Temporal Frequency and Velocity-Like Tuning in the Pigeon Accessory Optic System

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Short Title: Direction-selectivity in the AOS

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Abstract

Neurons in the accessory optic system (AOS) and pretectum are involved in the analysis of optic flow and the generation of the optokinetic response. Previous studies found that neurons in the pretectum and AOS exhibit direction-selectivity in response to large-field motion and are tuned in the spatio-temporal domain. Furthermore, it has been emphasized that pretectal and AOS neurons are tuned to a particular temporal frequency, consistent with the “correlation” model of motion detection. We examined the responses of neurons in the nucleus of the basal optic root (nBOR) of the AOS in pigeons to large-field drifting sine wave gratings of varying spatial and temporal frequencies (SF, TF). nBOR neurons clustered into two categories: “Fast” neurons preferred low SFs and high TFs, and “Slow” neurons preferred high SFs and low TFs. The fast neurons were tuned for TF, but the slow nBOR neurons had spatio-temporally oriented peaks that suggested velocity-tuning (TF/SF). However, the peak response was not independent of SF, thus we refer to the tuning as “apparent velocity tuning” or “velocity-like tuning”. Some neurons showed peaks in both the fast and slow regions. These neurons were TF-tuned at low SFs, and showed velocity-like tuning at high SFs. We used computer simulations of the response of an elaborated Reichardt detector to show that both the TF-tuning and velocity-like tuning shown by the fast and slow neurons, respectively, may be explained by modified versions of correlation model of motion detection.
Introduction

The pretectum and the accessory optic system (AOS) have been implicated in the processing of the visual consequences of self-motion, known as optic flow (Gibson, 1954), and the generation of the optokinetic response (OKR) to facilitate retinal image stabilization (for reviews see Simpson, 1984; Simpson et al., 1988; Grasse and Cynader, 1990). The AOS and pretectum are highly conserved in vertebrates. The mammalian pretectal nucleus of the optic tract (NOT) is homologous to the nucleus lentiformis mesencephali (LM) in birds, whereas the avian nucleus of the basal optic root (nBOR) of the AOS is homologous to the medial and lateral terminal nuclei (MTN, LTN) of the mammalian AOS (Simpson, 1984; McKenna and Wallman, 1985a; Fite, 1985; Weber, 1985; Simpson et al., 1988). In numerous species, it has been shown that pretectal and AOS neurons have large receptive fields in the contralateral eye, and exhibit direction-selectivity to moving large-field stimuli (NOT: Collewijn, 1975a,b; Hoffmann and Schoppmann, 1981; Volchan et al., 1989; Mustari and Fuchs, 1990, LM: Katte and Hoffmann, 1980; McKenna and Wallman, 1985b; Winterson and Brauth, 1985; Fite et al., 1989; Fan et al., 1995; Wylie and Frost, 1996, MTN/LTN: Grasse and Cynader, 1982; Grasse et al., 1984; Cooper and Magnin, 1986; Natal and Britto, 1987; Soodak and Simpson, 1988, nBOR: Burns and Wallman 1981; Morgan and Frost 1981; Gioanni et al. 1984; Rosenberg and Ariel, 1990; Wylie and Frost 1990a). The AOS and pretectum provide input to olivo-vestibulocerebellar pathways that respond best to patterns of optic flow resulting from self-translation and self-rotation (Simpson et al., 1981; Graf et al., 1988; Wylie and Frost, 1993, 1999; Wylie et al., 1993, 1998).
Using large-field drifting sine wave gratings of varying spatial frequency (SF) and temporal frequency (TF), a few studies have shown that AOS and pretectal neurons are tuned in the spatio-temporal domain. Ibbotson et al. (1994) recorded from the NOT of wallabies and found that there were two groups of neurons: those that preferred high SFs and low TFs vs. those that preferred low SFs and high TFs. As velocity = TF/SF, these two groups were referred to as “slow” and “fast” neurons, respectively. Strikingly similar observations were found in the pigeon LM and nBOR (Wylie and Crowder, 2000; Crowder and Wylie, 2001). Wolf-Oberhollenzer and Kirschfeld (1994) also recorded the responses of pigeon nBOR neurons to sine wave gratings, but they used a restricted range of SFs (<0.185 cpd), which did not include the SFs that maximally stimulate slow neurons (0.25-2Hz in pigeon nBOR and LM, and wallaby NOT; Ibbotson et al., 1994; Wylie and Crowder, 2000; Crowder and Wylie, 2001). Both Ibbotson et al. (1994) and Wolf-Oberhollenzer and Kirschfeld (1994) emphasized that neurons were tuned to TF rather than stimulus velocity, consistent with the “correlation” model of motion detection (Reichardt, 1957, 1961; Barlow and Levick, 1965; van Santen and Sperling, 1985) as opposed to the “gradient” models, which predict velocity tuning over a broad range of SFs and TFs (e.g. Marr and Ullmann, 1981; Buchner, 1984, Srinivasan, 1990).

In the present study we recorded the responses of neurons in the pigeon nBOR to drifting sine wave gratings, but used a broader range of SFs than those used by Wolf-Oberhollenzer and Kirschfeld (1994). We found that, whereas the fast cells were tuned to TF, the responses of the slow cells were more closely related to velocity than to TF. Although it has been assumed that the correlation model of motion detection (Reichardt, 1957, 1961; Barlow and Levick, 1965; van Santen and Sperling, 1985) is not well suited
for the measurement of image velocity, some versions of the correlation model produce
responses which are dependent on image speed (eg. Zanker et al., 1999). The data are
discussed with regard to these recent elaborations of the correlation model of motion
detection.

