J Neurophysiol 94: 1336–1345, 2005.
First published May 4, 2005; doi:10.1152/jn.01224.2004.

Orientation Tuning, But Not Direction Selectivity, Is Invariant to Temporal Frequency in Primary Visual Cortex

Bartlett D. Moore IV, Henry J. Alitto, and W. Martin Usrey
Center for Neuroscience, University of California, Davis, California

Submitted 1 December 2004; accepted in final form 28 April 2005

Moore, Bartlett D. IV, Henry J. Alitto, and W. Martin Usrey. Orientation tuning, but not direction selectivity, is invariant to temporal frequency in primary visual cortex. *J Neurophysiol* 94: 1336–1345, 2005. First published May 4, 2005; doi:10.1152/jn.01224.2004. The activity of neurons in primary visual cortex is influenced by the orientation, contrast, and temporal frequency of a visual stimulus. This raises the question of how these stimulus properties interact to shape neuronal responses. While past studies have shown that the bandwidth of orientation tuning is invariant to stimulus contrast, the influence of temporal frequency on orientation-tuning bandwidth is unknown. Here, we investigate the influence of temporal frequency on orientation tuning and direction selectivity in area 17 of ferret visual cortex. For both simple cells and complex cells, measures of orientation-tuning bandwidth (half-width at half-maximum response) are ~20–25° across a wide range of temporal frequencies. Thus cortical neurons display temporal-frequency invariant orientation tuning. In contrast, direction selectivity is typically reduced, and occasionally reverses, at nonpreferred temporal frequencies. These results show that the mechanisms contributing to the generation of orientation tuning and direction selectivity are differentially affected by the temporal frequency of a visual stimulus and support the notion that stability of orientation tuning is an important aspect of visual processing.

INTRODUCTION

Orientation tuning is a fundamental property shared by most neurons in primary visual cortex (V1). Despite differences between cortical neurons in terms of their preferred orientation, individual neurons are similar to each other in terms of their tuning bandwidth—a measure reflecting the range of orientations that excite a cell and typically quantified as the half-width at half-height of response peaks in orientation-tuning curves. Across species—including rats, ferrets, cats, tree shrews, and primates—mean orientation-tuning bandwidth is ~20–25° (Alitto and Usrey 2004; Chisum et al. 2003; Gilbert 1977; Girman et al. 1999; Henry et al. 1974; Kato et al. 1978; Orban 1984; Ringach et al. 2002; Schiller et al. 1976; Usrey et al. 2003), suggesting that tuning bandwidth is optimized for a similar computational task. Along these lines, studies examining the statistics of natural scenes conclude that the filtering properties of cortical neurons, including orientation tuning, are optimized for conveying information about the natural world (Field 1987; Kording et al. 2004; Olshausen and Field 1996; Simoncelli and Olshausen 2001; van Hateren and van der Schaaf 1998).

Responses of cortical neurons depend not only on the orientation of a visual stimulus, but also on stimulus temporal frequency (Alitto and Usrey 2004; Foster et al. 1985; Hawken et al. 1996; Ikeda and Wright 1975; Movshon et al. 1978; Saul and Humphrey 1992). This raises the question of whether or not temporal frequency affects the bandwidth of orientation tuning. If orientation tuning is optimized for computational processing, it might be important for neurons to maintain a constant tuning bandwidth across a range of temporal frequencies. However, orientation tuning might broaden with increasing temporal frequency, provided *1*) intracortical connections play an important role in sharpening orientation tuning beyond that established by the spatial arrangement of thalamic input (Alonso et al. 2001; Gardner et al. 1999; Reid and Alonso 1995; Shapley et al. 2003; Sillito 1975; Usrey et al. 2003; but see Ferster et al. 1996), and *2*) responses of cortical neurons are diminished to a greater extent than those of LGN neurons at high temporal frequencies (Alitto and Usrey 2004; Hawken et al. 1996; Movshon et al. 1978; Orban et al. 1985). Alternatively, orientation-tuning bandwidth might decrease with temporal frequency, provided *N*-methyl-D-aspartate (NMDA) receptors contribute significantly to thalamocortical processing. Modeling efforts indicate that high temporal frequencies should demodulate NMDA receptors, thereby reducing the f1 of thalamocortical input to cortical neurons relative to the DC input and, as a result, orientation-tuning bandwidth of cortical neurons is predicted to decrease (Krukowski 2000; Krukowski and Miller 2001). Using bar stimuli, Hammond and Smith (1983) reported that orientation tuning neither increases nor decreases with stimulus velocity. Because bar stimuli are not well suited to demodulate NMDA receptors, it remains to be determined whether or not orientation tuning is affected by the temporal frequency of a periodic stimulus, such as drifting gratings. If orientation-tuning bandwidth is indeed invariant to temporal frequency, as has been shown for stimulus contrast (Alitto and Usrey 2004; Anderson et al. 2000; Sclar and Freeman 1982; Skottun et al. 1987), this finding would indicate that the neuronal circuitry mediating the construction and maintenance of orientation tuning is designed to preserve orientation tuning over a wide range of conditions.

While it is unknown whether or not temporal frequency affects the orientation-tuning of cortical neurons, past work from areas 17 and 18 of adult cats shows that temporal frequency can affect the direction selectivity of cortical neurons (Saul and Humphrey 1992; see also Holub and Morton-Gibson 1981; McLean and Palmer 1994; Reid 1988; Reid et al. 1991; Saul and Feidler 2002). In particular, responses to stimuli drifting in nonpreferred directions often increase with

Address for reprint requests and other correspondence: W. M. Usrey, Ctr. for Neuroscience, Univ. of California, Davis, CA 95616 (E-mail: wmusrey@ucdavis.edu).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

temporal frequencies above preferred values. Given the influence of temporal frequency on direction selectivity, the question remains, does temporal frequency influence orientation tuning?

We performed single-unit recordings from area 17 of ferret visual cortex to determine whether or not orientation tuning and direction selectivity are influenced by the temporal frequency of a visual stimulus. Our results show that both simple cells and complex cells display temporal-frequency invariant orientation tuning. In contrast, we show that temporal frequencies above and below the preferred temporal frequency often decrease the direction selectivity of cortical neurons and occasionally result in a reversal of direction selectivity. These results are compared with those from other studies and the implications of differential effects of temporal frequency on orientation tuning and direction selectivity are discussed.

METHODS

Animal preparation

All surgical and experimental procedures conformed to National Institutes of Health guidelines and were carried out with the approval of the Animal Care and Use Committee at the University of California, Davis. Ten adult ferrets (*Mustela putorius furo*, 1–1.5 yr old) were used in this study. Animals were anesthetized for surgery with an intramuscular injection of ketamine (40 mg/kg) and acepromazine (0.04 mg/kg). A tracheotomy was performed, and animals were placed in a stereotaxic apparatus where anesthesia was maintained with 1.0–1.5% isoflurane in oxygen and NO (2:1). A thermostatically controlled heating blanket was used to maintain body temperature at 37°C. Eyes were dilated with 1% atropine sulfate, fitted with contact lenses, and focused on a tangent screen located 76 cm in front of the animal. A midline scalp incision was made, and a small craniotomy was made above area 17 of visual cortex. All wound margins were first infused with lidocaine. The temperature, ECG, EEG, and expired CO_2 were monitored continuously throughout the experiment.

After completion of all surgical procedures, animals were paralyzed with vecuronium bromide (0.2 mg/kg/h) and artificially ventilated. Proper depth of anesthesia was ensured throughout the experiment by *1*) monitoring the EEG for changes in slow-wave/spindle activity and *2*) monitoring the ECG and expired CO_2 for changes associated with a decrease in the depth of anesthesia. If any of these measures indicated a decrease in depth of anesthesia, the concentration of isoflurane was increased.

Electrophysiological recordings and visual stimuli

Cortical recordings were made from individual neurons in area 17 with receptive fields located between ~5 and 15° eccentric using tungsten in glass electrodes (Alan Ainsworth, London, UK). The laminar location of recording sites was not determined. Neuronal responses were amplified, filtered, and recorded to a PC computer equipped with a Power 1401 data acquisition interface and the Spike 2 software package (Cambridge Electronic Design, Cambridge, UK). Spike isolation was based on waveform analysis (on-line and off-line) and presence of a refractory period, as indicated by the autocorrelogram (Usrey et al. 2000, 2003).

