Spatiotemporal Frequency Tuning Dynamics of Neurons in the Owl Visual Wulst

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Pinto L, Baron J. Spatiotemporal frequency tuning dynamics of neurons in the owl visual wulst. J Neurophysiol 103: 3424–3436, 2010. First published April 14, 2010; doi:10.1152/jn.01151.2009. The transformation of spatial (SF) and temporal frequency (TF) tuning functions from broad-band/low-pass to narrow band-pass profiles is one of the key emergent properties of neurons in the mammalian primary visual cortex (V1). The mechanisms underlying such transformation are still a matter of ongoing debate. With the aim of providing comparative insights into the issue, we analyzed various aspects of the spatiotemporal tuning dynamics of neurons in the visual wulst of four awake owls. The wulst is the avian telencephalic target of the retinotectal pathway and, in owls, bears striking functional analogy with V1. Most neurons in our sample exhibited fast and large-magnitude adaptation to the visual stimuli with response latencies very similar to those reported for V1. Moreover, latency increased as a function of stimulus SF but not TF, which suggests that parvo- and magno-like geniculate inputs could be converging onto single wulst neurons. No net shifts in preferred SF or TF were observed along the initial second of stimulation, but bandwidth decreased roughly during the first 200 ms after response latency for both stimulus dimensions. For SF, this occurred exclusively as a consequence of low-frequency suppression, whereas suppression was observed both at the low- and high-frequency limbs of TF tuning curves. Overall these results indicate that SF and TF tuning curves in the wulst are shaped by both feedforward and suppressive mechanisms, similar to what seems to be the case in the mammalian striate cortex.

INTRODUCTION

Tuning to the spatial (SF) and temporal frequencies (TF) of visual stimuli is progressively refined along the mammalian retinotectal pathway with expressiveness band-pass characteristics being apparent only at the level of the primary visual cortex (V1) (Hawken et al. 1996; Maffei and Fiorentini 1973; Shapley and Lennie 1985). The mechanisms behind such refinement are still a matter of ongoing debate. While some models propose that the emergent properties of V1 neuronal receptive fields can be explained by appropriate combinations of feedforward projections from the lateral geniculate nucleus (LGN) (e.g., Allen and Freeman 2006; Frazor et al. 2004; Hubel and Wiesel 1962), others advocate the importance of intracortical processing for shaping SF and TF tuning curves with particular emphasis on suppressive mechanisms (e.g., Bauman and Bonds 1991; Bredfeldt and Ringach 2002; Hawken et al. 1996; Ringach et al. 2002).

A fruitful way of approaching this issue in studies that employ extracellular recordings has been the analysis of the temporal dynamics of response functions, whereby one can often tease apart mechanisms that have distinct time scales. With regard to SF tuning, this approach has grounded the elaboration of several mechanistic hypotheses (Bredfeldt and Ringach 2002; Frazor et al. 2004; Malone and Ringach 2008; Mazer et al. 2002). Surprisingly, to the best of our knowledge, no studies have yet characterized the temporal dynamics of TF tuning functions.

To shed more light into the mechanisms underlying the transformations that occur in SF and TF tuning functions of neurons in the primary visual areas of the thalamofugal pathway, we sought to analyze the dynamics of spatiotemporal tuning of neurons recorded from an alternative model system, the owl visual wulst. The latter constitutes a very interesting comparative model to the study of V1 as these two structures, albeit presumably not having originated from common ancestry, show remarkable physiological and hodological similarities (Karten et al. 1973; Shimizu and Bowers 1999). For instance, owl wulst neurons are tuned to stimulus orientation, binocular disparity, direction of motion, SF and TF, in ways that closely parallel their striate cortical counterparts (Baron et al. 2007; Nieder and Wagner 2000, 2001a,b; Pettigrew 1979; Pinto and Baron 2009). Studying the visual wulst of the owl may thus provide important insights on the constraints that have driven such evolutionary convergence.

In the present study we show that, in a similar fashion to V1, wulst neurons have longer response latencies for stimuli of higher SFs. Moreover, most wulst neurons have strong response adaptation soon after stimulus onset. In terms of SF tuning dynamics, no significant shifts in preferred frequency were observed, but there was a consistent decrease in tuning bandwidth explained by a strong suppression at low frequencies. A decrease in tuning width was also seen for TF, although for this dimension suppression occurred at both the high- and low-frequency limbs of the tuning curves. Our data support the idea that SF and TF tuning curves in the owl wulst are shaped by a combination of feedforward and suppressive intratelencephalic mechanisms.

METHODS

We analyzed data from 90 complex cells recorded from the visual wulst of four awake burrowing owls (*Athene cunicularia*). These cells were part of a larger dataset that has previously been used to characterize spatiotemporal frequency and speed tuning under steady-state conditions (Pinto and Baron 2009). Details on the experimental procedures can be found therein. Briefly, we performed extracellular recordings of single neurons while presenting full-contrast sine-wave gratings, drifting in the cells’ preferred direction, in several combinations of spatial and temporal frequencies (SF and TF, respectively).
Most often, we presented a total of 36 different conditions (10 trials each) with SFs ranging from 0.25 to 8 cycle/° and TFs going from 0.25 to 8 Hz, both in 1 octave steps. Stimuli were presented in a pseudorandom, blockwise order, with a baseline period of 1 s, stimulus duration of 4 s and inter-trial interval of 2 s. The animal protocols used in this study were approved by the Ethics Committee for Animal Experimentation (CETEA, License 2004/01) of the Federal University of Minas Gerais and were conducted in conformance with the guidelines established by the National Institutes of Health and the European Communities Council Directive of 24 November 1986 (86/609/EEC). The owls were maintained in an outdoors aviary under a license from the Brazilian Institute for the Environment and Natural Renewable Resources (IBAMA, License 02015.004197/03).

