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Feature detection of visual neurons in the nucleus of the basal optic root in pigeons

Yuan Wang, Yong Gu and Shu-Rong Wang*

Laboratory for Visual Information Processing, Institute of Biophysics, Chinese Academy of Sciences, Beijing, China

ABSTRACT: Previous studies have shown that the nucleus of the basal optic root in birds is involved in optokinetic nystagmus, and its neurons respond not only to large-field stimuli but also to a single object moving through their excitatory receptive fields. The present study provides electrophysiological evidence that basal optic neurons in pigeons respond vigorously to motion of a black leading edge. The orientation of the edge is also an essential factor affecting visual responses of these cells, showing that any deviation of the edge from the direction perpendicular to the preferred direction decreases visual responses in most cases. Furthermore, visual responses increase as the edge is lengthened within the excitatory receptive field. However, a square, semicircle and isosceles with an area ratio of 1.00: 0.39: 0.50 but with an identical leading edge elicit almost the same responses, which are not dependent on the shape and area of visual stimuli. It suggests that these feature extraction properties, similar to those of neurons in the nucleus lentiformis mesencephali, may be specialized for detecting optokinetic stimuli rich in luminance contrasts, but not for realizing pattern recognition. © 2000 Elsevier Science Inc.

KEY WORDS: Feature detection, Nucleus of the basal optic root, Optokinetic nystagmus, Pigeon, Receptive field.

INTRODUCTION

The nucleus of the basal optic root (nBOR) in birds has been suggested to be homologous to the terminal nuclei of the accessory optic tract in mammals [9,25]. It receives input from the retinal displaced ganglion cells [10,21,30], visual forebrain [3,31], contralateral nBOR and ipsilateral nucleus lentiformis mesencephali (nLM) [2,25,29], and projects to diverse regions including the contralateral nBOR, ipsilateral nLM, vestibulocerebellum and oculomotor complex [1,2,4,10,14,34,39,40]. These connections imply that it may play an important role in generating optokinetic nystagmus, which stabilizes an object image on the retina by compensatory eye movements.

Electrophysiological studies have shown that neurons within the nBOR and its mammalian homologues respond best to large-field stimuli moving at low velocities in particular directions (frog: 16; turtle: 32; chicken: 5; pigeon: 3,4,14,26,36–38; owl: 41; rabbit: 33; rat: 28; cat: 15; monkey: 27). They usually prefer up-, back- and downward motion of visual stimuli. Visual neurons in the

avian nBOR also respond in an inhibitory manner to stimuli moving in the direction opposite to the preferred direction [3,11, 26,41]. In addition to this response property, Zhang et al. [42] have also found two additional types of receptive field organization in the pigeon nBOR, one possessing only an excitatory receptive field (ERF) and the other having both ERF and inhibitory receptive field (IRF) with an identical directionality.

However, little is known about what particular features are essential in evoking visual responses in nBOR cells, though it has been indicated that nLM neurons in pigeons are sensitive to the leading edge of visual stimuli moving through their ERFs [13]. To figure out the feature extraction properties of nBOR neurons in birds, the present study was, therefore, undertaken by using extracellular recording and quantitative analysis techniques.

MATERIALS AND METHODS

The experiments were performed on 31 adult pigeons (*Columba livia*) of either sex, weighing 290–450 g, following guidelines regarding the use of animals in neuroscience research. The pigeon 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. The caudal forebrain on the left side was exposed, and the overlying dura mater excised. The nictitating membrane of the right eye was removed to keep the eye open, and the other eye was covered. The nucleus was reached according to its stereotaxic coordinates [22] and confirmed by visual responses. Extracellular recordings of action potentials were obtained using a micropipette filled with 2 M NaCl and 100 mM $CoCl_2$. Neuronal signals were amplified and then displayed on an oscilloscope, as well as fed into a workstation computer (Indigo 2 , Silicon Graphics, Inc., Mt. View, CA, USA) for on-line processing.