Visual stimuli were created with a VSG2/5 visual stimulus generator (Cambridge Research Systems, Rochester, UK). Stimuli were presented on a gamma-calibrated Sony monitor with a mean luminance of 40 candelas/m^2. Drifting sinusoidal grating stimuli (75% contrast, optimal spatial frequency) were used to characterize visual responses. Neuronal responses to gratings were used to generate orientation and temporal-frequency tuning curves. Grating stimuli were shown for 4 s, followed by 2 s of mean gray. After the period of mean gray, a new grating was shown with a different orientation or temporal frequency. Once a complete sequence of stimuli was presented, the process was repeated three to five times.

Cell classification

Using drifting sinusoidal gratings of optimal orientation and spatial frequency, cortical neurons were classified as simple cells or complex cells on the basis of the ratio of the first Fourier coefficient (f1) to mean response (simple cells: f1/mean >1.0; complex cells: f1/mean <1.0; see Skottun et al. 1991). Subsequent analysis of neuronal responses was performed using either the cell's f1 (simple cells) or mean response (complex cells).

Temporal-frequency tuning

Temporal-frequency tuning curves were made from neuronal responses of each neuron to drifting sinusoidal gratings (0.5–32 Hz; 70% contrast; preferred orientation and spatial frequency). Response curves were interpolated with a cubic spline to determine the preferred temporal frequency. Given each neuron's response to 0.5-Hz stimuli (<0.5 Hz for some cells), the lowest temporal frequencies to elicit responses 50 and 20% of maximum [TF(50L) and TF(20L), respectively] were determined. Similarly, given each neuron's response to 32-Hz stimuli, the highest temporal frequencies to elicit responses 50 and 20% of maximum [TF(50H) and TF(20H), respectively] were determined. Accordingly, neurons with perfect band-pass tuning for temporal frequency would have equal response rates for TF(50L) and TF(50H) and equal response rates for TF(20L) and TF(20H). For neurons with varying degrees of low-pass behavior, response rates for TF(50L) and TF(20L) would always be greater than response rates for TF(50H) and TF(20H), respectively.

To quantify the degree of band-pass versus low-pass behavior of neurons, a band-pass index was determined using the equation

$$\text{Band-Pass Index} = \frac{R_{(\text{pref. TF})} - R_{(\text{low TF})}}{R_{(\text{pref. TF})} + R_{(\text{low TF})}}$$

where $R_{(\text{pref. TF})}$ is the response at the preferred temporal frequency and $R_{(\text{low TF})}$ is the response at the lowest temporal frequency examined (generally 0.5 Hz).

For those neurons with responses that dropped to 50% of maximum at temporal frequencies above and below the preferred ($n = 26/32$), temporal-frequency tuning bandwidth (full-width, in octaves) was determined at half-maximum response.

Orientation tuning and direction selectivity

To determine the influence of temporal frequency on orientation tuning, orientation-tuning curves were generated using gratings drifting at five different temporal frequencies [the preferred temporal frequency, TF(20L), TF(50L), TF(50H), and TF(20H)]and presented in steps of 12°.

To quantify the effect of temporal frequency on orientation-tuning bandwidth, individual orientation-tuning curves were first fit to a Gaussian distribution

$$R(\text{ori}) = K \times \exp\left(\frac{-(X-\mu)^2}{2 \times \sigma^2}\right) + \text{baseline}$$

where K represents the maximum response rate, x represents the orientations used, μ represents the preferred orientation, σ represents the SD, and baseline is the DC-offset of the Gaussian distribution. This procedure allowed us to estimate the bandwidth of orientation tuning—a value equal to peak half-width at half-height or 1.17σ. A small subset of neurons ($n = 6$) was encountered that lacked orientation tuning at all temporal frequencies; these neurons were excluded from analysis.

Direction selectivity was assessed for each neuron using a direction index

$$\text{Direction Index} = \frac{R_1 - R_2}{R_1 + R_2}$$

where R_1 is equal to the response of a neuron to gratings drifting in the preferred direction, and R_2 is equal to the response of a neuron to gratings drifting in the opposite direction (Fig. 6, *inset*). Orientations corresponding to R_1 and R_2 were determined using the preferred temporal frequency for each neuron. These R_1 and R_2 orientations were used to determine R_1 and R_2 values at nonpreferred temporal frequencies. In so doing, direction index values would be negative if R_2 was greater than R_1 at nonpreferred temporal frequencies.

Statistical analysis

When statistical analysis was required to compare two distributions, we first used Lilliefors modification of the Kolmogorov-Smirnov test to determine if the distributions in question were significantly different from normal distributions of unspecified mean and variance ($\alpha = 0.05$). If the distributions were not statistically different from normal, an ANOVA was used to compare the two populations. However, if the populations were statistically different from normal distributions, a Wilcoxon rank-sum test was used. When population means are provided, they are accompanied by the SE.

RESULTS

Temporal-frequency tuning in ferret primary visual cortex

We recorded visual responses from 32 neurons in area 17 of ferret visual cortex. For each neuron, temporal-frequency tuning curves were made from responses to drifting sinusoidal gratings presented over a range of temporal frequencies (typically 0.5 Hz–32 Hz; see METHODS). Examples of temporal-frequency tuning curves from two representative simple cells and two representative complex cells are shown in Fig. 1, *A*, *B*, *D*, and *E*; average tuning curves are shown in Fig. 1, *C* and *F*. To determine the extent to which individual neurons displayed band-pass tuning for temporal frequency, we calculated a band-pass index (see METHODS). According to this index, values near 1.0 represent neurons with strong band-pass behavior, whereas values near zero represent neurons with low-pass behavior. Similar to other species, most neurons in ferret visual cortex display band-pass temporal-frequency tuning (Fig. 1*G*; mean band-pass index = 0.74 ± 0.01) (Alitto and Usrey 2004; Foster et al. 1985; Hawken et al. 1996; Ikeda and Wright 1975; Movshon et al. 1978; Saul and Humphrey 1992). Among our sample of cortical neurons, simple cells displayed greater band-pass tuning than complex cells (band-pass index = 0.87 ± 0.05 vs. 0.63 ± 0.07, respectively; $P < 0.01$). For those