Data analysis

Isolation of recorded units was reassessed off-line using a custom software developed by Dr. Nan-Hui Chen at the Max Planck Institute for Brain Research in Frankfurt, Germany, which performs semi-automatic clustering based on a dynamic template matching procedure (for details, see Baron et al. 2007; Pinto and Baron 2009). Spike density functions were generated for each neuron by convolving trial-averaged peristimulus time histograms (PSTH) of 1-ms bin size with a Gaussian kernel (sigma = 3 ms, total width = 15 ms) and were the basis for all the analyses described in the following text. Complex cells were defined as those with a PSTH f1/f0 modulation index smaller than 1 (De Valois et al. 1982; Skottun et al. 1991). Statistical significance of evoked responses for each stimulus condition was assessed by comparing a period of 500 ms preceding stimulus onset with one of equal length following it with either paired Student’s t-test or Wilcoxon’s sign rank test, depending on whether data were normally distributed (see General statistics).

RESPONSE LATENCY CALCULATION. Latency was calculated for stimulus conditions with statistically significant evoked response using the maximum likelihood estimation method devised by Friedman and Priebe (1998). This method has been shown by the authors to provide more reliable latency estimates than other commonly used methods (e.g., statistical criteria based on a Poisson distribution) (Maunsell and Gibson 1992). In part, this is because it is less vulnerable to biases introduced by, for example, low ratios of initial response rate/spontaneous rate (Friedman and Priebe 1998). While this assumption of maximum likelihood estimation of latency was devised to detect one inflection point in cumulative PSTHs and relies on the assumption of a step change in firing rate (Friedman and Priebe 1998). This model was chosen because it provides a means to make more direct comparisons with results obtained from the mammalian visual cortex and because relevant information, such as the time constant of adaptation, can be derived directly from the model’s parameters. We did not attempt to adapt the model used for computing response latency (Eqs. 1–3) to describe this later part of the response. This is so because the method of maximum likelihood estimation of latency was devised to detect one inflection point in cumulative PSTHs and relies on the assumption of a step change in firing rate (Friedman and Priebe 1998). While this assumption is approximately true for response onset transients, it is unlikely to hold for processes with slower time courses, such as response adaptation.

TUNING DYNAMICS. We assessed the temporal evolution of SF and TF tuning functions by sliding a 10-ms window with 1-ms steps over the first 1,000 ms after response latency determined for each condition. For conditions without significant evoked response, we chose the mean population latency at the best condition as the starting point (55 ms, see RESULTS). Spatial frequency tuning was evaluated at the preferred temporal frequency and vice versa. For each time window, mean response rates as a function of stimulus frequency were fitted with the following model, from which tuning parameters were extracted

\[ R(f) = A \times \left\{ \exp \left[ \frac{-(\log f_0 - \log f)^2}{2(\sigma_f + \frac{1}{f^2})} \right] - \exp \left[ \frac{-1}{f^2} \right] \right\} \]

The preceding equation is a modified Gaussian function used by Priebe et al. (2006) to fit one-dimensional (1D) speed tuning curves and that provided good fits for the steady-state SF and TF tuning data in our previous study (Pinto and Baron 2009). In the equation, \( f_0 \) is the independent variable, i.e., the temporal frequency of the grating in hertz or its spatial frequency in cycle/°; \( A \) is the maximum response amplitude; \( f_p \) is the preferred frequency of the cell, \( \sigma_f \) is the spread of the Gaussian and \( \xi \) is a skewness parameter. Note that even though we have previously defined tuning bandwidth as full width at half height, in the present study, \( \sigma_f \) was used instead. The reason is that for curves with a low-pass profile, it is not always possible to compute bandwidth at half height, and what we are presently interested in is how the width of the tuning curve varies with time. All the same, full width at half height and \( \sigma_f \) are highly correlated (Pearson correlation coefficient =
0.97 and 0.80, for SF and TF respectively, \( P < 0.001 \) for both as assessed in steady state. We also computed other quantities from the tuning curves on each 10-ms window: low spatial frequency suppression (LSFS), defined as the ratio between the response at the lowest SF tested and the response at the best SF (Xing et al. 2004); high spatial frequency suppression (HSFS), defined as the ratio between the response at the highest tested SF and the response at the preferred frequency; and the equivalents for TF, namely LTFS (low temporal frequency suppression) and HTFS (high temporal frequency suppression).

GENERAL STATISTICS AND FITTING PROCEDURE. Datasets were systematically screened for normality using the Lilliefors modification of the Kolmogorov-Smirnov test. If normality was verified, we applied a \( t \)-test to compare the means of two populations or an analysis of variance (ANOVA) test if comparisons were made between more than two populations. Conversely, if datasets had nonparametric distributions, the Wilcoxon rank-sum or Kruskal-Wallis tests were used as nonparametric equivalents of the \( t \)- and ANOVA tests, respectively. Statistical dependence between variables was measured using the nonparametric Spearman’s rank correlation test. Correlation coefficients derived from this test are reported as \( \rho \). The significance level used for all the tests was \( P < 0.05 \). Unless otherwise specified, central tendency measures are presented as arithmetic mean \( \pm \) SE.

All curves were fitted using the nonlinear least-squares trust region algorithm implemented in “fit” function in Matlab (MathWorks, Natick, MA). A maximum of 1,000 iterations were allowed. Goodness of fit was evaluated using \( r^2 \) values and the fit \( F \) statistics (Daniel and Wood 1980).

RESULTS

Response latency

Figure 1 summarizes our findings on response latency as estimated with the maximum likelihood method (see METHODS). As exemplified in A, which shows spike density functions for the same neuron with stimuli of different SFs at the cell’s preferred TF, we observed a systematic positive relation between stimulus SF and response latency, that is, latency was on average longer for higher SFs (B). Kruskal-Wallis test confirmed that these frequency-specific latency differences were significant [degrees of freedom (df) = 5, \( P < 0.001 \)]. More-
over, a comparison solely between the latencies at the smallest and highest SFs tested also yielded a significant difference (58.4 ± 4.0 and 92.9 ± 13.9 ms for SF = 0.25 and 8 cycle/°, respectively; Wilcoxon rank sum, \( P = 0.018 \)). Interestingly, this phenomenon has also been reported for neurons in macaque and cat V1 and is thought to express differential contributions of the parvo and magno streams from the LGN onto a given striate neuron (Frazor et al. 2004; Mausell and Gibson 1992; Mazer et al. 2002). No significant differences were given striate neuron (Frazor et al. 2004; Mausell and Gibson 1999), but the stimuli used in those studies had a broadband SF content and consequently several embedded nonspecified TF values, which makes unclear how latency is affected by specific TFs.

Figure 1E shows the distribution of response latencies of wulst complex cells estimated at their preferred SF–TF combination. Latency values were nonnormally distributed around a median of 48 ms with a skew toward lower latency values.

**Time course and magnitude of response adaptation**

Spike density functions at preferred SF and TF were fitted with a model of exponential decay from the initial peak to the end of the stimulation period, which provided good descriptions for our data in most instances (78/90 significant fits according to \( F \) statistics). We observed a variety of profiles regarding the degree of response adaptation, ranging from cells with sharp transients followed by fast and pronounced adaptation (e.g., cells depicted in Fig. 2, \( A \) and \( B \)) to those with fairly sustained responses throughout the stimulation period (\( C \) and \( D \)).

The rate of response adaptation was captured by the exponential decay time constant, \( \tau \), which is a free parameter of the model equation used to fit the spike density functions, and the distribution of which is shown in Fig. 2E. Overall, the rate of response adaptation was high in our sample, with most cells (46/78) displaying time constants below 100 ms. Mean \( \tau \) was of 192.9 ± 51.6 ms, and median was of 47.7 ms. In other words, distribution was heavily skewed toward low values, showing that most complex cells in the owl wulst adapt rapidly to full-contrast drifting sinusoidal gratings of optimal direction, SF and TF.

The magnitude of response adaptation was quantified by the sustained response ratio, which ranges from 0 to 1, with lower values indicating strong adaptation. Distribution of the ratio is shown in Fig. 2F. Average population behavior was of strong adaptation, with asymptotic responses having a mean of 26 ± 1% of the magnitude of the peak responses (ratio range: 0.02 – 0.65).

We also attempted to categorize cells as “transient” or “sustained” on the basis of whether their discharge rate computed over a 50-ms period after response latency was significantly higher than an equal-sized period 100 ms later (sign rank test). Using this criterion, 80% of the cells were classified as
“transient.” Finally, we also computed the time elapsed between the estimated response latency and initial response peaks, finding an arithmetic mean of $36.5 \pm 3.7$ ms (range: 10–89 ms).

**Tuning in the transient and sustained parts of the response**

To explore the relative importance of transient and steady-state activity in establishing the spatiotemporal tuning properties of wulst neurons, we constructed tuning curves for transient and sustained periods and compared tuning parameters between them. For this analysis, transient period was defined individually for each cell as the time epoch between response latency and $\tau$ (mean duration: 260.0 ± 53.0 ms, median: 130.9 ms), and the sustained period started 2,000 ms after the transient and had the same duration. Using a fixed period length of 200 ms for all cells yielded very similar results (not shown).

Figure 3 compares SF and TF tuning between the two epochs. A and B show representative tuning curves for SF and TF, respectively, computed on the sustained (black) and transient (gray) parts of the response. Inspection of these curves reveals several interesting phenomena. First, for SF, while the preferred frequency changes little, tuning width is much wider during the transient period than the sustained period. For TF, the preferred frequency and tuning width are comparable between the two periods, but there is a trend towards a slightly higher frequency in the transient period.

