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 of 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. 1979; 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...
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 (<20%) preferred backward (nasal to temporal) motion. 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 5–10 μ exposed tips were used to record extracellular potentials. A stepping motorized hydraulic microdrive system (Frederick Huer 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 the systematic manipulation of the direction and size of the stimuli. 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°/s. The microelectrode was then advanced in 5 μ 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 cinematographic 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 30 μ 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 nBORI. 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 was 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).