UDC 612.843.7:612.825.262

B. A. HARUTIUNIAN-KOZAK,[1] A. L. GHAZARYAN,[1] M. M. MOMJIAN,[1] D. K. KHACHVANKIAN,[1] and H. R. ASLANIAN[1]

CONTRAST-DEPENDENT RESTRUCTURING OF NEURONAL VISUAL RECEPTIVE FIELDS IN THE CAT EXTRASTRIATE CORTEX

Received March 28, 2016

Spatial modifications of neuronal visual receptive fields (RFs) in the cat extrastriate cortex were studied. The response properties and spatial organization of the RFs of area 21a neurons were investigated using visual stimuli of two opposite contrasts, with particular attention to the stationary structure of these RFs. It was found that the infrastructure of the RF of a visually sensitive neuron undergoes certain restructuring related to the contrast of the visual stimuli used. In most cases, discharge centers of the RF subfields changed their response profile and spatial localization within the RF depending on the stimulus contrast. Stationary RFs defined by presentation of flashing spots of two opposite contrasts (bright and dark) differed from each other quantitatively and qualitatively, indicating the influence of background illumination on the pattern of neuronal responses. It is hypothesized that the RF surrounding significantly influences central processing of incoming visual information and image recognition in the extrastriate cortex.

KEYWORDS: extrastriate cortex, visual receptive field (RF), stationary structure, contrast, spatial modifications, RF surrounding.

INTRODUCTION

The concept of the receptive field (RF) of a visually driven neuron in the retina and visual cortex of vertebrates was introduced by the pioneering studies of Hartline [1, 2] and Hubel and Wiesel [3–5]. The RF was defined as a certain limited portion of the visual space, where a change in the luminance intensity results in changes in the excitability of a visually sensitive neuron (excitation or inhibition). Considerable progress has been achieved in elucidating the regularities of central processing of visual information in the brain, especially in the striate and extrastriate visual cortices. Numerous studies [6–10] have shown that the characteristics of response patterns in the primary visual cortex and extrastriate cortical areas are mostly determined by spatial and temporal constraints of their RF stationary structure defined by presentation of visual stationary flashing stimuli. Later on, important findings were reported [11, 12], which showed even cells with a single "*on*" or "*off*" subregion in their stationary RF may reveal diversified response patterns to applications of moving visual stimuli. This was indicative of the existence of hidden adjacent inhibitory subregions in the visual space surrounding the tested RF. Furthermore, recent studies have shown that the RFs of visually driven neurons in the primary and extrastriate cortical areas are not static but show considerable spatiotemporal changes depending on the type of visual stimulus used [13–16]. The spatiotemporal RF structure may undergo substantial quantitative and qualitative modifications due to influences from the RF surrounding [17, 18]. Thus, central processing of visual information relies on the precisely correlated and coordinated integrative activity of neurons in hierarchically organized network structures of the brain, including the extrastriate visually sensitive areas. Thus, it is highly probable that spatial modulations of the RF sizes observed earlier [19–22] may significantly influence central processing of visual information.

In this study, we examined in detail both qualitative and quantitative characteristics (sizes and configurations) of the RFs of visually driven neurons

[1] Laboratory of Sensory Physiology, Institute of Applied Problems of Physics, National Academy of Sciences of Armenia, Yerevan, Armenia.
Correspondence should be addressed to B. A. Harutiunian-Kozak (e-mail: rnigagik@gmail.com),
A. L. Ghazaryan (e-mail: ana13am@yahoo.com),
M. M. Momjian (e-mail: mmelkon@yandex.ru) ,
D. K. Khachvankian (e-mail: khachvankyan@mail.ru) or
H. R. Aslanian (e-mail: hayk_aslanyan@yahoo.com).

upon application of stationary flashing and moving visual stimuli. The main goal of the experiments was to identify how the spatial substructure of neuronal RFs in the extrastriate area 21a defined by stationary flashing spots of two opposite contrasts (bright and dark) correelates with the features of responses of the neuron to moving visual stimuli. This study continues the examination of central processing of visual information in the extrastriate cortical area 21a. We found that the RF stationary structure is not constant but greatly depends on the contrast of the visual stimulus used; it is highly probable that influences from the areas surrounding the RF play a significant role in central processing of visual information and precise perception of visual images.