Methods

Surgery and Extracellular recording

The methods employed conformed to the Guidelines established by the Canadian
Council on Animal Care and were approved by the Biosciences Animal Welfare and
Policy Committee at the University of Alberta. Details for anaesthesia, extracellular
recording, stimulus presentation and data analysis have been described by Wylie and
Crowder (2000). Briefly, pigeons were anaesthetized with a ketamine (65 mg/kg) -
xylazine (8 mg/kg) mixture (i.m.) and supplemental doses were administered as
necessary. Based on the pigeon stereotaxic atlas (Karten and Hodos, 1967), sufficient
bone and dura were removed to access the nBOR with vertical penetrations. Recordings
were made with tungsten microelectrodes (2-5MΩ impedance) or glass micropipettes
filled with 2M NaCl (tip diameters 4-5 microns; impedance 2-5MΩ). 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 peri-stimulus time histograms were constructed with
Spike2 software (CED).
Stimulus Presentation

After neurons in the nBOR were isolated, the direction preference and the approximate locations of the receptive field boundaries were qualitatively determined by moving a large (90° × 90°) hand-held stimulus in various areas of the visual field. Directional tuning and spatio-temporal tuning were determined quantitatively with sine-wave gratings that were generated by a VSGThree graphics computer (Cambridge Research Designs, Cambridge UK), and back-projected onto a tangent screen that was located 50cm from the bird (90° × 75°). Direction tuning was tested using gratings of an effective SF and TF at 15° or 22.5° increments, while spatio-temporal tuning was tested using gratings of varying SF (0.03-2 cycles per degree (cpd)) and TF (0.03-16 cycles per second (Hz)) moving in the preferred and anti-preferred directions. Each sweep consisted of 4 sec of motion in one direction, a 3 sec pause, 4 sec of motion in the opposite direction, followed by a 3 sec pause. Firing rates were averaged over 3-5 sweeps. Contour plots of the mean firing rate in the spatio-temporal domain were made using Sigma Plot.

Histology

In some cases, when tungsten microelectrodes were used, electrolytic lesions were placed at the recording site (30µA for 8-10 seconds, electrode positive). At the end of each experiment, animals were given a lethal dose of sodium pentobarbitol (100 mg/kg i.p.) and immediately perfused with saline followed by 4% para-formaldehyde. Brains were extracted, post-fixed for 2-12 hours (4% para-formaldehyde with 20% sucrose) and then left in 30% sucrose for at least 24 hours. Frozen sections (45 µm thick in the coronal plane) through the nBOR were collected. Sections were mounted onto gelatine-
coated slides, and counterstained with neutral red. Light microscopy was used to localize electrode tracts and lesion sites.

Results

Extensive quantitative data, including directional and spatio-temporal tuning to sine wave gratings of varying SF and TF, was obtained from 53 nBOR neurons in 26 animals. Most neurons, although broadly tuned, were excited in response to motion in a particular direction (“preferred” direction) and inhibited below the spontaneous rate (SR) in response to motion in the (approximately) opposite direction (anti-preferred direction). Each neuron’s direction preference was assigned by calculating the maximum of the best cosine fit to the tuning curve. As shown in figure 1, there was an obvious clustering into four groups. Five (9%), 9 (17%), 15 (28%) and 24 (45%) neurons preferred forward (temporal to nasal), backward (nasal to temporal), downward, and upward motion, respectively. These data are in agreement with previous studies of the pigeon nBOR. Wylie and Frost (1990a) found that upward, downward and backward cells are equally abundant, but forward cells were rare (see also, Gioanni et al., 1984; Rosenberg and Ariel, 1990). It has been noted that a small subpopulation of nBOR neurons have binocular receptive fields and respond best to particular patterns of optic flow resulting from either self-rotation or self-translation (Wylie and Frost, 1990b, 1999; Wylie et al., 1998). No such neurons were recorded in the present study.

Spatio-temporal Properties of nBOR neurons
Figure 2 shows the responses of an nBOR neuron to gratings drifting in the preferred (up) and anti-preferred (down) directions. PSTHs to 36 combinations of SF (abscissa) and TF (ordinate) are shown. Each PSTH is for a single sweep, where each sweep consisted of 4 sec motion in the preferred direction (upward motion, solid line), followed by a 3 sec pause, followed by 4 sec of motion in the anti-preferred direction (downward motion, broken line). Note that this cell showed strong excitation to motion in the preferred direction and strong inhibition to motion in the anti-preferred direction. The neuron responded to several of the gratings, but the degree of the excitation and inhibition was variable. Note that for 1cpd/0.03Hz the neuron showed excitation rather than inhibition to motion in the anti-preferred direction. The asterisk (*) and pound (#) symbols respectively indicate the peak excitatory and inhibitory responses in the spatio-temporal domain (0.25cpd/0.125Hz) based on the average firing rate over the 4 sec epoch. This average encompassed the steady-state and transient responses during the epoch. An onset transient, variable in size, was present in response to motion in the preferred direction for most gratings. Onset transients to motion in the anti-preferred direction were less common, as were offset transients to motion in the both directions. In this report we do not further address these transients and other temporal factors (such as oscillations in the responses apparent in some PSTHs in Fig. 2). (Wolf-Oberhollenzer and Kirschfeld (1994), Ibbotson et al. (1994), Price and Ibbotson (2002) provided extensive descriptions of temporal factors).