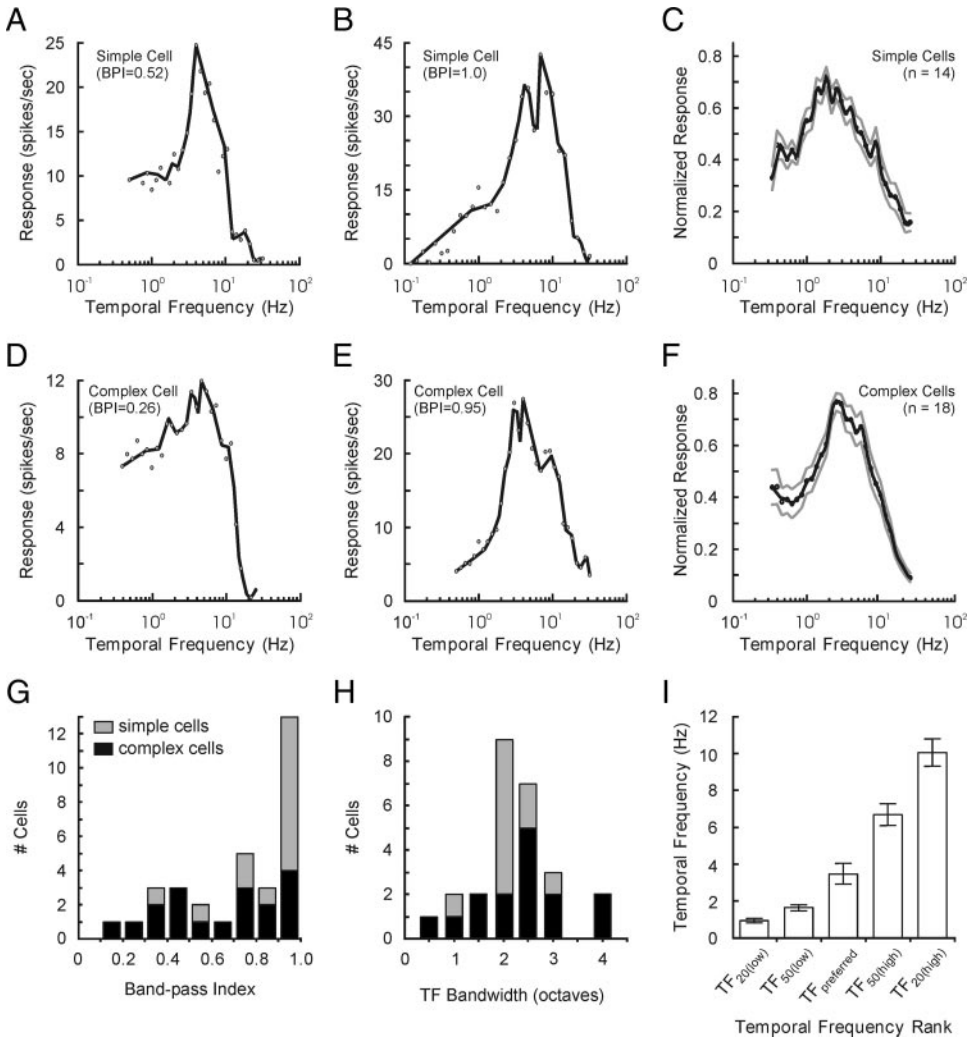

FIG. 1. Temporal-frequency tuning in ferret primary visual cortex. *A* and *B*: temporal-frequency tuning curves for 2 representative simple cells with band-pass index values of 0.52 and 1.0. *C*: average tuning curve for 14 simple cells. *D* and *E*: temporal-frequency tuning curves for 2 representative complex cells with band-pass index values of 0.26 and 0.95. *F*: average tuning curve for 18 complex cells. Black lines indicate the cubic spline fit; gray lines indicate SE. *G*: distribution of band-pass index values for the entire set of cortical neurons ($n = 32$). Most neurons display band-pass temporal frequency tuning. *H*: distribution of temporal-frequency bandwidths for those neurons ($n = 26$) with responses that dropped to ≥50% at temporal frequencies below and above the preferred. *I*: mean temporal frequencies measured at each of the 5 ranks used in this study—TF(20L), TF(50L), TF-(preferred), TF(50H), and TF(20H). Across the population, mean temporal frequencies for the 5 ranks were 0.93 ± 0.10, 1.6 ± 0.14, 3.47 ± 0.54, 6.68 ± 0.58, and 10.05 ± 0.75 Hz, respectively. Median values were 0.5, 1.5, 3.5, 7.8, and 14.5 Hz, respectively.

neurons with responses that decreased to 50% of maximum at temporal frequencies below and above the preferred (n = 26/32), the mean bandwidth was 2.22 ± 0.16 octaves (Fig. 1*H*). Bandwidth values for simple cells were not significantly different from those of complex cells (1.98 ± 0.13 vs. 2.44 ± 0.27 octaves, respectively; $P = 0.85$).

For each neuron in our sample, there was a preferred temporal frequency that evoked a maximal response. Among our sample of cortical neurons, the mean preferred temporal frequency was 3.47 ± 0.54 Hz (Fig. 1*I*). There was not a significant difference in the preferred temporal frequency of simple cells compared with complex cells (3.9 ± 1.1 vs. 3.1 ± 0.4 Hz, respectively; $P = 0.67$). Given each neuron's response to stimuli drifting at the lowest temporal frequency presented (0.1–0.5 Hz), we identified the two lowest temporal frequencies to evoke a response 50 and 20% of maximum [TF(50L) and TF(20L); see METHODS]. Similarly, given each neuron's response to 32-Hz stimuli, we identified the highest temporal frequencies to elicit responses 50 and 20% of maximum [TF(50H) and TF(20H)]. Among our sample of neurons, mean temporal frequencies for TF(50L) and TF(20L) were 1.6 ± 0.14 and 0.93 ± 0.10 Hz, respectively (Fig. 1*I*), and mean temporal frequencies for TF(50H) and TF(20H) were 6.68 ± 0.58 and 10.05 ± 0.75 Hz, respectively (Fig. 1*I*).

Influence of temporal frequency on orientation tuning

To investigate the influence of temporal frequency on orientation tuning in primary visual cortex, we made orientation-tuning curves for individual neurons using drifting sinusoidal gratings presented at each neuron's preferred temporal frequency, the two temporal frequencies *below* the preferred that corresponded to the TF(50L) and TF(20L), and the two temporal frequencies *above* the preferred that corresponded to the TF(50H) and TF(20H). Orientation-tuning curves for each neuron at each temporal frequency were fit by Gaussian functions to determine the orientation tuning half-widths at half-maximum response (Fig. 2*A*; see METHODS). At the preferred temporal frequency for each neuron, orientation tuning half-width was, on average, 24.9 ± 1.8° (Fig. 2*B*). While orientation tuning half-width was typically less for simple cells than complex cells (22.9 ± 1.8 vs. 26.5 ± 2.7°, respectively), the difference was not significant ($P = 0.37$; but see Alitto and Usrey 2004).

Across our sample of cortical neurons, orientation-tuning bandwidth was not affected by temporal frequency. Figure 3 shows orientation tuning curves from four representative neurons at five different temporal frequencies: the preferred temporal frequency, the two temporal frequencies below the preferred [TF(50L) and TF(20L)], and the two temporal frequencies above the preferred [TF(50H) and TF(20H)]. Although temporal frequency affected the firing rate of these example neurons, orientation-tuning bandwidth remained constant. A quantitative comparison of orientation-tuning bandwidth values at the preferred temporal frequency and the two temporal frequencies below and above the preferred is shown in Fig. 4. In each case, data points are mostly located on or near the line of unit slope, indicating no effect of temporal frequency on half-width measures. While there is some scatter around the line of unit slope, as a population there was not a significant difference between the mean orientation tuning half-width

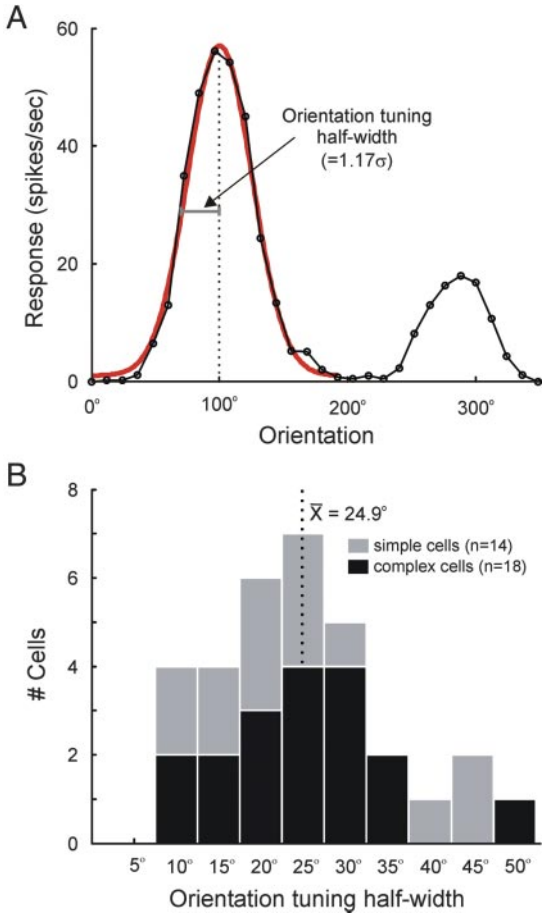

FIG. 2. Orientation tuning in ferret primary visual cortex. *A*: orientation-tuning bandwidth is determined by fitting each neuron's response (black circles) to a Gaussian distribution (red line) and assessing the half-width at half-height (1.17 × σ). *B*: distribution of orientation-tuning half-width measures for 32 cortical neurons using gratings drifting at each neuron's preferred temporal frequency. Bandwidth measures are not significantly different for simple and complex cells.

associated with the preferred temporal frequency (24.9 ± 1.8°) and the two temporal frequencies below the preferred [TF(50L) = 24.2 ± 2.0°, $P = 0.87$; TF(20L) = 23.1 ± 2.3°, $P = 0.53$] or the two temporal frequencies above the preferred [TF(50H) = 22.8 ± 1.9°, $P = 0.86$; TF(20H) = 20.4 ± 2.4°, $P = 0.16$].

To address the possibility that temporal-frequency invariant orientation tuning might depend on the temporal-frequency tuning properties of neurons, we sorted neurons into two groups based on their band-pass index (<0.5 vs. >0.5; Fig. 1*G*) and re-examined orientation tuning at each of the five temporal frequencies [TF(preferred), TF(50L), TF(20L), TF(50H), and TF(20H)]. There was not a significant difference in orientation tuning for the two groups of neurons at any of the five temporal frequencies (P = 0.5, 0.7, 0.5, 0.1, and 0.5, respectively; data not shown).

Influence of temporal frequency on direction selectivity

For many neurons in our sample, gratings presented at temporal frequencies above or below the preferred temporal frequency often decreased the neuron's direction selectivity. This effect is exhibited by three of the representative neurons

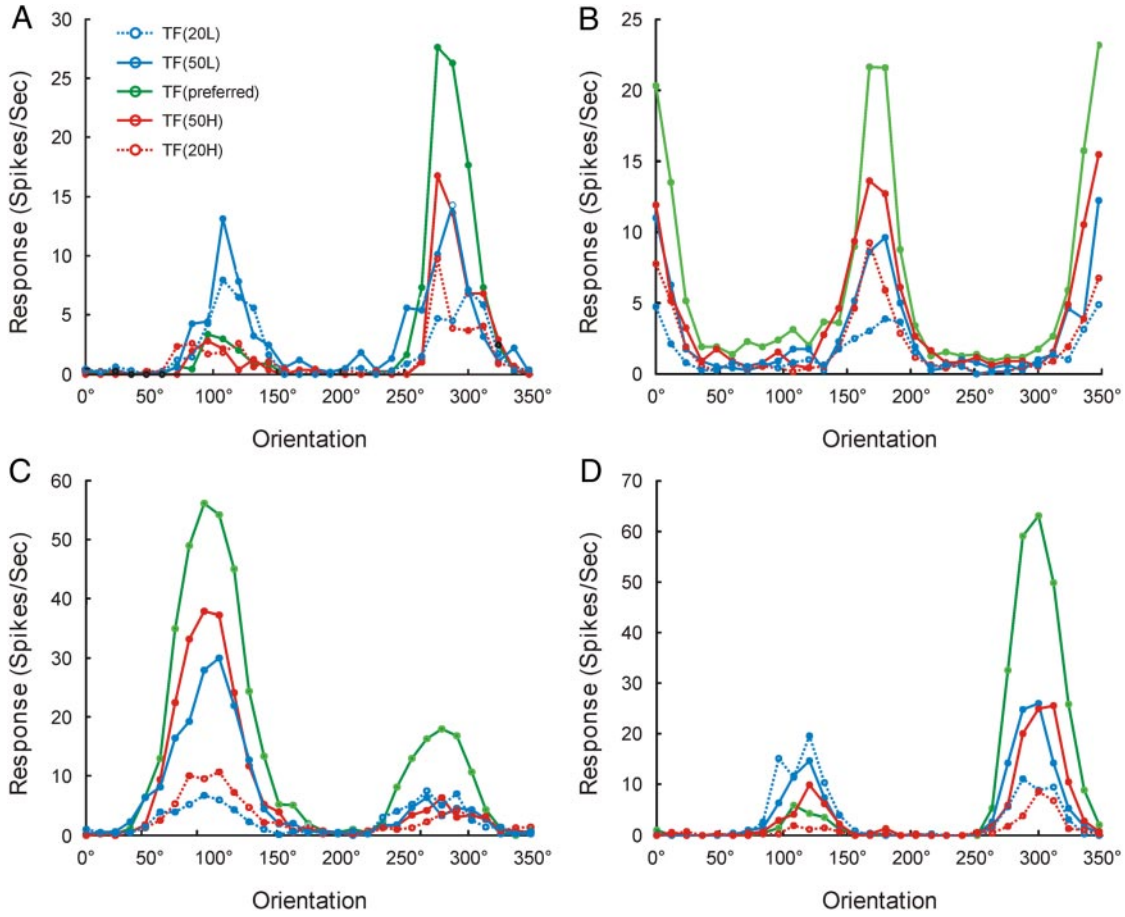

FIG. 3. Orientation tuning curves from 4 representative cortical neurons at 5 different temporal frequencies. Orientation tuning at the preferred temporal frequency is indicated in green. Orientation tuning at TF(20L) and TF(50L) are indicated by blue dashed and blue solid lines, respectively. Orientation tuning at TF(20H) and TF(50H) are indicated by red dashed and red solid lines, respectively. *A, C*, and *D*: tuning curves from 3 neurons that are strongly direction selective at the preferred temporal frequency and less selective for direction at nonpreferred temporal frequencies. *B*: tuning curves from a neuron that lacks direction selectivity at all temporal frequencies.

in Fig. 3, *A*, *C*, and *D*. Focusing on the neuron in Fig. 3*A*, this neuron preferred gratings drifting at 290 and 110°. At the preferred temporal frequency, 3 Hz, the neuron was strongly direction selective and responded most vigorously to gratings drifting at 290°. As expected, responses to gratings drifting at 290° decreased with temporal frequencies above and below the preferred. In contrast, responses to gratings drifting at 110° *increased* with temporal frequencies below the preferred and decreased, at a reduced rate, for temporal frequencies above the preferred.

To assess quantitatively the influence of temporal frequency on direction selectivity, we defined the two peaks in an orientation-tuning curve as *peak 1* (the peak with the greatest response at the preferred temporal frequency) and *peak 2* (the peak, centered ~180° from peak 1, with a reduced response at the preferred temporal frequency). We compared peak 1 responses versus peak 2 responses at the preferred temporal frequency, two temporal frequencies below the preferred [TF(50L) and TF(20L)], and two temporal frequencies above the preferred [TF(50H) and TF(20H)]. For the scatter plots shown in Fig. 5, points along the line of unit slope represent neurons with little or no direction selectivity, whereas points below unit slope represent neurons with varying degrees of direction selectivity. At the preferred temporal frequency, most neurons are represented with data points well below unity. Accordingly, differences in peak 1 and peak 2 responses were statistically significant ($P = 0.01$). As temporal frequency increased and decreased from the preferred, differences between peak 1 and peak 2 responses decreased progressively (Fig. 5, dashed lines) and were not significantly different from each other at the lowest [TF(20L)] and highest [TF(20H)] temporal frequencies examined [TF(20L), $P = 0.67$; TF(20H), $P = 0.1$; TF(50L), $P = 0.04$; TF(50H), $P = 0.03$].

To assess the influence of temporal frequency on direction selectivity further, we calculated direction index values (see METHODS) based on the responses of each neuron to gratings drifting at the preferred temporal frequency and the two temporal frequencies below [TF(50L) and TF(20L)] and above [TF(50H) and TF(20H)] the preferred (Fig. 6). At the preferred temporal frequency, direction index values ranged from 0 to 1.0 (mean = 0.48 ± 0.06), with values near or equal to 1.0 indicating strong direction selectivity and values near zero indicating weak direction selectivity. At temporal frequencies below and above the preferred temporal frequency, direction index values shifted toward zero, indicating a decrease in direction selectivity and, in some cases, were negative, indicating a reversal in the preferred direction. As a population, direction index values for neurons excited by gratings drifting

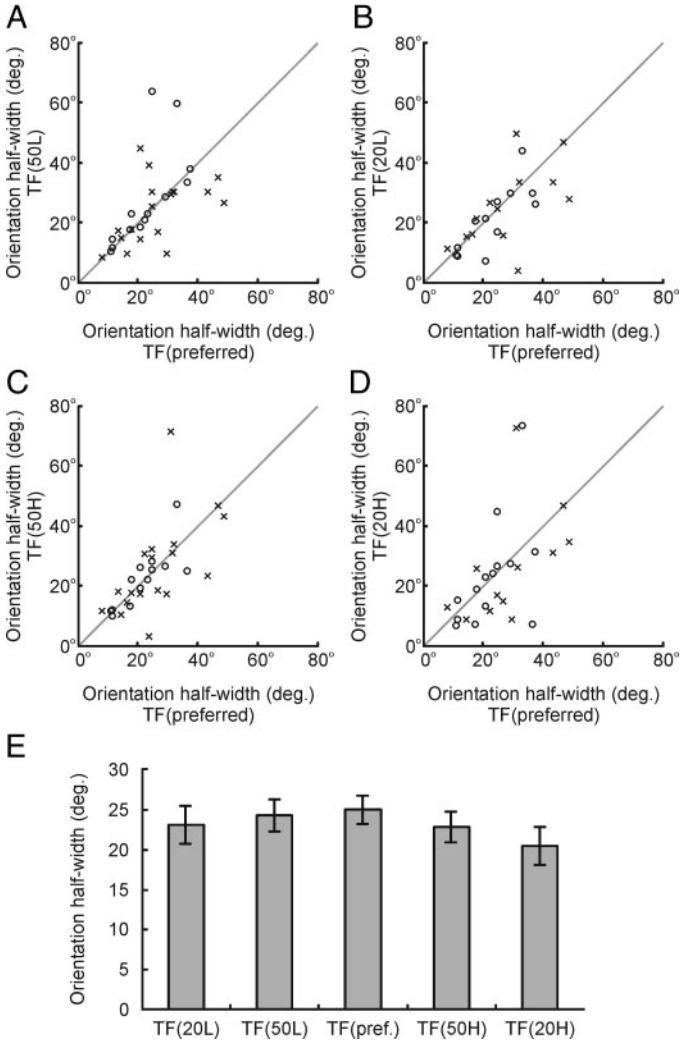

FIG. 4. Orientation-tuning is invariant to temporal frequency. *A–D*: scatter plots showing the relationship between each neuron's orientation-tuning half-width at the preferred temporal frequency and the half-width at temporal frequencies corresponding to TF(50L), TF(20L), TF(50H), and TF(20H). Simple cells indicated with circles; complex cells indicated with crosses. *E*: histogram showing the mean half-width for orientation tuning at all temporal frequencies examined. Across the population, there is not a significant effect of temporal frequency on orientation tuning half-width.