METHODS

The methods used were described in detail in earlier publications [23, 24]. The animals (cats) were initially anasthetized with alpha-chloralose (60 mg/kg, i.m). Tracheotomy and cannulation of the femoral artery were performed. Throughout the experiment, anesthesia was maintained by alpha-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). An opening (6 × 10 mm) was made in 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 myorelaxant Ditilin (diiodide dicholine ester of succinic acid, 7 mg/kg) was injected i.m. Artificial respiration (19 min^{-1}) with a stroke volume of 20 ml/kg body mass was administered. The body temperature was kept at ~38 °C with a heating pad. The pupils were dilated by topical application of 0.1% atropine solution; the corneas were protected from drying with zero-power contact lenses. Nictitating membranes were retracted by instilling Neo-synephrine (1%) into the conjunctival sac. The arterial blood pressure was continuously monitored and maintained at 90-100 mm Hg. The heart activity and EEG were continuously monitored throughout the experiment.

Extracellular recording of cortical single unit activity was provided by tungsten microelectrodes coated with vinyl varnish, with bare tips (1–3 μm) and 10-15 MΩ impedance. Action potentials were conventionally amplified, triggered, and passed to a digital analyzer for on-line analysis and data storage, using the averaged poststimulus/peristimulus time histogram (PSTH) mode for 16 realizations. The RF borders for each visually responsive neuron were defined by presentation of hand-held stimuli and plotted on a perimeter screen. The optic disc and *area centralis* (AC) were plotted on the screen, and the RF position in the visual field was referenced to the AC location [25]. Then the RF borders were carefully outlined by stationary flashing light spots (0.5-l.0 deg) positioned consecutively in the test zones across the hand-plotted RF area. The static properties of neurons were estimated also by a stationary flashing dark spot.

After this, moving visual stimuli (spots, bars, edges, and slits of different sizes and contrasts) were applied at a speed of 20 deg/sec. The 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. Bright stimuli were 15 lx against the 2 lx background, while dark stimuli were, conversely, 2 lx luminance against the 15 lx background.

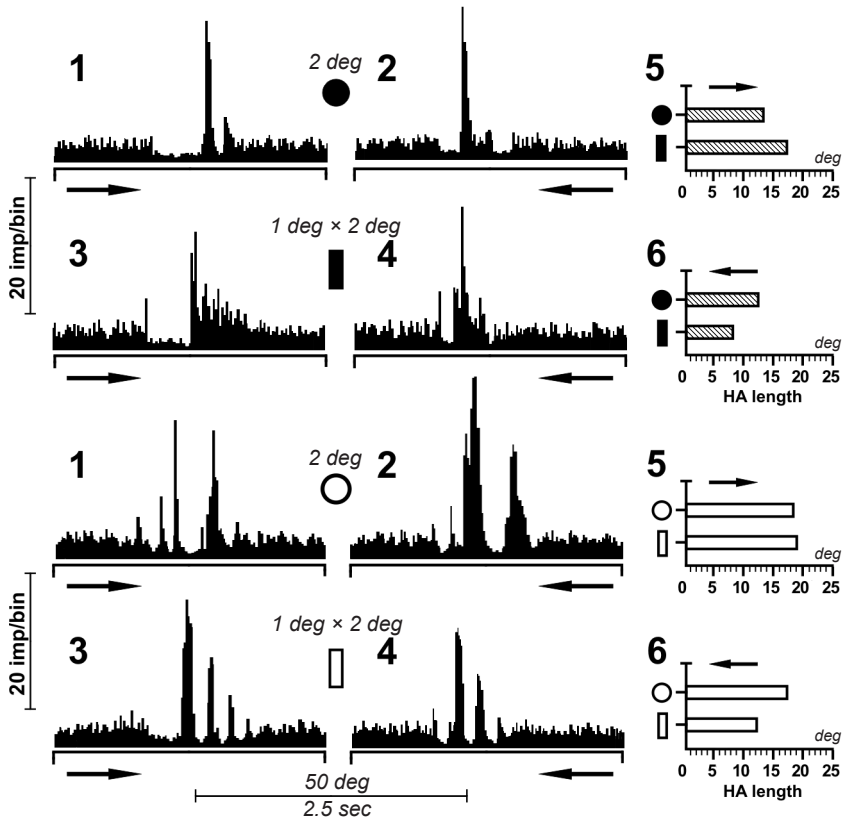
In some cases, coagulation was performed at the successive cortical recording points followed by perfusion of the animal with 10% formalin solution. The electrode tracks were reconstructed after examination of 50 μm-thick histological sections.

