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Fast and slow neurons in the nucleus of the basal optic root in pigeons

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Abstract

The nucleus of the basal optic root (nBOR) is involved in the generation of the optokinetic response. Previous studies showed that most nBOR neurons exhibit direction-selectivity in response to largefield motion. We investigated the responses of pigeon nBOR neurons to drifting sine wave gratings of varying spatial and temporal frequency (SF,TF). Two groups of neurons were revealed. The first group preferred gratings of low SF (mean, 0.07 cycles per degree (cpd)) and high TF (mean, 0.76 Hz) ('fast' stimuli). The second group preferred gratings of high SF (mean, 0.56 cpd) and lower TF (mean, 0.33 Hz) ('slow' stimuli). Previous studies have demonstrated fast and slow neurons in pretectal nucleus lentiformis mesencephali, which is also involved in the generation of the optokinetic response. © 2001 Elsevier Science Ireland Ltd. All rights reserved.

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The pretectum and the Accessory Optic System (AOS) are involved in the analysis of optic flow and the generation of the optokinetic response (OKR; for reviews see Refs. [9,13,14]). Neurons in the nucleus of the basal optic root (nBOR) of the AOS and the pretectal nucleus lentiformis mesencephali (LM) exhibit direction-selectivity in response to largefield stimuli moving in the contralateral visual field [1,6,12,15,18]. Wylie and Crowder [17] examined the responses of pigeon LM neurons to drifting sine-wave gratings varying in spatial and temporal frequency (SF, TF). Two groups of neurons were found: fast neurons preferred low SFs/high TFs (0.03-0.25 cycles per degree (cpd), 0.5-16 Hz) and slow neurons preferred high SFs/low TFs (0.35-2 cpd, 0.125-2 Hz). Fast and slow neurons have also been found in the nucleus of the optic tract (NOT), the mammalian homolog of the LM [10]. Wolf-Oberhollenzer and Kirschfeld [16] examined the responses of pigeon nBOR neurons to drifting sine wave gratings but the SF range used (0.024-0.185 cpd) did not encompass that of the slow LM neurons. In the present study, we recorded from pigeon nBOR neurons in response to drifting sine wave gratings using a broad range of SFs and TFs. We found

that, as is the case in LM, there are fast and slow cells in the nBOR.

The methods employed conformed to the Guidelines established by the Canadian Council on Animal Care and were approved by the University of Alberta Biosciences Animal Welfare Committee. Details for anaesthesia, extracellular recording, stimulus presentation and data analysis have been described by Wylie and Crowder [17]. Briefly, pigeons were anaesthetized with a ketamine (65 mg/kg)xylazine (8 mg/kg) mixture (i.m.) and supplemental doses were administered as necessary. The animals were placed in a stereotaxic device and sufficient bone and dura were removed to expose the brain and allow access to the nBOR based on the pigeon stereotaxic atlas [11]. Recordings were made with either tungsten microelectrodes (10 μ m exposed tips; impedance 2–5 M Ω) or glass micropipettes filled with 2 M NaCl (tip diameter 4-5 µm; impedance 2-5 M Ω). The extracellular signal was amplified, filtered, displayed on an oscilloscope and fed to a window discriminator. TTL pulses representing single spikes were fed to a 1401plus (Cambridge Electronic Designs (CED)) and peristimulus time histograms were constructed with Spike2 software (CED). The stimuli were high contrast (0.95) sine wave gratings produced using a visual stimulus generator (VSGThree, Cambridge Research Services). The stimuli were displayed on a SONY multiscan 17se II monitor that

