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RECEPTIVE FIELD CHARACTERISTICS OF NEURONS IN THE NUCLEUS OF THE BASAL OPTIC ROOT IN PIGEONS

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Abstract—Optokinetic nystagmus is a reflex to stabilize an object image on the retina by compensatory eye movements. In lower vertebrates, the nucleus of the basal optic root participates in generating this reflex. Visual responses of 135 neurons were extracellularly recorded from the nucleus in pigeons and their receptive field properties were analysed on-line with a workstation. These cells could be categorized into slow (84%), intermediate (3%) and fast (13%) cells, preferring motion velocities of 0.25–8, 16 and 32–64 deg./s, respectively. Using whole-field gratings as stimuli revealed that 97% of the cells were selective for direction of motion and 3% were not. The directional cells preferred motion in the dorsoventral (35%), nasotemporal (34%), ventrodorsal (23%), or temporonasal (8%) directions. The omnidirectional neurons were equally excited or inhibited by motion in all directions. The receptive field of basal optic neurons usually consisted of an excitatory receptive field and an inhibitory receptive field, both of which possessed opposite (heterodirectional) or identical (homodirectional) directionalities. In the case of homodirectional co-existence of both fields, whether whole-field gratings could produce visual responses from the cells would depend on the interaction between excitation and inhibition evoked in their excitatory and inhibitory receptive fields, respectively. Therefore, in some cases a single object was more effective than whole-field gratings in eliciting visual responses from basal optic neurons in pigeons.

All of these receptive field properties revealed by on-line computer analysis may underlie the detection of optic flow and the induction of optokinetic responses. © 1999 IBRO. Published by Elsevier Science Ltd.

Key words: directionality, nucleus of the basal optic root, optokinetic nystagmus, pigeon, receptive field, velocity preference.

The nucleus of the basal optic root (nBOR) is a mesodiencephalic structure of the accessory optic system in birds. Its retinal input arises primarily, if not exclusively, from the displaced ganglion cells.[10,20,28,29] It also receives extraretinal afferents from the visual forebrain[4,30] and the raphe nuclei,[34] as well as from the contralateral nBOR and the ipsilateral nucleus lentiformis mesencephali (nLM),[3,23] which is a pretectal component of the accessory optic system. nBOR sends diverse projections to various regions in the midbrain, diencephalon and cerebellum, including the contralateral nBOR, ipsilateral nLM, reticular formation, central gray, pontine nuclei, vestibulocerebellum and oculomotor complex.[3,5,10,15,33,42,43] This nucleus has been suggested to be homologous to the medial, lateral and dorsal terminal nuclei of the accessory optic tract in mammals.[9,23] In fact, several anatomical studies have found that avian nBOR could also be divided into three regions: nBOR proper, lateral nBOR and dorsal nBOR.[3,33] These findings imply that nBOR in birds may play an important role in generating optokinetic nystagmus, stabilizing an object image on the retina by eye movements.

Electrophysiological studies performed in various species have shown that neurons in nBOR and in its mammalian homologues prefer whole-field stimuli moving at low velocities in particular directions (for example, frog,[17] turtle,[31] chicken,[6] pigeon,[4,5,15,24,37–39] owl,[44] rabbit,[32] rat,[26] cat[16] and monkey[25]). These neurons usually prefer upwards and downwards motion of visual stimuli. Their direction selectivities could be modulated by the visual wulst in pigeons[4] and by the cortex in mammals.[16,27] Both electrophysiological studies[38,44] and 2-deoxyglucose mapping technique[22,23] have verified the existence of a directional parcellation within avian nBOR. However, very little is known about the functional organization of the receptive fields (RFs) in this accessory nucleus, although several physiological studies have indicated that nBOR cells possess large RFs and respond in an inhibitory manner to stimuli moving in the direction opposite to the preferred direction.[4,11,24,44] Recently, we have found that RFs of nLM neurons in pigeons are well organized, and they respond both to whole-field gratings and to small targets.[12,13] These neurons are essentially edge detectors.[13]

In view of the findings that both nBOR and nLM are responsible for oculomotor reflex stabilizing an

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Abbreviations: ERF, excitatory receptive field; IRF, inhibitory receptive field; nBOR, nucleus of the basal optic root; nLM, nucleus lentiformis mesencephali; RF, receptive field.

object image on the retina, the present study was therefore undertaken to further reveal the receptive field properties of nBOR neurons, and to compare them with those of nLM neurons in pigeons, by using extracellular recording and quantitative analysis techniques.

