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EXPANSION OF RECEPTIVE FIELDS IN THE EXTRASTRIATE VISUAL CORTEX: DEPENDENCE ON THE TRAJECTORY OF A MOVING STIMULUS

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Regularities of spatial expansion of receptive fields (RFs) of visually sensitive neurons at application of moving visual images were investigated in the cat extrastriate visual cortex (area 21a). The RF size and their spatial infrastructure were first defined by presentation of stationary flashing stimuli, and horizontal and vertical axes (HA and VA, respectively) of classical RFs were determined. Then the lengths of the above axes were carefully measured by spatial scanning of the RFs with moving visual stimuli. It was found that dynamic expansion of the RF sizes was, as a rule, linked to the trajectory of a moving stimulus across the RF. Stimulus motion along the RF HA resulted in significant extension of this axis but not of the VA, while the its motion along the RF VA usually caused extension of only this axis, while another axis underwent negligible changes. These results demonstrate that spatial expansion of the RFs correlates mainly with the trajectory of stimulus motion across the RF. Such an effect probably results from excitation of the neuron under study by adjacent cortical neural networks. Thus, neural circuits localized outside the RF play a decisive role in modulation of the qualitative and quantitative characteristics of classical RFs, hence ensuring precise central processing of incoming visual information.

Keywords: visual perception, extrastriate visual cortex, area 21a, receptive field, spatial expansion, trajectory of stimulus motion.

INTRODUCTION

Organization of neural mechanisms ensuring recognition and precise diversification of perceived visual images still remains the main question related to the principles of central processing of visual information. According to the results of earlier investigations [1–4], it was generally accepted that the stationary spatial structure of the receptive field (RF) of a visually driven neuron plays a decisive role in central processing of visual information, and perception and accurate diversification of visual images are mostly determined precisely by this factor. Many studies have been conducted for detailed investigation of fine mechanisms providing discrimination of the image form, size, and motion by single visually sensitive neurons in the primary visual cortex and extrastriate cortical structures [5–10]. Recently, it has been shown [11–14] that spatial dimensions of the neuronal RF are not static and may undergo substantial modifications, namely spatial expansion or shrinking, especially when a moving visual stimulus has been presented. So, it was hypothesised that activation of the networks surrounding the cortical RF plays an important role in central processing of incoming visual information. In our experiments, we investigated regularities of the RF spatial dynamics in relation to the trajectory of visual stimulus motion across the RF. As a first step, spatial scanning of the RF was carried out by stepwise motion of visual stimuli along the RF horizontal and vertical axes (HA and VA, respectively). The main problem was to find out whether expansion of the RF size at application of moving stimuli occurs along all RF spatial parameters or at a definite orientation. This approach enabled us to explore the extent and regularities of RF expansion and to analyze

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the relative importance of the influence of the RF surrounding contributing to central processing of visual information.

METHODS

The methods used were described in detail earlier [10]. The experiments were performed on 17 adult cats weighing 2.5-3.5 kg. The animals were initially anaesthetized with alfa-chloralose (60 mg/kg per hour, i.m.). Tracheotomy and cannulation of the femoral artery were performed. Throughout the experiment, the anesthesia was maintained by intravenously given chloralose (10-20 mg/kg per hour). The animal's head was fixed in a stereotaxic apparatus (Horsley-Clark, modified for visual research). Extracellular recording of single cell activity in the extrastriate area 21a was provided by tungsten microelectrodes covered by vinyl varnish, with an 1-3-μm exposed tip and a 10-15 MΩ impedance. Action potentials (APs) were conventionally amplified, triggered, and passed to a digital analyzer for on-line analysis and data storage, using the post/peristimulus time histogram (PSTH) mode. Stimulus cycles were repeated 16 times for averaging.