To graphically illustrate tuning in the spatio-temporal domain, contour plots were constructed for both the preferred and anti-preferred directions (see Fig. 3). Because large-field motion in the preferred direction elicits excitation and motion in the anti-
preferred direction elicits inhibition, we refer to these as excitatory response plots (ER plots) and inhibitory response plots (IR plots), respectively. TF and SF were plotted on the ordinate and abscissa, respectively, and firing rate (relative to the SR) was plotted on the z-axis. The diagonal lines overlaying the contour plots indicate particular velocities (TF/SF). In these plots, the black represents the SR, red represents excitation, and green represents inhibition. Progressively brighter and less saturated reds/greens represent greater magnitudes of excitation/inhibition, such that the peaks are shown as off-white.

The neurons shown in figure 3A and B clearly had two peaks in their ER plots. For the neuron in figure 3A there was a primary peak at 1cpd/0.5Hz (60 spikes/s) and a smaller secondary peak at 0.125cpd/16Hz (20 spikes/s). For the neuron in figure 3B there was a primary peak at 0.063cpd/16Hz (45 spikes/s) and a smaller secondary peak at 0.5cpd/0.125Hz (35 spikes/s). The neuron shown in figure 3C had a single peak in its ER (200 spikes/s above SR) to high SF gratings (0.5-1cpd) drifting at mid-low TFs (0.5-2Hz). Of the 53 ER plots, 25 showed a single peak (e.g. Fig. 3C) and 28 showed multiple peaks (e.g. Fig. 3A,B). The IR plot in figure 3B showed a similar profile to the ER plot for that neuron, but this was not the case for the neuron shown in figure 3C. The neuron in figure 3C was maximally excited (200 spikes/s) by high SFs drifting at mid-TFs in the preferred direction, but maximally inhibited (-12 spikes/s) by mid SFs (0.25pd) drifting at high TFs (16Hz) in the anti-preferred direction. For 16 neurons the ER and IR plots showed a similar tuning profile (as in Fig. 3B, see also Fig. 2). However, for 33 neurons, the tuning in the spatio-temporal domain was quite different for the ER and IR plots (as in Fig. 3C).
Quantitative Analysis of the ER Plots

Stimulus velocity (in degrees per second; °/s) is calculated as TF/SF. Thus, from the contour plots it is straightforward to see if a cell is tuned to TF or velocity. A contour plot showing perfect velocity tuning would have an elongated peak, such that the slope is equal to 1. TF-tuning is exemplified by contour plots that are symmetrical about a horizontal line through the peak indicating a preference for the same TF over a range of SFs.

From Figure 3 it is clear that not all the neurons were tuned to TF. To quantify the orientation of the peaks in the ER plots, each peak was fit to a two-dimensional Gaussian function, using a slightly modified version of the method of Perrone and Thiele (2001):

\[ G(u, \omega) = \left( \exp\left(-\left(\frac{u'}{\sigma_u}\right)^2\right) \right) \times \left( \exp\left(-\left(\frac{\omega'}{\sigma_\omega}\right)^2\right) \right) + P \]

where

\[ u' = (u - x) \cos \theta + (\omega - y) \sin \theta \]

\[ \omega' = - (u - x) \sin \theta + (\omega - y) \cos \theta \]

\( u \) is \( \ln \) (SF), \( \omega \) is \( \ln \) (TF), \( \theta \) is the angle of the Gaussian, \((x,y)\) is the location of the peak of the Gaussian, \( \sigma_u \) and \( \sigma_\omega \) are the spread of the Gaussian in the \( u' \) and \( \omega' \) dimensions, respectively, and \( P \) is a constant. The values \( \sigma_u, \sigma_\omega, x, y, \theta \) and \( P \) were optimized to minimize the sum of the mean error between the real and \( G \) values using the solver function in Microsoft Excel.

Following Perrone and Thiele (2001), each ER peak was fitted to two different types of Gaussian functions: non-oriented and oriented. In the non-oriented function \( \theta \) was constrained to zero, while \( \theta \) was free to take on any value in the oriented Gaussian function. The square of the Pearson product moment correlation coefficient (\( r^2 \)) was
calculated for each Gaussian to measure the overall fit to the data. Averaged across the entire data set, which consisted of 52 fitted peaks, the \( r^2 \) values of the oriented and non-oriented fits were 0.84 ± 0.09 and 0.77 ± 0.11, respectively (mean + standard deviation). These were significantly different (single sample Student t-test \( p< 0.0001 \)). (There were 13 neurons that were not fit with Gaussians either because the two peaks in the ER plot appeared inseparable, or there were more than two peaks in the contour plot).

In Figure 3 oriented Gaussian fits to the ER plots of the 3 neurons are shown. For perfect velocity tuning \( \theta \) would equal 45° (i.e. a slope of 1), but for TF-tuning \( \theta \) would equal 0° or 90°. For the neurons in figure 3A and B, the peaks in the fast and slow region were fit separately, and the gray boarders indicate the range of SFs and TFs used for each fit. For the neuron in figure 3A, the \( \theta \) values for the fast and slow peaks were 85° and 42°, respectively. For the neuron in figure 3B, the \( \theta \) values for the fast and slow peaks were 87° and 37°, respectively. For the neuron in figure 3C, which had a single slow peak, \( \theta = 57° \).

Figure 4 shows the location (x,y; circles) and orientation (\( \theta \); solid line) of each oriented Gaussian fit. For those ER plots with two peaks, the location of the primary and secondary peaks were plotted as filled and empty dots, respectively. Following previous studies of the pretectum and AOS (Ibbotson et al., 1994; Wylie and Crowder, 2000; Crowder and Wylie, 2001), we use 4°/s as the boarder between “Fast” and “Slow” neurons, although the distinction in the data is not as apparent as in those previous studies. For fast cells the peak excitation occurred in response low-mid SFs (0.03-0.13 cpd) and mid-high TFs (0.5-16 Hz). For slow cells the peak excitation occurred in response to mid-high SFs (0.3-2 cpd) and low-mid TFs (0.06-2 Hz). Shown in Table 1,
which considers data from only the primary peaks, the average SF and TF of the fast ERs were 0.078 cpd and 2.84 Hz, respectively. The average SF and TF of the slow neurons were 0.53 cpd and 0.30 Hz, respectively. (All values were first transformed to the natural log, the average was calculated, and then the inverse transformation was performed). As indicated by the orientation of lines in Figure 4, for most peaks in the fast zone θ approximated 0° or 90° (suggesting TF-tuning), whereas θ approached 45° for most peaks in the slow zone (suggesting velocity-tuning).