at the preferred temporal frequency (0.48 ± 0.06) were significantly greater than values for gratings drifting at TF(20L) (0.08 ± 0.08; $P < 0.001$) and TF(20H) (0.25 ± 0.06; $P < 0.01$), and nearly significantly greater than values for gratings drifting at TF(50L) (0.33 ± 0.07; $P = 0.1$) and TF(50H) (0.32 ± 0.07, $P = 0.09$). Across the five temporal frequencies examined, direction index values for simple cells were not significantly different from those of complex cells ($P > 0.05$) except at the highest temporal frequency examined TF(20H), where direction index values of complex cells were significantly less than those of simple cells ($P = 0.03$). At each of the nonpreferred temporal frequencies, direction indices were also not significantly different for neurons with high band-pass index values (>0.5) compared with neurons with low band-pass index values (<0.5; data not shown).

Finally, we wished to determine whether or not the decrease in direction selectivity measured at nonpreferred temporal frequencies was a consequence of temporal frequency or the decreased firing rates that accompany nonpreferred temporal frequencies. To do so, we quantified the relationship between direction index and firing rate for the subset of cells that displayed direction index values >0.5 at the preferred temporal frequency. A similar analysis was performed on data collected from a separate set of cells where the contrast of the stimulus was varied to elicit a maximal response and responses ~50 and 20% of maximal (Alitto and Usrey 2004). As shown in Fig. 7, the relationship between firing rate and direction selectivity was significantly different for cells under the two conditions ($P = 0.008$). Specifically, while direction selectivity decreased at reduced firing rates when temporal frequency was varied, it generally remained constant or increased slightly at reduced firing rates when contrast was varied. This latter finding has also been reported for neurons in cat visual cortex (Peterson

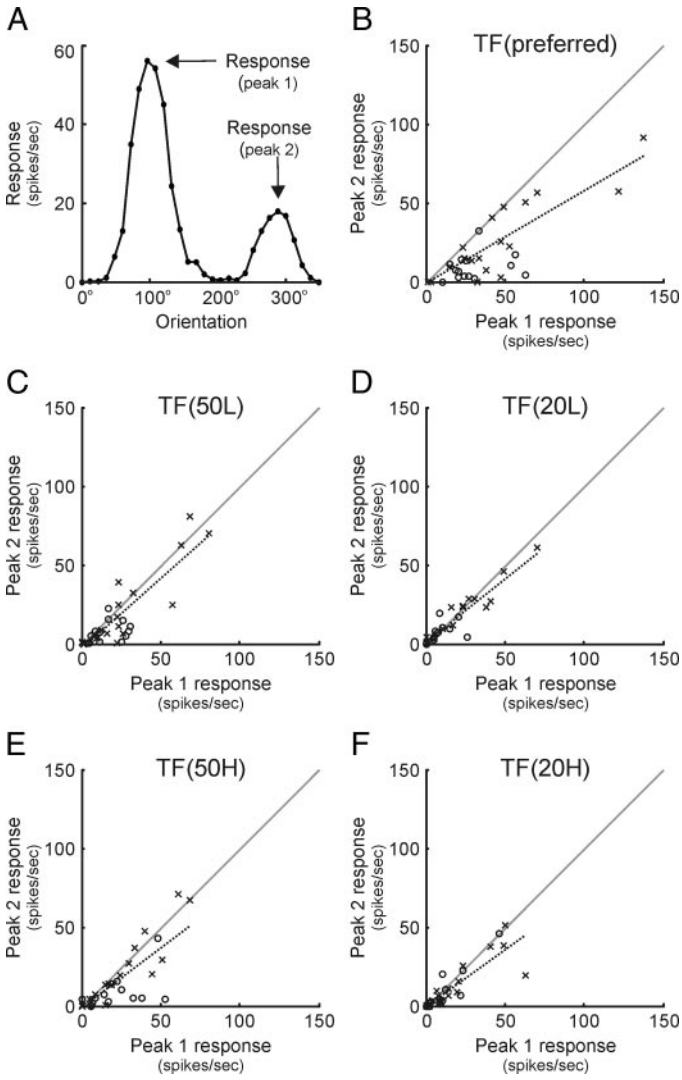

FIG. 5. Influence of temporal frequency on direction selectivity. *A*: diagram showing comparison made between peak 1 and peak 2 responses from a representative neuron's orientation-tuning curve. *B–F*: scatter plots showing relationship between peak 1 and peak 2 responses to gratings drifting at each neurons preferred temporal frequency and temporal frequencies corresponding to TF(50L), TF(20L), TF(50H), and TF(20H). Simple cells indicated with circles; complex cells indicated with crosses. Gray line indicates unit slope; dashed line indicates the linear fit of data points. Note that distributions shift toward unit slope for all nonpreferred temporal frequencies. Points above unit slope represent neurons with a reversal in preferred direction.

and Freeman 2003). Thus the reduced firing rate that accompanies nonpreferred temporal frequencies does not, in itself, seem to contribute to the reduction in direction selectivity.

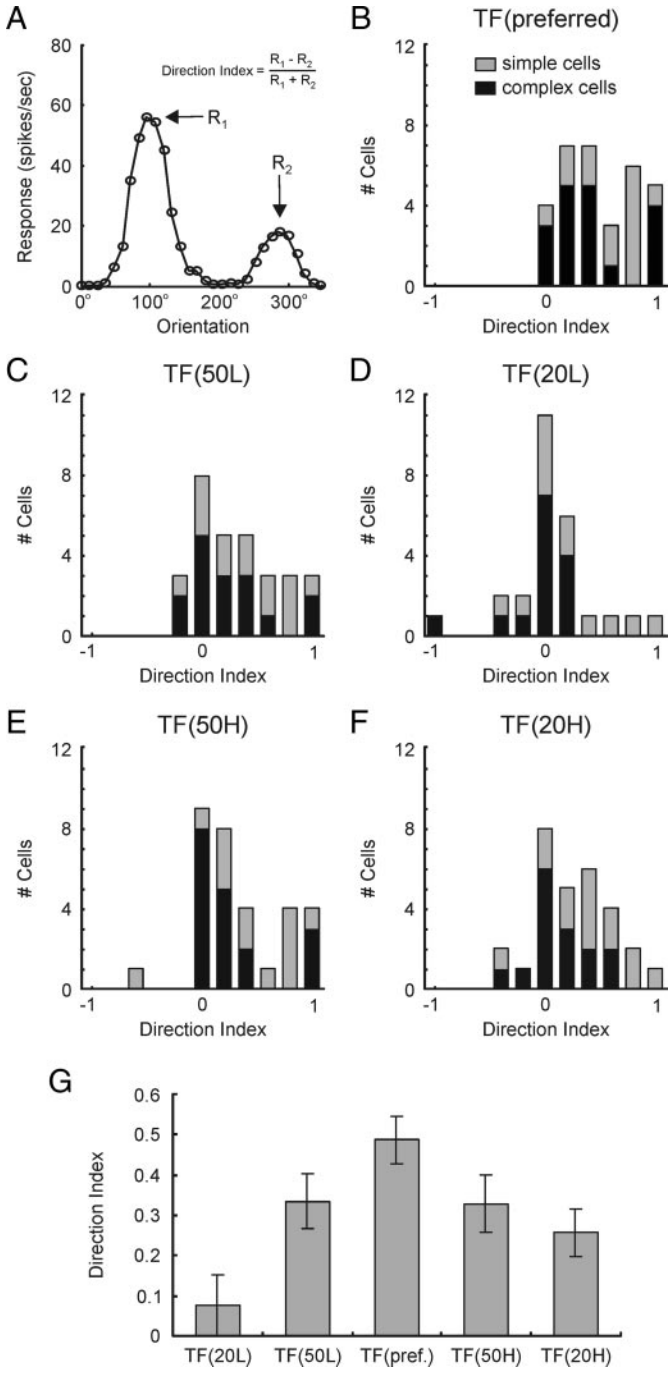

FIG. 6. Influence of temporal frequency on the direction index of cortical neurons. *A*: diagram showing method for calculating direction index. *B*: histogram showing distribution of direction index values at preferred temporal frequency. *C–F*: histograms showing distribution of direction index values at temporal frequencies corresponding to TF(50L), TF(20L), TF(50H), and TF(20H). Negative values represent neurons with a reversal in preferred direction. *G*: mean direction index values for each of the 5 temporal frequencies examined. Across the population, direction index values are greatest at the preferred temporal frequency and progressively less at temporal frequencies above and below the preferred.