The RF borders for each visually responsive cell were defined by presentation of hand-held stimuli and plotted on a semicircular perimeter screen placed in front of the animal's eyes at a 1 m distance. The optic discs and *area centralis* (AC) were plotted on the screen [15, 16], and the RF position in the visual field was referenced to the AC. For determination of approximate locations of the RFs (hand-plot), we used manually presented stimuli. Then, as a first step, the extent of single-neuron RF borders was carefully tested by presentation of stationary flashing light spots (0.5-1.0 deg) positioned consecutively side-by-side (test-subfields) within the hand-plotted RF area. The same procedure was repeated using dark flashing spots (0.5-1.0 deg). The lengths of the RF HA and VA were accurately measured. Then, some moving visual stimuli (spots, bars, and slits of different sizes and contrasts) were applied (speed of motion 20 deg/sec), and the lengths of RF axes under investigation were again defined by extrapolation from the spatiotemporal pattern of neuronal responses (PSTHs).

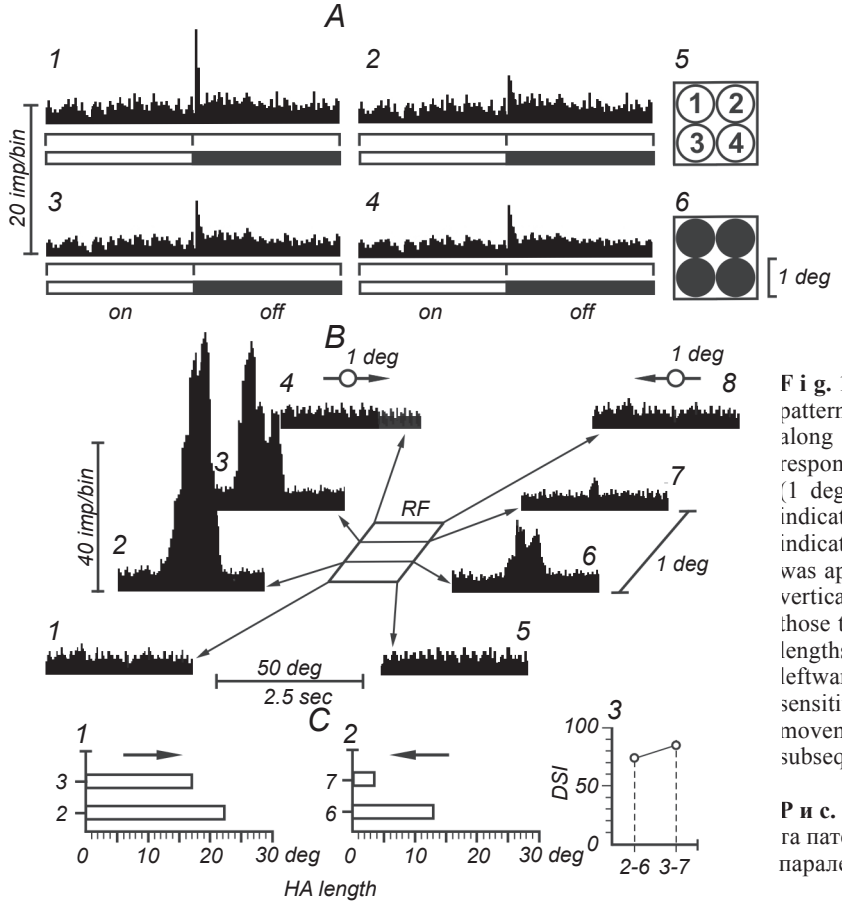
The values of the contrast for light and dark stimuli against the background were kept constant with the contrast defined as (Lmax – Lmin)/(Lmax + Lmin), where Lmax and Lmin are the maximum and minimum luminances, respectively. The bright stimuli were 15 lx against an 1 1x background, while dark stimuli were, conversely, 1 lx against the 15 lx background.

In some cases, successful recording points were coagulated, and this was followed by perfusion of the animal with a 10% formalin solution. The electrode track was reconstructed after examination of 50-μm-thick histological frontal sections.

