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Quantitative Reassessment of Speed Tuning in the Accessory Optic System and Pretectum of Pigeons

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Quantitative reassessment of speed tuning in the accessory optic system and pretectum of pigeons. *J Neurophysiol* 95: 546–551, 2006. First published September 28, 2005; doi:10.1152/jn.00921.2005. The correlation model of motion detection has been used to describe visual motion processing in the pretectum and accessory optic system (AOS). One feature of correlation detectors is that they are tuned to a particular temporal frequency (TF) independent of the spatial frequency (SF) but not to a particular stimulus speed (speed = TF/SF). Previous work has suggested that a subset of neurons in the AOS and pretectum of pigeons show apparent speed tuning. However, this study used relatively liberal between-groups statistics to assess speed tuning. From studies of the motion-sensitive neurons in primate cortex, a rigorous within-groups test of speed tuning has been offered. A meta-analysis of the spatiotemporal tuning of units in the AOS and pretectum of pigeons using this within-groups analysis of speed tuning has been performed. We conclude that speed tuning in the AOS and pretectum is rarer than previously estimated, and there is remarkable diversity in the impact of SF on tuning for speed. In total, 18.6% of the units showed significant speed tuning whereas 39.8% showed significant SF/TF independence. However, many cells (41.5%) fell along a continuum between speed tuning and SF/TF independence. This diversity has also been noted in primate cortex and may reflect a general property of motion-sensitive systems.

INTRODUCTION

The correlation model of motion detection has been used to describe many aspects of visual motion processing in a number of species from insects to primates (for reviews, see Borst and Egelhaaf 1989; Buchner 1984; Clifford and Ibbotson 2003; Srinivasen et al. 1999). This includes motion detectors in the pretectum and accessory optic system (AOS: Crowder and Wylie 2001; Crowder et al. 2003a; Ibbotson et al. 1994; pretectum: Crowder et al. 2003a,b; Wylie and Crowder 2000). Motion-sensitive neurons in the pretectum and AOS exhibit direction selectivity to large field “optic flow” stimuli and are involved in generating the optokinetic reflex. In mammals, the AOS includes the medial and lateral terminal nuclei, which are equivalent to the nucleus of the basal optic root (nBOR) in birds. Similarly, the pretectal nucleus of the optic tract (NOT) and the dorsal terminal nucleus of the AOS are the mammalian equivalent to the nucleus lentiformis mesencephali (LM) in birds (for reviews, see Simpson 1984; Simpson et al. 1988).

Recent electrophysiological studies that utilized large field sinusoidal gratings as stimuli showed that pretectal and AOS neurons show spatiotemporal tuning (wallaby NOT: Ibbotson

et al. 1994; pigeon nBOR and LM: Crowder and Wylie 2001; Crowder et al. 2003a; Wylie and Crowder 2000). Pretectal and AOS neurons can be classified into two groups based on spatiotemporal tuning: *slow* cells were maximally sensitive to motion at low temporal frequencies (TF < 1 Hz) and high spatial frequencies (SF > 0.25 cycles/°, cpd), whereas *fast* cells were sensitive to high TF (>1 Hz) and low SF (<0.25 cpd) (see also Ibbotson and Price 2001; Winship et al. 2005).

One feature of Reichardt correlation detectors is that they are not tuned to stimulus speed (TF/SF) but respond to a particular TF independent of the SF, i.e., they are “spatiotemporally independent” (Buchner 1984; Clifford and Ibbotson 2003; Egelhaaf et al. 1989; Ibbotson et al. 1994; Srinivasen et al. 1999). Spatiotemporally (SF/TF) independent motion detectors could be interpreted as tuned either to a particular TF (TF-tuned), a particular SF (SF-tuned) or tightly tuned to a particular SF/TF combination. Crowder et al. (2003a) quantitatively described spatiotemporal tuning in the AOS and pretectum by fitting the spatiotemporal contour plots with two-dimensional Gaussians and suggested that fast units in pigeon LM and nBOR showed SF/TF independence, whereas most of the slow cells showed apparent speed tuning. As the response maxima were not completely independent of SF, we (Crowder et al. 2003a) termed this “speed-like” tuning (see also Zanker et al. 1999). The assertions made by Crowder et al. (2003a) were based on between groups statistics that demonstrated that for the slow cells, oriented Gaussians typical of speed-like tuning provided better fits than nonoriented Gaussians typical of SF/TF independence. Nonoriented Gaussians provided better fits for fast cells. Using analyses similar to these, a recent study of motion-sensitive units in the middle temporal (MT) area of monkeys (Perrone and Thiele 2001; see also Simoncelli and Heeger 2001) suggested that most units were speed tuned. However, Priebe et al. (2003) offered another quantitative test of tuning for speed versus SF/TF independence using within-groups statistics and suggested that Perrone and Thiele (2001) greatly overestimated the degree of speed tuning. We feel that a cell-by-cell classification method as proposed by Priebe et al. (2003) may offer a more detailed description of spatiotemporal tuning. Therefore we have performed a meta-analysis of the spatiotemporal tuning of LM and nBOR units from our previous studies of pigeons (Crowder and Wylie 2001; Crowder et al. 2003a,b, 2004; Wylie and Crowder 2000) using the quantitative methods outlined by Priebe et al. (2003; see also Levitt