**FIG. 3.** Comparison between tuning parameters computed for the transient and sustained parts of the response, as determined from $\tau$. A: example of a SF tuning curve calculated on the transient (gray) and sustained (black) parts of the response of a cell. B: example of a cell TF tuning curve derived for each of the 2 periods, conventions as in A. C–F: on each scatter plot, gray filled lines correspond to the $x = y$ line, and dashed gray lines indicate slopes of linear fits. Histograms show the corresponding distributions of the differences between parameters obtained for the transient and sustained periods (SF: $n =$ 66; TF: $n =$ 47). Note that the different sample sizes are a consequence of the fact that TF tuning assessment resulted in fewer cells meeting our goodness of fit criteria than SF assessment. BW, bandwidth; trans, transient; sust, sustained; c/deg, cycle/°; rho, Spearman’s rank correlation coefficient.
smaller in the sustained than in the transient period, apparently mostly due to suppression at low frequencies. For TF, the reduction in tuning bandwidth in the sustained part of the response appears even more striking and seems to be related to suppression at both extremes of the curve. Moreover, there is some decrease in the preferred frequency in this period as compared with the response transient. A quantification of these observations is presented in C–F, which plot the preferred SF and TF and respective tuning bandwidths for the two periods. In all four panels, the scatter plots show the correlations between the values, and the histograms show the distribution of the difference between the parameters for transient and sustained periods. As can be seen in C, preferred SF was significantly correlated for these periods (rho = 0.47, P < 0.01) and not significantly different between the two (mean difference: 0.20 ± 0.14 octaves, median: −0.15 octaves, sign rank test against a 0-median distribution: P = 0.09). D shows the comparison for SF bandwidth. While the values for the two periods were less strongly correlated than for preferred frequency (rho = 0.27, P = 0.02), they were higher in the transient than in the sustained period for almost all cells as shown by a mean difference of 0.57 ± 0.10 octaves, which was significantly larger than zero (median: 0.45, sign rank test, P < 0.001). A different pattern of results was observed for TF. Preferred frequency values were highly correlated and significantly different from each other—they were on average higher in the transient than in the sustained period (E, rho = 0.63, P < 0.01, mean difference: 0.65 ± 0.15 octaves, Student’s t-test against a zero-mean distribution: P ≪ 0.01). Finally, F shows that TF bandwidth was not correlated between the epochs (rho = 0.13, P = 0.38) and was significantly larger in the transient part of the response (mean difference: 0.61 ± 0.32, sign rank test: P = 0.02).

In summary, while preferred SF remained the same throughout the response latency and another spanning the whole 1,000-ms period. This index was computed for each cell, the 10-ms window over the mean population values of several tuning parameters.

We believe that this time-dependent sampling difference between SF and TF is due to the fact that the fitting model we used is less likely to converge when the experimental data points form very flat curves; this was often the case for TF tuning at the beginning of the response.

To control for all the aforementioned confounding factors, we bootstrapped the data (sample size = 20, number of iterations = 1,000) and assessed how subsamples compared with the overall results reported in the following text. For every iteration, all tuning parameters were significantly correlated with those calculated from the whole dataset with correlation coefficients ranging from 0.12 to 0.80 with a mean of 0.50. It should also be noted that using a 50-ms window did not substantially alter the results (data not shown).

Taken together, the preceding considerations allow us to conclude that in spite of the noise introduced by the fine temporal scale of the analysis the results presented below reliably capture the dynamics of SF and TF tuning of wulst neurons.

**SF tuning dynamics**

Figure 4 shows three representative examples of the temporal evolution of TF tuning for the first 820 ms following response latency. Inspection of the figure reveals several aspects that characterize our cell sample. First, there is no consistent pattern of change in preferred SF over time at the population level. Some cells maintain their peak frequency fairly constant (Fig. 4B), whereas others exhibit a consistent decrease (A) or increase (C) with respect to this dimension. Second, tuning width narrows mainly due to a relative decrease of response at low frequencies, a phenomenon that appears to be more pronounced approximately within the first 50 ms. Third, no sizable changes in SF tuning profiles were observed after ~200 ms.

Figure 5 shows population results for SF tuning dynamics. Plots on the left (A, C, E, and G) show the temporal evolution of the mean population values of several tuning parameters. Right-hand side panels (B, D, F, and H) are histograms showing population distributions of an index we devised to quantify the sign of value changes along time. For each time window, we assigned a “+” if the value was greater than the value on the first window, and a “−” if the value was smaller. The index is given by (total “+” counts − total “−” counts)/(total “+” counts + total “−” counts) and ranges from −1 for cells for which all windows have values smaller than the first one and to +1 for cells with all windows having values larger than that on the first window. A value of 0 indicates an equal number of + and − counts, essentially suggesting random value fluctuations. To separate very rapid processes from the overall behavior throughout the analyzed period, this index was computed for two time windows, one going until 100 ms after response latency and another spanning the whole 1,000-ms window (white and black bars in histograms, respectively). Note that independent of the time scale, any monotonic pattern
of change in tuning parameter value would translate into change sign index values away from 0.

