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 dorso-ventral (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. It also receives extraretinal afferents from the visual forebrain and the raphe nuclei, as well as from the contralateral nBOR and the ipsilateral nucleus lentiformis mesencephali (nLM), which is a preterminal 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. This nucleus has been suggested to be homologous to the medial, lateral and dorsal terminal nuclei of the accessory optic tract in mammals. In fact, several anatomical studies have found that avian nBOR could also be divided into three regions: nBOR proper, lateral nBOR and dorsal nBOR. 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, turtle, chicken, pigeon, owl, rabbit, rat, cat and monkey). These neurons usually prefer upwards and downwards motion of visual stimuli. Their direction selectivities could be modulated by the visual wulst in pigeons and by the cortex in mammals. Both electrophysiological studies and 2-deoxyglucose mapping technique 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. 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. These neurons are essentially edge detectors.

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.
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 stereotoxic 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 and covered with an occluder. The nucleus of the basal optic thalamus was reached according to its stereotaxic coordinates and verified the recording sites. 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 stereotypically 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-prefering 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-prefering 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
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
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).

![Image of velocity-tuning curves](image)

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.

Excitatory receptive fields in 85% of cells and inhibitory receptive fields in 95% of cells in the pigeon nBORG 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 ± 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 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 nBORG cells are sensitive to large-field patterns moving slowly in particular directions. 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. 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 nBORG cells are quite similar to those of nLM neurons in pigeons. These similarities probably imply that both nBORG and nLM may receive similar retinal inputs from the displaced ganglion cells, and their functions would be in coordination.

Most cells recorded from nBORG 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 nBORG neurons in birds. The present study confirms the functional compartmentalization of directional neurons within avian nBORG and further finds that omnidirectional cells are located in the dorso-lateral part of the rostral nBORG. The direction preferences of nBORG cells are complementary to those of nLM neurons, which mostly prefer forward and backward motion. Recently, Wylie and Frost have suggested that the optokinetic system in pigeons is organized in accordance with the extraocular muscles. The average direction preference of backward units in nBORG is equivalent to the orientation of the lateral rectus, while the preferred direction of nLM forward units corresponds to the
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. 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. 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. Lesions made in the pigeon visual wulst and in the rat cortex 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, as well as by other afferents, for example, from the raphe nuclei.

Although some studies have reported that there exist large ERFs without inhibitory surrounds and directionality of excitation is approximately opposite to that of inhibition in avian nBOR, 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.

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.
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, suggesting that they may process different visual information. The functional organization of RFs of nBOR cells is similar to that of nLM cells, but quite different from that of visual cells in the optic tectum and in the nucleus isthmi 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.

It has been widely accepted that nBOR is specialized for processing whole-field motion information, and its cells respond best to stimuli moving slowly, either horizontally or vertically. Therefore, whole-field stimuli are usually used to study the directional and velocity preference of neurons in nBOR and in nLM, and also in their mammalian homologues. Previous studies 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...
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. 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.

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 and the induction of optokinetic nystagmus.

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