RESULTS

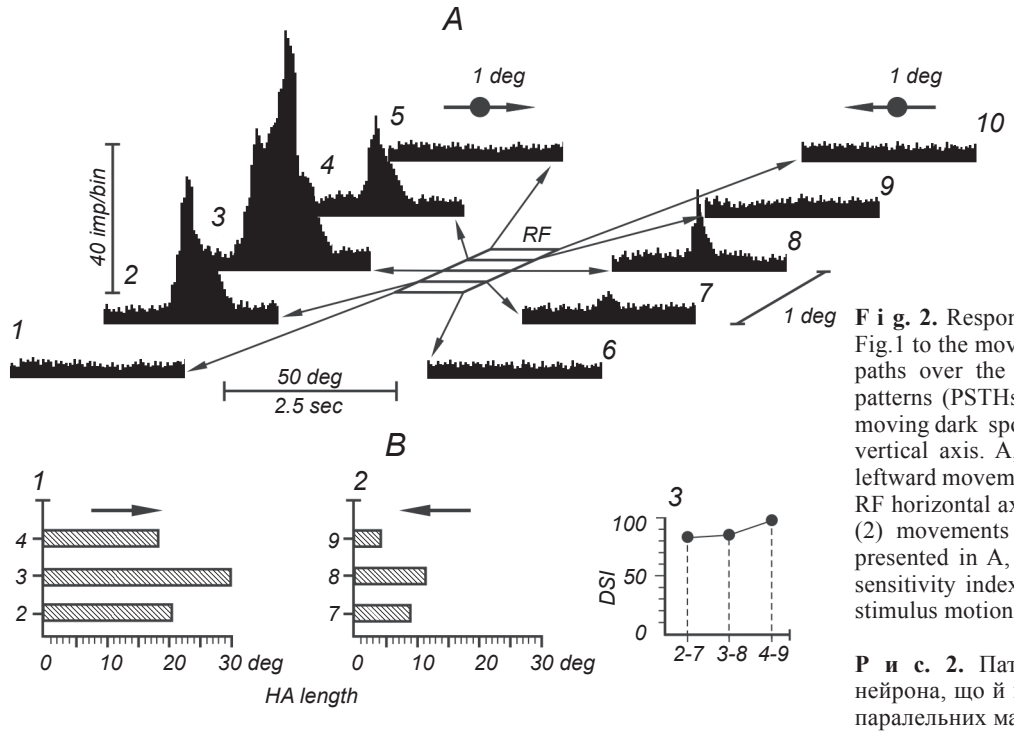
Response patterns of 54 visually driven neurons were recorded in the extrastriate area 21a of the cat cortex. The spatial dimensions and qualitative characteristics of RFs were determined and explored in detail by careful mapping of the stationary spatial structure of the neuronal RFs and by recording averaged PSTHs in response to presentation of stationary flashing spots positioned side-by-side (test-subfields) within the hand-plotted RF borders. The moving stimuli were applied mainly at horizontal and vertical orientations of motion, taking into account that these orientations are most effective in visual perception. Among 54 investigated neurons, 21 units had a homogenous RF stationary structure with the same type of response patterns to the flashing light spot ("*off*", "*on*" or "*on-off*") positioned in the RF test-subfields. As a first step, these neurons were selected for further investigation.

In Fig. 1A, responses of a neuron to the stationary flashing bright spot (1 deg) are shown. As is seen in this panel, the neuron generated *off* responses to the light spot positioned in the RF test-subfields (Fig. 1A, 1-4). The dimensions of the "classical" RF (CRF) are 2 deg along the HA and 2 deg along the VA (Fig. 1A, 5, 6). Spatial scanning of the same RF was provided at different levels of the RF VA by horizontally moving bright and dark spots. In Fig. 1B, 1-8, the response patterns of the neuron evoked by the bright spot (1 deg) moving horizontally with 1 deg steps at consecutive VA levels of the RF are shown. The lengths of RF HA were measured on the basis of the response profiles at consecutive VA levels of stimulus motion. As is seen in Fig. 1C, 1, 2, significant extensions of the HA lengths were observed at both rightward (22.5 and 17.5 deg) and leftward (13.7 and 3.7 deg) directions of motion when the moving stimulus crossed central regions of the RF, while upper and lower RF borders tested by the same stimulus were unresponsive (Fig. 1B, 1, 4, 5, 8). Thus, the RF HA was manifold elongated, while the VA remained about 2 deg long,



F i g. 1. Properties of the static receptive field and response patterns of a neuron at presentation of a moving bright spot along parallel paths over the receptive field (RF). A, 1-4) responses of the neuron to the stationary flashing bright spot (1 deg) positioned in the RF test-fields (5); filled circles indicate "*off*" responses (6). Open bar under histograms indicates the "*on*" phase of the flash, the bright spot (1 deg) was applied at different levels with (1-deg steps) of the RF vertical axis. B, responses to rightward movements (1-4), B, those to leftward movements of the stimulus (5-8). C, 1, 2) lengths of the RF horizontal axes estimated at rightward and leftward motions of the bright spot. C, 3) plot of the direction sensitivity index (DSI) at consecutive paths of the stimulus movement across the RF. Explanations are the same for all subsequent figures.