RESULTS

The main goal of our experiments was to determine whether the neuronal stationary RF structure is constant or can be modified depending on the contrast of the applied stationary flashing visual stimulus. Our experiments showed that there are substantial differences between the stationary RF spatial structures of visually driven neurons depending on the contrasts of stationary flashing spots. A total of 57 neurons was investigated; these were the cells from which sufficiently complete sets of static and dynamic response patterns were obtained and thoroughly explored. After hand-plot determination of the position of the neuronal RF in the visual coordinate system, the RF sizes and characteristics of the response patterns were measured by presentation of flashing bright and dark spots positioned consequently in the test subfields over the entire RF surface. Afterwards, moving visual stimuli were applied. In some cases, spatial scanning of the RF along the horizontal axis (HA) was performed at different levels of the RF

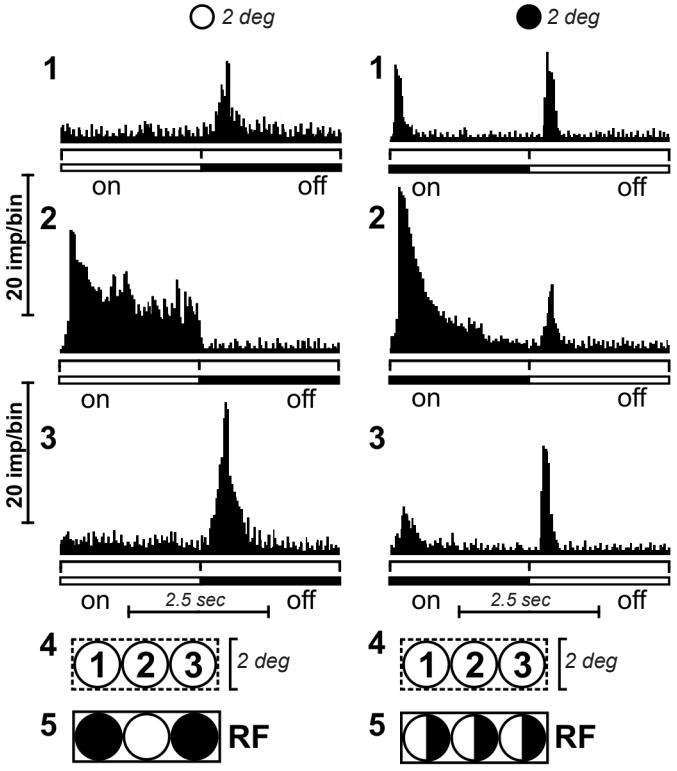
vertical axis (VA). The main goal of such scanning procedure was to obtain complete characteristics of the sensitivity of the examined neuron to moving stimuli over the visual space if the motion of a visual stimulus in the horizontal orientation across the RF leads to the corresponding parallel modification of the RF along the VA too.

Among 57 neurons investigated thoroughly, most units (43 neurons) demonstrated drastic modifications of the RF stationary structure depending on the contrast of the visual stimulus used. In Fig. 1, response patterns of the examined neuron are presented; moving visual stimuli of different shapes (spots and quadrangles) having two opposite contrasts (bright and dark) were used. As is seen in Fig. 1A, the 2-deg dark spot moving from the left to the right along the RF HA evoked a response profile consisting of initial suppression of background activity (an inhibitory phase) followed by a bimodal excitatory response (Fig. 1A, 1). When the stimulus moved in the opposite direction, initial suppression of background activity was elicited again, and then a monomodal excitation was followed by an inhibitory phase of the response (Fig. 1A, 2). Motion of a dark bar (1 deg × 2 deg) along the same track through the RF evoked initial suppression of background activity too, but the excitatory response was monomodal, with the discharge bursts occurring after the suppression phase (Fig. 1A3, 4). Significant spatial expansion of the RF HA was observed at stimulus movements in both directions (Fig. 1A, 5, 6). Significantly different response profiles of this neuron were observed upon changing the stimulus contrast into the opposite one. The response patterns became multimodal, and the response profiles upon motion of a bright spot (Fig. 1B, 1, 2), and also upon bright bar motion (Fig. 1B, 3, 4) differed from each other. Additionally, certain differences between expansions of the RF size were observed too; these differences depended on the contrast, shape, and direction of motion of the applied stimulus (Fig. 1B, 5, 6). Detailed exploration of the stationary spatial structure of the RF of this neuron appeared to be highly important for finding out whether the stationary RF structure also undergoes certain modifications depending on the contrast of stationary flashing spots used. Thus, detailed exploration of the stationary spatial structure of the same neuronal RF was provided using stationary flashing bright and dark spots (2 deg) consequently



F i g. 1. Response patterns of an area 21 neuron to presentation of moving stimuli of opposite contrasts. A) Peristimulus histograms (PSTHs) of the responses to rightward and leftward movements of a dark spot (2 deg; 1 and 2) and a dark rectangle (1 deg × 2 deg; 3 and 4) along the receptive field (RF) horizontal axis (HA), and lengths of the HA measured at rightward and leftward movements of the above visual stimuli (5 and 6). B) PSTHs of the responses (1–4) and HA lengths (5 and 6) for the movements of the analogous but bright stimuli, respectively. Arrows indicate the directions of stimulus motions; open and filled symbols indicate bight and dark stimuli, respectively.

