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The visual response properties of neurons in the nucleus of the basal optic root of the pigeon: a quantitative analysis

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Summary. The response characteristics of single-units in the nucleus of the basal optic root (nBOR) of the pigeon accessory optic system (AOS) were investigated using standard extracellular techniques. The receptive fields (RFs) were large (20–115° long) and elliptical and were found throughout the contralateral visual field with the exception of the red field. The RFs did not have inhibitory surrounds and there was no evidence of retinotopic organization. Most neurons responded to small moving spots although the optimal stimulus was wholefield motion of a particular direction. Analysis of 166 single-units showed that neurons preferring upward, downward and backward (nasal to temporal) motion were equally abundant (32.5, 32.5 and 31% respectively), while < 5% preferred forward (temporal to nasal) motion. Mapping studies demonstrated that UP units were located in the dorsal portion of the nucleus; DOWN units were found ventral to UP units; BACK units were found along the ventral surface of the nucleus; and FORWARD units were found in the posterior-dorsolateral margin of the nucleus. Most cells were excited by wholefield motion in the preferred direction and inhibited by motion approximately 180° in the opposite direction, however, some cells lacked the excitatory component while others lacked the inhibitory component. Neurons were grouped into six categories based on the relative contributions of excitation and inhibition. These results are compared with investigations of the AOS of other vertebrates.

Key words: Accessory optic system – Nucleus of the basal optic root – Wholefield visual motion – Directionally Specific neurons – Pigeon

Introduction

An increasing body of evidence suggests that a distinct visual pathway, the Accessory Optic System (AOS), provides information about self-produced motion to generate compensatory head and eye movements in response to displacement of the retinal image (see Simpson (1984) for a recent review). The AOS is associated with the vestibular and oculomotor systems (Brecha et al. 1980), and lesions of the AOS typically result in the disruption of optokinetic nystagmus (OKN) (Fite et al. 1979; Frost 1982; Gioanni et al. 1983a, 1983b; Wallman et al. 1981).

The avian AOS consists two of structures; the nucleus of the basal optic root (nBOR) and the pretectal nucleus lentiformis mesencephali (LM). Based on cell morphology, the nBOR has been subdivided into three regions, nBOR proper (nBORp), nBOR dorsalis (nBORd) and nBOR lateralis (nBORl) (Brauth and Karten 1977; Brecha et al. 1980). The nBOR receives direct retinal projections from the displaced ganglion cells (DGCs) (Karten et al. 1977; Fite et al. 1981; Reiner et al. 1979) and projects to vestibular and oculomotor structures (Brauth and Karten 1977; Brecha and Karten 1979; Brecha et al. 1980).

In the chicken, electrophysiological and 2-deoxyglucose studies by Wallman, McKenna and their colleagues (Burns and Wallman 1981; McKenna and Wallman 1981, 1985a, 1985b; Rojas et al. 1985; Wallman et al. 1981) found that neurons in nBORd and nBORp prefer upward or downward motion, and neurons in nBORl and LM prefer forward (temporal to nasal) motion. The 2-DG studies also demonstrated that neurons preferring upward motion are found in the dorsal part of the nucleus while neurons preferring downward motion are found in the ventral part of the nucleus (McKenna and Wallman 1981, 1985a, 1985b; Wallman et al. 1981).

Like the chicken AOS, 2-DG and electrophysiological have found that the pigeon LM processes forward motion (Chown et al. 1984; Morgan et al. 1983; Winterson and Brauth 1985), and 2-DG studies have shown that the pigeon nBOR processes primarily vertical motion (Frost et al. 1980; Morgan et al. 1983). However, there are some discrepancies with respect to electrophysiological studies of the pigeon nBOR. Britto et al. (1981) used small spots or bars of light as stimuli and found that about half of the neurons preferred stimuli moving upward or downward in the contralateral visual field. Morgan and Frost (1981) reported that nBOR neurons do not respond to small spots, though all units responded to the movement of large

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patterns of random dots or visual noise. Most neurons preferred upward or downward motion, although some (<20%) preferred backward (nasal to temporal) motion. Gioanni et al. (1984) recorded from nBOR in alert pigeons restrained in an optokinetic drum which could be rotated in different directions. They found that most neurons preferred upward and backward motion in the contralateral eye.

It is possible that the discrepancies between these studies i.e., inconsistencies in the direction preferences of nBOR neurons, could be due to either the type of preparation used (alert vs. anaesthetized pigeons) or a sampling bias since Gioanni et al. (1984) recorded from a small number of cells. In the present investigation a quantitative analysis of the visual response properties of nBOR neurons was studied in anaesthetized pigeons. In addition, the receptive fields of nBOR neurons were plotted and the effect of varying stimulus size was studied. Furthermore, since 2-DG studies found that the chicken nBOR is functionally compartmentalized (McKenna and Wallman 1981, 1985a, 1985b; Wallman et al. 1981), the nBOR was systematically mapped out by making multiple penetrations in a systematic grid-like pattern. This would allow a comparison of the functional structure of the chicken and pigeon nBOR.

Material and methods

Experiments were performed on thirty-five adult feral pigeons (*Columba livia*) anaesthetized with 20% urethane (10 ml/kg i.p.). Animals were positioned in a stereotaxic instrument with modified beak and ear bars in order that the orientation of the skull conformed with the atlas of the pigeon brain (Karten and Hodos 1967). A hole was made in the left side of the skull and a microelectrode was stereotaxically positioned to penetrate the left nBOR (coordinates: anterior 4.0 mm, lateral 1.8 mm). The right eyelid was retracted.

Glass insulated tungsten microelectrodes with 5–10μ exposed tips were used to record extracellular potentials. A stepping motorized hydraulic microdrive system (Frederick Haer and Co.) was used to advance the electrode through the brain. Standardized square-wave pulses, each representing a single spike were stored in a PDP 11–23 computer to produce peri-stimulus time histograms (PSTHs). The stimulus presentation was synchronized with the sweep of the computer.