Figure 5 shows the responses of two cells as a function of velocity (left column) and TF (right column). Responses to low SFs (0.03 – 0.125 cpd) and high SFs (0.25 – 1 cpd) are separated into top and bottom panels, respectively. The neuron in figure 5A showed velocity tuning to high SFs with a peak response at 1°/s (bottom-left panel). At low SFs, this neuron was more closely tuned to TF (top-right panel; peak at 0.125 Hz) than velocity. Figure 5B also shows a neuron that was more closely tuned for velocity (peak at 0.1 – 1°/s) at high SFs, but TF-tuned at lower SFs, with a sharp peak at 16Hz.

**Direction Tuning in Fast and Slow Zones**

Figure 6 shows three down cells (A,C,D) and one back cell (B) from which direction tuning curves were collected using slow gratings (solid line, 0.5cpd/0.5Hz) and fast gratings (dashed line, 0.063/4Hz). Firing rate relative to the SR (gray circle) is plotted as a function of the direction of motion in polar coordinates (i.e. the SR has been set to zero; outside the gray circle= excitation, inside = inhibition). The neurons in figure 6A,C and D preferred the slow gratings, showing a much greater depth of modulation. The neuron in figure 6B responded to slow and fast gratings equally. Solid and dashed
arrows represent the neuron’s preferred direction for slow and fast gratings, respectively, as calculated from the best-fit cosines to the tuning curves. The neurons in figure 6A and C showed very little variation in preferred direction in response to slow and fast gratings. The neurons in figure 6B and D had differences of about 20° in their preferred directions in response to slow and fast gratings, but these were the largest changes we observed. No cells showed large enough differences in direction preference to be classified as one direction-type in response to slow gratings and another direction-type in response to fast gratings.

Discussion

In the present study we examined the responses of neurons in the pigeon AOS to large-field drifting sine wave gratings. nBOR neurons clustered into two groups based on the location of peak response in the spatio-temporal domain: fast cells which preferred low SFs and high TFs, and slow cells that preferred high SFs and low TFs, although many neurons showed peaks in both the fast and slow regions. Most of the fast peaks were tuned to a specific TF (see Figs. 3A,B, 4, 5) whereas most of the slow peaks showed apparent velocity tuning, insofar as the 2-dimensional Gaussians fit to the slow peaks were oriented at about 45° (see Figs. 2-5). Strictly speaking, the slow neurons cannot be called velocity-tuned because the response is SF dependent. For example, the ER plot shown in Figure 3C shows a peak oriented at approximately 45°, suggestive of velocity tuning. However, the response to 1cpd/2Hz (2°/s) was about 200 spikes/s, whereas the response to 0.25cpd/0.5Hz (2°/s) was 150 spikes/s. A velocity-tuned neuron would respond equally well to a preferred velocity, irrespective of the SF, and the peak in the
ER plot would appear as an elongated ridge (Zanker et al., 1999). Thus, we use the term “velocity-like” tuning, or apparent velocity tuning.

Comparison with Previous Studies of the Pretectum of Birds and Mammals

Ibbotson et al. (1994) were the first to demonstrate that neurons in the pretectum (wallaby NOT) were tuned in the spatio-temporal domain to either low SF/high TFs (fast cells) or high SFs/low TFs (slow cells). Subsequently, Wylie and Crowder (2000) showed that neurons in the pretectum (nucleus LM) of pigeons contained such fast and slow neurons. Following Ibbotson and Price (2001), a direct comparison of the pigeon and wallaby pretectal data is offered in Table 1, along with data from the pigeon nBOR from the present study. The mean velocity of the slow and fast NOT neurons was 0.8 and 50°/s, respectively, remarkably similar to what we found for the pigeon LM (1.08 and 52°/s, respectively). Such similarities may arise from convergent evolution in response to similar visual environments, or point toward a highly conserved visual system of ancient origin (Ibbotson and Price, 2001). Table 1 shows that the TF, SF and velocity preferences of the fast and slow nBOR neurons are similar to their counterparts in the LM. Note that the percentage of fast cells in the nBOR is much less than that in the LM (also see Crowder and Wylie, 2001).

In our previous study of the spatio-temporal tuning in the pigeon LM (Wylie and Crowder, 2000), we reported that velocity tuning was rare. In fact, of 35 ER plots only 1 appeared as velocity-tuned, whereas 14 were TF-tuned. The results of the present study prompted us to re-examine the LM data, with emphasis on the slow cells. The data set from Wylie and Crowder (2000) consisted of 12 slow cells, but we have subsequently
recorded from an additional 8 slow LM neurons (e.g. from Crowder et al., in press). Two-
dimensional Gaussian functions were fit to the peaks in the LM ER plots, and the
locations (x,y) and orientations (θ) of each oriented Gaussian fit is shown in figure 4,
alongside the same data from the nBOR cells. Of the 20 slow peaks, 12 had slopes that
approached 45° (i.e. within 20°). Thus, it appears that slow neurons in nBOR and LM
show apparent velocity tuning.