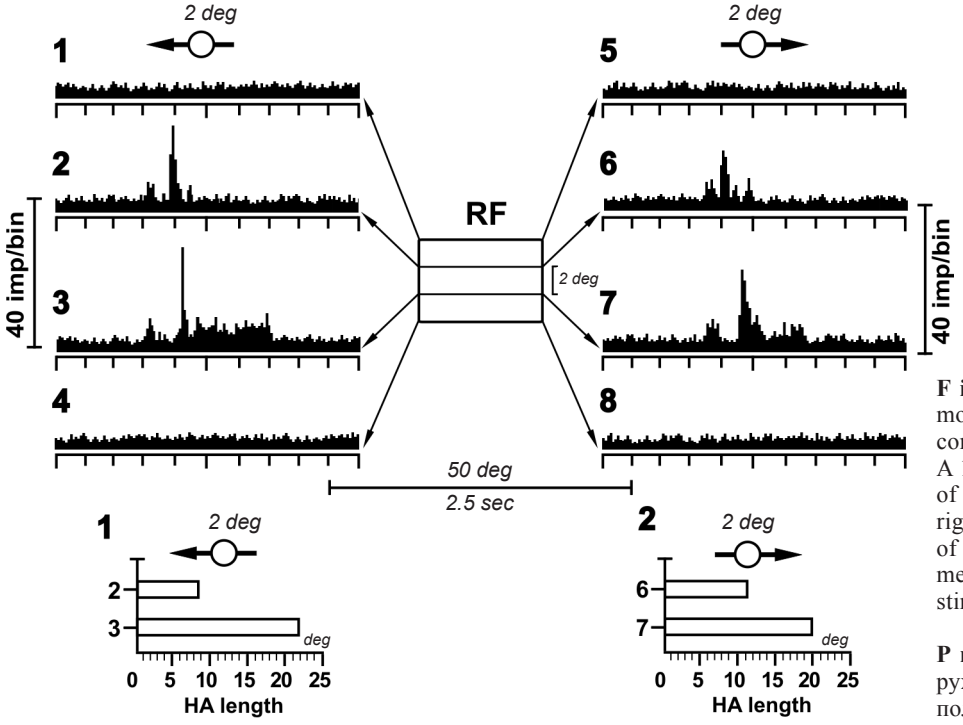
Р и с. 1. Патерни відповідей нейрона кортикального поля 21а на рух темних (*A*) та яскравих (*B*) стимулів із протилежними контрастами.



F i g. 2. Stationary spatial structure of the neuronal RF defined by presentations of bright and dark flashing spots. A 1–3) PSTHs of the responses to the stationary flashing bright spot (2-deg in diameter); 4) consecutive positions of the presented spots in the RF test zones; 5) schematic representation of the RF spatial functional structure. B 1–5) Response patterns (1–3), positions of the stimuli (4), and RF spatial structure (5) at presentation of a dark 2-deg spot. Open and dark circles in 5 indicate "*on*" and "*off*" responses, while half-dark circles indicate "*on-off*" ones; such symbols are used in all other figures.

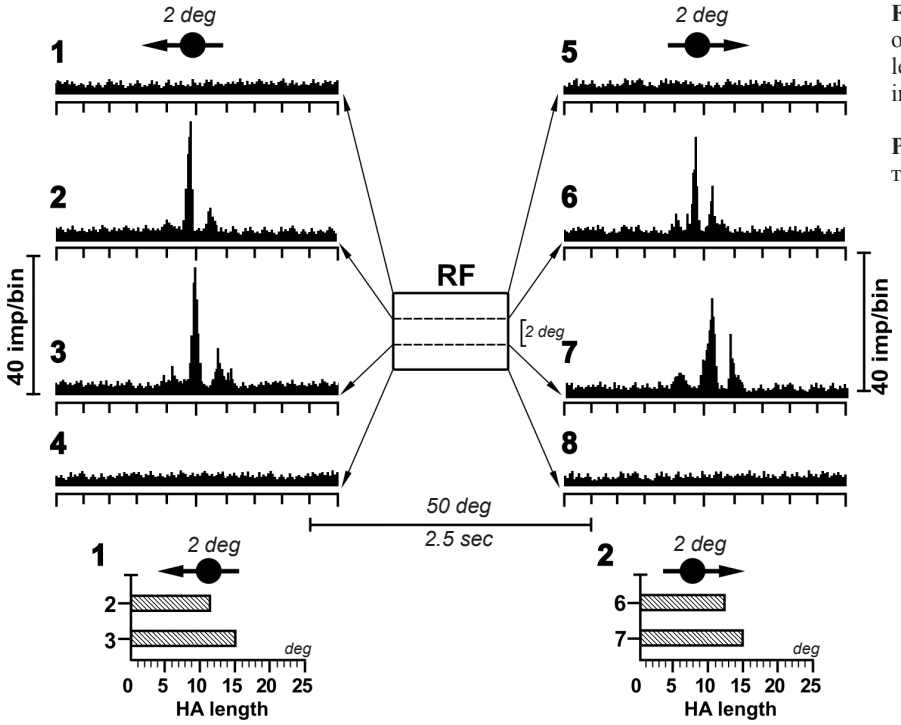
Р и с. 2. Стаціонарна просторова структура рецептивного поля нейрона, визначена при пред'явленні яскравих і темних плям, що спалахують.