Stimuli were produced by a Grinnell 270 Image Processing System with a PDP 11-23 host computer, and backprojected by an Electrohome EDP 57 projection monitor onto a tangent screen (see Frost et al. 1988). The screen was 125 cm wide × 265 cm high and was placed 29 cm in front of the bird's right eye. All stimuli consisted of kinematograms (coherent motion of random dots, Frost et al. 1988). The PDP 11–23 allowed for systematic manipulation of the direction and size of the stimuli.

To search for nBOR neurons, the room was darkened and a Julesz random dot pattern measuring approximately 125 × 125° visual angle (henceforth called a 'wholefield' stimulus) was moved alternately back-and-forth along the vertical axis at a velocity of 5°/s. The random dots measured approximately 0.5°. The microelectrode was then advanced in 5μ steps with the microdrive. Neurons in nBOR were identified because of their unique response to this type of stimulation. Once a single-unit was isolated the approximate location of its receptive field was located with a hand-held shadow caster. The vertical position of the projector was then adjusted to ensure stimulation of as much of the receptive field as possible.

By presenting wholefield stimuli moving in 8 directions, 45° apart, a "coarse" tuning analysis of the directional preference of the isolated unit was determined. In some cases a "fine" tuning analysis was carried out by presenting wholefield visual stimuli moving in 24 directions, 15° apart. The duration of each sweep was 5s and PSTHs were averaged over three sweeps for each direction. The system automatically randomized the presentation of trials. The spontaneous firing rate (SR) of the cell was measured by projecting a stationary wholefield random dot stimulus on the screen and averaging over three 5s sweeps.

The location of the receptive field (RF) boundaries was determined by moving a kinematographic disc (radius = 6°) across the length of the screen at nine different transit positions (equal intervals) horizontally or vertically depending on the preferred direction of motion. The RFs were reconstructed from the stored PSTHs, which were averaged across three sweeps. When possible, the textured disc was moved in both the preferred and non-preferred directions so that the excitatory receptive field (ERF) and inhibitory receptive field (IRF) could be reconstructed.

The effect of the stimulus size was tested by varying the length of a bar moved across the centre of the RF in the preferred and non-preferred directions. Also, in some cases, opaque sheets of paper with apertures of various sizes were placed over the screen, thus limiting the area of the RF exposed to wholefield stimuli.

On some penetrations lesions were made in nBOR by passing a current of 10 μamps through the electrode for 7–10s. At the end of the experiment the bird was perfused transcardially with 0.75% saline followed by 10% formal saline. The head was stored in a cold 20% sucrose solution for three days and then in 10% formal saline. Brains were blocked and cut in 30μ sections in a cryostat. These were then mounted, dried and stained with cresyl violet to verify electrode placements.

Results

For single unit studies, between 1 and 10 penetrations were made into each nBOR. (Twenty-three of the birds received 5 or fewer penetrations). Histology confirmed the position of electrodes in nBOR and indicated that all areas of the nBOR complex were sampled, although few tracks were found in nBORl. Within each penetration between 0 and 5 single units were isolated. In total, 196 single-units in nBOR were isolated. Quantitative data along at least one stimulus dimension is available from 166 cells.

Preferred and non-preferred directions of motion

The spontaneous rate (SR) in response to a stationary pattern of random dots was measured from 166 cells. SR varied from 0 to 82.8 spikes/s (mean = 12.3 spikes/s), although most cells had a low SR. 53% of the neurons had a SR less than 5 spikes/s, and 77% had a SR less than 10 spikes/s.

All single-units encountered were specific for direction of wholefield motion. Quantitative data regarding directional tuning is available for 166 cells. The data were subjected to vector analysis in order to calculate the mean preferred and non-preferred directions of motion. Rather than simply designating the peak firing rate and lowest firing rate as the preferred and non-preferred directions of motion, vector analysis takes into account the firing rate in all directions to calculate the mean vectors of preferred and non-preferred directions of motion (see Grasse and Cynader 1982; Burns and Wallman 1981).

All 166 cells were subjected to "coarse" directional tuning analysis and 95 of these cells were also subjected to "fine" tuning analysis. In such cases, an average of the two resultant mean preferred (and non-preferred) directions was taken. Within neurons, the average difference between the direction of the mean preferred vectors calculated by "coarse" and "fine" tuning analysis was 4.1°. Similarly the average difference between the mean non-preferred vectors was 8.5°.

The vector analysis revealed four major classes of neurons. The mean preferred and non-preferred directions of motion for each unit are displayed in polar coordinates within directional classes in Fig. 1. The horizontal orientation (i.e. 0 and 180°) in Fig. 1 is based on measurements of the orientation of the pigeon head during walking and flying (Erichsen et al. 1989). All directions discussed are with respect to movement in the visual field. Fifty-four neurons (32.5%) preferred wholefield stimuli moving upward (UP units). Similarly, fifty-four neurons (32.5%) were classified as DOWN units. Fifty-one neurons (30.7%) preferred motion from nasal to temporal visual field, that is, backward motion (BACK units), while only 7 neurons (4.2%) were classified as FORWARD units, preferring motion from temporal to nasal visual field.

