Spatiotemporal frequency tuning dynamics of neurons in the owl visual wulst

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Abstract
The transformation of spatial (SF) and temporal frequency (TF) tuning functions from broad-band/lowpass to narrow bandpass 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 retinothalamofugal 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 intratelencephalic suppressive mechanisms, similarly 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 retinothalamofugal pathway, with expressive bandpass characteristics being apparent only at the level of the primary visual cortex (V1) (Maffei and Fiorentini 1973; Shapley and Lennie 1985; Hawken et al. 1996). 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. Hubel and Wiesel 1962, Frazor et al. 2004; Allen and Freeman 2006), 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; Hawken et al. 1996; