Spatiotemporal Tuning of Directional Neurons in Mammalian and Avian Pretectum: A Comparison of Physiological Properties

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Ibbotson, Michael R. and Nicholas S. C. Price. Spatiotemporal tuning of directional neurons in mammalian and avian pretectum: a comparison of physiological properties. *J Neurophysiol* 86: 2621–2624, 2001. Responses were recorded from 72 neurons in the wallaby's nucleus of the optic tract (NOT) during stimulation with drifting sinusoidal gratings at a range of temporal and spatial frequencies (TF and SF). Most cells (70/72) were TF tuned, but two were velocity tuned. The neurons are placed into two descriptive groups: fast and slow cells, which prefer SF/TFs of 0.06–0.6 cpd/0.4–20 Hz and 0.13–1 cpd/<1 Hz, respectively. The peak spatiotemporal tunings of the neurons are compared for motion in preferred and anti-preferred directions with little variation observed in most cases. The spatiotemporal properties of wallaby NOT are compared with those of pigeon lentiformis mesencephali: the avian homologue of NOT. The neurons in the pigeon and wallaby nuclei segregate into fast and slow cells that operate in similar spatiotemporal domains. The fast and slow cells segregate largely on the basis of TF in wallabies and SF in pigeons, but their respective velocity tuning properties are very similar. In both species, the mean velocity tuning for fast and slow cells is approximately 50°/s and 1°/s, respectively.

INTRODUCTION

The pretectal nucleus of the optic tract (NOT) in mammals and the lentiformis mesencephali (LM) in birds are retinorecipient nuclei that detect wide-field image motion and drive optokinetic responses (e.g., Mustari and Fuchs 1990; Wylie and Crowder 2000). The LM is the avian homologue of NOT (McKenna and Wallman 1981). Neurons in both nuclei are direction selective with most neurons preferring temporal-to-nasal motion through the contralateral eye's visual field. Wylie and Crowder (2000) measured the responses of pigeon LM neurons to drifting sinusoidal gratings that varied in spatial and temporal frequencies (SF and TF). They found that ~40% of the 31 neurons had similar TF response profiles for all SFs (TF tuned), two neurons were velocity tuned, and the others had multiple peaks in the spatiotemporal domain. The neurons fell into two populations based on the peak responses to the preferred direction of motion. *Fast* cells preferred low SFs and high TFs (0.03–0.25 cpd, 0.5–16 Hz), and *slow* cells preferred high SFs and low TFs (0.3–2 cpd, 0.1–2 Hz). The peak spatiotemporal tuning for preferred and anti-preferred motion were different for 25/31 neurons, suggesting possible differences in motion coding for the two directions (Fu et al. 1998). Here the spatiotemporal properties of neurons in the wallaby NOT are reported and compared with Wylie and Crowder's (2000) pigeon data.

METHODS

Recordings were made from 72 cells in the NOTs of 18 wallabies prepared for extracellular recording as described previously (Ibbotson et al. 1998). The stimuli were monochromatic spatial sinusoidal gratings moved at TFs of 0.05–24.4 Hz. The gratings had SFs of 0.05–1.5 cpd (mean luminance 45 cd · m^{-2}) and were presented on a monitor subtending 90° (horizontally) by 67°.

RESULTS

Figure 1*A* shows the SF/TFs that generated the maximum preferred direction responses for the NOT cells. Cluster analysis using Ward's method of agglomeration with squared-Euclidean distance measures (Johnson and Wichern 1992) was used to group the cells based on the locations of their peak responses in the spatiotemporal domain. Cluster analysis is used here because it allows a direct comparison with the results of Wylie and Crowder (2000), who used it to segregate neurons in the LM of the pigeon on the basis of peak spatiotemporal tuning. Cluster analysis searches a set of data for natural groupings, and since the most significant groupings are automatically established, statistical significance testing is inappropriate (Johnson and Wichern 1992). Cluster analysis of the NOT data produced several levels of clustering that ranged from 1 to 72 groups. We chose a grouping that divided the cells into two clusters and closely matched the qualitative observation that two cell populations exist, distinguished by preferences for speeds above or below 4°/s (diagonal lines, Fig. 1, *A* and *C*). Fast cells respond optimally at high TFs (0.4–20 Hz) and SFs of 0.06–0.6 cpd (●, Fig. 1*A*), while slow cells respond optimally at low TFs (<1 Hz) and higher SFs (0.13–1 cpd; ○, Fig. 1*A*). For comparison, Fig. 1*C* shows the peak spatiotemporal tuning of neurons in the pigeon LM (from Wylie and Crowder 2000), which also segregate into fast (●) and slow (○) cells. We have plotted the image velocity (TF/SF) producing the largest response for each wallaby and pigeon cell (Fig. 1, *B* and *D*). The values obtained were binned on a logarithmic scale ranging from 0.125 to 256°/s. The velocity tuning of pigeon and wallaby cells reveals two cell populations with a trough at 4°/s (Fig. 1, *C* and *D*).