Single-units with a SR less than 1 spike/s were not assigned a non-preferred direction, nor were units in which motion in all directions resulted in excitation (see below). Similarly, single-units in which motion in all directions resulted in inhibition did not have a preferred direction of motion (see below). These units were classified with those cells which had the same non-preferred direction. For example, a cell which did not respond to upward motion,

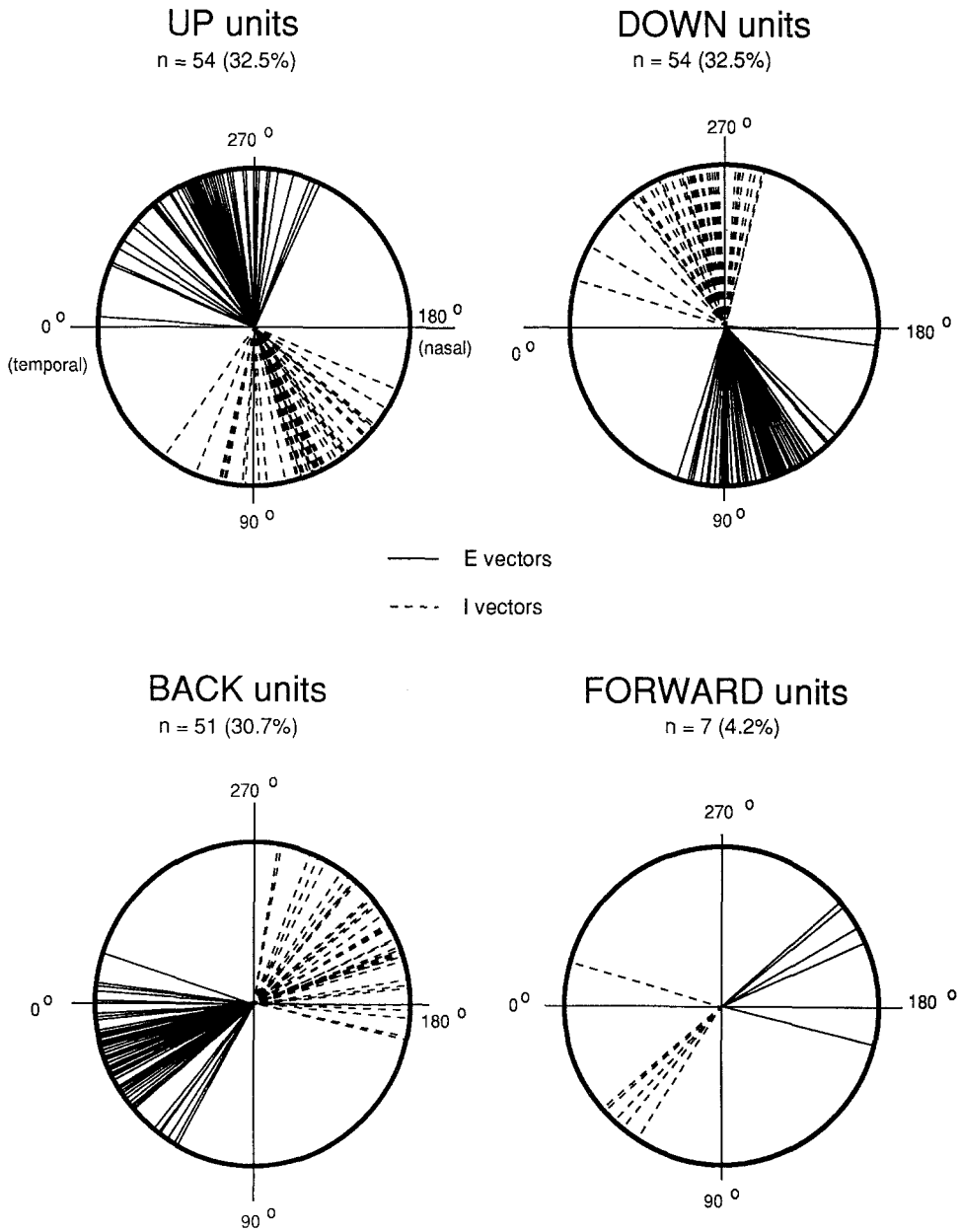

Fig. 1. The mean preferred and non-preferred directions of nBOR neurons. These are plotted in polar coordinates within directional classes. Solid lines represent the preferred direction and the broken lines represent the non-preferred directions. Directions are corrected to conform with measurements of head orientation during walking and flying (Erichsen et al. 1989)

but was inhibited by downward motion, was grouped with UP units, since they too were inhibited by downward motion.

The preferred and non-preferred hypermean directions of motion for each of these classes were calculated by averaging the mean preferred and non-preferred directions respectively. These are shown in polar coordinates in Fig. 2. Note that within classes the hypermean preferred and non-preferred directions are within 10° of being opposite to one another.

Within cells, the average difference between the mean preferred and non-preferred directions was 179.3°, although there was considerable variation (range = 125 to 225°). Figure 3 shows a frequency histogram of the difference between the mean preferred and non-preferred directions of motion. Note that the distribution is symmetrical about 180° and that the difference is within 15° of 180° for 77% of the sample.

Some authors (Simpson 1984; Soodak and Simpson 1988; Wallman and Velez 1985) point out that vector analysis may not accurately indicate the peak excitation and inhibition if the directional tuning profile is asymmetrical. Thus, for those units subjected to a fine tuning analysis, the direction of stimulus motion which produced the greatest firing rate was taken for each unit and averaged within directional classes. The resultant average was compared with the hypermean preferred direction as calculated by vector analysis for the same group of cells. The difference between these two measures was within 1° for both UP and DOWN classes, and within 5° for the BACK class: Vector analysis does not seem inappropriate for the analysis of directional tuning of the present sample.

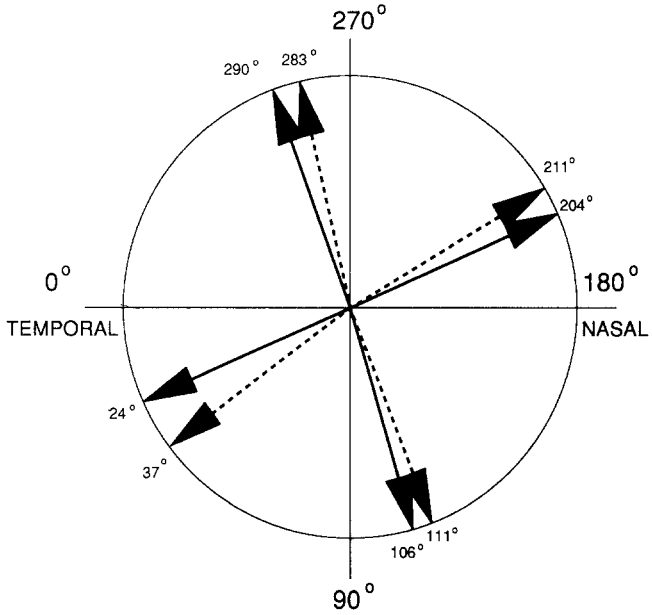

Fig. 2. Hypermean preferred and non-preferred directions of motion of the four directional classes. Solid and broken arrows represent hypermean preferred and non-preferred directions respectively. These vectors were obtained by averaging data from Fig. 1. Note that the preferred directions of different classes are about 90 or 180° apart and that within classes the preferred and non-preferred directions are about 180° apart

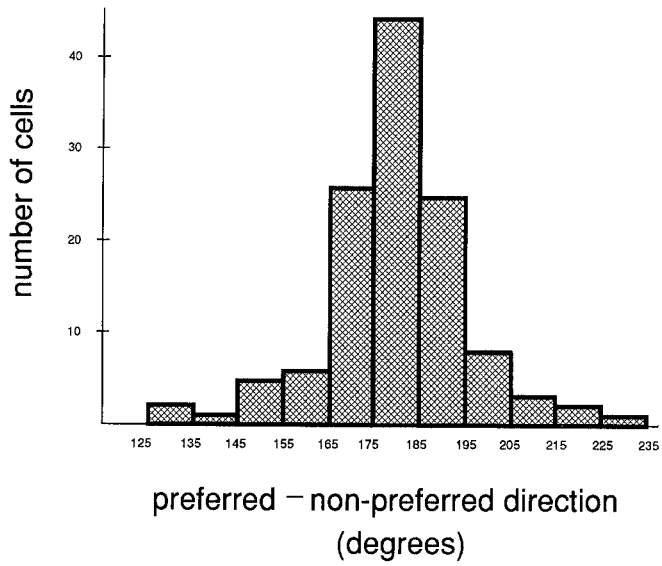

Fig. 3. A frequency histogram of the difference between the preferred and non-preferred directions of nBOR neurons. Note that the distribution is symmetrical about 180°

Functional compartmentalization of nBOR

The single-unit recording sessions suggested that neurons preferring the same direction of motion were clustered into zones within the nBOR. On any given penetration, as the electrode was advanced UP units were usually encountered first, followed by DOWN units, which in turn were followed by BACK units. In order to map out the entire nucleus, 19 penetrations were made systematically throughout the nBOR of one animal. Subsequent histology revealed that the entire nucleus had been effectively sampled, with the exception of nBORl. Two additional birds received 13 and 12 penetrations through nBOR, which sampled the lateral portion of nBOR in one bird, and the anterior portion of nBOR in the other. Neither of these birds received penetrations into nBORl. The penetrations were 200μ apart along the medial-lateral dimension and 300μ apart along the rostral-caudal dimension. Multi-unit recordings were taken every 50 or 100μ and a qualitative assessment of the direction preference was made.

The same general subdivision was observed in all three birds. Within birds, the subdivisions were not absolute, since the preferred direction of a few multiunits was not that of adjacent multiunits. Figure 4 shows the subdivisions of nBOR based on a compilation of the multiunit responses from all three birds.

Relative excitation and inhibition of neurons

Observation of directional tuning profiles suggested that cells could be divided into six groups based on the relative magnitudes of excitation and inhibition in response to wholefield motion in the preferred and non-preferred directions respectively (see Fig. 5). The majority of the cells, category E_i (n = 100, 60.2%), were greatly excited by