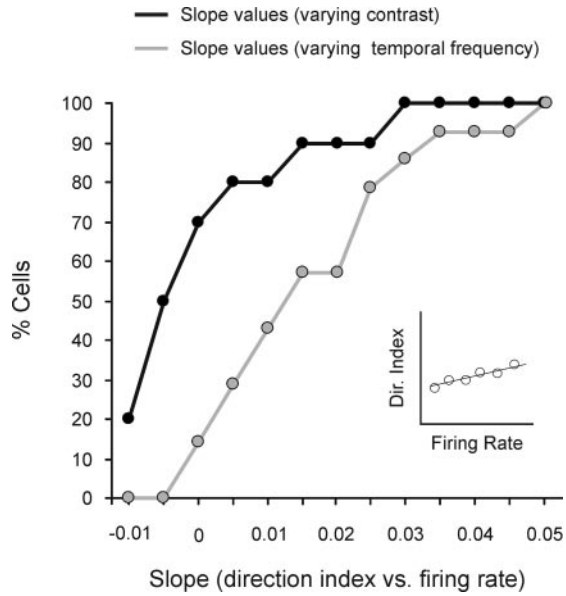

FIG. 7. Cumulative probability distribution showing the relationship between direction index and firing rate for cells stimulated with drifting gratings that varied in either temporal frequency (gray line, $n = 14$ cells) or contrast (black line, $n = 10$ cells). For cells studied under conditions of varying temporal frequency, a contrast of 70% was used; for cells studied under conditions of varying contrast, the preferred temporal frequency was used. All cells contributing to this analysis had direction index values of 0.5 or greater at the preferred temporal frequency and high contrast condition. For each cell, the relationship between firing rate and direction index was quantified as the slope of the best fitting line (see *inset*). Slopes of the 2 populations were significantly different from each other ($P < 0.01$, Wilcoxon rank-sum test), indicating that influence of temporal frequency on direction index is not simply due to changes in firing rate.

DISCUSSION

The goal of this study was to determine the influence of temporal frequency on orientation tuning and direction selectivity in ferret primary visual cortex. Our results show that orientation tuning is invariant to temporal frequency for both simple cells and complex cells. In contrast, direction selectivity is often reduced, and occasionally reverses, at nonpreferred temporal frequencies. In the sections below, we compare our results to those of previous studies and consider their functional implications for visual processing.

Temporal-frequency tuning from retina to cortex

In cats and monkeys, neurons along the visual pathway—from retina to primary visual cortex—display characteristic shifts in their temporal-frequency tuning properties. Most notable of these is a decrease in both the preferred temporal frequency and high temporal-frequency cut-off of cortical neurons compared with retinal ganglion cells and lateral geniculate nucleus (LGN) neurons (Benardete et al. 1992; Derrington and Lennie 1984; Foster et al. 1985; Hawken et al. 1996; Lee et al. 1989; Movshon et al. 1978; Mukherjee and Kaplan 1995; O'Keefe et al. 1998; Orban et al. 1985; Usrey and Reid 2000). This shift in temporal-frequency tuning, or low-pass filtering, is also present in ferrets, where a recent study found the high temporal-frequency cut-off, TF(50H), of cortical neurons to be significantly less than that of LGN neurons (5.6 ± 0.5 vs. 19.8 ±2.9 Hz, respectively; Alitto and Usrey 2004). Although a somewhat greater TF(50H) is re-

ported for ferret cortical neurons in this study (8.3 ± 1.0 Hz), this value is still significantly less than that reported for LGN neurons.

Within primary visual cortex of cats and monkeys, simple cells and complex cells generally have similar preferred temporal frequencies (e.g., cat: 2.8 ± 0.3 vs. 3.4 ± 0.5 Hz, respectively, Saul and Humphrey 1992; macaque monkey: 9.6 ± 7.5 vs. 11.2 ± 7.5 Hz, respectively, Hawken et al. 1996). In the ferret, our results show that simple cells and complex cells also have similar preferred temporal frequencies (3.9 ± 1.1 vs. 3.1 ± 0.4 Hz, respectively). It is worth noting that our sample of orientation tuned cortical neurons ($n = 32$) almost certainly does not include all cell types from all layers, thus differences may exist in the tuning properties of certain classes of neurons. Along these lines, a small population of visually responsive neurons was encountered that lacked orientation tuning (6/38, see also Bullier and Henry 1979; Hirsch et al. 2003; Usrey et al. 2003). These neurons were therefore excluded from further analysis.

Effects of temporal frequency on orientation tuning and direction selectivity

Orientation tuning is similar across species. In cat (Gilbert 1977; Kato et al. 1978), macaque monkey (De Valois et al. 1982; Henry et al. 1974; Ringach et al. 2002; Schiller et al. 1976), tree shrew (Chisum et al. 2003), rat (Girman et al. 1999), and ferret (this study; see also Alitto and Usrey 2004; Usrey et al. 2003), cortical neurons display a range of tuning bandwidths with most neurons, particularly those in the output layers, having a bandwidth near the mean, ~25° (half-width at half-maximum response). This similarity of tuning bandwidth is rather remarkable when one considers the many differences in cortical processing between species, including differences in the cortical layer where orientation tuning emerges (e.g., layer 4 in cats and ferrets, layers 2/3 in tree shrews; Fitzpatrick 1996; Hubel and Wiesel 1962; Usrey et al. 2003), distinct patterns of intrinsic circuits (Binzegger et al. 2004; Callaway 1998; Fitzpatrick 1996), and dramatic differences in area occupied by primary visual cortex (e.g., macaque V1: 1,320 mm^2, Daniel and Whitteridge 1961; tree shrew V1: ~60 mm^2, estimated from Tigges and Shantha 1969). Even within species, orientation tuning is constant and varies little with eccentricity or mean luminance (Bisti et al. 1977; Schiller et al. 1976; Wilson and Sherman 1976; see also Beaton and Blakemore 1981). This similarity is further emphasized when orientation tuning is examined under different levels of stimulus contrast. In all species examined, neurons in primary visual cortex display contrast-invariant orientation tuning, whereby orientation-tuning bandwidth remains constant (~25° on average), regardless of stimulus contrast (Alitto and Usrey 2004; Anderson et al. 2000; Sclar and Freeman 1982; Skottun et al. 1987). In this study, we now show that orientation tuning is also invariant to temporal frequency. Taken together, these results suggest that orientation tuning is likely optimized for a common computational task and/or constrained by similar ecological or economical demands. Along these lines, the filtering properties of cortical neurons, including orientation tuning, appear well matched for the statistics of natural scenes (Field 1987; Kording et al. 2004; Olshausen and Field 1996; Simoncelli and Olshausen 2001; van Hateren and van der Schaaf 1998).

Unlike orientation tuning, direction selectivity is influenced by temporal frequency. Similar to results from the cat (Saul and Humphrey 1992; see also Holub and Morton-Gibson 1981; McLean and Palmer 1994; Reid 1988; Reid et al. 1991), we show that direction selectivity of neurons in ferret visual cortex often decreases at high temporal frequencies—for some neurons, even to the point of reversal in preferred direction. Our results also show that direction selectivity often decreases with temporal frequencies below the preferred, an effect not reported previously for adult animals, but one that has been shown in young animals (Saul and Feidler 2002). Although the cellular mechanisms that underlie temporal-frequency variant direction selectivity are unknown, it seems likely that the temporal frequency of a stimulus affects the timing and strength of synaptic inputs—both excitatory and inhibitory—such that temporal summation and spike generation are altered (Buchs and Senn 2002; Carandini et al. 2002; Chance et al. 1998; Krukowski and Miller 2001; Priebe and Ferster 2003; Saul and Humphrey 1992).