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et al. 1994). Applying these criteria, speed tuning in nBOR and LM is less than previously estimated.

METHODS

We analyzed the spatiotemporal tuning of 42 nBOR and 76 LM units collected from previous studies in pigeons (Crowder and Wylie 2001; Crowder et al. 2003a,b, 2004; Wylie and Crowder 2000). Details of the surgery, electrophysiological recording and stimulus presentation can be found in these papers. All methods conform to the guidelines established by the Canadian Council on Animal Care and approved by the Biosciences Animal Care and Policy Committee at the University of Alberta. Briefly, we recorded the responses of nBOR and LM neurons in anesthetized pigeons to sine-wave gratings of varying SF and TF moving in the preferred direction (contrast = 0.95; mean luminance = 65 cd/m²; refresh rate = 80 Hz). Most units were tested with a standard protocol of 36 SF/TF combinations (SF = 0.031, 0.063, 0.125, 0.25, 0.5, and 1 cpd; TF = 0.031, 0.125, 0.5, 2, 8, and 16 cycle/s, Hz). Additionally, 16 units were tested with TFs of 0.0625, 0.25, 1, and 4 Hz; 21 units were tested with TF of 24 Hz; and 30 units were tested with SF of 2 cpd. Contour plots of the mean firing rate as a function of SF (abscissa) and TF (ordinate) were generated with Sigma Plot (see Fig. 2, left). The location of maximal excitation was referred to as the primary peak of the contour plot. Many cells also display a secondary peak, but these were not considered in this analysis.

Analysis of speed tuning versus TF tuning

To determine the influence of SF on speed tuning, each excitatory response contour plot was fit to a two-dimensional (2-D) Gaussian function using the equation described by Priebe et al. (2003)

$$R(sf, tf) = A \cdot e^{-\frac{(\log_2(sf) - \log_2(sf_0))^2}{\sigma_{sf}^2}} \cdot e^{-\frac{(\log_2(tf) - \log_2(tf_0))^2}{\sigma_{tf}^2}}$$

where tf_0 depends on SF and is defined as

$$tf_p(sf) = 2^{(Q-1) \cdot (\log_2(sf) - \log_2(sf_0)) + \log_2(tf_0)}$$

From this unconstrained Gaussian fit, the location of maximal excitation (sf_0 , tf_0) of the contour plot of spatiotemporal tuning and the relationship between preferred speed and SF (indicated by the exponent Q) could be determined. When Q is equal to zero, there is no relationship between SF tuning and speed preference, i.e., the neuron remains tuned to a particular speed of motion across all SFs. When Q is equal to -1 , preferred speed is strongly dependent on SF such that as SF increases by 1 log unit, the preferred speed of the neuron decreases by 1 log unit. That is, a Q value of -1 indicates that the SF tuning and TF tuning of the neuron are independent, i.e., the unit is SF/TF independent.