Р и с. 1. Властивості статичного рецептивного поля (РП) та патернів відповідей нейрона на рух яскравої плями по паралельних маршрутах через РП.

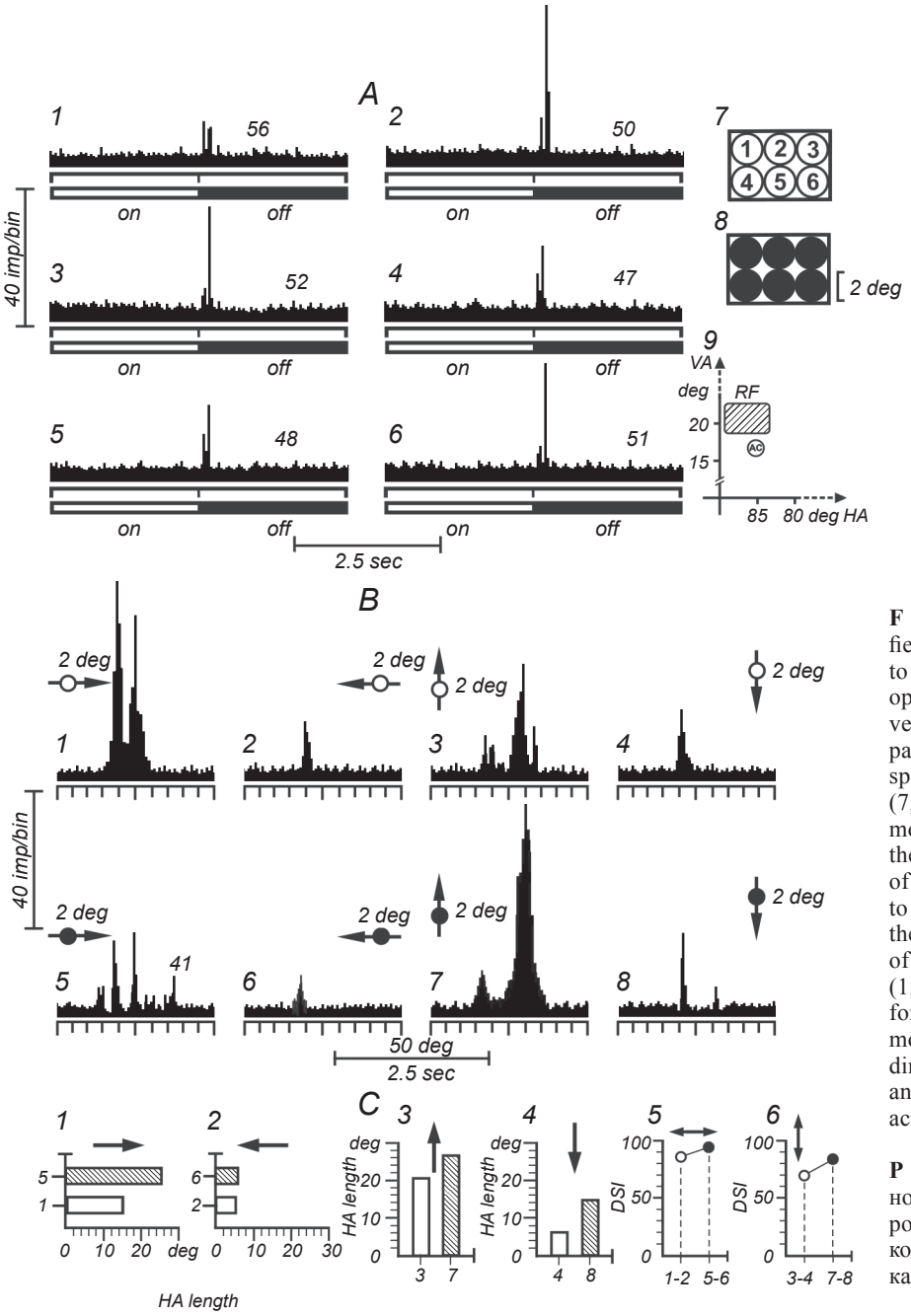


F i g. 2. Response patterns of the neuron shown in Fig.1 to the movements of a dark spot along parallel paths over the receptive field. A, 1-10) response patterns (PSTHs) of the neuron to the horizontally moving dark spot (1 deg) at consecutive levels of RF vertical axis. A, 1-5) rightward movements, 6-10) leftward movements. B, 1,2) lengths estimated of the RF horizontal axes at the rightward (1) and leftward (2) movements of the dark spot along the paths presented in A, 1-10. B, 3) Plots of the direction sensitivity index (DSI) at each parallel path of the stimulus motion (numbers under the plot).

Р и с. 2. Патерни відповідей того ж самого нейрона, що й на рис. 1, на рух темної плями по паралельних маршрутах через рецептивне поле.

as compared with the magnitude defined previously by means of the stationary flashing spot. In addition, the response patterns of this neuron revealed a high degree of the direction sensitivity index (Fig. 1C, 3). Spatial scanning at consecutive levels of the RF VA of the same neuron was performed using a horizontally moving stimulus of the opposite contrast (dark 1-deg spot). As is seen in Fig. 2A, 1-10, negligible changes in the VA length (±1.5 deg) were observed. At the same time, at the horizontal orientation, especially in the case of the preferred direction of stimulus motion, the HA expansion through the RF central regions reached a 29.7 deg magnitude (Fig. 2B, 1, 2). The clear-cut pattern emerged from the above results was that the VA of the RF did not expand at the horizontal orientation of visual stimulus motion.

As a next step, the neuronal RFs were scanned by a moving visual stimulus at the vertical motion orientation, to find out whether the RF HA undergoes some modulation at application of vertically moving visual stimuli. The RF stationary spatial structure of another neuron of this group is shown in Fig. 3.