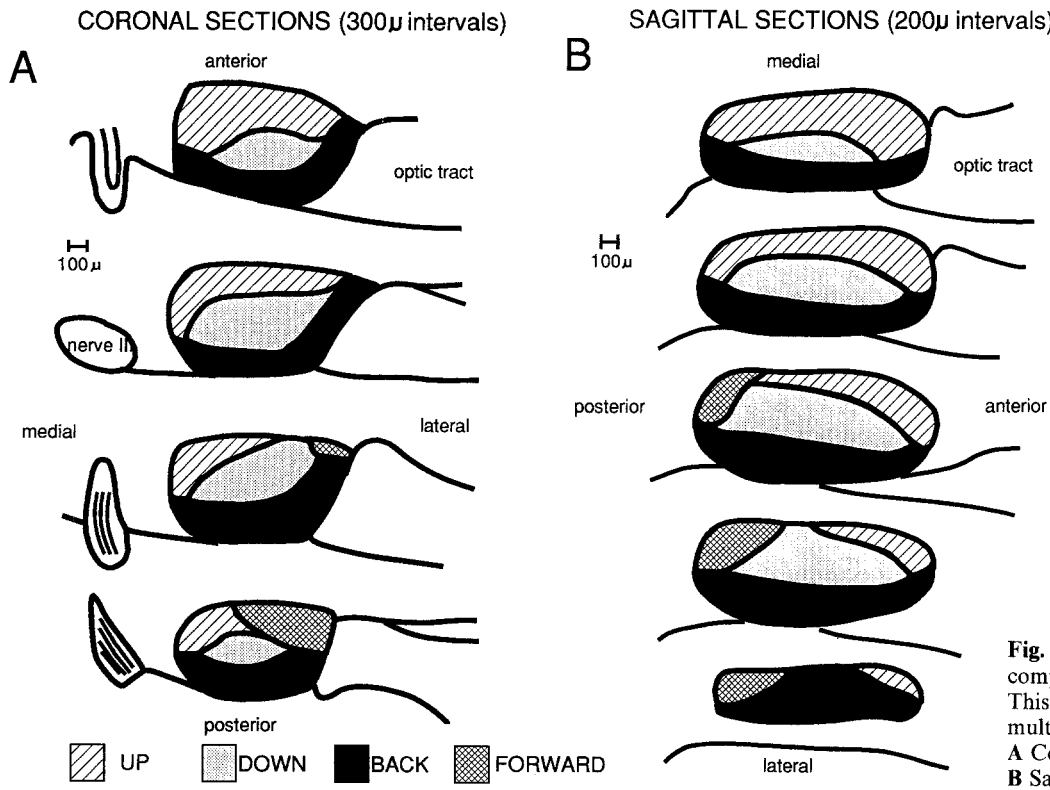

Fig. 4A, B Functional compartmentalization of nBOR. This is based on the compilation of multiunit responses from 3 birds. **A** Coronal sections, 300 μ intervals. **B** Sagittal sections, 200 μ intervals

wholefield motion in the preferred directions, and inhibited by motion in non-preferred direction, usually to zero spikes/s, for up to 180 degrees of the polar distribution. Cells with a SR less than 1 spike/s which were not activated by wholefield motion in some directions were also included in this subgroup. In general, E_i cells had a low SR (mean = 7.51 spikes/s). Figures 5A–C show the directional tuning profiles of 3 representative neurons of the E_i subgroup. Note that the cell in 5A is narrowly tuned relative to the cells in Fig. 5B, C. This was characteristic of E_i cells with low SRs (less than 4 spikes/s). Figures 5B, C resemble cardioid functions with the typical 'notch'. All cells in subgroup E_i resemble cardioid functions or have narrower tuning profiles as in Fig. 5A.

A second category (E_o) (Fig. 5D, E) consisted of 16 cells (9.6%) which showed directional response profiles similar to those of E_i cells with respect to motion in excitatory directions but not in inhibitory directions. Despite having high SRs (mean = 20.2 spikes/s), E_o cells showed no inhibition of SR in response to motion in the non-preferred direction, or showed a small amount of inhibition over a number of different directions.

Category E_e (Fig. 5F, G) consisted of 9 cells (6.0%) with low SRs (mean = 4.9 spikes/s). For these cells, wholefield motion in all directions resulted in an increase in firing rate, although these cells still exhibit a direction preference.

Category I_e consisted of 17 (10.2%) neurons with high SRs (mean = 24.2 spikes/s) which, although primarily affected by motion in the non-preferred direction, showed some excitation in response to motion in the preferred direction (Fig. 5H, I). Note that the tuning is extremely broad in the preferred directions.

Ten neurons (6.0%) with high SRs (mean = 21.7 spikes/s) formed the category I_o (Fig. 5J, K). These neurons were inhibited by motion in all directions, yet still displayed a definite non-preferred direction.

The remaining 14 (8.4%) neurons formed a less homogeneous category (R; rare cells for the lack of a better name) than the other five (Fig. 5L). These neurons had high SRs (mean = 20.4 spikes/s) and were broadly tuned or not well modulated by wholefield motion in both preferred and non-preferred directions.

Most of the I_e and I_o cells were found at the very top of the nucleus or the very bottom of the track on penetrations in the caudal portion of the nucleus. Often there was little of the audible nBOR activity in the background within 100–200μ of an isolated I unit. Their position within the nucleus, suggests that they may have been isolated in nBORd, however, this could not be histologically verified.

Receptive field (RF) properties

The RFs of 120 neurons were plotted by moving the 6° kinematographic disc across the screen at different transit positions. For 75 of the cells, only the ERF was plotted and for 18 cells only the IRF was plotted. Both the ERF and IRF were plotted for 27 cells.

The response to the kinematographic disc was not uniform across the receptive field; rather, the cell exhibited a 'hot-spot' of peak excitation (or inhibition) in or near the centre of the RF. This is illustrated in Fig. 6A, which shows the response of a neuron to the stimulus moving across the screen in the preferred direction. Similarly, Fig. 6B shows the response of a neuron to the stimulus moving in the