We also computed a $\Delta_{\text{w}}$ number that compares the initial and final parameter values over a period going from 0 to $w$ ms by calculating the difference between the means of the last and first 10 time points of this period. Both the index and delta distributions were compared against a zero-mean (median) distribution using the sign-rank or Student’s $t$-test, depending on the normality of data distribution (see METHODS).

As noticeable from the very broad distribution of the change sign index in Fig. 5B, and confirming what is illustrated by the three cells shown in Fig. 4, we observed a variety of behaviors regarding the temporal evolution of preferred SF, resulting in no obvious frequency shifts at the population level. Even though there is a slight increase in preferred SF roughly for the first 30 ms that follow response latency, sign index was not significantly different from 0, neither for the first 100 ms (median: 0.16; Wilcoxon rank sum, $P = 0.30$) nor for the whole 1,000 ms (median: 0.08, $P = 0.17$). Accordingly, neither $\Delta_{\text{(100)}}$ nor $\Delta_{\text{(1000)}}$ were statistically different from a 0-mean distribution ($\Delta_{\text{(100)}} = 0.12 \pm 0.15$ octaves, $P = 0.55$; mean $\Delta_{\text{(1000)}} = 0.39 \pm 0.18$ octaves; Student’s $t$-test, $P = 0.08$). Note, however, that if we select conservatively the cells in our sample with a change sign index $>0.5$ ($75\%$ of + counts), we find an expressive subpopulation of 30%. This sub-population has a $\Delta_{\text{(100)}}$ distribution that differs significantly from 0 (Student’s $t$-test, $P \ll 0.001$) with a mean of $1.21 \pm 0.19$ octaves.

Tuning bandwidth displayed a sharp drop until roughly 50 ms, decreasing more smoothly until 200–250 ms of response and stabilizing thereafter. This is captured by the fact that although sign indices computed for 100 and 1,000 ms are both significantly different from zero (Wilcoxon rank sum, $P \ll 0.001$), the former is significantly more negative than the latter [Wilcoxon rank sum, $P \ll 0.001$, median(100) = −0.85 and median(1000) = −0.47]. The opposite behavior was seen in the distributions of $\Delta_{\text{(100)}}$ and $\Delta_{\text{(1000)}}$; while both were different from 0-mean distributions (Wilcoxon rank sum, $P = 0.03$ and $P \ll 0.01$, respectively), the negative shift in tuning bandwidth had greater magnitude when assessed over the entire 1,000-ms period [median($\Delta_{\text{(100)}}$) = −0.13 octaves, median($\Delta_{\text{(1000)}}$) = −0.37 octaves; Wilcoxon rank sum, $P = 0.05$], which confirms that fully fledged SF bandwidth reduction requires $>100$ ms to take place. The observed reduction in bandwidth was accompanied by an increase of similar time course in low-frequency suppression, as expressed by a fairly sizable decrease in LSFS (mean $\Delta_{\text{(100)}} = -0.09 \pm 0.03$, mean $\Delta_{\text{(1000)}} = -0.20 \pm 0.05$, both significantly smaller than 0—Student’s $t$-test, $P \ll 0.01$; but not significantly different from each other, Student’s $t$-test, $P = 0.10$). Moreover, change sign indices

FIG. 4. Three representative examples of the temporal evolution of SF tuning with best-fitting curves sampled from time points indicated on the plots, where each cell is shown in a different panel (A–C). The black dots correspond to mean response and the bars indicate SE. The gray arrows indicate the location of preferred frequency as assessed on the 1st temporal window.
significant negative correlation was found between $\Delta_{1000}$ (LSFS) and $\Delta_{1000}$ (preferred SF; Fig. 8B, $\rho = -0.42, P < 0.001$). As we have shown in the preceding text, only a portion of our sampled cells displayed positive shifts in optimal SF during the first 100 ms after response latency. We therefore decided to repeat the above correlation test for this sub-population. Curiously, this selection resulted in a nonsignificant correlation ($\rho = -0.31, P = 0.17$).

**TF tuning dynamics**

Two representative examples of TF tuning dynamics are depicted in Fig. 6. Both cells display an interesting behavior regarding preferred TF: there is an initial increase, followed by a decrease, with little net shift. Also, as seen for SF, tuning bandwidth decreases, and more pronouncedly so for the initial 50–100 ms. Unlike SF, however, this narrowing of the tuning curve is accompanied by relative response suppression at both low and high frequencies.