The Gaussian function was used to classify units as speed-tuned or SF/TF independent using a partial correlation analysis (Levitt et al. 1994; Priebe et al. 2003). For the partial correlation analysis, each peak from our sample was fit to two constrained Gaussians: to provide a SF/TF independent prediction, Q was constrained to -1 (see Fig. 2, right); 2) to provide a speed-tuned prediction, Q was constrained to 0 (see Fig. 2, middle). We computed the partial correlation of the actual data with the speed-tuned or independent prediction using the following equations

$$R_{ind} = \frac{(r_i - r_s \cdot r_{is})}{\sqrt{((1 - r_s^2)(1 - r_{is}^2))}}$$

$$R_{speed} = \frac{(r_s - r_i \cdot r_{is})}{\sqrt{((1 - r_i^2)(1 - r_{is}^2))}}$$

where R_{ind} and R_{speed} are the partial correlations of the real data to the SF/TF independent and speed-tuned predictions, respectively; r_i is

equal to the correlation of real data with the independent prediction; r_s is the correlation of the real data with the speed-tuned prediction; and r_{is} is the correlation of the two predictions.

The statistical significance of R_{speed} and R_{ind} was calculated with a Fisher Z-transform on the correlation coefficients $\{Zf = 1/2 \cdot \ln[(1 + R)/(1 - R)]\}$, and then calculating the difference between these z scores (Papoulis 1990)

$$z_{diff} = (Zf_{ind} - Zf_s) / ((1/N_{ind} - 3) + 1/(N_s - 3))^{1/2}$$

where Zf_s is the Fisher Z-transform for R_{speed} , Zf_{ind} is the Fisher Z-transform for R_{ind} , and $N_s = N_{ind}$ = number of SF/TF combinations used in the best-fit Gaussian. A z score of 1.65 was selected to denote significance. With this statistic, cells were categorized as speed tuned if $z_{diff} \leq -1.65$ and R_{speed} was significantly >0 . Likewise cells were categorized as SF/TF independent if $z_{diff} \geq 1.65$ and R_{ind} was significantly >0 . Cells not meeting these criteria were termed unclassifiable ($1.65 > z_{diff} > -1.65$). This partial correlation technique has been used previously to assess motion integration in visual neurons (e.g., Crowder and Wylie 2002; Gizzi et al. 1990; Movshon et al. 1985; Scannell et al. 1996). The conventional criterion of a probability of 0.1 (i.e. $z_{diff} > 1.65$ or $z_{diff} < -1.65$) (Crow et al. 1960) has been justified by the fact that this method is not a true test of statistical significance but a convenient way to reduce data (Crowder and Wylie 2002; Gizzi et al. 1990; Movshon et al. 1985; Scannell et al. 1996).

RESULTS

Figure 1 plots primary peaks locations of all 118 units as determined from the best-fit Gaussians. A Ward's cluster analysis on peak locations showed that the two largest clusters corresponded to fast and slow cells. Of the 76 LM units (hexagons), 45 (59.2%) were classified as fast cells (mean TF:mean SF = 4.28 Hz:0.15 cpd; range TF = 0.45–16.0 Hz, SF = 0.05–0.28 cpd) and 31 (40.8%) were slow cells (mean TF:mean SF = 0.48 Hz:0.57 cpd; range TF = 0.09–2.09 Hz, SF = 0.14–1.00 cpd). Of the 42 nBOR units (\blacktriangledown , ∇), 4 (9.5%) were fast cells (mean TF:mean SF = 5.87 Hz:0.11 cpd; range TF, 0.51–12.69 Hz, SF = 0.07–