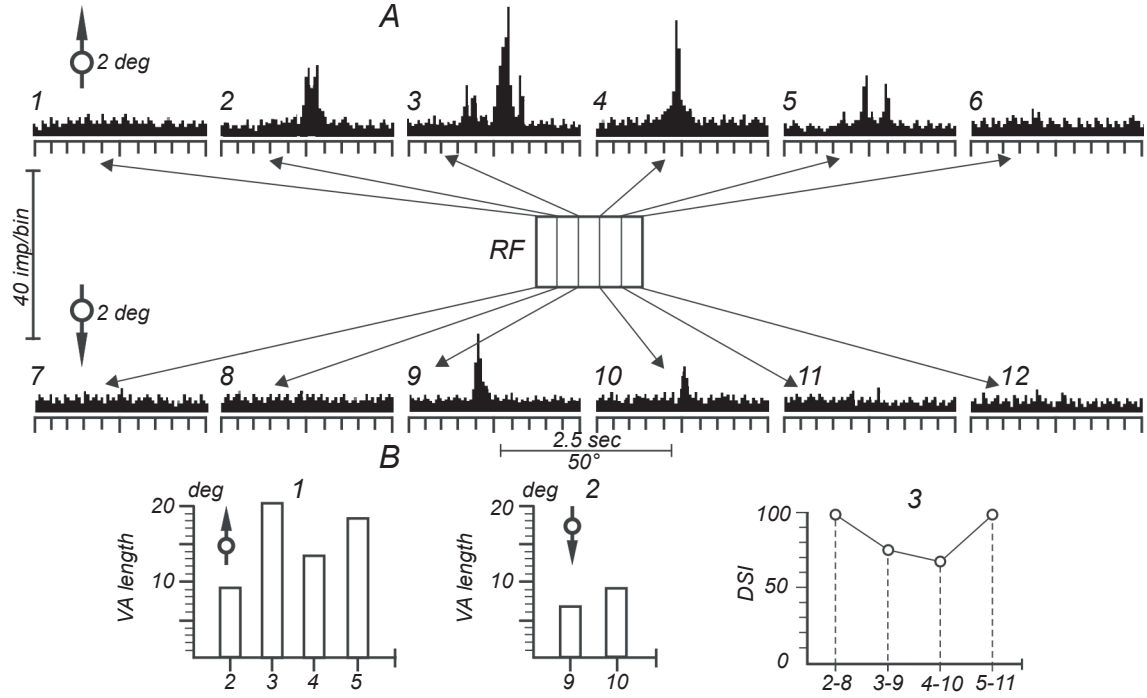


F i g. 3. Stationary structure of the receptive field (RF) and response patterns of a neuron to presentation of moving stimuli of two opposite contrasts along the horizontal and vertical axes of the RF. A, 1-6) Response patterns to presentation of the flashing bright spot (2 deg) positioned in the RF test fields (7, 8). B, 1-4) Response patterns to the movement of the bright spot (2 deg) along the horizontal (1, 2) and vertical (3, 4) axes of the RF; 5-8) responses of the same neuron to the movement of a dark spot (2 deg) along the horizontal (5, 6) and vertical (7, 8) axes of the RF. C, 1-4) Plots of the RF horizontal (1, 2) and vertical (3, 4) axis lengths measured for each orientation and direction of stimulus motion (shown by arrows). C, 5, 6) Plots of the direction sensitivity index at horizontal (5) and vertical (6) movements of visual stimuli across the RF.

Р и с. 3. Стаціонарна структура рецептивного поля (РП) та патернів відповідей нейрона на рух стимулів двох протилежних контрастів вздовж горизонтальної та вертикальної осей РП.

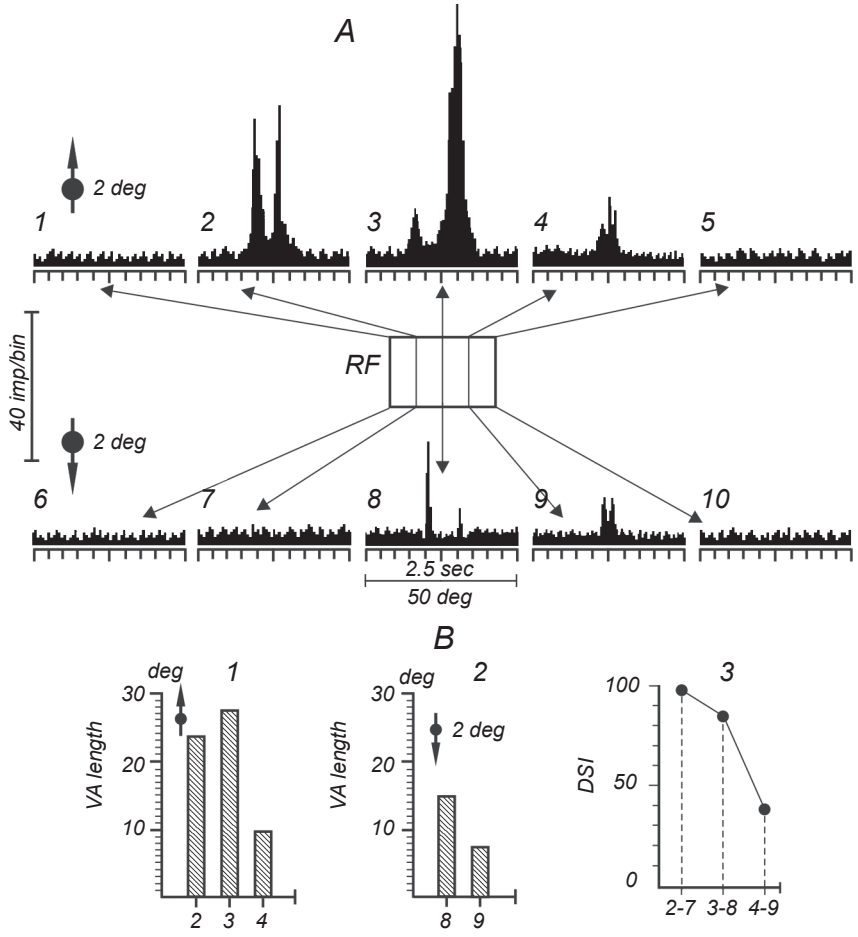
The neuron revealed *off* response patterns from each test subfield (Fig. 3A, 1-6); thus, the stationary structure of the RF was homogenous *off* with the 6-deg HA length and 4-deg VA length (Fig. 3A, 7, 8). At application of a bright 2 deg spot moving along the RF HA, a direction-sensitive pattern of the response (Fig. 3B, 