*Implications for Models of Motion Detection*

Initially proposed by Reichardt (1961), the correlation model of motion detection
has been very successful in describing motion processing in animal vision (for reviews
see Buchner, 1984; Borst and Egelhaaf, 1989; Srinivasen et al., 1999; Clifford and
Ibbotson, 2003). The classic correlation detector consists of two subunits, or “half
detectors”, each selective for motion in opposite directions. When the outputs of these
two half-detectors are subtracted from each other a highly directional motion detector is
created (see also Appendix A, Fig. 8). Recent elaborations of the basic correlation-type
detector have involved the addition of spatial and temporal pre-filters (e.g. Dawson and
DiLollo, 1990; Ibbotson and Clifford, 2001; Price and Ibbotson, 2002). The energy model
is a variant of this basic scheme, and generates similar response properties to elaborated
correlation-type detectors (Adelson and Bergen, 1985; Zanker et al., 1999).

One of the most prominent features of the correlation model of motion detection
is its dependence on the spatial structure and contrast of the visual stimulus (Reichardt
1961; Buchner, 1984). Furthermore, correlation motion detectors are tuned to a particular
TF rather than a particular velocity (for reviews see, Buchner, 1984; Egelhaaf et al.,
1989; Ibbotson et al., 1994; Wolf-Oberhollenzer and Kirschfeld 1994; Srinivasan et al., 1999). This TF-tuning has been used as an identifying characteristic of the correlation scheme for many years (e.g. Wolf-Oberhollenzer and Kirschfeld 1994). Behavioral and physiological studies of insects over the last 40 years have emphasized that the motion detectors underlying the optokinetic “turning response” are of the correlation type (Srinivasan et al., 1999). The amplitude of the turning response is dependent on TF rather than the velocity of the stimulus, and the responses of the optic flow sensitive neurons in the visual neuropile exhibit properties consistent with the correlation model, including tuning for TF rather than velocity (e.g. Reichardt, 1969, Eckert, 1980; Hausen, 1984; Buchner, 1984; Borst and Egelhaaf, 1989; Egelhaaf et al., 1989, 1990; O’Carroll et al., 1996). Moreover, there is behavioral and physiological evidence from cats, monkeys and humans indicating that detectors of the correlation type are involved in motion analysis in mammals (Tolhurst and Movshon, 1975; Miles and Kawano, 1987; see also Nakayama, 1985; Borst and Egelhaaf, 1989).

Evidence in favor of the correlation scheme has also been reported for the oprokinetic system. Neurons in the wallaby NOT were sensitive to contrast and most were tuned to TF (Ibbotson et al., 1994; Ibbotson and Price, 2001). Turke et al. (1996) recorded optokinetic head movements in unrestrained pigeons in response to horizontally drifting gratings of varying SF, contrast, and stimulus velocity. They noted a strong dependence on contrast and TF rather than velocity. In a study of responses of neurons in the pigeon nBOR, Wolf-Oberhollenzer and Kirschfeld (1994) reported that most neurons were TF-tuned, but only one neuron tested showed velocity tuning. This is in stark contrast to our findings. However, neither Wolf-Oberhollenzer and Kirschfeld (1994) nor
Turke et al. (1996) used the higher SFs that would maximally excite the slow nBOR cells discussed in the present study. Indeed, the classic correlation motion detection model cannot account for the velocity-like tuning of slow nBOR neurons.

Recently, Zanker et al. (1999) explicitly showed that altering the subtraction step, or “balance”, of the two half-detectors critically affects the tuning of the detector. The classic correlation scheme described above is a fully balanced detector, where the inputs from the two anti-symmetric half detectors are equally weighted. Recall that this fully balance detector is TF-tuned. Conversely, Zanker et al. (1999) showed that a fully unbalanced detector, which is essentially a lone half-detector, is velocity-tuned. Finally, a partially balanced detector had responses between these two extremes, with velocity tuning that was weakly dependent on SF (Zanker et al., 1999). It is possible that the velocity-like tuning in the slow zone of nBOR neurons represents the output of a partially balanced correlation-type motion detector. We illustrate this in Figure 7, which shows the ER plots of simulations generated by a model of an elaborated Reichardt detector. The details of the model can be found in Appendix A. We used a model from Dawson and DiLollo (1990), but with delay filters given by (Clifford et al., 1998) and temporal pre-filters described by Ibboston and Clifford (2001) and Price and Ibboston (2002).

Moreover, following Zanker et al. (1999) we manipulated the balance by varying the gain \( \alpha \) of the subtraction step where the response \( = (S_1) - (\alpha \times S_2) \). When \( \alpha = 1 \) the detector is fully balanced, and when \( \alpha = 0 \) the detector is fully unbalanced (i.e. a half-detector) (Zanker et al., 1999). In Figure 7A we have modeled the ER plot of a slow cell with a peak response to 1cpd/0.5Hz. When \( \alpha = 1 \) (left) the ER plot shows TF-tuning, but when \( \alpha = 0.5 \) (right) velocity-like tuning is evident. When a 2-dimensional Gaussian is fit to
this peak $\theta = 56^\circ$, but clearly the response is dependent upon SF. Thus, we suggest that
the slow nBOR neurons might represent the output of partially balanced correlation
detectors, perhaps approaching half-detectors. Other electrophysiological evidence from
the fly’s visual system (Egelhaaf et al., 1989) and the wallaby pretectum (Ibbotson et al.
1994; Ibboston and Clifford, 2001; Price and Ibbotson, 2002) also suggests that the
underlying motion detectors are not perfectly balanced.