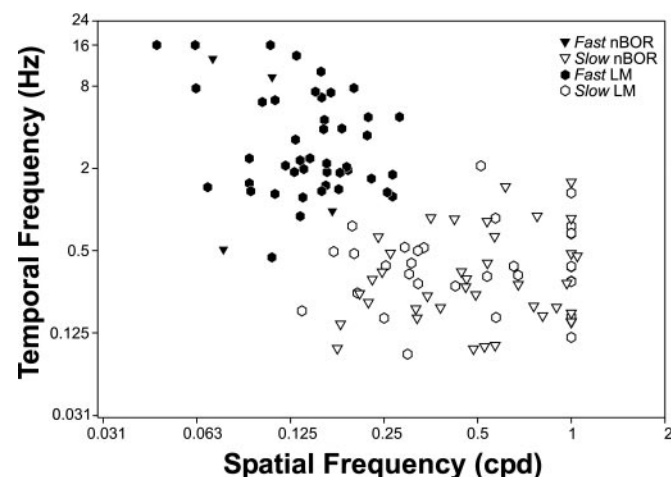
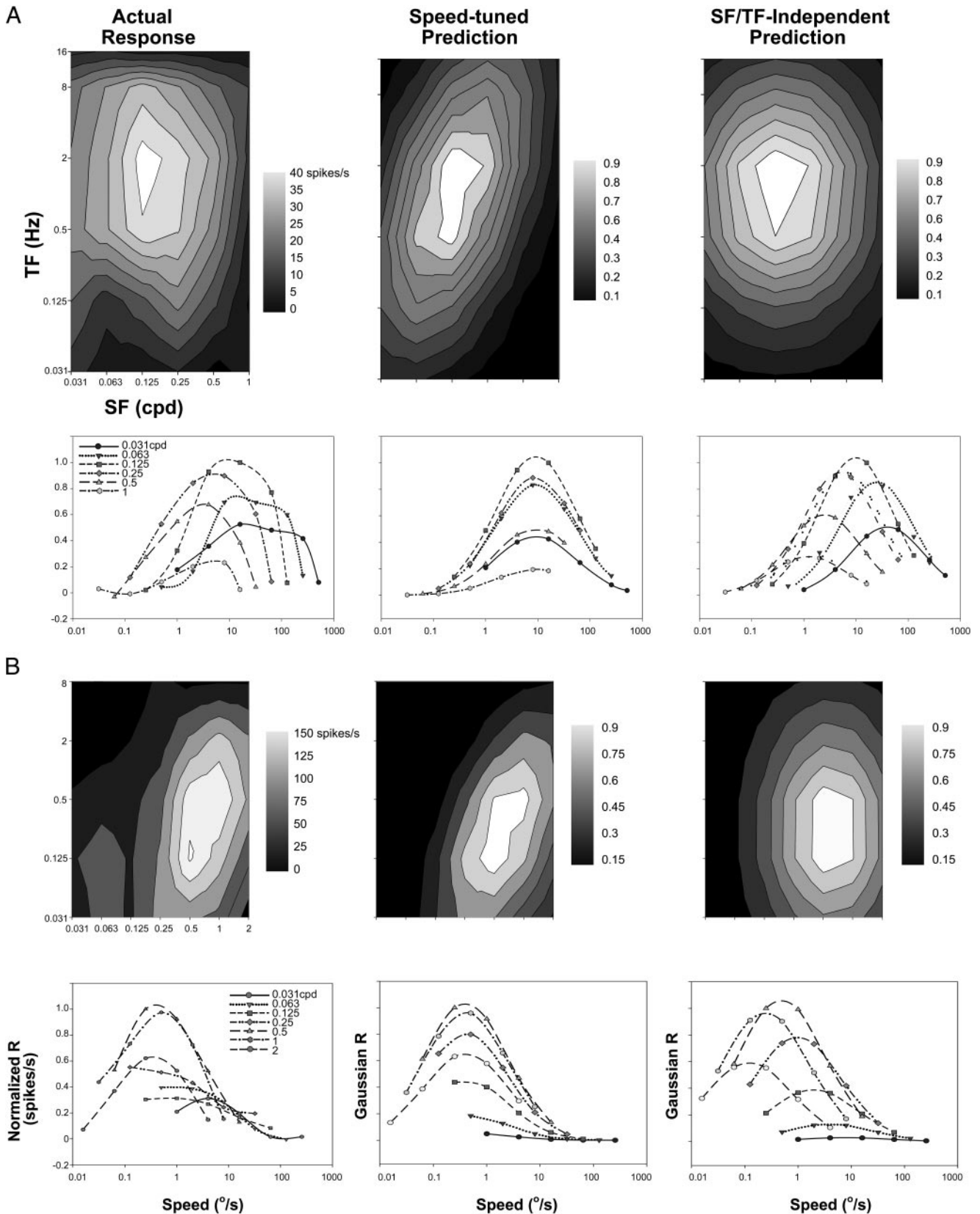


FIG. 1. The locations of the primary peaks in the spatiotemporal domain for 42 units in the nucleus of the basal optic root (nBOR) and 76 units from the lentiformis mesencephali (LM) (from Crowder and Wylie 2001; Crowder et al. 2003a,b, 2004; Wylie and Crowder 2000) [abscissa, spatial frequency (SF); ordinate, temporal frequency (TF)]. \blacktriangledown and ∇ and hexagons show peaks of nBOR and LM units, respectively. \blacktriangledown and black hexagons, fast cells; ∇ and white hexagons, slow cells, as classified by Ward's cluster analysis (see METHODS).