1, 2) with a high degree of DI (Fig. 3C, 5) was observed. At stimulus motion in the preferred direction, a substantial HA expansion was observed (Fig. 3C, 1). The motion of the same bright spot at the vertical orientation along the VA induced AP bursts at the upward direction of motion (preferred) and weaker responses at the downward motion of the bright spot (Fig. 3B, 3, 4). The RF VA also was manifold expanded (Fig. 3C, 3, 4). Application of a visual stimulus of opposite contrast (dark 2 deg spot) moving along the HA resulted in expansion of the HA in the preferred direction (Fig. 3B, 5, 6). The motion of the dark spot at vertical orientation resulted in expansions of the VA both at the upward (Fig. 3B, 7, C3) and downward directions of motion (Fig. 3B, 8, C4), revealing a high degree of the DSI (Fig. 3C, 5, 6). Then, the length of the RF horizontal axis was defined by vertically moving stimuli at spatial scanning of the RF along the HA at 1-deg step motion perpendicular to the RF HA (Fig. 4A). Significant extension of the RF VA was observed at the upward (preferred) direction of motion. As is shown in Fig. 4A, 1-12, B1, 2, the VA lengths measured along the consecutive stimulus motion trajectories across the RF exceeded manifold that of the stationary RF VA length measured by means of the stationary flashing spot, while the RF HA length remained near the tentative values based on the RF HA length measured by the stationary flashing spot.