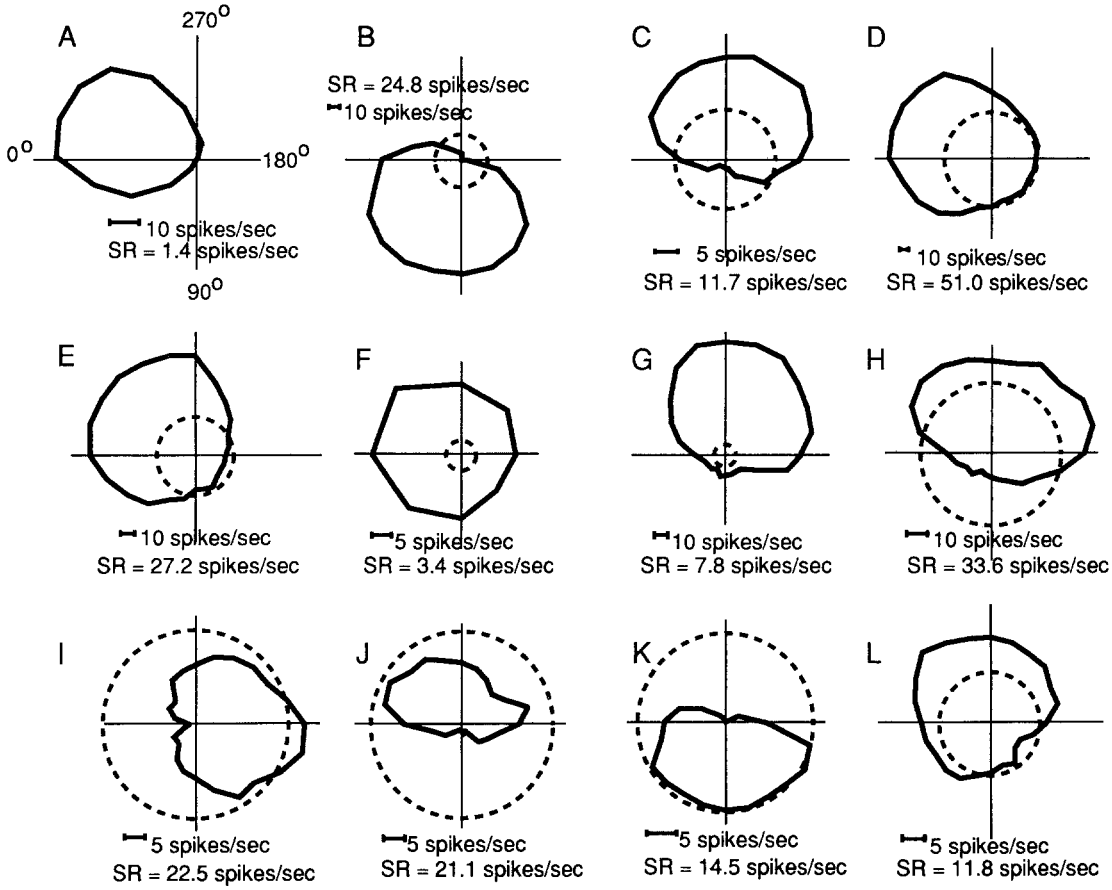

Fig. 5A–L. Directional tuning profiles of 12 nBOR neurons illustrating the categorization based on the relative contributions of excitation and inhibition. In each case the firing rate in response to wholefield visual stimuli is plotted as a function of the direction of motion in polar coordinates. The broken circles represent the spontaneous rate (SR). 0° = backward motion; 90° = downward; 180° = forward; 270° = upward. **A–C,** category E_i; **D, E,** E_o cells; **F, G,** E_e cells; **H, I,** I_e cells; **J, K,** I_o cells; **L** is an R cell

non-preferred direction. There was no evidence of antagonistic inhibitory surrounds.

All RF reconstructions revealed a circular (15 cells) or elliptical shape. As an index of shape, the ratio (long axis)/(short axis) was used. This measure varied from 1.00 (i.e. circular), to 3.57 (i.e. long ellipse). The mean of this measure was 1.61. In most cases (72 of 105) the long axis of elliptical receptive fields was oriented horizontally. The RFs were rather large, with the long axis ranging in length from 20 to 115° visual angle (mean = 62.4°). The length of the short axis ranged from 13 to 92° (mean = 39.9°). In terms of area, ERF sizes ranged from 198 to 7040 deg^2 (mean = 2060 deg^2). The range in RF sizes was similar for both ERFs and IRFs, however, the IRFs were larger on average (mean ERF size = 1769 deg^2; mean IRF size = 2750 deg^2). For the 27 cells in which both the ERF and IRF were plotted, in 21 cases in IRF was larger (up to 14 times) than the ERF, while the reverse was true for only 3 cells. For 3 cells the ERF was equal in size to the IRF. A paired-difference t-test supported the notion that within cells, the IRF was larger that the ERF ($t = 3.84$, $df = 26$, $p < 0.005$). The mean difference (IRF-ERF) was 1646 deg^2 (range = −2780 to 5768 deg_2). In cases where the IRF was larger than the ERF, it was noted that the ERF was centred in the IRF for only 7 cells. The other 9 cells had the ERF positioned in a part of the IRF such that the two shared common boundaries.

Receptive fields were found throughout the monocular visual field, with the exception of the red field (nasal inferior visual field). (The red field is an area of retinal specialization thought to be involved with binocular vision (Martinoya et al. 1981)). Most RFs were found in the superior-nasal visual field, however this may simply represent a selection bias since the stereotaxic instrument blocked portions of the temporal visual field, and the screen did not extend into the most peripheral 20° of the temporal visual field. Figure 7 shows a reconstruction of the RFs for 10 cells to illustrate the distribution throughout the visual field. Despite the fact that RFs from as many as 24 cells from the same nBOR were reconstructed, there was no conclusive evidence that the nBOR was retinotopic.

Responses to small stimuli

Most cells (38 of 44) would respond to a bar measuring 2.5 × 1.3° or less as it was moved across the RF in the preferred and non-preferred directions. For the other 6 cells a bar measuring 1.3 × 10° or less produced a response.