disposed within the RF test subfields. In Fig. 2A1-3, the response patterns of the same neuron are shown; a flashing bright spot positioned side by side within the RF borders within the test subfields was presented (Fig. 2A, 4). As is seen in Fig. 2A1-3, the RF stationary structure consists of the *off*, *on*, and *off* discrete subfields. Thus, the RF size was estimated by the presentation of the 2-deg-wide bright flashing spot (Fig. 2A, 5). The same neuron tested by the dark flashing spot (Fig. 2B, 1-3) showed quite dissimilar (from the qualitative aspect) stationary RF structure. In this case, the RF consisted of three *on-off* subfields (Fig. 2B, 4, 5), but the RF size remained unchanged. The observed discrepancies between the response



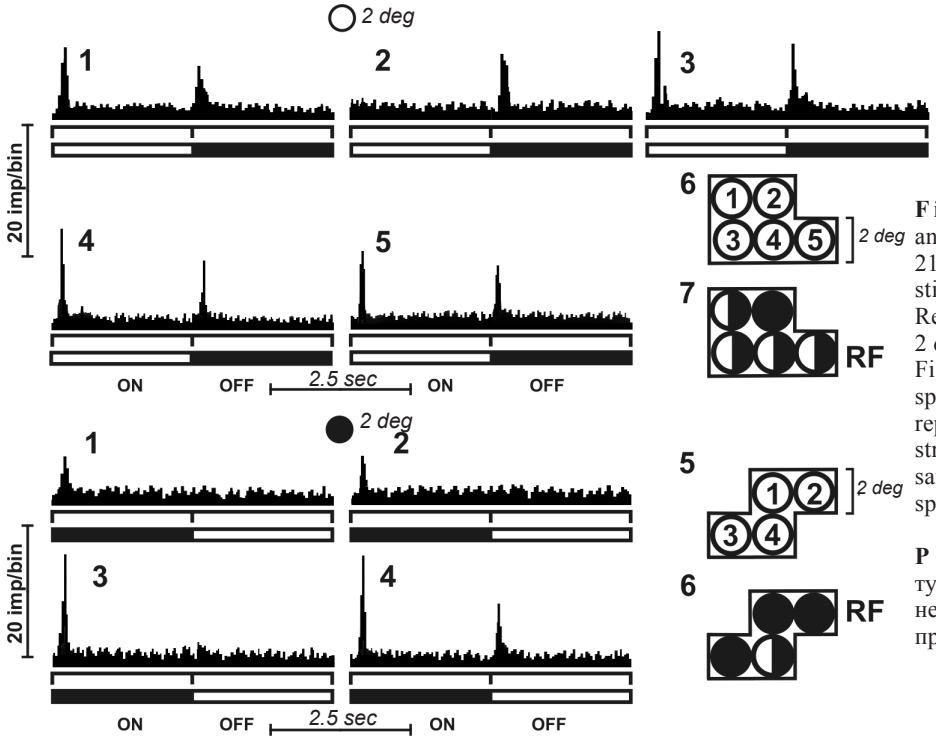
F i g. 3. Response patterns of a neuron to motions of a bright (2 deg) spot at different consecutive levels of the RF vertical axis. A 1–8) Response profiles to the movements of the above spot in the leftward (1–4) and rightward (5–8) directions. B 1, 2) Lengths of the RF horizontal axis at each VA level measured at two opposite directions of stimulus motion.

Р и с. 3. Патерни відповідей нейрона на рух яскравої плями через рецептивне поле по паралельних траєкторіях.



F i g. 4. Response patterns of a neuron to motions of a dark (2 deg) spot at different consecutive levels of the RF vertical axis. Panels A and B and indications are the same as in Fig. 3.

Р и с. 4. Патерни відповідей нейрона на рух темної плями по паралельних траєкторіях.