In Fig. 5, vertical motion with the opposite contrast of the moving stimulus (dark 2-deg spot) is shown for spatial scanning of the RF perpendicularly to the RF HA. As is seen in Fig. 5A, 1-10, a substantial extension of the VA occurred, especially at the preferred upward direction of dark spot motion (Fig. 5B, 1, 2). However, the length of the RF HA did not exceed the value of about 6 deg. Thus, dynamic changes of the RF sizes



F i g. 4. Response patterns of the neuron to the movement of a bright spot vertically (perpendicularly to the RF horizontal axis) at consecutive steps over the RF. A, 1-6) Response patterns to the upward movement of the bright spot (2 deg) by 2 deg steps crossing the RF horizontal axis. A, 7-12) Response patterns to the downward movement of the bright spot. Arrows indicate the path of stimulus movement. B, 1, 2) Lengths of the receptive field VA estimated at consecutive steps (2 deg) along of RF horizontal axis at upward (B, 1) and downward (B, 2) movements of the bright spot. B, 3) Plot of the direction sensitivity index (DSI) for each consecutive path of the bright spot movement (numbers under the plot).

Р и с. 4. Патерни відповідей нейрона на вертикальні рухи яскравої плями (перпендикулярно горизонтальній осі рецептивного поля) з послідовним зміщенням траєкторії.



F i g. 5. Response patterns of the neuron shown in Fig. 3 and 4 to the vertically moving dark spot over the RF. A, 1-5) Response patterns to the upward movement of the dark spot across the RF at 2 deg steps along the RF horizontal axis. A, 6-10) Response patterns to the downward movement of the dark spot. B, 1, 2) Lengths of the RF vertical axes estimated for each path of the dark spot upward (B, 1) and downward (B, 2) movements. B, 3) Plot of the direction sensitivity index measured for each path of the vertically moving dark spot (numbers under the plot).