EXPERIMENTAL PROCEDURES

The experiments were performed on 33 adult pigeons (*Columba livia*; purchased from the Beijing pigeon market), weighing 340–480 g, both sexes, following the Policy on the Use of Animals in Neuroscience Research approved by the Society for Neuroscience in 1995. The animal was anesthetized with urethane (20%, 1 ml/100 g body weight) and then placed in a stereotaxic apparatus. The body temperature was maintained at 41°C by a heating pad. Surgical exposure of the caudal forebrain on the left side was done in a conventional manner and the dura mater overlying the exposed part was excised. The nictitating membrane of the right eye was cut to keep the eye open and the other eye was covered with an occluder. The nucleus of the basal optic root was approached according to its stereotaxic coordinates[21] and confirmed by visual responses. Extracellular recordings of action potentials were obtained using a micropipette (2–3 μm tip diameter) filled with solution containing 2 M NaCl and 100 mM $CoCl_2$. Cobalt-sulfide markings of 11 recording sites verified the reliability of our isolating nBOR units. Neuronal signals from nBOR cells were amplified and then displayed on an oscilloscope, as well as fed into a workstation computer for on-line processing.

Visual stimuli were generated by the workstation (Silicon Graphics Indigo 2) and rear-projected through a three-color projector (Electrohome ECP4101) on to a screen 180 cm in height and 220 cm in width, which was 40 cm distant from the viewing eye, and made an angle of 24 deg. with the longitudinal axis of the pigeon body. Because the angle between the eye-center to bill-tip line of a stereotaxically fixed pigeon and the horizontal meridian of the visual field is 72 deg., while it is 34 deg. during normal behaviors such as flying, walking, perching and standing,[8] the horizontal meridian was rotated clockwise by 38 deg. The relationship between the position and orientation of the pecten plotted with an ophthalmoscope, the visual axis, the horizontal and vertical meridians verified the correctness of this rotation. Under this situation, the screen area that could be visually simulated was 140 deg. horizontally and 130 deg. vertically.

Two types of visual stimulus used in the present study were previously described.[14] In brief, type I was a whole-field grating pattern consisting of equal-width black and white stripes, with contrast of 0.97 and spatial frequencies of 4.5–6.0 cycles/m. These gratings were randomly moved in eight directions (0 deg.—nasal, 45 deg., 90 deg.—dorsal, 135 deg., 180 deg.—temporal, 225 deg., 270 deg.—ventral, 315 deg.) at a series of angular velocities ranging from 0.25 to 128 deg./s with a multiplication factor of 2. They were used to measure the directionality and preferred velocities of nBOR cells. Type II was a single square (6×6 deg.) moving at particular velocities in particular directions to scan the whole screen randomly along a series of parallel paths. This single target was used to study the functional organization of RFs of nBOR neurons. To explore the inhibitory receptive fields (IRFs) of the neurons with negligible spontaneity, a grating pattern moving within a display window over their excitatory receptive fields (ERFs) was used to evoke these cells to discharge. The directionalities, velocity preferences and functional organization of RFs of nBOR cells were on-line analysed with the workstation. The total distribution of excitatory vectors representing directional selectivity of nBOR neurons was obtained using Gaussian fitting. For an individual cell, its directional-response data were fitted with Gauss formula to determine the direction in which the cell produced the maximal responses; this direction was considered to be the preferred direction of this cell.

In some experiments, cobalt ions were microiontophoretically ejected using positive pulses of 10 μA in intensity, 0.5 s in duration and 1 Hz in frequency, for 10 min to histologically verify the recording sites.[12,35] Under deep anesthesia, the brain was immediately removed from the skull and then immersed for 25–30 min in saline containing ammonium sulfide to form a black precipitate of cobalt sulfide. The brain tissue was fixed in 10% formalin solution and soaked in 30% sucrose solution overnight. Frozen sections were cut at 80 μm thickness, mounted, counterstained with Cresyl Violet, dehydrated and covered for subsequent observation with a microscope.