Population results are displayed in Fig. 7 with the same layout as Fig. 5. First, the pattern of preferred TF shifts illustrated in Fig. 6 is also clear at the population level: an initial upward shift in the first 100 ms is followed by a downward inflection of the curve, which reaches an asymptote soon after 200 ms. This initial positive shift is statistically significant, as both $\Delta_{1000}$ (mean: 1.57 ± 0.48 octave) and sign change index (100) (mean: 0.32 ± 0.11) differ from a 0-mean distribution (Student’s $t$-test, $P < 0.01$ for both). Likewise, the following decrease in peak TF is also significant [mean $\Delta_{1000}$ = −1.25 ± 0.45 octave, Student’s $t$-test, $P < 0.01$; median index (100–1000): −0.67, Wilcoxon test, $P < 0.001$]. When one looks at the whole 1,000-ms period, the upward and downward shifts cancel out, resulting in no significant net changes in preferred TF (mean index: −0.08 ± 0.09; mean $\Delta_{1000}$ = −0.05 ± 0.31; Student’s $t$-test, $P = 0.30$ and $P = 0.89$, respectively). Interestingly, changes in preferred TF are positively and significantly correlated with changes in high-frequency suppression [Spearman correlation, preferred TF vs. HTFS, $\Delta_{1000}$: $\rho_0 = 0.36$, $P = 0.05$; $\Delta_{1000}$: $\rho_0 = 0.41$ (Fig. 8C), $P = 0.01$; sign index (100–1,000): $\rho_0 = 0.30, P = 0.02$]. In other words, positive shifts in peak TF seem to be related to decreased relative suppression at high frequencies; conversely, decreases in preferred TF are apparently related to increased high-frequency suppression.

As suggested by the examples in Fig. 6, TF tuning bandwidth displays a sharp decrease in the course of the initial 100 ms, roughly stabilizing thereafter. Notably, this is a fairly shorter time scale than the one observed for SF (200–250 ms). Not surprisingly, for this tuning parameter, $\Delta_{1000}$ (mean: −1.13 ± 0.30) and $\Delta_{1000}$ (mean: −1.07 ± 0.36) were both significantly smaller than zero (Student’s $t$-test, $P < 0.01$) and not significantly different from each other (paired Student’s $t$-test, $P < 0.01$). Moreover, similarly to what was observed for SF bandwidth, sign change index for 100 ms (median: −0.91) was significantly smaller than that for 1,000 ms (median: −0.69; Wilcoxon test, $P < 0.01$) and both had distributions that differ statistically from a 0-mean one (Wilcoxon test, $P < 0.01$ for both). We also observed a decrease in LTFS, i.e., an increase in relative low-frequency suppression with stimulation time. In both analysis periods, sign change index was smaller than zero (Wilcoxon test, $P < 0.01$ for both), with a median of −0.63 for the initial 100 ms and −0.68 for the
whole period, a statistically nonsignificant difference (Wilcoxon test, $P = 0.55$). The same can be said for $\Delta_{100}$ (mean $= -0.20 \pm 0.07$) and $\Delta_{1000}$ (mean $= -0.31 \pm 0.06$; difference between the two is not significant, paired Student’s $t$-test, $P = 0.25$). Also similarly to what we report for SF, TF tuning bandwidth is highly correlated with LTFS regardless of the measure or analysis period used [TF bandwidth vs. LTFS; $\rho = 0.50$ and $P = 0.001$, $\Delta_{1000}$: $\rho = 0.82$ and $P \ll 0.001$ (Fig. 8D); sign index(100): $\rho = 0.40$ and $P = 0.02$, sign index(1000): $\rho = 0.54$ and $P < 0.001$]. Unlike SF, on the other hand, TF relative high-frequency suppression significantly increases with time by approximately the same magnitude as low-frequency suppression. Nevertheless, LTFS and HTFS differ in their time courses. It is clear from Fig. 7G that while LTFS drops for the first 100 ms, HTFS remains stable, starting to decrease only after this period. Indeed both $\Delta_{100}$ (mean $= -0.07 \pm 0.05$) and $\Delta_{1000}$ (mean $= -0.24 \pm 0.06$, and sign index 100 (median $= -0.09$) and 1,000 (median $= -0.71$) are significantly different from each other ($P \ll 0.05$ for both, paired Student’s $t$-test for $\Delta$ and Wilcoxon test for the index) with the measures for the whole period, but not for the initial 100 ms, being significantly different from zero [Student’s $t$-test, $\Delta_{1000}$; $P = 0.14$, $\Delta_{1000}$: $P \ll 0.01$; Wilcoxon test, sign index(100): $P = 0.52$, sign index(1,000): $P \ll 0.001$]. As expected from their different time courses, HTFS is uncorrelated with either LTFS or TF bandwidth (Spearman correlation, $\rho < 0.25$ and $P > 0.1$ for all possible correlations).

**DISCUSSION**

In this study, we analyzed several aspects of the dynamics of owl visual wulst neuronal responses to full-contrast sinusoidal gratings of varying SFs and TFs, drifting in the optimal motion direction. Our results may be summarized as follows. First, most neurons displayed increasingly longer response latencies as SFs got higher for gratings of optimal TF. Variation of TF at the optimal SF, however, did not result in significantly different latencies. Analysis of the time course and magnitude of response adaptation at the optimal SF-TF combination revealed that wulst neurons display a continuum of degrees of adaptation that tends to concentrate on the more transient end of the spectrum: most cells have rapid and intense adaptation to the stimuli. Regarding SF tuning dynamics, no significant shifts in preferred frequency were noticed, but bandwidth significantly decreased roughly for the initial 200 ms following onset of response, a change that was correlated with an increase in suppression at low, but not high, frequencies. TF tuning bandwidth also decreased during the initial 100–150 ms, which was paralleled by a sizable low-frequency suppression. Temporal evolution of preferred TF had a less straightforward behavior: it displayed an initial increase, decreasing after 100 ms, without any net changes when the whole 1000-ms analysis period was considered. These changes were related to the degree of high-frequency suppression.