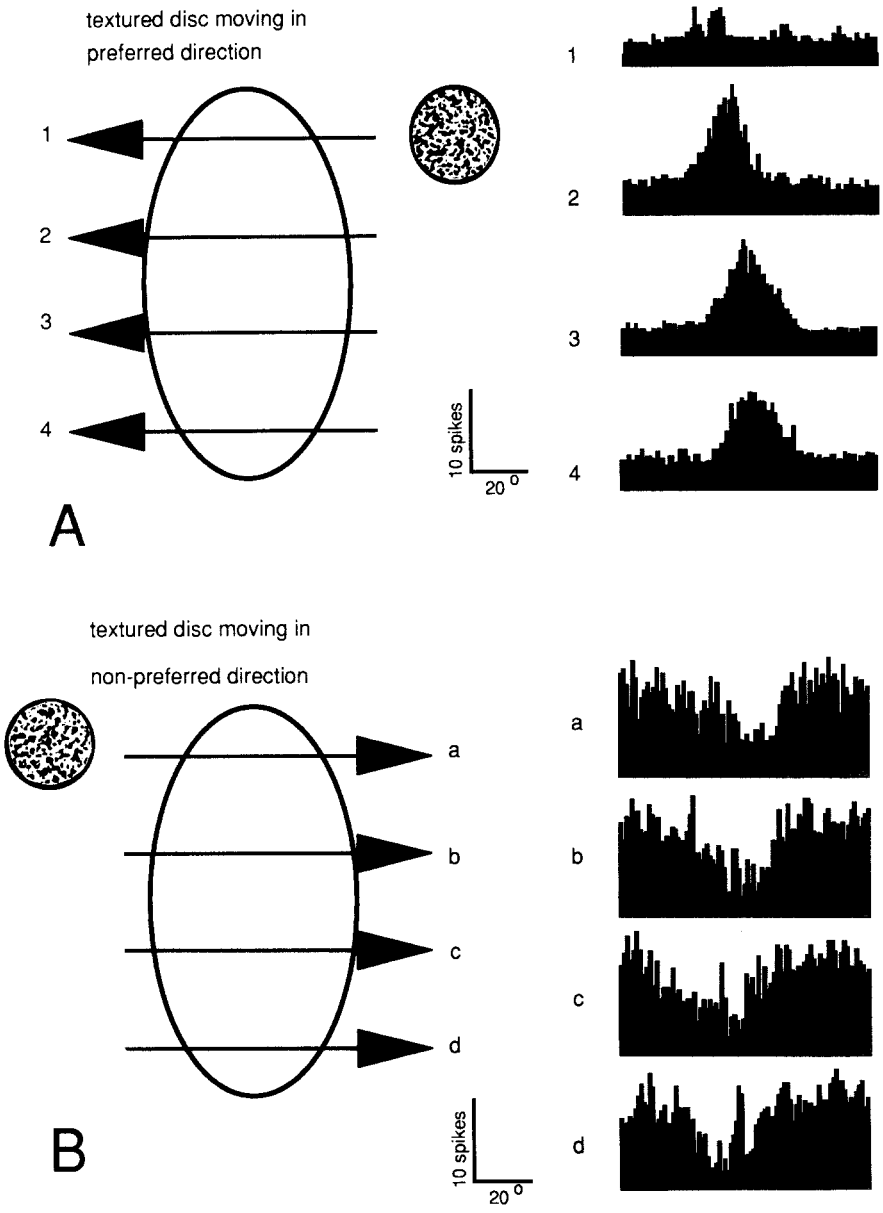

Fig. 6A, B. PSTHs of nBOR neurons in response to a textured disc traversing the RF in the preferred (**A**) and non-preferred (**B**) directions. A textured disc was moved along the screen at equally spaced transit positions. RF boundaries were determined from the PSTHs at each transit position. Note the *hot-spot* of peak excitation in **A** (transit 2) and peak inhibition in **B** (transit b)

The response of the cell increased as the length of the bar increased, depending on the length of the RF. Using the opaque sheets of paper with apertures of various sizes, it was noted the whole RF need not be stimulated to obtain a maximal response. For some cells the response of the cell was greatest when the whole RF was stimulated, however for other cells, stimulation of as little as 27% of the RF resulted in a maximum response.

Discussion

The AOS of the pigeon vs. the chicken and other vertebrates

The present study found that UP, DOWN and BACK (nasal to temporal) units are equally represented in the pigeon nBOR, but few FORWARD were found. UP units were found dorsal to DOWN units, and BACK units were found along the ventral surface of the nBOR. The small number of FORWARD units were found in the posterior dorsolateral region of the nBOR. Similar to the pigeon nBOR, in the chicken DOWN units were found ventral to UP units (Burns and Wallman 1981; McKenna and Wallman 1981, 1985a, 1985b). However, unlike the pigeon nBOR, in the chicken FORWARD units are found in the nBORl, which is lateral and rostral to the nBORp and nBORd (McKenna and Wallman 1981, 1985a, 1985b). A substantial population of BACK units has not been reported for the chicken nBOR.

Britto et al. (1981) reported that most neurons in pigeon nBOR responded to spots and bars of light moving either upward or downward. However, Gioanni et al. (1984) and Morgan and Frost (1981) found that some neurons responded best to backward wholefield motion. Moreover, Gioanni et al. (1983b) found that lesions of

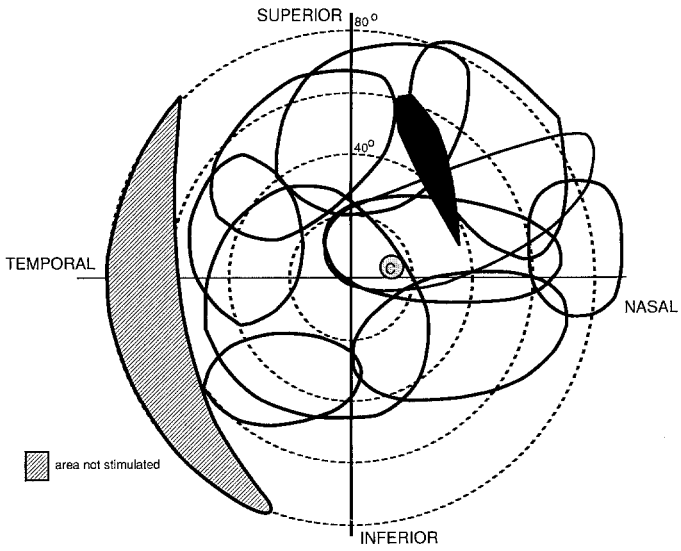

Fig. 7. The distribution of the RFs of nBOR neurons in the contralateral visual field. The reconstructions of 10 RFs are shown. The position of the RFs were calculated using both ends of the pecten as reference points. Note that RFs were not found in the inferior temporal visual field. C = area centralis

pigeon nBOR impaired nasal to temporal OKN but not temporal to nasal OKN. In chickens, vertical and torsional OKN, but not horizontal OKN, are disrupted by lesions of nBOR (Wallman et al. 1981). Thus, it appears that in pigeons, but not in chickens, the nBOR is important in processing backward motion.