RESULTS

Visual responses of 135 cells were extracellularly recorded from stereotaxically defined nBOR region, and 11 recording sites marked with cobalt sulfide were all localized within the nucleus. These cells were firing spontaneously, with an average rate of 22.3 ± 16.5 spikes/s (mean ± S.D., $n = 135$). According to their direction-selective responses to whole-field stimulation, nBOR cells could be classified into two main groups: 131 (97%) directional and 4 (3%) omnidirectional cells. The directional group contained three types of neurons. The first type of cells ($119/131 = 91\%$) responded maximally to whole-field stimulation moving at optimal velocities in the preferred directions, and were inhibited by motion in directions approximately opposite to the preferred directions (Fig. 1A). The second type of cells ($4/131 = 3\%$) maximally discharged to motion in the preferred directions, but no inhibition occurred in any direction. The third type of cells ($8/131 = 6\%$) responded in an inhibitory manner to moving whole-field gratings. The inhibition was also directionally tuned, with the weakest inhibition occurring in the forward, upward or backward directions. Among the directional cells, 30 cells preferred upward, 46 downward, 45 backward and 10 forward motion. Therefore, it appeared that nBOR cells in pigeons preferred vertical and backward motion of whole-field stimuli (Fig. 1B). The omnidirectional group defined by non-directional responses to whole-field stimuli included two cells that were almost equally excited or inhibited by motion in all directions, and two object-preferring cells that responded to single target but not to whole-field gratings. Systematic recordings made in one pigeon showed that neurons with a similar directionality tended to be clustered together. Generally speaking, upward-preferring cells were localized in the dorsal part of the nucleus, ventral were downward cells, and backward cells were in the most ventral part; forward cells were localized in the dorsomedial part of the caudal nBOR and omnidirectional cells in the dorsolateral part of the rostral nBOR.

The velocity preference of 37 cells was measured using whole-field stimuli moving at a series of

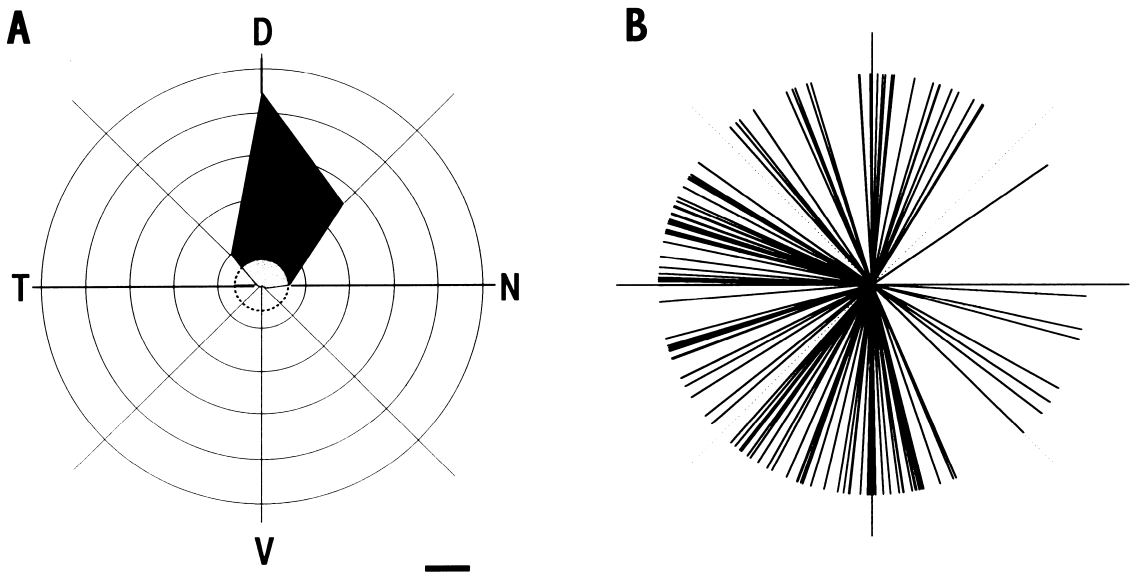

Fig. 1. (A) Directional tuning profile of a nBOR neuron that was maximally excited by upward motion (grey polygon) and inhibited by downward motion (greyish sector) of whole-field gratings (spatial frequency: 4.5 cycles/m; black–white contrast: 0.97) moved randomly in eight directions. (B) Total distribution of directionalities of 131 nBOR neurons that was obtained by Gaussian fitting based on the directional–response data obtained from measurements in eight directions. Gaussian fitting could find the preferred direction of each of these cells, which may be one of the eight directions, or some other direction. N, D, T and V represent nasal, dorsal, temporal and ventral, respectively. Dotted circle, spontaneous activity = 14 spikes/s; Scale bar: (A) = 24 spikes/s.

velocities in the preferred directions. Our data analysis indicated that 31 cells (84%) preferred slow motion (0.25–8 deg./s), one cell (3%) preferred an intermediate velocity (16 deg./s) and five cells (13%) responded maximally to fast-moving gratings (32–64 deg./s) (Fig. 2). Generally speaking, the pigeon nBOR cells were broadly velocity-tuned. No apparent correlation between directionalities and velocity preferences was observed in these cells.

By scanning a square (6 × 6 deg.) at a velocity of 8 deg./s over the whole screen, the RF properties were analysed in 35 nBOR cells. As an example, Fig. 3 shows that this cell had an ERF and an IRF in the upward direction (A) and an ERF alone in downward direction (B). Six out of 35 cells only had ERFs, and 29 others possessed both ERFs and IRFs. Care should be taken to analyse the field organization of broadly direction-tuned cells, because more than one ERFs or IRFs mapped with single target moving in different directions may actually be the same one, evidenced by the fact that these ERFs or IRFs had the same "sensitive center" and similar shapes. This was not the case with the cell whose ERFs and IRF are shown in Fig. 3. The ERF mapped by upward motion and the one by downward motion were quite different in their locations, sensitive centers and shapes (Fig. 3C, D). Among 29 cells with both ERFs and IRFs, one ERF and one IRF existed in 19 cells, one ERF and two IRFs or the reverse in six cells, two ERFs and two IRFs in two cells, and two others had up to four ERFs and/or IRFs each. These co-existent ERFs and IRFs appeared in the same direction (homodirectional) (Fig. 3A, C) or in different directions (heterodirectional). If ERF and IRF were homodirectional, whole-field stimulation could not elicit visual responses in the cases that contribution of ERF was balanced by that of IRF; otherwise, the cell would show either excitatory or inhibitory responses. In this situation, a single object was very effective in eliciting either excitatory or inhibitory responses from accessory optic neurons.

The present study indicated that accessory optic cells in pigeons responded both to whole-field stimuli and to a single object moving through their RFs (Fig. 4). Some cells could respond vigorously to a moving object as small as 0.5 deg. Comparison of visual responses of 35 neurons to whole-field gratings (spatial frequency: 4.5 cycles/m) with those to a single square (6 × 6 deg.) moving at 8 deg./s in the preferred directions showed that both stimulations produced equivalent responses in 17 cells (48%), 15 of which had one ERF each and two others had homodirectional co-existence of ERF and IRF; whole-field stimuli were more effective in eight cells (23%), seven of which had one ERF each and one cell had both ERF and IRF, and less effective in 10 cells (29%), eight of which had homodirectional ERF and IRF and two others only had ERF, than the single target in eliciting visual responses, if only considering the responsive peak frequencies. In some homodirectional cells, only the single target could produce excitation or inhibition, because

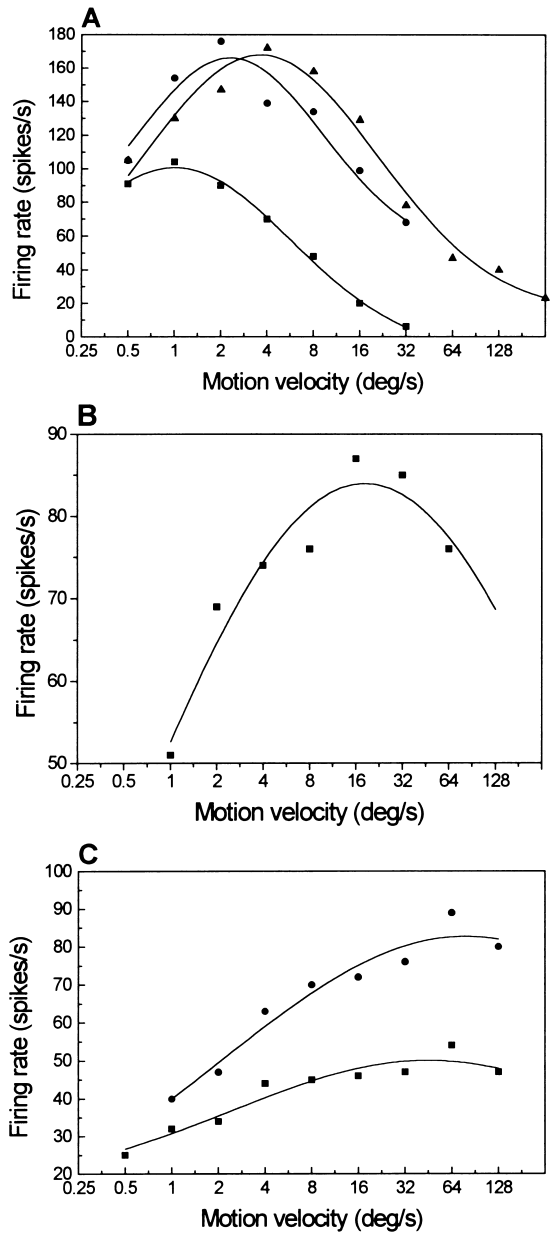

Fig. 2. Examples of velocity-tuning curves of three slow cells (A, solid circles, triangles and squares), an intermediate cell (B), and two fast cells (C, solid circles and squares). Visual stimuli were whole-field gratings with a spatial frequency of 4.5 cycles/m and black-white contrast of 0.97, which were moved at a series of angular velocities 0.25–128 deg./s by a multiplication factor of 2. Note that these cells are broadly tuned.

whole-field gratings may simultaneously stimulate both ERFs and IRFs, resulting in the cancellation of excitation and inhibition. The cell shown in Fig. 4A–B appeared to be a good example of this situation. In cells with sole ERFs or in heterodirectional cells, whole-field gratings could produce peak firing frequencies similar to those evoked by a single object, but the total number of spikes was quite different in these cases because of continuous stimulation by gratings (Fig. 4C, D).

Excitatory receptive fields in 85% of cells and inhibitory receptive fields in 95% of cells in the pigeon nBOR were elliptical in shape. The other fields were round-shaped. The long and short axes of ERFs were 67.2 ± 30.0 deg. and 47.4 ± 22.4 deg. (mean $\pm$ S.D. $n = 52$) and those of IRFs were 75.4 ± 33.6 deg. and 56.1 ± 28.3 deg. ($n = 50$), respectively. They were mainly elongated in the vertical and horizontal directions. About two-thirds of RF centers were localized in the superior visual field, and more than half of the centers were in the posterior visual field (Fig. 5). These fields were heterogeneous in responsiveness, characterized by the fact that there existed a "sensitive center" within an ERF or IRF, where a single object moving at the optimal velocity in the preferred direction could elicit the strongest responses and the more peripheral the region the object was moving through, the weaker the responses it could produce from the cell under study.

DISCUSSION

Several electrophysiological studies have indicated that the pigeon nBOR cells are sensitive to large-field patterns moving slowly in particular directions.[4,37,38] The present study not only confirms the previous findings, but also shows that these cells could respond both to whole-field stimuli and to a single object, and their optimal velocities range from 0.25 to 64 deg./s. This velocity range is much wider than that described before.[38,39,44] According to their velocity preferences, these cells could be classified into slow (< 8 deg./s, 84%), intermediate (16 deg./s, 3%) and fast (32–64 deg./s, 13%) cells. Surprisingly, the optimal velocities and the proportion of each group of nBOR cells are quite similar to those of nLM neurons in pigeons.[12] These similarities probably imply that both nBOR and nLM may receive similar retinal inputs from the displaced ganglion cells,[10,20,29] and their functions would be in co-ordination.

Most cells recorded from nBOR prefer motion in the upward, downward and backward directions, with a small fraction of cells preferring forward motion, in accordance with previously reported distributions of directional selectivities of nBOR neurons in birds.[38,44] The present study confirms the functional compartmentalization of directional neurons within avian nBOR,[38,44] and further finds that omnidirectional cells are located in the dorsolateral part of the rostral nBOR. The direction preferences of nBOR cells are complementary to those of nLM neurons, which mostly prefer forward and backward motion.[12] Recently, Wylie and Frost[40] have suggested that the optokinetic system in pigeons is organized in accordance with the extraocular muscles. The average direction preference of backward units in nBOR is equivalent to the orientation of the lateral rectus, while the preferred direction of nLM forward units corresponds to the