In a well-established model of direction selectivity, direction selectivity emerges as a result of converging inputs from nondirection selective neurons that have 90° (quadrature) spatiotemporal phase differences (Adelson and Bergen 1985; Watson and Ahumada 1985). While neurons in the visual cortex of macaque monkeys have been identified that display the appropriate phase relationship of the quadrature model (De Valois and Cottaris 1998; De Valois et al. 2000), similar neurons have not been found in cat visual cortex (Peterson et al. 2004). A recent study has shown, however, that the phase relationship required for quadrature can be met if one includes inputs from the LGN, presumably from neurons with lagged responses (Peterson et al. 2004). With that in mind, timing differences between lagged and nonlagged neurons in the adult cat LGN are known to decrease with increasing temporal frequency over the range of temporal frequencies that also decrease direction selectivity of cortical neurons (Saul and Humphrey 1992). If lagged LGN inputs indeed provide the necessary phase difference for quadrature, the effects of temporal frequency on LGN timing might be the basis for the effects of temporal frequency on direction selectivity. Finally, in models of direction selectivity that incorporate synaptic depression, one can adjust the input parameters to produce a decrease in direction selectivity similar to that reported in this study for stimuli drifting at both high and low temporal frequencies (see Fig. 5 in Chance et al. 1998).

Perceptual correlates

Our finding that orientation tuning of cortical neurons is invariant to temporal frequency while direction selectivity is variant raises the question of whether there are perceptual correlates of these neuronal properties. While this line of inquiry is certainly speculative, results from a number of psychophysical studies are consistent with the response properties reported here for ferret V1 neurons. In a series of psychophysical experiments, Snowden (1992) reported that estimates of orientation-tuning bandwidth based on perceptual discrimination are not affected by temporal frequency (but see Sharpe and Tolhurst 1973). This result is dependent on the spatial frequency of the stimulus, however, as estimates of orientation-tuning bandwidth are reported to increase with

temporal frequency when subjects are shown low spatial frequency stimuli (Snowden 1992; but see Phillips and Wilson 1984). Because all of the recordings in this study were made using each neuron's preferred spatial frequency, it is unknown whether or not temporal frequency has an influence on orientation tuning at low spatial frequencies. With this caveat, our finding that individual neurons in primary visual cortex display temporal-frequency invariant orientation tuning is consistent with psychophysical results and suggests a link between neuronal activity in primary visual cortex and perceptual performance.

Results from studies examining the influence of temporal frequency on direction sensitivity in humans are also consistent with our findings. In humans, measures of detection and discrimination of motion are band-pass for temporal frequency (Derrington and Henning 1993; Gegenfurtner and Hawken 1995), indicating that perception may follow neuronal activity in primary visual cortex. Finally, for a subset of neurons in this study, the preferred direction of drifting gratings actually reverses at low and/or high temporal frequencies. Similarly, Purves et al. (1996) reports that human observers often experience a weakening and reversal of periodic stimuli shown at high and low temporal frequencies. It is tempting to suggest that this effect—likened to the wagon wheel illusion (but see Pakarian and Yasamy 2003)—may also find its roots in the activity of neurons in primary visual cortex.

ACKNOWLEDGMENTS

We thank K. Britten, B. Olshausen, D. Warland, and F. Briggs for insightful discussions during the course of this project and K. Henning and D. Sperka for expert technical assistance.

GRANTS

This work was supported by National Eye Institute Grants EY-13588, EY-12576, and EY-15387, the McKnight Foundation, the Esther A. and Joseph Klingenstein Fund, and the Alfred P. Sloan Foundation.

REFERENCES

Adelson EH and Bergen JR. Spatiotemporal energy models for the perception of motion. *J Opt Soc Am A* 2: 284–299, 1985.

Alitto HJ and Usrey WM. Influence of contrast on orientation and temporal frequency tuning in ferret primary visual cortex. *J Neurophysiol* 91: 2797–2808, 2004.

Alonso JM, Usrey WM, and Reid RC. Rules of connectivity between geniculate cells and simple cells in cat primary visual cortex. *J Neurosci* 21: 4002–4015, 2001.

Anderson JS, Lampl I, Gillespie DC, and Ferster D. The contribution of noise to contrast invariance of orientation tuning in cat visual cortex. *Science* 290: 1968–1972, 2000.

Beaton A and Blakemore C. Orientation selectivity of the human visual system as a function of retinal eccentricity and visual hemifield. *Perception* 10: 273–282, 1981.

Benardete EA, Kaplan E, and Knight BW. Contrast gain control in the primate retina: P cells are not X-like, some M cells are. *Visual Neurosci* 8: 483–486, 1992.

Binzegger T, Douglas RJ, and Martin KA. A quantitative map of the circuit of cat primary visual cortex. *J Neurosci* 24: 8441–8453, 2004.

Bisti S, Clement R, Maffei L, and Mecacci L. Spatial frequency and orientation tuning curves of visual neurones in the cat: effects of mean luminance. *Exp Brain Res* 27: 335–345, 1977.

Buchs NJ and Senn W. Spike-based synaptic plasticity and the emergence of direction selective simple cells: simulation results. *J Comput Neurosci* 13: 167–186, 2002.

Bullier J and Henry GH. Ordinal position of neurons in cat striate cortex. *J Neurophysiol* 42: 1251–1263, 1979.

Callaway EM. Local circuits in primary visual cortex of the macaque monkey. *Annu Rev Neurosci* 21: 47–74, 1998.

Carandini M, Heeger DJ, and Senn W. A synaptic explanation of suppression in visual cortex. *J Neurosci* 22: 10053–10065, 2002.

Chance FS, Nelson SB, and Abbott LF. Synaptic depression and the temporal response characteristics of V1 cells. *J Neurosci* 18: 4785–4799, 1998.

Chisum HJ, Mooser F, and Fitzpatrick D. Emergent properties of layer 2/3 neurons reflect the collinear arrangement of horizontal connections in tree shrew visual cortex. *J Neurosci* 23: 2947–2960, 2003.

Daniel PM and Whitteridge D. The representation of the visual field on the cerebral cortex in monkeys. *J Physiol* 159: 203–221, 1961.

Derrington AM and Henning GB. Detecting and discriminating the direction of motion of luminance and colour gratings. *Vision Res* 33: 799–811, 1993.

Derrington AM and Lennie P. Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. *J Physiol* 357: 219–240, 1984.

DeValois RL and Cottaris NP. Inputs to directionally selective simple cells in macaque striate cortex. *Proc Natl Acad Sci USA* 95: 14488–14493, 1998.

DeValois RL, Cottaris NP, Mahon LE, Elfar SD, and Wilson JA. Spatial and temproal receptive fields of geniculate and cortical cells and directional selectivity. *Vision Res* 40: 3685–3702, 2000.

DeValois RL, Yund EW, and Hepler N. The orientation and direction selectivity of cells in macaque visual cortex. *Vision Res* 22: 531–544, 1982.

Ferster D, Chung S, and Wheat H. Orientation selectivity of thalamic input to simple cells of cat visual cortex. *Nature* 380: 249–252, 1996.

Field DJ. Relations between the statistics of natural images and the response properties of cortical cells. *J Opt Soc Am A* 4: 2379–2394, 1987.

Fitzpatrick D. The functional organization of local circuits in visual cortex: insights from the study of tree shrew striate cortex. *Cereb Cortex* 6: 329–341, 1996.

Foster KH, Gaska JP, Nagler M, and Pollen DA. Spatial and temporal frequency selectivity of neurones in visual cortical areas V1 and V2 of the macaque monkey. *J Physiol* 365: 331–363, 1985.

Gardner JL, Anzai A, Ohzawa I, and Freeman RD. Linear and nonlinear contributions to orientation tuning of simple cells in the cat's striate cortex. *Vis Neurosci* 16: 1115–1121, 1999.

Gegenfurtner KR and Hawken MJ. Temporal and chromatic properties of motion mechanisms. *Vision Res* 35: 1547–1563, 1995.

Gilbert CD. Laminar differences in receptive field properties of cells in cat primary visual cortex. *J Physiol (Lond)* 268: 391–421, 1977.