Р и с. 5. Патерни відповідей того ж самого нейрона, що й на рис. 3 та 4, на вертикальні рухи темної плями через рецептивне поле.

were quite evident along two vertical trajectories of the moving stimulus, while the HA parameters remained practically unchanged. Generally, all neurons of this group with the homogenous structures of their RFs demonstrated similar characteristics of RF size modulation at application of moving visual stimuli. Differences were related mainly to the quantitative aspects of individual response patterns of certain neurons.

DISCUSSION

Modifications of the neuronal RF sizes in the primary visual cortex were investigated earlier [17–21], and the importance of influences coming from the RF surrounding were outlined as a main source of the observed RF size changes. We have provided further investigation of the problem trying to find out whether the dynamics of visually sensitive neuron RF sizes is a general phenomenon, and whether application of moving stimuli along certain orientation of the RF axis evokes simultaneous RF size expansions involving all orientations of the RF axes. Our experimental results showed that dynamic changes in the RF spatial dimensions of visually sensitive neurons in the extrastriate area 21a having a homogenous structure of the stationary RF occur mainly at a certain trajectory of motion of the applied visual stimulus across the RF. One may infer that, along the path of motion, the visual stimulus causes excitation of surrounding neurons of the RF environment, especially of those having horizontal intracortical connections with the cells localized along the track of stimulus motion; these cells influence the neuron under investigation. It may be concluded that a visual stimulus, in the course of its motion along the trajectory, excites neighboring neurons of the RF environment, especially those with intracortical horizontal connections. Besides, it also cannot be ruled out that feedback influences on the cortical neuron are activated by the applied visual stimulus [22, 23]. Thus, it is obvious that adjacent

neuronal circuits, similarly to those in the primary visual cortex, play in the extrastriate cortical area 21a a decisive role in modulation of the qualitative and quantitative characteristics of neuronal RFs in the course of central processing of incoming visual information. Our data suggest that excitation of neuronal circuits outside the neuronal RF is strongly determined by the trajectory of a moving visual image, thus ensuring more specialized diversification at central processing of incoming visual information concerning the precise perception of the shape, size, and direction of motion of percepted images.

All experimental procedures involving animals were approved by the Ethical Commission at the Yerevan State Medical University and corresponded to the international standards.

The authors of this study, D. K. Khachvankian, A. L. Ghazaryan, B. A. Harutiunian-Kozak, M. M. Momjian, and H. R. Aslanian, confirm that the research and publication of the results were not associated with any conflicts regarding commercial or financial relations, relations with organizations and/or individuals who may have been related to the study, and interrelations of co-authors of the article.

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РОЗШИРЕННЯ РЕЦЕПТИВНИХ ПОЛІВ У ЕКСТРАСТРІАТНІЙ ЗОРОВІЙ КОРІ: ЗНАЧЕННЯ ТРАЄКТОРІЇ СТИМУЛУ, ЩО РУХАЄТЬСЯ

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Р е з ю м е

Закономірності просторового розширення рецептивних полів (РП) при пред'явленні візуальних образів, що рухаються, досліджували на екстрастріатній зоровій корі кота (поле 21a). Величина та просторова інфраструктура РП зоровочутливих нейронів спочатку визначалися пред'явленням стаціонарних стимулів, що спалахують; при цьому визначали горизонтальні та вертикальні осі (ГО та ВО відповідно) РП. Потім точно вимірювали довжину вказаних осей, використовуючи просторове сканування РП візуальними стимулами, що рухаються. Було виявлено, що динамічне збільшення величин РП було, як правило, пов'язане з траєкторією руху стимулу через РП. Рух стимулу вздовж ГО РП зумовлював істотне збільшення довжини цієї осі, але не довжини ВО; в той же час рух стимулу вздовж ВО РП звичайно викликав «розтягування» тільки даної осі, тоді як ГО зазнавала мінімальних змін. Отримані результати вказують на те, що просторове розширення РП корелює насамперед із траєкторією руху стимулу через РП. Такий ефект, вірогідно, зумовлений збудженням досліджуваного нейрона під впливом кортикальних нейронних мереж, розташованих поблизу цієї клітини. Отже, нейронні мережі, локалізовані поза РП, відіграють вирішальну роль у модуляції якісних та кількісних характеристик класичних РП, забезпечуючи таким чином точнішу центральну обробку візуальної інформації, що надходить.

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