In the present study we found that the fast nBOR neurons exhibit TF tuning.
Although one could conclude that this implies that the underlying motion detectors are
fully balanced, with Figure 7B we show that this is not necessarily the case. On the left,
we modeled a fully balanced detector tuned to $1\text{cpd}/8\text{Hz}$, with rather restrictive temporal
pre-filters. Note the TF-tuning. On the right we show the response of the model with the
same parameters except $\alpha = 0$. The peak, which has been pushed to the lower range of
SFs, appears TF-tuned. Clearly the shape of the peak in the spatio-temporal domain is
dependent upon both the pre-filter settings and the balance of the detector. Dror et al.
(2001) demonstrate that other processes such as response compression and adaptation are
also critical when considering velocity estimations by Reichardt detectors.

Another model of motion detection that may be applied to the current results is
the Weighted Intersection Mechanism (WIM) model developed by Perrone and Thiele
(2002). The WIM model of velocity sensitivity was developed to show how MT neurons
in the primate extra-striate cortex could build velocity-tuned spatio-temporal peaks by
summing the spatio-temporal inputs from a sustained V1 neuron and a transient V1
neuron. In this model, the spatio-temporal tuning of the sustained V1 neuron must differ
slightly from the tuning of the transient V1 neurons, this difference produces a diagonal
peak in the spatio-temporal domain enabling narrow velocity tuning (Perrone and Thiele, 2002). Although this model appears to be tailor-made for the geniculo-striate pathway, it demonstrates that the spatio-temporal tuning from multiple inputs can be combined to shape the spatio-temporal tuning of an afferent neuron. This shaping has already been shown experimentally in the AOS and pretectum. The spatio-temporal tuning of LM neurons is drastically altered when input from the nBOR is inactivated by tetrodotoxin (Fowder et al., in press). Similar results are expected for nBOR neurons if the LM were inactivated. Antidromic stimulation studies in the turtle AOS indicate that the receptive fields of AOS neurons result from the pooling of multiple directionally selective retinal inputs (Kogo et al., 1998). The spatio-temporal tuning of these retinal inputs could be combined to form velocity-like tuning.

Function of fast and slow neurons

Ibbotson et al. (1994) provide an extensive discussion of the potential role of the slow and fast NOT neurons in the generation and maintenance of optokinetic nystagmus (OKN). Immediately after the onset of an optokinetic stimulus, there is a 50-100msec latent period before ocular following begins (e.g. Collewijn, 1972). During this period, the retinal slip velocity (RSV) is high, and Ibbotson et al. (1994) suggest that the fast NOT neurons are responsible for initiating ocular following (the “direct” phase of OKN; Cohen et al., 1977; Miles et al., 1986; Gellman et al., 1990). Moreover, they suggest that the fast neurons are involved in the charging of the velocity storage mechanism (“indirect” phase of OKN) when stimulus speeds are high. Ibbotson et al. (1994) note that rapidly moving visual images become blurred, which is consistent with the fact that
the fast NOT neurons respond best to low SFs. The slow NOT neurons would become active when the RSV is low, and they would continue to charge the velocity storage mechanism at these slow velocities. Pigeons lack the direct phase of OKN, but they do possess a velocity storage mechanism (Gioanni, 1988; Nalbach, 1992). This precludes the fast LM and nBOR neurons in pigeons from a role in the direct component of OKN, as proposed for the fast NOT neurons. However, it is reasonable to imagine that the fast and slow nBOR and LM neurons are involved in charging the velocity storage mechanism as proposed for the fast and slow NOT neurons. Those neurons with peaks in both the fast and slow regions would be active when RSV is high and low.

Srinivasan et al. (1999) offer another function for the fast and slow cells (see also Heeger, 1987; Simoncelli and Heeger, 1998). They refer to single motion detector with a peak in the spatio-temporal domain as a “correlator”. The spatio-temporal tuning of a single correlator would look similar to a contour plot of a pretectal or AOS neuron with a sharp peak in the spatio-temporal domain. The response of a single correlator is ambiguous because all points that lie on a given response contour in the spatio-temporal domain represent combinations of SFs and TFs that elicit the same response. If contrast is allowed to vary, another degree of uncertainty is added. Because the response of the motion detector will increase with contrast (until saturation is reached), all points on a given response contour will be confounded with points on a weaker response contour if the contrast representing the weaker contour is appropriately increased. The above ambiguity can be removed if more than one correlator is incorporated into the movement detecting process, with each correlator having different spatio-temporal frequency optimum. The velocity of a stimulus would be coded by the relative activity of the
correlators. Manipulating the contrast of the stimulus would affect all correlators equally, but the stimulus velocity would still determine the ratio of the activity between the correlators. In this scheme, velocity of a stimulus can be estimated unambiguously and independently of spatial structure or contrast based on the population response (Srinivasan et al., 1999). Srinivasen et al. (1999) noted that visual systems of insects have two classes of direction-selective neurons differing with respect to preferred TF (Horridge and Marcelja, 1992) and the optokinetic system in crabs has three such classes of neurons (Nalbach, 1990).

When this model is applied to the AOS and pretectum, the fast and slow cells take on the roles of two classes of correlators. Theoretically, the RSV could be reliably be encoded by the pattern of activity in nBOR neurons, and the velocity storage mechanism would be provided with a velocity signal that is unambiguous and independent of spatial structure or contrast of the visual stimulus. Furthermore, this velocity information could be utilized for other behaviours such as flight speed and “odometry” which require an unambiguous velocity signal (Srinivasen et al., 1999).
Appendix A

For the simulations shown in Figure 7 we examined the responses of an elaborated version of the Reichardt detector, depicted in Figure 8, to 36 SF/TF combinations. It was created by modifying a model originally proposed by Dawson and Di Lollo (1990) by incorporating alternative temporal filters proposed by Ibbotson and Clifford (2001) and Price and Ibbotson (2002). The stimuli for the model, designed to closely resemble the stimuli used during the neural recordings, consisted of a blank gray screen (at mean luminance) for 2 seconds, followed by a drifting sine wave grating for 2 seconds. The elementary motion detector (EMD) consists of two subunits (A, B) that we assume to be separated by 2°. The model consists of 5 stages; (i) prefILTERING (ii) delay filtering, (iii) multiplication, (iv) subtraction, and (v) phase averaging.