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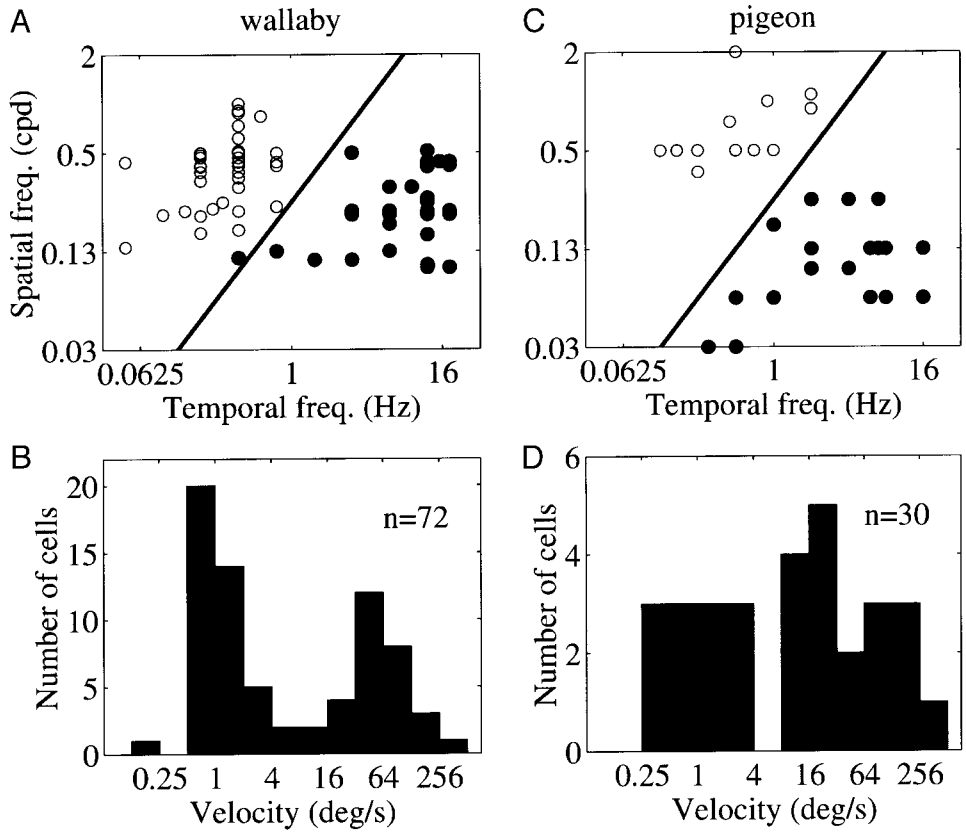

FIG. 1. Locations of peak spatial/temporal frequency (SF/TF) tuning for wallaby nucleus of the optic tract (NOT; *A*) and pigeon lentiformis mesencephali (LM; *C*). Histograms of peak velocity tuning for NOT (*B*) and LM (*D*). Pigeon data from Wylie and Crowder (2000). *A* and *C*: ●, fast cells; ○, slow cells. Diagonal lines in *A* and *C* show 4°/s.

Figure 2*A* shows a wallaby fast cell's responses to preferred direction motion as a spatiotemporal contour plot. The peak response occurs at SF/TFs of 0.3 cpd and 7 Hz. There is a distinct vertically oriented ridge in the contour plot showing similar sized responses for a TF of 7 Hz across a range of SFs, so the cell is TF tuned. In contrast, the responses of a wallaby slow cell form a diagonal ridge (Fig. 2*B*), where the TFs generating peak responses equate with approximately the same velocity for a range of SFs (peak responses occur at approximately 1°/s). Only 2/72 (3%) wallaby neurons were velocity tuned, while most were TF tuned (Fig. 2, *A* and *C*). Some (12/31) fast cells had multiple excitatory peaks, but one peak was always dominant, e.g., the fast cell in Fig. 2*A* has a second region of excitation at SF/TFs of 0.5 cpd/0.4 Hz.