Visual stimuli were generated by the workstation, and rear-projected through a three-color projector (Electrohome ECP4101, Electrohome Limited, Kitchener, Ontario, Canada) onto a screen of 180 cm in height and 220 cm in width, which was in 40 cm distance from the viewing eye and at an angle of 24° with the longitudinal axis of the pigeon body. Because the angle between the eye center-bill tip line of the stereotaxically fixed pigeon and the horizontal meridian of the visual field is 72°, while it is 34°
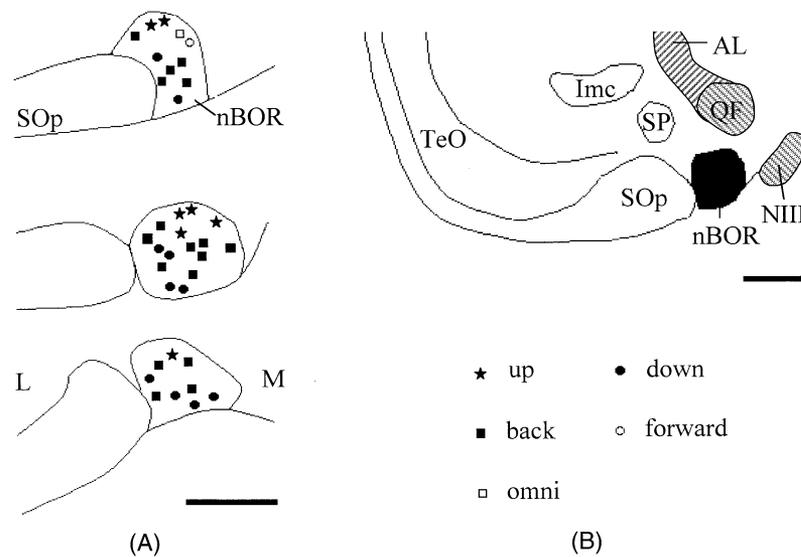
FIG. 1. Location of the nucleus of the basal optic root (nBOR) in a cross-section of pigeon's brain at AP 4.25 (B) and topographic distribution of 36 recording sites marked with cobalt (A), showing that locations of nBOR cells are related to their directional selectivities. Symbols with words represent up-, back-, down-, forward directionalities, and empty square with omni indicates the recording site of an omnidirectional cell. Sections are arranged rostrocaudalward from up to bottom. L and M represent lateral and medial sides. Abbreviations: AL, ansa lenticularis; Imc, nucleus isthmi pars magnocellularis; NIII, nervus oculomotoris; QF, tractus quintofrontalis; SOp, stratum opticum; SP, nucleus subpretectalis; TeO, tectum opticum. Scale bars: 1 cm.

during normal behaviors [8], the horizontal meridian was therefore rotated clockwise by 38°.

The following visual stimuli were used: (1) A random-dot pattern consisting of 2° black squares of 250 dots/ m² in density was used to measure the preferred direction and optimal velocity of nBOR cells. It was randomly moved in 8 directions (0, 45, 90, 135, 180, 225, 270, 315°) at angular velocities ranging from 0.2–150°/s. (2) A black square (5–13°) was moved randomly along a series of parallel paths at the optimal velocity in the preferred direction to plot the location and extent of ERF. The luminance of the black object and white background was 0.1 cd/m² and 6.6 cd/m², respectively. (3) A black square, semicircle, and isosceles triangle, with an area ratio of 1.00:0.39:0.50 but identical leading edge of 4.5–15.4°, were used to examine effect of shape and area on visual responses. (4) A spot of light equal in size to ERF of a nBOR cell examined was used for testing ON-OFF responses.

By the end of experiments, cobalt ions were ejected using positive pulses of 10 μA in intensity, 0.5 s in duration, 1 Hz in frequency, for 10 min to histologically verify the recording sites [12,13,35]. The pigeon was killed under deep anesthesia, its brain was immediately removed from the skull and then immersed for about 15 min in saline containing ammonium sulfide to form a cobalt sulfide spot. The brain block was fixed in 4% paraformaldehyde for 6–12 h, 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 microscopic observations.

RESULTS

Fifty-eight cells were extracellularly recorded from nBOR and their visual responses to various stimuli examined. Among them were 55 (95%) unidirectional, 2 (3%) bidirectional, and 1 (2%)

omnidirectional cells. The unidirectional cells preferred backward (40%), downward (34%) or upward (22%) motion, with only a small portion of cells (4%) preferring forward motion of a visual stimulus. The recording sites of 36 cells were marked with cobalt and all located within nBOR (Fig. 1), showing that 7 upward-preferring cells were in the dorsal (5 cells) and central (2 cells) parts; 16 backward cells in the dorsal (3), central (10) and ventral (3) parts; 11 downward cells in the dorsal (1), central (3) and ventral (7) parts; 1 forward cell and 1 omnidirectional cell were in the dorsocaudal part of the nucleus. Generally speaking, upward cells were located dorsally, downward cells ventrally, and between were backward cells.