**FIG. 6.** Two representative examples of the temporal evolution of TF tuning where each cell is shown in a different panel (A and B). Conventions are the same as in Fig. 4.
Cortical neurons that response latency increases as a function of stimulus SF, a finding that has been interpreted as evidence for the convergence of LGN parvo and magno inputs onto a single V1 neuron (Frazor et al. 2004; Mazer et al. 2002). According to this explanation, tuning to higher SFs is characteristic of LGN parvocellular neurons, which have lower conduction velocities than magnocellular neurons (Kaplan and Shapley 1982; Schiller and Malpeli 1978). This hypothesis is further strengthened by the fact that lesions to the magnocellular layers of the LGN increases the response latency of cells in V1 (Maunsell and Gibson 1992).

In the owl, Pettigrew (1979) reported that cells in the nucleus geniculatus lateralis par dorsalis (GLd), the avian equivalent of the LGN, at least hodologically (see Güntürkün and Karten 1991 and references therein), are readily dividable into X- and Y-like functional classes. This conclusion was based on results from a number of tests classically used to establish such classes in the mammalian visual pathway and include tests of sustained versus transient responses to flashing spots, response to fast movement and contrast-reversal, and latency measures after optic chiasma stimulation. This finding, together with our SF-dependent latency shift result, allows us therefore to speculate that a convergence of magno- and parvo-like inputs also takes place in the wulst. In addition, we have previously reported that there is a significant negative correlation between preferred SF and TF of single neurons in the wulst; this further suggests that these cells can be under various degrees of influence of putative parvo and magno inputs (Pinto and Baron 2009).

The lack of significant relationship between latency and TF displayed by wulst neurons is at first glance unexpected. Following the same aforementioned line of reasoning, at the

Convergence of parvo- and magno-like signals onto wulst neurons?

It is fairly well established for macaque and cat striate cortical neurons that response latency increases as a function of
cells’ preferred SF, one would expect to see decreasing latencies for increasing TFS, as parvocellular LGN neurons tend to respond better to lower TFS (Derrington and Lennie 1984; Hicks et al. 1983). However, as shown by these authors, magno- and parvocellular TF tuning profiles in the mammalian LGN are largely overlapping. A later study by Hawken et al. (1996) found no significant differences between the two populations. If this is also the case in owl GLd, the differential timing of parvo- and magno-like inputs to the wulst is likely to be blurred for a relatively large range of TFS.

As a final comment on response latency, it is interesting to note that its overall distribution closely matches the one seen in the mammalian striate cortex (e.g., Frazor et al. 2004; Maussell and Gibson 1992; Mazer et al. 2002; Schmolesky et al. 1998). The present study also demonstrates the existence of a close resemblance between the owl wulst and the mammalian striate cortex in terms of the magnitude and the temporal profile of response adaptation (e.g., Hegdé and Van Essen 2003, 2004; Müller et al. 2001; Palanca and DeAngelis 2003; Zhang et al. 2008). Most notably, the distribution of τ and sustained response ratio reported by Müller et al. (2001) in primate V1 are strikingly similar to what we find in the owl wulst. Given that in the natural world sensory input features are continuously changing, it is possible that transient activity, rather than steady-state dynamics, may be particularly important for neural coding.

Moreover, this pattern of response adaptation may be taken as another piece of indirect evidence for the intermixing of parvo- and magno-like signals in the wulst—a similar argument to the one put forward for the macaque striate cortex (Maussell and Gibson 1992). As a cautionary note, however, one should emphasize the fact that the characterization of transient and sustained response profiles in the visual cortex has typically performed with stationary stimuli (Hegdé and Van Essen 2003, 2004; Müller et al. 2001; Palanca and DeAngelis 2003; Zhang et al. 2008). Most notably, the distribution of τ and sustained response ratio reported by Müller et al. (2001) in primate V1 are strikingly similar to what we find in the owl wulst. Given that in the natural world sensory input features are continuously changing, it is possible that transient activity, rather than steady-state dynamics, may be particularly important for neural coding.

The biophysical mechanism of response adaptation in V1 is still unclear. Mechanisms identified as contributors include short-term synaptic depression (Abbott et al. 1997), intrinsic membrane properties associated with conductance changes and membrane hyperpolarization (Carandini and Ferster 1997), and specific intracortical networks of inhibitory neurons (Ahmed et al. 1997). However, a comparison between stimulus-dependent neuronal response profiles in the mammalian LGN and striate cortex suggests that part of the decay is accomplished within the cortex (Müller et al. 2001). Arguably the same type of mechanism could explain the differences we observed in SF and TF tuning of wulst neurons between the transient and sustained periods, especially concerning bandwidth. Interestingly, Müller et al. (2001) reported that the contrast and/or the response gain of V1 neurons are usually smaller if the calculation of mean response rates includes the sustained period than if it is based only on the initial response transient. It is thus conceivable that if the same holds true for the owl wulst, changes in tuning bandwidth could simply reflect changes in contrast gain. However, preliminary data from our group show that both spectral and orientation tuning of wulst neurons are invariant to stimulus contrast (C. Amorim and J. Baron, unpublished observations), similarly to V1 (Sclar and Freeman 1982; Skottun et al. 1987). Thus the responses of wulst neurons seem to result from a complex interaction between mixed parvo- and magno-like feedforward input and intratradence-philic mechanisms. A finer-grained analysis of the temporal dynamics of SF and TF tuning further supports this notion, as discussed in the following text.