0.17 cpd) and 38 (90.5%) were slow cells (mean TF:mean SF = 0.41 Hz:0.57 cpd; range TF = 0.10–1.59 Hz, SF = 0.18–1.05 cpd).

Figure 2 shows two representative units: a fast LM unit (Fig. 2A) and a slow nBOR unit (Fig. 2B). Figure 2, left, shows the contour plots of the spatiotemporal tuning for the two units;



below each contour plot, the normalized response is plotted as a function of speed for all SFs. From the unconstrained Gaussian fit (not shown), the unit in Fig. 2A had a peak in the fast zone at 1.22 Hz/0.14 cpd, and a Q value of -1.00 , strongly suggesting SF/TF independence. The unit in Fig. 2B had an primary peak in the *slow* region at 0.28 Hz/0.68 cpd, and a Q value of -0.27 , suggesting speed tuning principally independent of SF. The speed tuning curves for this unit indicate tuning to $\sim 0.5^\circ/\text{s}$ for all SFs > 0.031 cpd.

Predictions used for the partial correlation analysis are also shown in Fig. 2. The right column shows the SF/TF-independent prediction for each unit (Q constrained to -1). The *middle column* shows the speed-tuned prediction (Q constrained to 0). Contour plots are shown directly above the corresponding speed tuning curves for the tested SFs. Note that the speed tuning curves for the speed-tuned prediction show a maximal response to the same speed of motion across all SFs. The unit in Fig. 2A appears more closely approximated by the SF/TF independent prediction, whereas the speed-tuned prediction provides a better approximation of the unit in Fig. 2B. The z_{diff} scores for these units support this observation: the unit in Fig. 2A had a z_{diff} of 4.69, whereas the unit in B had a z_{diff} of -3.10 , indicating that the fast and slow units were significantly SF/TF independent and speed tuned, respectively.

Figure 3, A and B, shows scatter plots of R_{speed} versus R_{ind} for all the nBOR and LM units, respectively. The black lines separate the data space into three regions (based on the criteria described in METHODS): speed tuned, SF/TF independent, and unclassified. Of the 38 slow nBOR units, 15 (39.5%) showed significant speed tuning, 20 were unclassified and 3 (7.9%) were SF/TF independent. Of the four fast nBOR units, three were SF/TF independent, and one was unclassified. Of the 31 slow LM units, 6 (19.4%) showed significant speed tuning, 15 were unclassified, and 10 (32.2%) were SF/TF independent. Of the 45 fast LM units, 1 (2.2%) showed significant speed tuning, 13 were unclassified, and 31 (68.9%) were SF/TF independent. Thus combining data from the nBOR and LM: fast units tend to be SF/TF independent (34/49, 69.4%) or unclassified (14/49, 28.6) but not speed tuned (1/49, 2.0%); slow units tend to be speed tuned (21/69, 30.4%) or unclassified (35/69, 50.7%) but not SF/TF independent (13/69, 18.8%).

With the unconstrained fits, fast LM units had a mean Q value of -0.95 ± 0.05 (SE), slow LM units had a mean Q

value of -0.68 ± 0.09 , fast nBOR units had a mean Q value of -1.00 ± 0.20 , and slow nBOR units had a mean Q value of -0.42 ± 0.06 . Because the mean Q values suggested differences between fast and slow neurons, and LM and nBOR neurons, we performed a one-way ANOVA comparing the Q scores of the four groups of neurons. Post hoc analysis using the Tukey's HSD method revealed that the Q scores of slow nBOR units were significantly different from all other groups (fast LM, $P < 0.001$; slow LM, $P < 0.042$; fast nBOR, $P < 0.034$). In addition, the Q values of the fast LM units were significantly different from slow LM scores ($P < 0.023$).

Because speed tuning was more apparent for the slow neurons and SF/TF independence was more common for the fast units (as indicated by both mean Q values and the partial correlation analysis), in Fig. 3C, we plotted the preferred speed (TF/SF) of each nBOR (∇) and LM unit (black hexagons) as a function of Q value. Regression lines for nBOR and LM units were plotted separately using SigmaPlot. There was a significant negative correlation between the log of preferred speed and the value of Q (all units, $P \ll 0.001$, $R = -0.529$; nBOR units, $P < 0.001$, $R = -0.505$; LM units, $P < 0.001$, $R = -0.404$); i.e., as preferred speed increased, Q approached -1 (SF/TF independence), whereas tuning for slower speeds was associated with Q values closer to 0 .