Figure 2*D* shows the spatiotemporal tuning for anti-preferred motion from the slow cell in Fig. 2*C*. The primary inhibitory region occurs at similar SF/TFs to the excitatory region in the preferred direction (Fig. 2*C*). However, the anti-preferred tuning function has a second area of suppression at high TFs and low SFs, which occurred in 30% of slow cells. The TF producing the maximum or minimum response for preferred and anti-preferred motion, respectively, is plotted for 20 wallaby cells (Fig. 2*E*: points overlap). The peak TF tuning is similar for both directions of motion in 18 cells. For two neurons (*), the maximum suppression of spontaneous firing for anti-preferred motion occurred at higher TFs than the peak excitation for preferred direction motion. Figure 2*F* plots the peak SF tuning for preferred direction motion against the SF producing maximum suppression for anti-preferred motion ($n = 20$). Most cells show small differences in optimum SF tuning for the two motion directions; however, the cells that showed differences in TF tuning also showed differences in SF tuning (*).

DISCUSSION

Neurons in the wallaby NOT and pigeon LM segregate into fast and slow cells with a dividing velocity of approximately 4°/s. In wallaby NOT the separation between fast and slow cells is mainly due to differences in TF tuning, whereas in pigeon LM the separation is due to SF tuning. Despite these differences, the peak velocity tuning (TF/SF) is similar in the two species. The mean peak velocity tuning for the fast and slow cells in the NOT are 0.79 and 50°/s, compared with 0.93 and 56°/s in LM. These are remarkably similar values for species from different phylogenetic orders and might indicate similarities in the visual environment during eye movements, which could have driven convergent evolution. Alternatively, the spatiotemporal tuning properties of the oculomotor nuclei could represent a conserved system of ancient origin. Studies on other species using drifting sinusoidal gratings and comparisons with the statistics of natural moving scenes are needed to decide between the possibilities. Indications from experiments using random dot patterns show some similarities between the present data and other species. For example, 35 and 39% of wallaby and pigeon fast cells prefer velocities ≥65°/s, while 33% of monkey neurons tested with velocities ≥4°/s prefer the same speeds (from Fig. 8*C*, Mustari and Fuchs 1990).

Wylie and Crowder (2000) found that LM neurons rarely (6/31) had identical peak spatiotemporal tuning for anti-preferred and preferred motion, possibly because the exci-