Comparison with SF tuning dynamics in V1

The temporal dynamics of SF tuning in V1 has been assessed by several investigators (Bredfeldt and Ringach 2002; Frazor et al. 2004; Malone and Ringach 2008; Mazer et al. 2002; Nishimoto et al. 2005). Most of these studies have focused on how preferred SF changes within the first tens of milliseconds and consistently found it to shift from low to high values. This trend was not so consistent across our sample of visual wulst neurons: only 30% showed a largely continuous increase in optimal SF during the first 100 ms of response. Note, however, that average SF shifts measured by reverse correlation are rather small, and their distribution does not seem to be so different from ours [0.62 ± 0.69 octave in Bredfeldt and Ringach (2002); 0.23 ± 0.28 octave in Nishimoto et al. (2005)]. Using a different and less directly comparable measure of SF shift, a similar conclusion was also reached in the reverse correlation study of Mazer et al. (2002). The largest shift in preferred SF was reported by Frazor et al. (2004) (0.91 octave), who employed a different methodology, using static grating stimulation for a longer period of time than reverse correlation procedures (200 ms). However, as the authors note, this effect was largely attributable to latency shifts as realignment of PSTHs by response latency mostly abolishes it.

To what extent this apparent dissimilarity between our results and those obtained by reverse correlation studies in the striate cortex is real or due to differences in stimulation paradigms and/or analytical procedures is not so clear. To start with, it is important to mention that we used moving gratings, contrary to previous studies that employed stationary gratings. We did so because we wanted to characterize the dynamics of both SF and TF tuning. However, depending on the degree of separability of these two dimensions, and its development in time, complex interactions may arise and modify the temporal evolution of SF tuning seen with stationary gratings. Two findings would argue against this scenario: first, steady-state spatiotemporal tuning was shown to be separable for the large majority of wulst neurons (Pinto and Baron 2009); second, receptive field characterization based on reverse correlation has been shown to be in good agreement with that obtained by traditional steady-state stimulation using drifting gratings (Nishimoto et al. 2005). It is also possible that steps of one octave that we used in our stimulation paradigm were too coarse to capture small shifts in SF. Such potential undersampling problem may have not been compensated by our fitting model. Another potential factor that may have masked temporal evolution of SF peaks is the nonnegligible amount of fits that had to be excluded from the analysis due to our rather conservative rejection criterion. However, the results of our bootstrapping control analysis show that the effect caused by
missing data points is unlikely to change the main conclusion of the present study.

To date, only one study has provided information on the temporal evolution of SF tuning bandwidth in the striate cortex (Bredfeldt and Ringach 2002). Although the measure of tuning width used in this previous study is not directly comparable to ours, both converge to the same conclusion, namely a rapid sharpening in SF tuning after response onset. In accordance with Bredfeldt and Ringach (2002), this change was also found to be significantly correlated with response suppression at frequencies below but not above the one preferred by the cell. Furthermore, our results indicate that refinement of tuning selectivity may extend for longer periods (~200–250 ms) than those considered in the reverse correlation study of Bredfeldt and Ringach (~100 ms). However, as previously discussed, one should keep in mind that this difference could also be due to our use of drifting gratings.

**TF tuning dynamics in the owl wulst**

Our results on the dynamics of TF tuning suggest that two different processes shape the transformation of TF responses between the GLd and the visual wulst. First, there is a rapid decrease in tuning bandwidth that is highly correlated with an increase in low-frequency suppression. Given the fast time scale, it is reasonable to speculate that this could be due at least partly to feedback processes. Second, the fact that the sizable decrease seen in high-frequency suppression does not start until 100 ms after response latency likely indicates the participation of intratelencephalic mechanisms. Such suppression is correlated with a reduction in preferred TF that follows an initial transient increase in that tuning parameter. These results are overall consistent with the known transformations of TF tuning that occur between the LGN and V1 of macaque monkeys, as assessed in steady-state responses (Hawken et al. 1996). These authors have shown that there is a sizable reduction in high-frequency cutoff between these two processing stages along with a more discrete reduction in preferred TF. Moreover, as we show in the present study, these two parameters seem to be positively correlated (Hawken et al. 1996).

Unfortunately, however, we are unaware of any studies that have addressed the issue of TF tuning dynamics in the mammalian primary visual cortex. Given all the similarities between the physiology of the wulst and V1 observed in this and in past studies, we hypothesize that TF tuning dynamics has a similar profile in V1, which would be interesting to study. Another topic for future investigation is the complex behavior of preferred TF during the initial portion of the response. For instance, one could test whether it is at all related to the dynamics of fixations and, in the owl, head motion. Although owls have negligible eye movements (Steinbach and Money 1973), they do display a wide repertoire of head movements, including saccades, fixations, translations and rotations (Knudsen et al. 1995; Ohayon et al. 2006).

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