Stage I: Prefiltering. In the original Dawson and Di Lollo (1990) model, spatial and temporal band-pass prefILTERING was performed to represent photoreceptor responses. In that model, impulses were used as stimuli, a difference of Gaussians (DOG) was used to perform spatial filtering, and temporal filtering was accomplished via an impulse response function defined by Adelson and Bergen (1985). In the current study, we were interested in studying the model’s responses to drifting sine gratings. For such stimuli, spatial DOG filtering produces a sinusoid of the same frequency and phase. Because of this, we did not employ spatial prefilters, although we assume that such prefILTERING is carried out by the visual system. Ibbotson and Clifford (2001) also adopted this approach in their simulations.
In the current model, the raw signal \( s(t) \) that was presented to a subunit of the EMD at time \( t \) was defined as:

\[
s(t) = \begin{cases} 
L, t \leq 2 \\
L + C \times \sin((f_s \times x) - (f_t \times t) - P), t > 2
\end{cases}
\]

where \( L \) is mean luminance in arbitrary units, \( C \) is contrast in arbitrary units, \( f_s \) is spatial frequency in cycles/radian, \( f_t \) is temporal frequency in \( 2\pi \times \) cycles/second, \( x \) is the spatial location of the subunit’s detector, \( P \) is a phase shift of the signal (radians), and \( t \) is time (seconds). In the simulation, the value of \( x \) for the left detector was 0, and the value of \( x \) for the right detector was \( \pi/90 \) radians (\( 2^\circ \)).

Temporal filtering was then performed by convolving the signal for each detector with a band pass filter of the type used by Price and Ibbotson (2002):

\[
h(t) = \begin{cases} 
\frac{1}{\tau_1} \exp \left( \frac{-t}{\tau_1} \right) - \left( \frac{\beta}{\tau_2} \right) \exp \left( \frac{-t}{\tau_2} \right), t > 0 \\
0, t \leq 0
\end{cases}
\]

This filter is a difference between exponential functions, where \( \tau_1 \) and \( \tau_2 \) are the time constants of these respective functions in seconds, and \( \beta \) is the gain of the temporal filter, which has a value between 0 and 1.

**Stage II: Delay filtering.** In order to detect motion, delayed versions of the signals being detected by both receptors in the EMD were computed. In the original Dawson and Di
Lollo (1990) model, this was accomplished by a pure phase shift. In the current model, this was instead achieved by convolving the prefiltered signals from stage I with a first-order low-pass filter that was used by Clifford et al. (1998):

\[
d(t) = \begin{cases} 
0, & t \leq 0 \\
\left(\frac{1}{\tau}\right)\exp\left(-\frac{t}{\tau}\right), & t > 0 
\end{cases}
\]

where \(t\) is time (seconds), and \(\tau\) is the time constant of the filter in seconds.

**Stage III: Multiplication.** In the multiplication step, the left-delayed signal was multiplied by the right-undelayed signal to produce the signal from the left half of the detector (S\(_1\)). The signal from the right half of the detector (S\(_2\)) was calculated in a similar fashion, by multiplying the right-delayed signal by the left-undelayed signal.

**Stage IV: Subtraction.** In the subtraction step, the signal from the right half of the EMD (S\(_2\)) was subtracted from that from the left half of the detector (S\(_1\)), but scaled by \(\alpha\) which controls the “balance” of the detector (Zanker et al., 1999), such that

\[
\text{Output} = (S_1) - (\alpha \times S_2), \quad 0 \leq \alpha \leq 1
\]

When \(\alpha = 1\), the detector is fully balanced, but with \(\alpha < 1\), the detector is said to be partially balanced. With \(\alpha = 0\), the fully unbalanced EMD is referred to as a “half-detector” (Zanker et al., 1999).
*Stage V: Phase Averaging.* The final step, phase-averaging, serves the purpose of spatial integration that is found in models that employ an array of EMDs (e.g. Zanker et al., 1999; Ibbotson and Clifford, 2001; Price and Ibbotson, 2002). Because the response of an EMD is sensitive to the phase of the grating (e.g. Buchner, 1984), and because we were using a rather short duration of motion for the slower TFs, we averaged the response of the detector to 4 different stimuli. The only difference between each of these stimuli in terms of phase, which was manipulated by varying the value of P in the equation for the drifting sinusoid that was provided earlier. The values of P for the four different stimuli were 0, π/2, π, and 3π/2 radians (i.e. 0, 90, 180, and 270 degrees).
Acknowledgements

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Figure Captions

Figure 1.
Directional tuning of neurons in the nucleus of the basal optic root. The orientation of each arrow represents the preferred direction for each neuron, as calculated from the peak of the best-fit cosine to the direction-tuning curve. U, B (N-T), D, and F(T-N) represent up, back (nasal to temporal), down, and forward (temporal to nasal) motion.