We examined effects of several parameters of stimuli on visual responses of nBOR cells. Forty-five cells were examined for sensitivity to luminance-contrast. This sensitivity was described by a ratio (R) defined as $R = (f_b - f_s)/(f_w - fs)$, where f_b and f_w were maximum discharge rates in response to moving black and white leading edges, respectively, and f_s was spontaneous rate [13]. The R values were 0.71–0.79 in 1 (2%) cell, 0.80–1.19 in 8 (18%) cells, 1.20–1.99 in 12 (27%) cells, 2.00–4.99 in 14 (31%) cells, and > 5.00 in 10 (22%) cells, indicating that most nBOR cells produced stronger responses to black edge than white one (Fig. 2). Visual responses of 29 cells were examined to the onset and offset of a spot of light that was located within and equal in size to ERFs. Optic stimulation produced ON-response in 2 cells, ON-OFF responses in 2 cells, and OFF-response in 19 cells. Six others did not respond at all. Of these six cells, 5 were more sensitive to black edge than white one, and 1 equally responded to both edges. One of ON-cells equally responded to black and white edges, and the other preferred black edge. Among OFF-cells, 14 preferred black edge to white one, and 5 had an equal sensitivity to both edges.
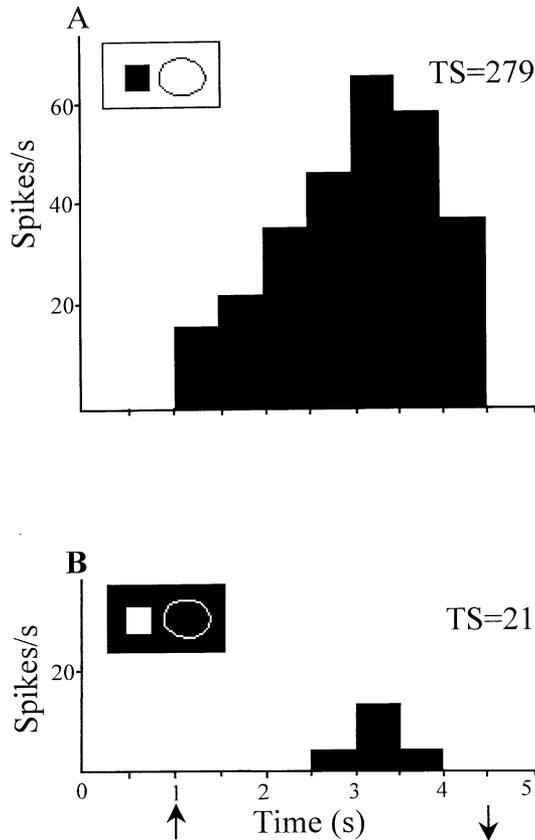
FIG. 2. Histograms showing visual responses of a nBOR cell to black square (A) and white square (B) moving at 8.4°/s in the backward direction through its excitatory receptive field (oval, 38° × 25°). Arrows pointing up- and downward represent the start and end of motion of the leading edge, respectively. Abbreviation: TS, total number of spikes counted for three sweeps.

Two ON-OFF cells responded to black edge more strongly than white one.

Fifty cells were examined for visual responsiveness to stimuli of various shapes and areas, but with an identical leading edge. Though a black square, semicircle and isosceles triangle were different in shape and had an area ratio of 1:0.39:0.50, they evoked almost the same responses in terms of the total number of spikes. As shown in Fig. 3, the ratio of total number of spikes elicited by these figures was 1:0.99:1.02. The fact that visual responses of nBOR cells did not depend on the shape and area of stimuli with an identical leading edge was true for all 50 cells examined, including 47 unidirectional, 2 bidirectional and 1 omnidirectional cells. The orientation and length of the leading edge were also essential factors affecting responsive strength of nBOR cells. In 15 of 23 cells examined, any deviation of the leading edge from its orientation perpendicular to the preferred direction resulted in decrease in firing rate (Fig. 4). Seven cells did not show changes in firing rate, and the other even increased its firing rate when the deviation was enlarged. Furthermore, increase in length of the leading edge perpendicular to the preferred direction resulted in a rapid increase in firing rate. Figure 5 indicated that the firing rate of a nBOR cell increased to 98% of its maximum when the leading edge was lengthened to 40°, though the cell's ERF was 68° × 85°. The firing rate reached its maximum when the edge was equal to the ERF dimension, beyond which the firing rate saturated and the length tuning curve reached a plateau.

