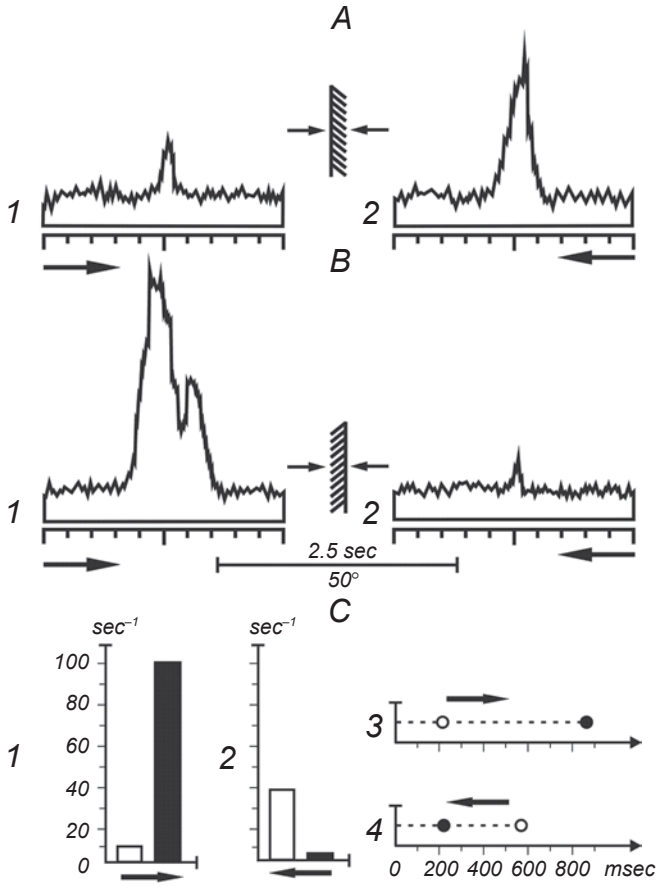
Thus, response facilitation, most likely, results from excitation of the surrounding RF visual space and integration of the neighboring neurons into the overall output. Furthermore, as illustrated in Fig. 3A, 1,2, the light spot elicited a bimodal response pattern with two discharge peaks related to two opposite directions of the movement, with the preferred direction from left to right (DSI = 55.2). Therefore, spatial restructuring of the RF (appearance of two discharge centers) is evident in this case. The response pattern evoked by 8º dark spot movement corresponded to monomodal responses (single discharge centre), but with the same preferred direction, rightward (DSI = 40.7) (Fig. 3B, 1,2). However, there were some differences in the number of evoked APs and in the response duration (Fig. 3C, 1-4) between the response patterns evoked by the same stimuli, but of two opposite contrasts.

We next attempted to learn if the shape of the moving stimuli affects the directional asymmetry patterns of the neuron responses. In Fig. 4A, 1-2, B, 1,2, responses of the same neuron to moving of the bars 2º × 10º with two opposite contrasts are illustrated. The moving bright bar crossing the RF along its horizontal axis evoked bimodal discharges at a rightward direction, which is also the preferred direction (DSI = 82.4), compared to a significantly lower number of APs evoked at the opposite direction of motion (Fig. 4A, 1,2). The reversal of the stimulus contrast (dark bar) led to the change of the preferred direction (DSI = 64.0), which in this case became leftward (Fig. 4B, 1,2). Taking into account that the RF spatial structure corresponds to homogenous *on-off* one, these modifications of the neuronal activity profile may indicate a probable temporary restructuring of the RF spatial organization. The comparison of the numbers of spikes evoked by the moving bright and



F i g. 5. Profiles of direction-sensitive asymmetric neuronal responses to moving bright and dark slits. Designations are analogous to those for Figs. 2-4.

Р и с. 5. Профілі чутливих до напрямку руху асиметричних відповідей нейрона на пред'явлення рухливих яскравих та темних щілин.

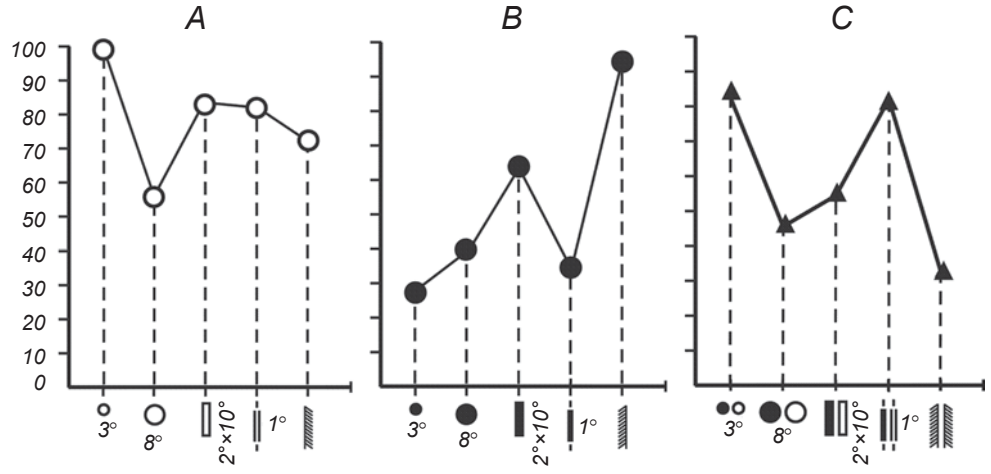


F i g. 6. Profiles of neuronal response to moving edges. Designations are analogous to those for Figs. 2-5.