F i g. 5. Differences in the stationary structures and configurations of the RF of another area 21 neuron defined upon presentation of visual stimuli having two opposite contrasts. A, 1–5) Responses of a neuron to presentation of the 2 deg flashing bright spot; 6–7) the same as in Fig. 2 (consecutive positions of the presented spot in the RF test zones and schematic representation of the RF spatial functional structure, respectively). B, 1–4, 5, and 6) The same as in A but upon presentation of a dark spot. Indications are similar to those in Fig. 2.

Р и с. 5. Відмінності стаціонарної структури і конфігурації рецептивного поля нейрона, визначені при застосуванні двох протилежних контрастів зорових стимулів.

patterns are likely due to changes in the background illumination, which was dark in the case of application of the bright spot and opposite (bright) upon application of the dark flashing spot. Thus, certain influences from the RF surrounding on the activity profile of the examined neuron cannot be ruled out.

The question arises: Does the RF undergo any modifications in its VA when visual stimuli moving along the HA are applied? As the next step, spatial scanning of the neuronal RF was carried out at

consecutive different VA levels by horizontally moving bright and dark spots. In Fig. 3A, 1-8, the patterns of responses of a neuron upon presentation of the bright spot (1 deg) moving horizontally at consecutive VA levels of the RF are shown. The HA of the RF of this neuron defined by the stationary flashing bright spot was 6 deg long, and the VA was 4 deg long. As is seen in Fig. 3A, significant expansions of the RF HA were observed at both rightward and leftward directions of stimulus motion (Fig. 3B, 1, 2). The upper and lower borders of the RF tested by the same stimulus were unresponsive (Fig. 3A, tracks 1, 4, 5, 8). Thus, the RF HA is elongated several times, while the VA length remained at the 4 deg value, which was the VA magnitude defined by the stationary flashing spot. Afterwards, scanning of the RF of the same neuron by horizontal movements of the dark spot (2 deg) was performed (Fig. 4A, 1-8). Spatial expansions of the RF defined by the horizontally moving dark spot at four consecutive levels of the VA showed no respective changes in the VA length (4 deg). The extent of RF expansions is, however, smaller compared to that evoked by bright spot motion (Fig. 4B, 1, 2), and diversification of the response profiles occurred. Thus, substantial differences were observed between the neuronal response patterns to two opposite contrasts of the moving visual stimuli.

The stationary spatial structure of the neuronal RF was explored in detail by presentation of visual stimuli of two opposite contrasts. Flashing spots were introduced within the hand-plotted RF region sequentially, side by side, in the RF test-subfields over the entire RF surface (Fig. 5A, 6, B, 5). As is shown in Fig. 5A, B, the response profiles evoked by the flashing bright spot (Fig. 5A, 1-5) and flashing dark spot (Fig. 5B, 1-4) strongly differed from each other depending on the spatial position of the spot within the RF borders. Depending on the stimulus contrast, the RF shapes also varied significantly (Fig. 5A, 7, B, 6). The observed diversifications and modifications of the neuronal response patterns to flashing stimuli of two opposite contrasts are most probably due to changes in the level of background illumination (dark during application of the bright spot and, conversely, bright during application of the dark flashing spot). Taking into account that the stationary spatial structure of the RF of a visually sensitive neuron determines the response profiles of the neuron to presentation of moving stimuli, it seems quite logical that dynamic restructuring of the RF stationary spatial organization during application of moving visual stimuli plays an important role in modifications of the neuronal response patterns we observed.

DISCUSSION

In our study, a special approach was used; it was directed toward exploration of the precise spatial structure of the stationary RFs of these cells. For examination of visually driven neurons localized in the extrastriate area 21a, two opposite contrasts of stationary flashing spot stimuli were used as a first step in revealing the neuronal mechanisms related to contrast discrimination and image perception by visually sensitive neurons of the brain structures. Our results demonstrated the existence of crucial differences in the stationary spatial RF structure depending on the contrast of the applied visual stimuli. For example, the tested subregion in the RF, when excited by a bright flashing spot, produced "*on*" responses, i.e., the neuron was excited by illumination of this subregion. The same RF subfield evoked also "*on*" responses to presentation of a dark flashing spot (instead of "*off*") at the darkening of the same subfield. Additionally, the RF spatial configurations upon changing these stimuli also become different (at least in most cases) depending on the stimulus contrast. As a preliminary hypothesis, we suggest that the background luminance that was different for bright and dark flashing stimuli may play an important (and even crucial) role in modifications of the above neuronal response patterns. Earlier, it was shown by Barlow et al. [26] that dark adaptation of the retina results in substantial changes in the RF spatial organization defined by stationary flashing visual stimuli. Later on, McIllwain [27] presented data according to which RFs in the lateral geniculate nucleus are strongly influenced by the RF surroundings; this was called by the author a "peripheral effect." Recent studies showed that descriptions based only on a "classical" mode of estimation of the RF of the neuron may not be sufficient for understanding the principles of central visual processing involving contextual information. Visual inputs from fields beyond the "classic" RF, called an extra-receptive field (ERF), were found to inhibit or facilitate responses elicited by stimulation of the above classic RF [28]. Thus, it is obvious that the influences coming from the surrounding of the RF due to changes in the background luminance parameters