DISCUSSION

Perrone and Thiele (2001) examined the spatiotemporal tuning of direction-sensitive neurons in area MT in rhesus monkeys. They reported that neurons had oriented peaks in contour plots of their spatiotemporal tuning and concluded that MT neurons are tuned for speed. While such an oriented response profile is necessary for speed tuning, Priebe et al. (2003) emphasized that it is not sufficient. Priebe et al. (2003) used a 2-D Gaussian function termed Q analysis, as well as a partial correlation analysis, to quantitatively test the influence of SF on the speed tuning of neurons in MT. They concluded that only $\sim 25\%$ of MT neurons were tuned for speed and suggested that without such quantitative analyses there is a danger in overestimating the incidence of speed tuning.¹

It seems that we (Crowder et al. 2003a) have fallen victim to the caveat noted by Priebe et al. (2003). Crowder et al. (2003a) suggested that the majority of slow neurons in nBOR and LM show speed-like tuning, whereas most fast units were TF tuned (i.e., SF/TF independent). Although we (Crowder et al. 2003a) used 2-D Gaussians to quantitatively analyze the spatiotemporal peaks and showed that oriented Gaussians provided better fits across the population, we did not statistically compare speed-tuned and SF/TF independent fits for individual cells. This was the aim of the present re-analysis. In this study, a meta-analysis of these data suggests that speed tuning is less common than previously implied. Only 39.5% of slow nBOR cells, and 19.4% of slow LM cells, showed significant speed tuning. Consistent

FIG. 2. Figure 2A and 2B respectively show representative units from the lentiformis mesencephali (LM) and the nucleus of the basal optic root (nBOR) and their corresponding SF/TF independent and speed-tuned predictions. The left column shows contour plots illustrating the firing rate in response to sine wave gratings of varying spatial (SF, abscissa) and temporal (TF, ordinate) frequencies. SF and TF are plotted on a logarithmic scale. The plot is shaded such that white represents the SF-TF combinations resulting in maximal excitation and black indicates minimal excitation. The unit in 2A had a primary peak in the *fast* zone, while the unit in 2B was tuned to *slow* gratings. The middle column shows the speed-tuned prediction, while the right column shows the spatio-temporally independent prediction. Below each contour plot, the unit's response is plotted as a function of the speed ($^\circ/\text{s}$) of the gratings across all SFs. In the left column, the normalized firing rate (R) is plotted on the Y-axis and speed is plotted on the X-axis. In the middle and right columns, the normalized Gaussian values are plotted on the Y-axis. The independent prediction provides a better fit for the unit in A, whereas the unit in B is more closely approximated by the speed-tuned prediction (see RESULTS).

¹ Priebe et al. (2003) also noted that tests using sine wave gratings of a single spatial frequency underestimate the true speed tuning of MT neurons.

with what we had previously suggested, only a single fast unit showed speed tuning and most (69.4%) fast cells exhibited SF/TF independence (3 of 4 nBOR cells, 31 of 45 LM cells). Approximately 41.5% of cells were unclassifiable, most of which were slow cells (61.2%). It is possible that we have underestimated the incidence of speed-tuned units if these units were tightly tuned relative to our sampling resolution. We do not feel this was a problem, how-

ever, because the response peaks in the contour plots of spatiotemporal tuning spanned multiple SF/TF combinations. Following Priebe et al. (2003), we suggest that the spatiotemporal response profile for motion-sensitive units in LM and nBOR is best described as a continuum between two extremes represented by the SF/TF independent and speed-tuned predictions. Fast cells fall toward the SF/TF independent end of the distribution, whereas slow cells generally fall closer to the speed-tuned prediction. Combined with similar results from experiments in V2 and MT (Levitt et al. 1994; Priebe et al. 2003), our data from the AOS and pretectum support the suggestion of Priebe et al. (2003) that diversity in the impact of SF on speed tuning may be a general property of motion-sensitive neurons.