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was placed 35 cm from the bird $(50 \times 40^{\circ} \text{ visual angle})$ or backprojected by an InFocus LP750 projector onto a tangent screen placed 50 cm from the bird $(90 \times 75^{\circ})$. Once a responsive cell was isolated, a directional tuning curve (15 or 22.5° increments) was obtained using gratings of an effective SF and TF. Each neuron's direction preference was calculated from the best-fit cosine. Subsequently, the spatio-temporal properties were determined by presenting gratings in the preferred and anti-preferred directions. Several different SFs (0.015-2 cpd) were presented at several different TFs (0.15-16 Hz). Each sweep consisted of 4-5 s motion in the preferred direction, a 3-5 s pause, 4-5 s of motion in the anti-preferred direction, followed by a 3-5 s pause. Firing rates were averaged from at least three sweeps. Contour plots of the mean firing rate in the spatiotemporal domain were made using Sigma Plot. The maximum in the contour plot was used to assign the preferred SF/ TF combination for each neuron. At the end of the experiments, the birds were given an overdose of sodium pentomg/kg intraperitoneally barbitol (100 (i.p.)) and immediately perfused with saline followed by 4% paraformaldehyde. The brains were extracted and sectioned such that the electrode tracts could be localized using light microscopy.

We recorded from 32 nBOR neurons. The average spontaneous rate (SR) was 35 spikes/s (range 11-70 spikes/s). Spatio-temporal contour plots for both the preferred and anti-preferred directions were obtained for all neurons. Because, for most neurons, largefield motion in the preferred direction elicits excitation and motion in the anti-preferred direction inhibits the spontaneous activity, we refer to these as excitatory response plots (ER plots) and inhibitory response plots (IR plots), respectively. Fig. 1 shows ER and IR plots of three neurons. For the majority of contour plots, there was a single peak in the spatiotemporal domain (e.g. ER plots of Fig. 1A,C; IR plot of Fig. 1C). The ER plot in Fig. 1B contains two clear peaks. Similarly, the IR plot in Fig. 1A also contains two peaks of approximately equal size. In total, 13 ER plots and ten IR plots showed multiple peaks. Wylie and Crowder [17] reported similar properties for LM neurons (26% of the ER and IR plots had multiple peaks).

In some cases, for a given neuron, the ER plot was similar to the IR plot. That is, the SF/TF combination eliciting excitation to motion in the preferred direction also elicited maximal inhibition when moved in the anti-preferred direction (e.g. Fig 1C). However, this was not the norm. For example, in Fig. 1B, the peak in the ER plot was at midhigh SFs and low TFs, whereas the peak in the IR plot was at mid-high SFs and mid-TFs. Of the 28 neurons for which we obtained both ER and IR plots, 19 (68%) had markedly different spatio-temporal response profiles for the ER and IR. Wylie and Crowder [17] found that the proportion of LM neurons showing an independence of IR and ER was even higher (81%).

In Fig. 2 the locations of the response maxima are shown

for the ER and IR plots of nBOR neurons. For those contour plots in which there were multiple peaks, the location of the primary peak was plotted. One IR and one ER plot that had multiple minima/maxima of equal size was excluded from this analysis, as was one IR plot that showed a broad plateau. On the upper left, the peaks from the nBOR ER plots are shown. A Ward's cluster analysis with squared-Euclidean distance measures revealed two distinct clusters. Ten neurons comprised a group that preferred low-mid SFs (0.031–0.125 cpd) and TFs in the range of 0.125–4 Hz. The second group consisted of 21 neurons that preferred midhigh SFs (0.3–1 cpd) and TFs in the range of 0.063–2 Hz. We refer to these groups as fast and slow ERs, respectively (velocity = TF/SF). The average SF, TF and velocity of the fast ERs were, 0.074 cpd, 0.76 Hz and 10.2°/s, respectively. The average SF, TF and velocity of the slow neurons were, 0.56 cpd, 0.33 Hz and 0.59°/s, respectively.

The upper right section of Fig. 2 shows locations of the peaks from the nBOR IR plots. Like the ERs, the locations



Fig. 1. Spatio-temporal tuning of neurons in nucleus of the basal optic root (nBOR). (A–C) show contour plots of the responses of three nBOR neurons to gratings of varying spatial frequency (abscissa) and temporal frequency (ordinate) drifting in the preferred (ER plots) and anti-preferred (IR plots) directions. The scale on the iso-contour lines represents the firing rate (spikes/s) above (+) or below (-) the spontaneous rate. The spontaneous rates for the cells in A, B and C were 70, 21, and 17.5 spikes/s, respectively.