DISCUSSION

Previous studies have shown that nBOR cells in pigeons respond to large-field stimuli and single object moving through their ERFs [36–38,41,42]. The present study indicates that nBOR cells are sensitive to the leading edge of a moving object. Random-dot patterns also can fire nBOR neurons, probably because there exist many high-contrast edges in these stimuli and nBOR cells are able to detect them, similar to visual properties of nLM neurons [13]. Visual cells in nBOR prefer black edge to white one, in agreement with contrast preference of units in the pigeon nLM [13] and in the rabbit nucleus of the optic tract (NOT) [6]. However, this preference does not result from OFF responses, because most cells without OFF responses also prefer black edge to white one. It is conceivable that a black object moving against white background is easier to be found by diurnal animals than a white object against black background. Accessory optic neurons are also selective for the orientation and length of the leading edge of visual objects. The
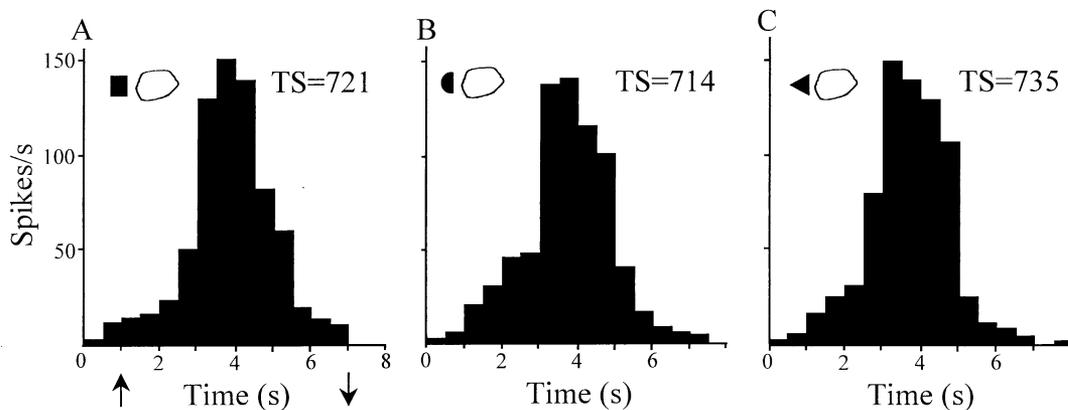

FIG. 3. Histograms showing that a nBOR cell responded to the black leading edges but not to the shape and area of a square (A), semicircle (B) and isosceles triangle (C). These edges were identical in length (10.7°) and orientated perpendicular to, and moved (8.3°/s) in the preferred direction through the cell's excitatory receptive field (oval, 60° × 48°). Arrows pointing up- and downward represent the start and end of the leading edge motion, respectively. Abbreviation: TS, total number of spikes counted for three sweeps.
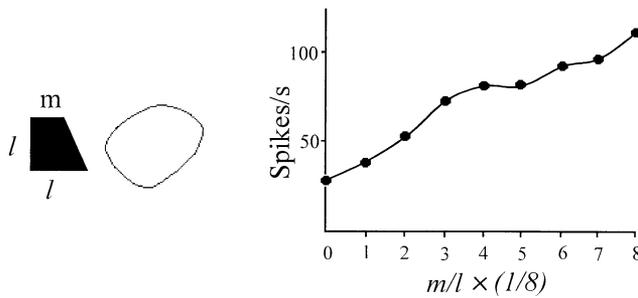
FIG. 4. Orientation tuning curve of a nBOR cell, showing relationship between firing rate and orientation of the leading edge of a single object (l = 35 cm). This object was moved at 12.3°/s in the cell's preferred direction through excitatory receptive field (oval, 42° × 65°). Firing rate was counted when the middle point of the leading edge was passing through the ERF center. Orientation here was described by m/l × 1/8 due to the computer program. Please note that abscissa 8 means that the leading edge is perpendicular to the preferred direction.