(especially via intracortical networks with horizontal connections [29–31]) play a highly important role in central processing of incoming visual information (by modulation and restructurization, both qualitative and quantitative, of the neuronal RF). In principle, these effects can provide crucial transformation of the characteristics of such RFs. It cannot be ruled out that neuronal afterdischarges and the activity of feedback synaptic connections are factors involved in realization of the above-described RF modifications.

All procedures followed were in accordance with the ethical standards of the responsible Committees on human experimentation (institutional and national) and with the Helsinki Declaration of 1975, as revised in 2000.

The authors of this study, B. A. Harutiunian-Kozak, A. L. Ghazaryan, M. M. Momjian, D. K. Khachvankian, 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.

Б. А. Арутюнян-Козак[1], А. Л. Газарян[1], М. М. Момджян[1], Д. К. Хачванкян[1], Х. Р. Асланян[1]

ЗАЛЕЖНІ ВІД КОНТРАСТУ ПЕРЕБУДОВИ СТАЦІОНАРНОЇ СТРУКТУРИ ЗОРОВИХ РЕЦЕПТИВНИХ ПОЛІВ У ЕКСТРАСТРІАТНІЙ КОРІ КОТА

[1]Інститут прикладних проблем фізики НАН Вірменії, Єреван (Вірменія).

Р е з ю м е

Досліджували просторові модифікації зорових рецептивних полів (РП) нейронів екстрастріатної кори кота. Властивості реакцій та просторова організація РП нейронів поля 21а визначали, використовуючи зорові стимули двох протилежних контрастів; особливу увагу приділяли стаціонарній структурі РП. Результати проведених експериментів показали, що просторова інфраструктура РП візуально чутливих нейронів піддається певній реструктуризації залежно від контрасту використаних візуальних стимулів. У більшості випадків розрядні центри субполів РП змінювали профіль їх відповідей і просторову локалізацію в межах РП залежно від контрасту використаного стимулу. Отже, стаціонарні структури РП, визначені за допомогою пред'явлення спалахуючих плям двох протилежних контрастів (яскравих та темних), істотно розрізнялися кількісно та якісно, що вказує на вплив фонового освітлення на патерн відповіді нейрона. Висунуто гіпотезу, згідно з якою впливи, що надходять від оточення РП, відіграють значну роль у центральній переробці отриманої візуальної інформації і формуванні образу в екстрастріатній корі.