Fig. 2. Locations of the peak excitatory and inhibitory responses of neurons in nucleus of the basal optic root (nBOR) to gratings of varying spatial frequency (abscissa) and temporal frequency (ordinate). In top-left and top-right, respectively, the locations of the peaks are shown for the ER plots and the IR plots of nBOR neurons. In bottom-left and bottom-right, respectively, the locations of the peaks are shown for the ER plots and the IR plots of neurons in the lentiformis mesencephali of pigeons (data from [17]). Included in this analysis are ER and IR plots that showed single peaks, as well as those that showed multiple peaks where there was a clear primary peak (the locations of the primary peaks, but not the secondary peaks, are plotted). Locations of peak responses are indicated with a letter corresponding to the preferred direction of the cell (F, forward (temporal to nasal); B, backward; U, upward; D, downward motion). Note that for the IR plots, (responses to motion in the anti-preferred direction), the preferred direction of the cell is indicated.

of the peak IRs fell into two groups, although the clustering is not as obvious (there are two peaks at high TFs that are outliers from both groups). The average SF, TF and velocity of the eight fast IRs were, 0.068 cpd, 0.68 Hz and 9.9°/s, respectively. The average SF, TF and velocity of the 16 slow IRs were, 0.51 cpd, 0.48 Hz and 0.94°/s, respectively. The average TFs of these two groups were not significantly different (*t*-test, P = 0.36).

The lower half of Fig. 2 shows the locations of the peak ERs and IRs for LM neurons (from Ref. [17]). The ERs of LM neurons clustered into fast and slow groups, however, the IRs of LM neurons do not. Note the higher proportion of LM neurons (61%) with fast ERs compared to the nBOR sample (32%). The ERs of the slow LM and nBOR neurons were not significantly different with respect to average SF, TF or velocity. The ERs of the fast LM and nBOR neurons were not significantly different with respect to average SF, however the average TF and velocity were significantly

lower for the fast nBOR neurons (TF; nBOR, 0.76 Hz; LM, 2.88 Hz; P < 0.01: velocity; nBOR, 10.2°/s; LM, 29.2°/s; P < 0.05).

Previous research has shown that the pigeon LM and nBOR are complementary with respect to direction preference of neurons. In the nBOR, neurons preferring upward, downward and backward (nasal to temporal) motion are equally abundant, but neurons that prefer forward (temporal to nasal) motion are rare (<10%) [6,18]. In contrast, most neurons ($\sim50\%$) in LM prefer forward motion, fewer neurons prefer backward motion, and neurons that prefer upward or downward motion are the least common [2,3,15,17]. Fig. 2 also shows the direction preference of each neuron. There is a clear interaction between the spatio-temporal preference and the direction preference for both LM and nBOR neurons. With respect to direction preference, in both LM and nBOR, it is the most common cell types that prefer slow stimuli. As seen in the plots of the

peak ERs, forward cells are slow cells in the LM. Upward, downward, and backward cells are slow cells in the nBOR. Fast cells code all directions in both nuclei.

The fact that the LM contains more neurons responsive to fast stimuli than does the nBOR, and the fact that the fast LM ERs prefer faster stimuli than their nBOR counterparts, is consistent with behavioral observations. In pigeons, the gain of the OKR in response to nasal to temporal (forward) motion does not decline until velocities of 20–40°/s. In contrast, the gain declines at lower velocities for stimuli moving backward, upward and downward [4,5]. Furthermore, and consistent with our physiological findings, lesion experiments by Gioanni et al. [7,8] showed that the LM is important for generating the OKR to stimuli drifting forward in the contralateral eye, whereas the nBOR is involved in driving the OKR to stimuli drifting upward, downward or backward.

Ibbotson et al. [10] found fast and slow neurons in the NOT in the wallaby. The discovery of fast and slow neurons in the nBOR suggests that this functional division is not a specific feature of pretectal neurons but of all optokinetic nuclei. Thus, we predict that fast and slow cells would be found in the mammalian AOS as well.

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