orientation selectivity may probably at least in part originate from the retinal ganglion cells that respond selectively to orientated edges moving in particular directions [23,24]. The response property of nBOR cells to moving objects is similar to that of the pigeon nLM cells [13] in that they increase firings with increasing object edge but not with shape and area of the objects, and different from that of the wallaby NOT cells, whose discharge rates increase as stimulus area is enlarged [18]. The length tuning curve of nBOR cells shows that the ERF center is maximally responsive, similar to the maximal effect in the ERF center of the pigeon nLM cells [12,13], and to the "hot spot" in the pigeon nBOR cells [37] and in ectostriatal neurons of the zebra finch [7]. The size and heterogeneous organization of ERFs in accessory optic neurons imply that they may receive inputs from a number of projecting neurons, which are connected to a nBOR cell with decreasing synaptic weights from the central to peripheral region of an ERF.

The present study shows that basal optic cells are sensitive to moving edges. Their response strength depends, in addition to direction and velocity of motion, on the direction of contrast, orientation, and length of the leading edge, but not on the shape and area of visual stimuli. It suggests that these feature extraction properties of nBOR cells, similar to those of nLM neurons [13], may be specialized for detecting optokinetic stimuli rich in contrasts, but not for realizing pattern recognition. Visual properties of basal optic neurons are different from those of tectal cells in two aspects: First, receptive fields of tectal cells is composed of a center and its antagonistic surround [17,19,20], whereas those of nBOR neurons are excitatory, without inhibitory surrounds, but their excitation can be suppressed by motion in the opposite direction [37,38,41]. Zhang et al. [42] have recently shown that nBOR cells in pigeons possess spatially separate ERFs and IRFs or ERFs alone. These excitatory and inhibitory fields have either opposite or identical directionalities. Therefore, in most cases, visual response strength of a nBOR cell increases with increasing length of the leading edge that is perpendicular to and moved in the preferred direction through ERF, because IRF, if any, does not exert any inhibitory action due to its opposite directionality (Fig. 5). Second, some tectal cells are sensitive to shape and size [17,19] of visual stimuli, but basal optic cells optimally respond to the leading edge. These differences between tectal and basal optic cells may result from differential retinal inputs (ganglion cells vs. displaced ganglion cells) and functional segregation (object discrimination vs. optokinetic nystagmus). Furthermore, several studies have shown that there exist functional interactions between nBOR and nLM in pigeons [1,29]. These interactions may at least in part underlie the selectivity of nLM neurons for horizontal motion [12] and that of nBOR neurons for vertical and backward motion [37,41,42]. It is probable that these two nuclei work in coordination to detect optokinetic stimuli.
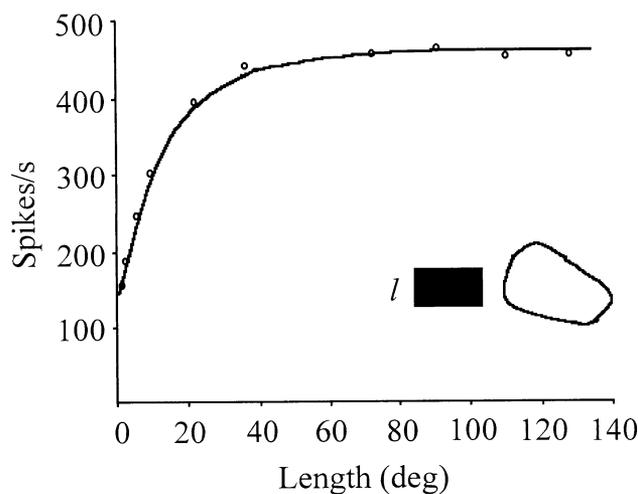
FIG. 5. Length tuning curve of a nBOR cell, showing relationship between firing rate produced by a black leading edge and its length (l) when it was perpendicular to and moved (5.5°/s) in the preferred direction through the cell's ERF (oval, 68° × 85°). Small circles were experimental data counted for three sweeps.

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