REFERENCES

1. H. K. Hartline, "The response of single optic nerve fibers of the vertebrate eye to illumination of the retina," *Am. J. Physiol.,* **121**, No. 2, 400-415 (1938).
2. H. K. Hartline, "The receptive field of the optic nerve fibers," *Am. J. Physiol.,* **130**, No. 3, 690-699 (1940).
3. D. H. Hubel and T. N. Wiesel, "Receptive fields of single neurons in the cat's striate cortex," *J. Physiol.,* **148**, No. 3, 574-591 (1959).
4. D. H. Hubel and T. N. Wiesel, "Receptive fields, binocular interaction and functional architecture in the cat's visual cortex," *J. Physiol.,* **160**, No. 1, 106-154 (1962).
5. D. H. Hubel and T. N. Wiesel, "Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of cat," *J. Physiol.,* **28**, No. 2, 229-289 (1965).
6. D. Debanne, D. E. Shultz, and J. Fregnac, "Activity-dependent regulation of "on" and "off" responses in cat visual receptive fields," *J. Physiol.,* **508**, No. 2, 523-548 (1998).
7. F. Mechler and D. J. Ringach, "On the classification of simple and complex cells," *Vis. Res.*, **42**, No. 8, 1017-1033 (2002).
8. J. R. Cavanaugh, W. Bair, and A. Movshon, "Nature and interaction of signals from the receptive field centre and surround in macaque V1 neurons," *J. Neurophysiol.*, **88**, No. 5, 2530-2546 (2002).
9. G. H. Henry, "Receptive field classes of cells in the striate cortex of the cat," *Brain Res.,* **133**, No. 1, 1-28 (1977).
10. L.A. Palmer and T. J. Davis, "Receptive field structure in cat striate cortex," *J. Neurophysiol.*, **46**, No. 2, 260-276 (1981).
11. P. O. Bishop, J. S. Coombs, and G. H. Henry, "Receptive fields of simple cells in the cat striate cortex," *J. Physiol.,* **231**, No. 1, 31-60 (1973).
12. J. Xing and G. A. Gerstein, "Networks with lateral connectivity. Development of neurons grouping and corresponding receptive field changes," *J. Neurophysiol.,* **75**, No. 1, 200-215 (1996).
13. B. Dreher, A. Michalski, R. H. T. Ho, et al., "Processing of form and motion in area 21a of cat visual cortex," *Vis. Neurosci.,* **10**, No. 1, 93-115 (1993).
14. U. T. Eysel, D. Eyding, and G. Schweigart, "Repetitive optical stimulation elicits fast receptive field changes in mature visual cortex," *NeuroReport,* **9**, No. 5, 949-954 (1998).
15. K. Suder, K. Funke, Y. Zhao, et al., "Spatial dynamics of receptive fields in cat primary visual cortex related to the temporal structure of thalamocortical feedforward activity," *Exp. Brain Res.,* **144**, No. 4, 430-444 (2002).
16. B. A. Harutiunian-Kozak, D. K. Khachvankian, G. G. Grigorian, et al., "Dynamic spatial organization of receptive fields of neurons in the 21a cortical area," *Neurophysiology,* **42**, No. 3, 175-184 (2010).
17. C. D. Gilbert and T. N. Wiesel, "Receptive field dynamics in adult visual cortex," *Nature,* **356**, No. 6365, 150-152 (1992).
18. A. Angelucci, J. B. Levitt, E. F. S. Walton, et al., "Circuits for local and global signal integration in primary visual cortex," *J. Neurosci.,* **22**, 8633-8646 (2002).
19. M. W. Pettet and C. D. Gilbert, "Dynamic changes in receptive field size in cat primary visual cortex," *Proc. Natl. Acad. Sci. USA,* **89**, 8366-8370 (1992).
20. A. Das and C. D. Gilbert, "Receptive field expansion in adult visual cortex is linked to dynamic changes in strength of cortical connections," *J. Neurophysiol.,* **74**, No. 2, 779-792 (1995).
21. B. J. Malone, V. R. Kumar, and D. L. Ringach, "Dynamics of

receptive field size in primary visual cortex," *J. Neurophysiol.,* **97**, No. 1, 407-414 (2007).
22. D. K. Khachvankian, B. A. Harutiunian-Kozak, H. R. Aslanian, et al., "Dynamic changes in receptive field sizes of visually sensitive neurons in extrastriate area 21a," *Eur. J. Nat. Sci.,* **2**, No. 23, 42-46 (2014).
23. D. K. Khachvankian, H. R. Aslanian, A. P. Antonian, et al., "Regularities of visual receptive field spatial expansion at the application of moving stimuli, " *Eur. J. Nat. Sci.,* **2**, No. 25, 45-48 (2015).
24. D. K. Khachvankian, H. R. Aslanian, B. A. Harutiunian-Kozak, et al., "Responses of cortical extrastriate area 21a neurons specialized in motion detection," *Neurophysiology*, **47**, No. 3, 19-25 (2015).
25. P. O. Bishop, W. Kozak, and G. J. Vakkur, "Some quantitative aspects of the cat's eye: axis and plane reference, visual field co-ordinates and optics," *J. Physiol.,* **163**, No. 3, 466-502 (1962).
26. H. B. Barlow, R. Fitzhugh, and S. Kuffler, "Change of organization in the receptive fields of the cat's retina during dark adaptation," *J. Physiol.,* **137**, No. 3, 338-354 (1957).
27. J. T. McIlwain, "Receptive fields of optic tract axons and lateral geniculate cells: extent of barbiturate sensitivity," *J. Neurophysiol.,* **27**, No. 6, 1154-1173 (1964).
28. C. Blakemore and E. Tobin, "Lateral inhibition between orientation detectors in cat visual cortex," *Exp. Brain Res.,* **15**, No. 4, 439-440 (1972).
29. C. Y. Li, Y. X Zhou, X. Pei, et al., "Extensive disinhibitory region beyond the classical receptive field of cat retinal ganglion cells," *Vis. Res.,* **32**, No. 2, 219-228 (1992).
30. C. L. Passaglia, C. Enroth-Cugell, and J. B. Troy, "Effects of remote stimulation on the mean firing rate of cat retinal ganglion cells," *J. Neuroscience*, **21**, No. 15, 5794-5803 (2001).
31. T. Akasaki, H. Sato, Y. Yoshimura, et al., "Suppressive effects of receptive field surround on neuronal activity in the cat primary visual cortex," *Neurosci. Res.*, **43**, No. 3, 207-220 (2002).