The chicken AOS, like the mammalian AOS does not have a substantial population of neurons processing backward motion (Collewijn 1975; Grasse and Cynader 1982, 1984; Hoffmann and Schoppmann 1975, 1981; Simpson et al. 1979, Soodak and Simpson 1988). However, the pigeon AOS and the amphibian AOS both contain numerous neurons which process backward motion. In both the frog *Rana pipiens* (Gruberg and Grasse 1984) and newt (Manteuffel 1982) nBOR there is an equal representation of neurons preferring upward, downward, backward and forward motion. In another species of frog, *Rana temporaria*, Cochran et al. (1984) found units preferring upward, downward, and backward motion in the nBOR, and units preferring forward motion in the pretectum. Thus, the AOS of the pigeon and *Rana temporaria* show remarkable similarity.

Relative excitation and inhibition

As illustrated in Fig. 5, neurons were categorized as a function of the amount of relative excitation and inhibition in response to wholefield motion in the preferred and non-preferred directions respectively. Most neurons (E_i) exhibited robust excitation in response to wholefield motion in the preferred direction, and robust inhibition in response to wholefield motion in the non-preferred direction. I_e cells showed robust inhibition but very little excitation in response to wholefield motion in the non-preferred and preferred directions respectively. Some neurons lacked the inhibitory component (E_o, E_e) while others (I_o) lacked the excitatory component. In their study of the alert pigeon, Gioanni et al. (1984) described similar classes of nBOR neurons.

Brauth and Karten (1977) have described classes of nBOR neurons based on cell morphology. The nBORp consists mainly of large stellate shaped cells, with and some medium ovoid and small spindle shaped cells. The nBORd contains only small spindle shaped cells. In the present study, I_e and I_o cells were often found in an area corresponding to nBORd. It follows that I units may be the small spindle shaped neurons. However, without histological verification, any functional claims about these units would be premature.

Is the nBOR processing visual information in vestibular coordinates?

Simpson and his colleagues (Simpson et al. 1979; Simpson 1984; Simpson et al. 1988) developed the hypothesis that the AOS is organized in vestibular coordinates. That is, neurons in the AOS respond best to wholefield motion which results from a movement which maximally stimulates a pair of semicircular canals. Burns and Wallman (1981) proposed a similar argument for the avian system based on their study of the chicken. In the chicken, the optic axis is 70° from the posterior semicircular canal and 20° from the anterior semicircular canal. Because of this, a head rotation maximally stimulating the ipsilateral posterior canal results in visual flow along a curved path, such that in the upper and lower visual fields, the resultant visual flow has anterior components. In contrast a head rotation which maximally stimulates the ipsilateral anterior canal results in visual flow along a nearly straight path. Burns and Wallman (1981) found that Up units responded best to upward motion and were maximally inhibited by downward motion; i.e. the preferred and non-preferred directions that were on average 180° apart. However, Down units had asymmetrical directional tuning curves; i.e. they responded best to downward and slightly anterior motion, and were maximally inhibited by upward and slightly anterior motion. These findings suggested that the UP units are organized with respect to the ipsilateral anterior canal, and respond best to linear motion. Likewise, Down units are organized with respect to the ipsilateral posterior canal, responding best to motion along an arc.

The findings of the present study cannot support this argument for two reasons. First, the above argument predicts that for DOWN units the IRF and ERF would be found in the upper and lower visual fields respectively (Burns and Wallman 1981, p. 177). In the present study, no such receptive field organization was found. Second, in the present study DOWN units were found to have preferred and non-preferred directions which were nearly collinear. The preferred and non-preferred directions were on average 183° apart for DOWN units (see Fig. 2). Burns and

Wallman (1981) found that the preferred and non-preferred directions were on average 157° apart for Down units.

Simpson (1984) points out that directional tuning curves are not always symmetrical and argues that in such cases the mean preferred direction as calculated by vector analysis would not represent the peak of the distribution. That is, vector analysis would result in the mean preferred and non-preferred directions being more collinear than the peak values in an asymmetrical distribution. However, Figure 5 illustrates that the direction tuning profiles of pigeon nBOR neurons are not as asymmetrical as those in the rabbit MTN (Soodak and Simpson, 1988). Moreover, an analysis of direction preference based on the peak firing rate of cells which underwent a fine tuning analysis indicated that vector analysis did not misrepresent the average preferred and non-preferred directions of the directional classes. In any case, Burns and Wallman (1981) did use vector analysis. The apparent discrepancy between the results of the present study and those of Burns and Wallman (1981) may be due to the fact that the latter study based their conclusions on analysis of a small sample (i.e. 7) of Down units. Alternatively this discrepancy could represent a species difference between chicken and pigeon.

Although it has been demonstrated that the rabbit AOS is organized in vestibular coordinates (Simpson et al. 1979, 1988; Simpson 1984; Soodak and Simpson 1988), the same type of correspondence between the vestibular system and the AOS may not exist in the pigeon. In the rabbit, most AOS RFs are located in an area on, and just above the horizon (Oyster et al. 1980), thus all neurons experience the same direction of visual flow in response to a given head rotation. However, in the pigeon, the nBOR RFs tend to be scattered throughout the retina, with the exception of the red field. If the pigeon AOS was to be organized in vestibular coordinates, then the direction preference of every cell would have to be unique. Cells with peripheral RFs would respond best to motion along an arc, while those with central RFs would prefer linear motion. Moreover the RFs in Fig. 7 which extend from the centre to the periphery of the visual field should prefer linear motion at the centre, but more curvilinear motion at the periphery. However, in the present study the preferred and non-preferred directions of nBOR neurons were independent of the RF position, and subfield stimulation did not reveal any differences in direction preference.

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