The hallmark of correlation motion detectors is SF/TF independence (Buchner 1984; Clifford and Ibbotson 2003; Egelhaaf et al. 1989; Ibbotson et al. 1994; Srinivasan et al. 1999). However, Zanker et al. (1999) demonstrated that a Reichardt detector can show speed-like tuning if the balance between its two constituent half detectors is altered. The more "unbalanced" the detector, the closer the approximation to true speed tuning. Pretectal and nBOR units have been modeled with this modified version of the Reichardt detector (Crowder et al. 2003a). We (Crowder et al. 2003a) argued that speed-like tuning observed in the slow nBOR neurons reflects the properties of an unbalanced Reichardt detector. With the continuum between speed tuning and SF/TF independence in mind, perhaps there is a continuum with respect to the degree of balance for the slow cells: cells classified as speed tuned are more unbalanced than those falling in the unclassified region. Conversely, fast cells would have balanced constituent half detectors.

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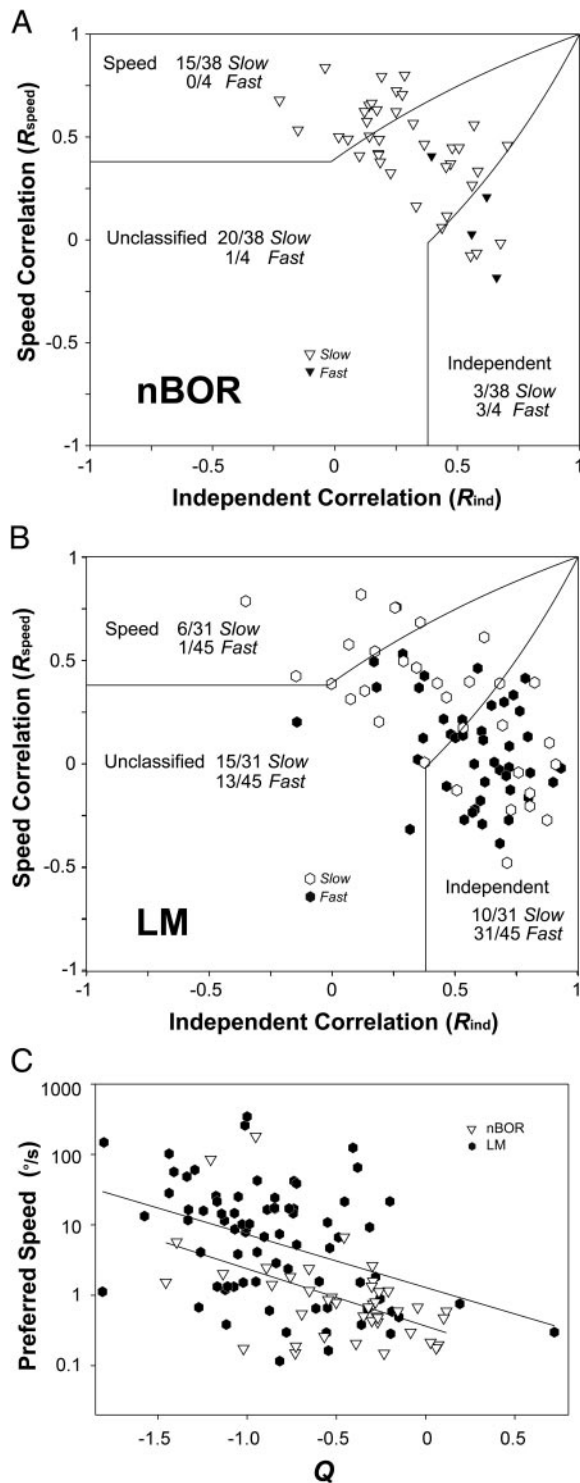


FIG. 3. Figure 3A and 3B show scatter plots of partial correlations for speed (R_{speed}) and spatio-temporally independent (R_{ind}) tuning for units in nBOR and LM, respectively. Each data point indicates the degree to which a particular unit from the nBOR (A) or LM (B) is correlated with speed-tuned and independent predictions. The data space is divided into three regions based on statistical criteria approximated by the solid black line. This line represents statistical significance for 31.6 SF/TF combinations, which was the average number of points in the Gaussian fits across all units. Speed-tuned, unclassifiable, or spatio-temporally independent cells fall in the upper left, middle, or lower right areas of the scatter plot, respectively. White and black symbols indicate *slow* and *fast* units, respectively. Figure 3C shows the Q values for all units plotted as a function of the log of preferred speed (black hexagons, LM; white triangles, nBOR). Regression lines for nBOR and LM units are plotted independently. A significant negative correlation ($P \ll 0.001$, $R = -0.529$) between Q and the log of speed preference was observed.

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