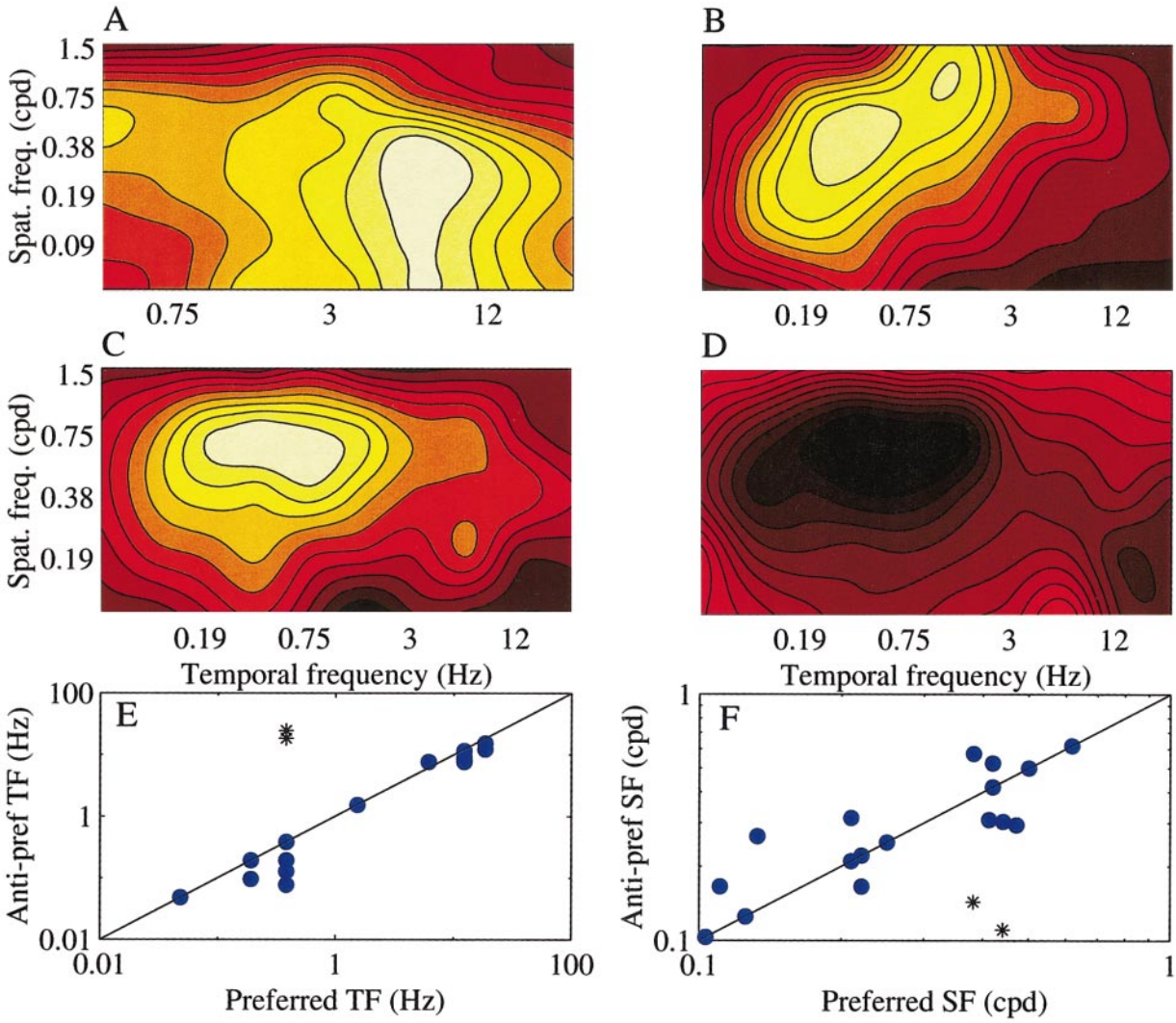

FIG. 2. Spatiotemporal tuning for preferred direction motion for a fast cell (*A*) and 2 slow cells (*B* and *C*). *D*: spatiotemporal tuning for anti-preferred motion (same slow cell as *C*). Yellow is excitation above the spontaneous level (30–66 spikes/s, depending on the cell), red-brown is the spontaneous rate, and black is suppression below spontaneous (15–46 spikes/s below spontaneous). The spatiotemporal plots were smoothed using a thin plate spline method to interpolate across SFs and TFs (Ibbotson et al. 1994). *E*: anti-preferred peak TFs and preferred direction peak TFs for 20 neurons. *F*: as in *E* but for SF. The cells marked (*) show large differences in peak tuning for opposite motion directions. Diagonal lines represent equal peak tuning for both motion directions.

tation arises from retinal inputs while the inhibitory input is extra-retinal (e.g., Brecha et al. 1980; Fu et al. 1998). Wallaby NOT neurons showed a closer match between peak preferred and anti-preferred SF/TF tuning. It is possible that similarities between spatiotemporal tuning for preferred and anti-preferred motion in wallabies could partially arise through reciprocal connections between the NOTs in each hemisphere. The appropriate connections have been identified in another marsupial, the opossum, and in that species excitation generated by preferred direction motion in one NOT is converted into inhibition in the other nucleus (Pereira et al. 1994).

Multiple regions of excitation and inhibition in the spatiotemporal contour plots of some wallaby NOT and pigeon LM cells suggest that inputs arise from multiple sources. For example, Ibbotson and Mark (1994) suggested that inhibition at low SFs and high TFs could arise from other nondirectional pretectal neurons optimally tuned to detect saccade-like displacements of the visual scene (Price and Ibbotson 2001). Such inputs would suppress NOT neurons during saccades and prevent inappropriate optokinetic responses. Nondirectional neurons have also been observed in the pretectum of the pigeon (Fu et al. 1998), and suppressive inputs from these cells may explain some of the inhibitory regions observed in LM neurons (Wylie and Crowder 2000).

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