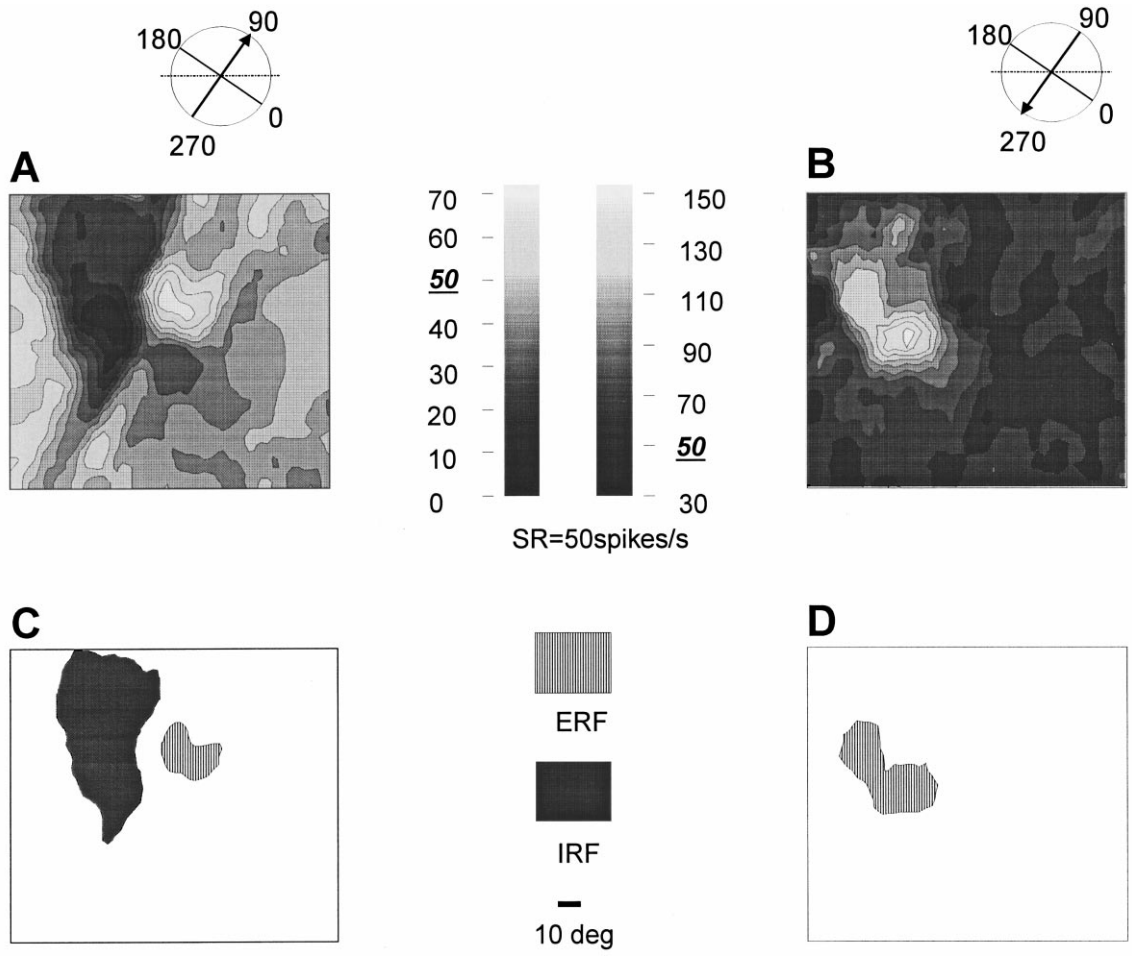

Fig. 3. Topography of excitatory receptive fields (ERFs) and inhibitory receptive field (IRF) of a nBOR neuron was mapped by equal firing rate lines as indicated by two frequency scales between A and B. The homodirectional ERF and IRF (A) were measured with a 6×6 deg. square moving at 8 deg./s in the ventrodorsal direction, whereas its opposite direction motion only showed an ERF (B). The location and extent of ERFs (hatched) and IRF (solid) were plotted on the screen, indicating that there existed a larger IRF and a smaller ERF in the upward direction (C) and sole ERF in the downward direction (D). Note that these two ERFs mapped in opposite directions were different in their location, extent and shape. In insets of polar coordinates, arrows represent direction of motion and dotted lines symbolize the horizontal line. The average spontaneous firing rate of this cell was 50 spikes/s, as underlined in the scales drawn between A and B.

orientation of the medial rectus. It appears that both nBOR and nLM concurrently play essential roles in generating optokinetic nystagmus. Avian nBOR has been suggested to be involved in the analysis of visual flow fields resulting from self-motion.[11,39,41,44] Therefore, direction preferences of nBOR neurons are fitted well with detecting either translation movements, either descent, ascent or forward motion, or rotational movements of the bird, such as roll or yaw motion.[39,41] This nucleus also receives a descending input from the ipsilateral visual wulst, and this telencephalo-nBOR projection is similar to the visual cortico-accessory optic pathway in mammals.[30] Lesions made in the pigeon visual wulst[4] and in the rat cortex[27] result in similar effects on the directional selectivity of accessory optic neurons, as shown by the findings that after telencephalic lesions visual responses of accessory cells to upward motion are dramatically reduced, and most cells now prefer temporal or downward–nasal directions. This directionality may also be modulated by the ipsilateral nLM projecting upon nBOR,[1] as well as by other afferents, for example, from the raphe nuclei.[34]

Although some studies have reported that there exist large ERFs without inhibitory surrounds[38,39,44] and directionality of excitation is approximately opposite to that of inhibition in avian nBOR,[4,15,38,39,44] the present study, for the first time, provides a detailed description of the functional organization of RFs in the pigeon nBOR cells. Most nBOR cells are heterodirectional, characterized by having ERF(s) in the preferred directions and IRF(s) in the approximately opposite directions. In contrast, both ERFs and IRFs in homodirectional cells have similar directionalities. In