Girman SV, Sauve Y, and Lund RD. Receptive field properties of single neurons in rat primary visual cortex. *J Neurophysiol* 82: 301–311, 1999.

Hammond P and Smith AT. Directional tuning interactions between moving oriented and textured stimuli in complex cells of feline striate cortex. *J Physiol.* 342: 35–49, 1983.

Hawken MJ, Shapley RM, and Grosof DH. Temporal-frequency selectivity in monkey visual cortex. *Vis Neurosci* 13: 477–492, 1996.

Henry GH, Dreher B, and Bishop PO. Orientation specificity of cells in cat striate cortex. *J Neurophysiol* 37: 1394–1409, 1974.

Hirsch JA, Martinez LM, Pillai C, Alonso JM, Wang Q, and Sommer FT. Functionally distinct inhibitory neurons at the first stage of visual cortical processing. *Nat Neurosci* 12: 1300–1308, 2003.

Holub RA and Morton-Gibson M. Response of visual cortical neurons of the cat to moving sinusoidal gratings: response-contrast functions and spatiotemporal interactions. *J Neurophysiol* 46: 1244–1259, 1981.

Hubel DH and Wiesel TN. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J Physiol* 160: 106–154, 1962.

Ikeda H and Wright MJ. Spatial and temporal properties of "sustained" and "transient" neurones in area 17 of the cat's visual cortex. *Exp Brain Res* 22: 363–383, 1975.

Kato H, Bishop PO, and Orban GA. Hypercomplex and simple/complex cell classifications in cat striate cortex. *J Neurophysiol* 41: 1071–1095, 1978.

Kording KP, Kayser C, Einhauser W, and Konig P. How are complex cell properties adapted to the statistics of natural stimuli? *J Neurophysiol.* 91: 206–212, 2004.

Krukowski AE. A model of cat primary visual cortex and its thalamic input. PhD Dissertation, University of California, San Francisco, 2000.

Krukowski AE and Miller KD. Thalamocortical NMDA conductances and intracortical inhibition can explain cortical temporal tuning. *Nat Neurosci* 4: 424–430, 2001.

Lee BB, Martin PR, and Valberg A. Sensitivity of macaque retinal ganglion cells to chromatic and luminance flicker. *J Physiol* 414: 223–243, 1989.

McLean J and Palmer LA. Organization of simple cell responses in the three-dimensional (3-D) frequency domain. *Vis Neurosci* 11: 295–306, 1994.

Movshon JA, Thompson ID, and Tolhurst DJ. Spatial and temporal contrast sensitivity of neurons in areas 17 and 18 of the cat's visual cortex. *J Physiol* 283: 101–120, 1978.

Mukherjee P and Kaplan E. Dynamics of neurons in the cat lateral geniculate nucleus: in vivo electrophysiology and computational modeling. *J Neurophysiol* 74: 1222–1243, 1995.

O'Keefe LP, Levitt JB, Kiper DC, Shapley RM, and Movshon JA. Functional organization of owl monkey lateral geniculate nucleus and visual cortex. *J Neurophysiol* 80: 594–609, 1998.

Olshausen BA and Field DJ. Emergence of simple-cell receptive field properties by learning a sparse code for natural images. *Nature* 381: 607–609, 1996.

Orban GA. *Neuronal Operations in the Visual Cortex.* Berlin, Germany: Springer Verlag, 1984.

Orban GA, Hoffmann KP, and Duysens J. Velocity selectivity in the cat visual system. I. Responses of LGN cells to moving bar stimuli: a comparison with cortical areas 17 and 18. *J Neurophysiol* 54: 1026–1049, 1985.

Pakarian P and Yasamy MT. Wagon-wheel illusion under steady illumination: real or illusory? *Perception* 32: 1307–1310, 2003.

Peterson MR and Freeman RD. Direction selectivity of neurons in striate cortex changes with stimulus contrast. *Soc Neurosci Abstr* 484.17, 2003.

Peterson MR, Li B, and Freeman RD. The derivation of direction selectivity in the striate cortex. *J Neurosci* 24: 3583–3591, 2004.

Phillips GC and Wilson HR. Orientation bandwidths of spatial mechanisms measured by masking. *J Opt Soc Am A* 1: 226–232, 1984.

Priebe NJ and Ferster D. Timing, not tuning, of excitatory and inhibitory inputs determines direction selectivity in simple cells of cat visual cortex. Program N. 229.7. *Abstract Viewer/Itinerary Planner.* Washington DC: *Soc for Neurosci* 2003.

Purves D, Paydarfar JA, and Andrews TJ. The wagon wheel illusion in movies and reality. *Proc Natl Acad Sci USA* 93: 3693–3697, 1996.

Reid RC. *Directional Selectivity and the Spatiotemporal Structure of the Receptive Fields of Simple Cells in Cat Striate Cortex*. PhD dissertation, Rockefeller University Press, 1988.

Reid RC and Alonso JM. Specificity of monosynaptic connections from thalamus to visual cortex. *Nature* 378: 281–284, 1995.

Reid RC, Soodak RE, and Shapley RM. Directional selectivity and spatiotemporal structure of receptive fields of simple cells in cat striate cortex. *J Neurophysiol* 66: 505–529, 1991.

Ringach DL, Shapley RM, and Hawken MJ. Orientation selectivity in macaque V1: diversity and laminar dependence. *J Neurosci* 22: 5639–5651, 2002.

Saul AB and Feidler JC. Development of response timing and direction selectivity in cat visual thalamus and cortex. *J Neurosci* 22: 2945–2955, 2002.

Saul AB and Humphrey AL. Temporal-frequency tuning of direction selectivity in cat visual cortex. *Vis Neurosci* 8: 365–372, 1992.

Schiller PH, Finlay BL, and Volman SF. Quantitative studies of single-cell properties in monkey striate cortex. II. Orientation specificity and ocular dominance. *J Neurophysiol* 39: 1320–1333, 1976.

Sclar G and Freeman RD. Orientation selectivity in the cat's striate cortex is invariant with stimulus contrast. *Exp Brain Res* 46: 457–461, 1982.

Shapley R, Hawken M, and Ringach DL. Dynamics of orientation selectivity in the primary visual cortex and the importance of cortical inhibition. *Neuron* 38: 689–699, 2003.

Sharpe CR and Tolhurst DJ. The effects of temporal modulation on the orientation channels of the human visual system. *Perception* 2: 23–29, 1973.

Sillito AM. The contribution of inhibitory mechanisms to the receptive field properties of neurones in the striate cortex of the cat. *J Physiol* 250: 305–329, 1975.

Simoncelli EP and Olshausen BA. Natural image statistics and neural representation. *Annu Rev Neurosci* 24: 1193–1216, 2001.

Skottun BC, Bradley A, Sclar G, Ohzawa I, and Freeman RD. The effects of contrast on visual orientation and spatial frequency discrimination: a comparison of single cells and behavior. *J Neurophysiol* 57: 773–786, 1987.

Skottun BC, De Valois RL, Grosof DH, Movshon JA, Albrecht DG, and Bonds AB. Classifying simple and complex cells on the basis of response modulation. *Vision Res* 31: 1079–1086, 1991.

Snowden RJ. Orientation bandwidth: the effect of spatial and temporal frequency. *Vision Res* 32: 1965–74, 1992.

Tigges J and Shantha TR. *A Stereotaxic Brain Atlas of the Tree Shrew* (*Tupaia glis*). Baltimore, MD: Williams and Wilkins, 1969.

Usrey WM, Alonso J-M, and Reid RC. Synaptic interactions between thalamic inputs to simple cells in cat visual cortex. *J Neurosci* 20: 5461–5467, 2000.

Usrey WM and Reid RC. Visual physiology of the lateral geniculate nucleus in two species of New World monkeys: *Saimiri sciureus* and *Aotus trivirgatis. J Physiol* 523: 755–769, 2000.

Usrey WM, Sceniak MP, and Chapman B. Receptive fields and response properties of neurons in layer 4 of ferret visual cortex. *J Neurophysiol* 89: 1003–1015, 2003.

van Hateren JH and van der Schaaf A. Independent component filters of natural images compared with simple cells in primary visual cortex. *Proc R Soc Lond B Biol Sci* 265: 359–66, 1998.

Watson AB and Ahumada AJ Jr. Model of human visual-motion sensing. *J Opt Soc Am A* 2: 322–341, 1985.

Wilson JR and Sherman SM. Receptive-field characteristics of neurons in cat striate cortex: changes with visual field eccentricity. *J Neurophysiol* 39: 512–533, 1976.