Figure 2.
Responses of a neuron in the nucleus of the basal optic root (nBOR) to drifting gratings of varying spatial and temporal frequency (SF, TF). Peri-stimulus time histograms (PSTHs) show the responses of the neurons to 36 combinations of SF (abscissa) and TF (ordinate). Single sweeps are shown, where each sweep consisted of 4 sec motion in the preferred direction (upward motion, solid line), then a 3 sec pause, followed by 4 sec of motion in the anti-preferred direction (downward motion, broken line). The asterisk (*) and pound (#) indicate the peak excitatory and inhibitory responses in the spatio-temporal domain based on the average firing rate over the 4 sec epoch, respectively.

Figure 3.
Spatio-temporal tuning of neurons in the nucleus of the basal optic root (nBOR). Contour plots of the responses of nBOR neurons to gratings of varying spatial frequency (abscissa) and temporal frequency (ordinate) are shown. A shows the response to gratings drifting in the preferred direction (ER plots) and the Gaussian
fit of the ER (see results) for a slow neuron. B and C show the responses to gratings drifting in the preferred and anti-preferred (ER and IR plots) directions as well as the Gaussian fits of the ER plots for two other neurons. For the ER and IR plots, the scale on the iso-contour lines represents the firing rate (spikes/sec) above (+) or below (-) the spontaneous rate, and the diagonal lines overlaying the contour plots indicate particular velocities (TF/SF). Note that the ordinate and abscissa are not symmetrical, and the diagonal lines represent a slope of 1 (i.e. 45°). For the Gaussian fits, the scale has been normalized. The gray lines encompass the range of SF and TF used to create each Gaussian fit. The correlation coefficient for each of the Gaussian fits is also indicated. For the ER and IR plots, as well as the Gaussian fits, black fill represents the SR, red represents excitation, and green represents inhibition.

Figure 4.

Spatio-temporal preferences of neurons in the nucleus of the basal optic root (nBOR, left) and pretectal nucleus lentiformis mesencephali (LM, right). Each circle represents the location (x,y) of the peak of the best fit two dimensional Gaussian to the peaks in excitatory response (ER) plots. For ER plots that had multiple peaks, primary and secondary peaks are shown as filled and empty circles, respectively. The dotted line indicates 4°/s, the boundary between the fast and slow zones in the spatio-temporal domain (Ibbotson and Price, 2001). The tail on each dot represents the orientation (θ) of the best fit Gaussian. Note that orientations of 45° indicate velocity-like tuning, and 0° or 90° indicate temporal...
frequency tuning. See results section for a detailed description of the Gaussian fitting procedure.

Figure 5.

Velocity and temporal frequency tuning of neurons in the nucleus of the basal optic root (nBOR). The responses of two cells (A and B) are shown as a function of velocity (abscissa, left column) and TF (abscissa, right column). Responses to low SFs (0.03 – 0.125 cpd) and high SFs (0.25 – 1 cpd) are separated into top and bottom panels, respectively. Firing rate (in spikes/sec) is shown on the ordinate for all graphs. Error bars indicate mean ± standard deviation.

Figure 6.

Directional tuning of neurons in the nucleus of the basal optic root (nBOR) to slow and fast stimuli. Polar plots illustrating the directional tuning of neurons in the nBOR in response to slow gratings (solid lines; SF= 0.5cpd, TF= 0.5Hz) and fast gratings (dashed lines; SF= 0.063cpd, TF= 4Hz). Firing rate (spikes/sec) relative to the spontaneous rate (SR; gray circle) is plotted as a function of the direction of motion in polar coordinates (i.e. the SR has been set to zero; outside the gray circle = excitation, inside = inhibition). Solid and dashed arrows represent the neuron’s preferred direction for slow and fast stimuli, respectively, as calculated from the best fit cosines to the tuning curves. U, B, D, and F represent up, back (nasal to temporal), down, and forward (temporal to nasal) motion, respectively.
Figure 7.

Spatio-temporal contour plots generated by an elaborated Reichardt detector model. Thirty-six combinations of spatial frequencies (abscissa) and temporal frequencies (ordinate) were entered into the model shown in Appendix A to build each contour plot. A shows a simulation for a slow cell, where the values for the temporal pre-filter were $\tau_1 = 20$ms, $\tau_2 = 10000$ms, $\beta = 1$, the time constant of the delay filter was $\tau = 0.4$s, and the $\alpha$ level was equal to 1 (left; i.e. balanced) or 0.5 (right; partially balanced). B shows a simulation for a fast cell, where the values for the temporal pre-filter were $\tau_1 = 10$ms, $\tau_2 = 1000$ms, $\beta = 1$, the time constant of the delay filter was $\tau = 0.015$s, and the $\alpha$ level was equal to 1 (left; i.e. balanced) or 0.0 (right; i.e. fully unbalanced). See figure 3 for details regarding contour plot presentation.

Figure 8

Schematic representation of the correlation model of motion detection with variable balance between half-detectors. See text in Appendix for details. BPTF = band pass temporal filter. LPTF = low pass temporal filter.
<table>
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<th>“Fast” Cells</th>
<th></th>
<th>“Slow” Cells</th>
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<td>SF (cpd)</td>
<td>TF (Hz)</td>
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<tr>
<td>Wallaby NOT</td>
<td>31 (43%)</td>
<td>[50°]</td>
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#meanTF/meanSF. *arithmetic mean.

**Table 1 caption**

Preferred spatial frequencies (SFs), temporal frequencies (TFs), and velocities of fast and slow neurons. Average SFs, TFs, and velocities of the primary peaks are shown for the fast and slow neurons in the pigeon nucleus of the basal optic root (nBOR; present study) and lentiformis mesencephali (LM; from Wylie and Crowder, 2001). The average velocities of fast and slow neurons found in the wallaby nucleus of the optic tract (NOT) are also shown (from Ibbotson and Price, 2001). See discussion for details.
Figure 3
Figure 4
Figure 5
Figure 6
Figure 7
Figure 8