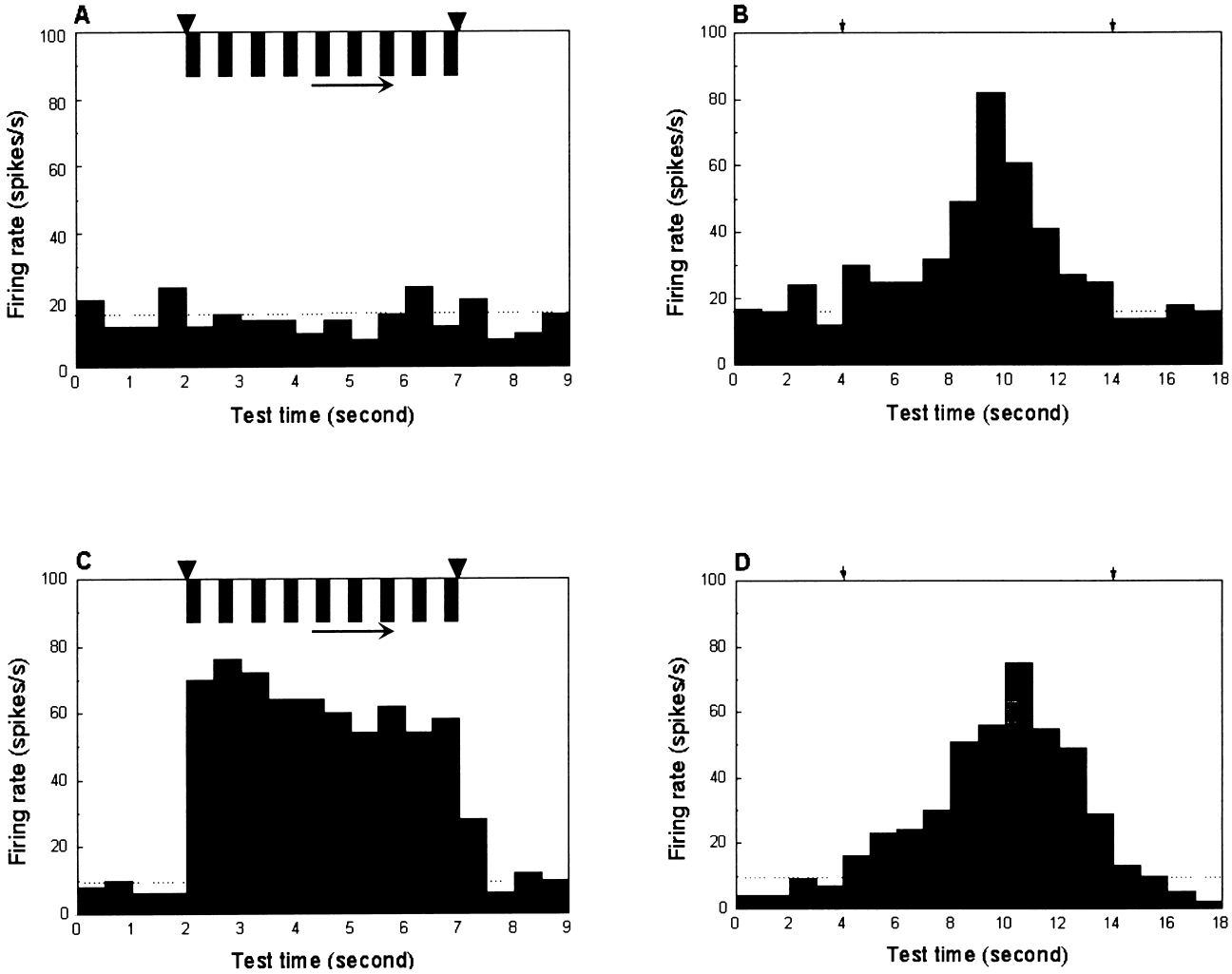

Fig. 4. Comparison of visual responses of two nBOR neurons (A–B, C–D) to whole-field square-wave gratings (spatial frequency: 4.5 cycles/m, black–white contrast: 0.97) (A, C) with those to a single square (6×6 deg., contrast: 0.97) (B, D). Both stimuli were moved at 8 deg./s in the upward direction (A–B) or backward direction (C–D). Note that cell A–B produced much stronger responses to a single object than to whole-field gratings, owing to homodirectional co-existence of ERF and IRF, whereas cell C–D, having sole ERF, produced comparable responses to both stimuli. Arrowheads represent the start and end of stimulus motion (thin arrows). Dotted lines symbolize spontaneous firing levels. Three sweeps were averaged.