Р и с. 6. Профілі відповідей нейрона на рухливі межі між яскравим та темним полями.

dark rectangles (Fig. 4C, 1,2) confirmed the above-mentioned hypothesis. Furthermore, a moving light 1°-wide slit covering the entire vertical meridian of the visual field evoked bimodal responses of the neuron at the rightward direction of motion (preferred direction, DSI = 81) and a monomodal pattern of the discharge distribution at the opposite direction (null direction) of the movement (Fig. 5A, 1,2). The moving dark slit of the same parameters significantly suppressed the discharge activity of the neuron eliciting responses of almost negligible number of discharges at two opposite directions of motion (DSI = 34.6) (Fig. 5B, 1,2). The prevalence of the white slit-evoked discharges compared to those to the dark one is clearly seen in Fig. 5C, 1-4, where the number of evoked spikes and the response duration are presented. Thus, the surround influences coming from the visual space outside of the neuron's stationary RF eventually exert certain diversified modulatory effects on the mechanisms of information processing of the neuron under investigation.

To address this possibility, a moving edge was used, so that the rightward direction of the movement provided lightening of the whole visual field, and the leftward motion darkend it. As is seen in Fig. 6A, 1,2, the moving edge evoked direction-specific asymmetric responses (DSI = 72.5) of the neuron, with the preferred direction from right to left. The opposite direction of the edge motion (rightward) evoked weak responses of the cell (null direction). The same neuron responded also with direction-sensitive asymmetric responses (DSI = 94.3) when the edge moved from left to right and darkened the RF. In this case, the preferred direction was from left to right (Fig. 6B, 1,2), i.e., opposite to the previous one (Fig. 6A, 1,2). In Fig. 7A, B, the variability of DSI and CSI are presented graphically in relation to the applied stimulus type and contrast. As is seen in Fig. 7A-C, even though the



F i g. 7. Dynamics of the direction sensitivity index (DSI) and contrast specificity index (CSI) in relation to the sizes and shapes of applied visual stimuli. A, B) Distribution of the DSI for bright (A) and dark (B) moving visual stimuli of different sizes and shapes. C) Distribution of the CSI for moving visual stimuli of different sizes and shapes (shown under the plots).

Р и с. 7. Динаміка індексу диференціональної чутливості та індексу специфічності щодо контрасту залежно від розмірів та форми візуальних стимулів, що пред'являються.

stationary RF structure of the neuron is homogenous *on-off*, the RF activity profiles of neuron responses are significantly different from each other relative to the magnitudes, shapes, and contrasts of the applied stimuli. The majority of investigated neurons (n = 15) with the homogenous RF stationary structure revealed substantial diversification and variability of the responses to moving visual stimuli, depending of the type and contrast of the applied stimuli.

DISCUSSION

The results of the experiments described above indicate that, in the extrastriate cortex of the cat, the response patterns of visually driven cortical neurons concerning detection of the movement direction are variable and may undergo dynamic changes at the contrast reversal of the visual stimuli used, as well as depending on the stimulus size and shape. The data presented confirm our earlier observations concerning the dynamic nature of the stationary subfield organization of neuronal RFs [14]. It was shown that the direction asymmetry in the neuronal response patterns is realized by a mechanism whose operation is largely dependent on dynamic qualitative and quantitative changes in the arrangement of subregions encountering the visual stimuli, as they move over the RF surface. Generally, it is accepted that central transformation and processing of sensory information describing the nature of the visual stimulus is resolved by a single neuron in conjunction with the synchronized activity of neuronal ensembles [13, 18-21]. According to a proposal by McIllwain and colleagues [22] confirmed later by a group of the authors [23-25], the observed RF/surround interactions between separate RFs indicate that the probability of functional interconnections between neighboring neurons is quite high. Thus, eventually mutual interactions among synchronously activated neighboring groups of the neurons may become highly important and effective in modulating the stationary structure of the RF, resulting in diversified compound processing of information concerning visual images. The results of the above-described experiments suggest that the cortical area 21a seems to be specifically involved in the analysis of visual image properties, such as object shapes, magnitudes, and direction of the image motion.

All experimental procedures were approved by the Ethics Commission at the Yerevan State Medical University and correspond to internationally accepted ethical principles for scientific experiments on vertebrate animals.

The authors, H. R. Aslanian, D. K. Khachvankian, B. A. Harutiunian-Kozak, G. G. Tokhmakhyan, T. S. Khachatrian, and J. A. Kozak, confirm that they have no conflict of interests.

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ЗДАТНІСТЬ ДО ДЕТЕКЦІЇ РУХУ ТА СТРУКТУРА СТАЦІОНАРНИХ РЕЦЕПТИВНИХ ПОЛІВ ПООДИНОКИХ НЕЙРОНІВ ЕКСТРАСТРІАТНОГО ПОЛЯ 21а КОРИ КОТА

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Р е з ю м е

Досліджували патерни відповідей поодиноких нейронів екстрастріатного поля 21а кори великих півкуль кота на пред'явлення рухливих візуальних стимулів, одночасно бе-

ручи до уваги структуру стаціонарних рецептивних полів (РП) цих нейронів. Спочатку виконували прецизійне картування стаціонарних РП за допомогою пред'явлення яскравих плям, що спалахували; після цього пред'являли рухливі візуальні стимули різних форм та розмірів з двома протилежними контрастами. Значна більшість досліджених нейронів із гомогенною організацією стаціонарних РП демонстрували істотно відмінні профілі активності, залежні від величини, форми та контрасту рухливих зорових стимулів, що пред'являлися. Отримані дані узгоджуються з моделлю, в рамках якої стаціонарна структура РП піддається специфічним динамічним модифікаціям завдяки одночасній активації оточення РП під дією рухливого візуального образу. Це забезпечує точніше залучення інформації щодо руху зображення до процесу детекції такого руху.

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