these cells, whole-field stimuli moving at optimal velocities in the preferred directions could elicit either excitatory, inhibitory or no responses, depending on functional interaction between the opposing receptive fields. This appears to be at least one reason why single target but not whole-field gratings can produce firings from some nBOR cells. The sensitive centers within RFs are similar to "hot spots" of large fields of ectostriatal neurons in pigeons in that both are of higher responsiveness, but different in that the sensitive centers are mainly distributed in the superior and posterior visual field but the hot spots are all located in the foveal region,[2,7] suggesting that they may process different visual information. The functional organization of RFs of nBOR cells is similar to that of nLM cells,[12] but quite different from that of visual cells in the optic tectum[18,19] and in the nucleus isthmi[36,45] in birds. The sensitive centers of ERFs and IRFs are primarily distributed along the horizontal and vertical lines and in the superior-posterior region of the visual field. This asymmetric distribution appears to be supplementary to that of RF centers of the pigeon nLM cells.[12]

It has been widely accepted that nBOR is specialized for processing whole-field motion information,[37] and its cells respond best to stimuli moving slowly, either horizontally or vertically.[44] Therefore, whole-field stimuli are usually used to study the directionality and velocity preference of neurons in nBOR and in nLM, and also in their mammalian homologues. Previous studies[38,44] have indicated that motion of small targets results in some modulation of neuronal activity in avian nBOR. The present study points out that visual responses evoked in most nBOR cells by a small single target are comparable

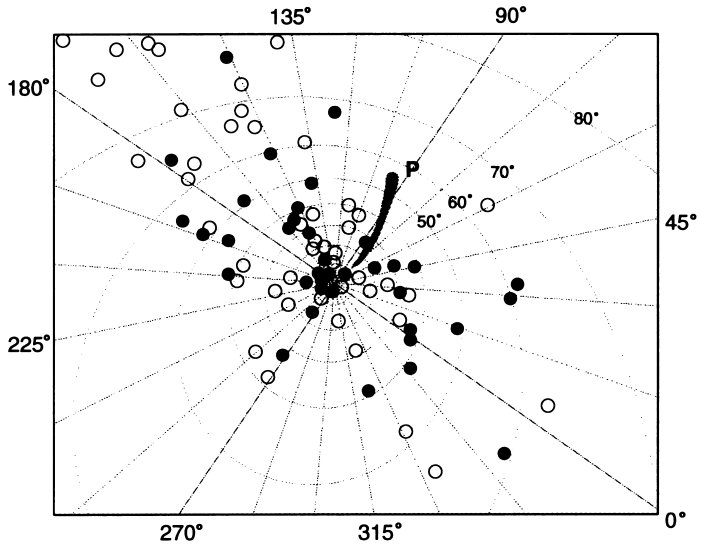

Fig. 5. Distribution of ERF (empty circles) and IRF (solid circles) centers of 35 accessory optic neurons in the visual field. Among these cells, six have ERFs alone, and each of the others has one to four ERFs and IRFs. Note that most ERF and IRF centers are located in the superior and posterior visual field. The horizontal meridian of the visual field is clockwise rotated by 38 deg. to meet its normal position relative to the eye-center to bill-tip line during the pigeon's normal behaviors such as flying, walking, perching and standing.[8]

to those evoked by whole-field stimuli. In homodirectional neurons, a single target moving at the optimal velocity in the preferred direction is much more effective than whole-field gratings in producing neuronal activity, because the latter pattern stimulates both ERF and IRF simultaneously. More recently, Wylie *et al.*[43] have indicated that providing information on motion parallax by detecting small stimuli moving relative to large stimuli may be one of the visual functions of nBOR neurons. It seems likely that sensitivity of accessory neurons in birds to small objects may also be involved in producing optokinetic responses.[12]

CONCLUSIONS

Visual neurons in the pigeon nucleus of the basal optic root are selective for the velocity and direction of stimulus motion. They prefer velocities of 0.25–64 deg./s and vertical and backward directions of motion. The main findings of the present study indicate that receptive fields of basal optic neurons are usually characterized by homodirectional or heterodirectional co-existence of ERFs and IRFs, whose interactions determine neuronal responsiveness. These nBOR cells respond not only to whole-field stimuli but also to a single object moving through their receptive fields. All of these RF characteristics may underlie the detection of optic flow[11,39,41,44] and the induction of optokinetic nystagmus.

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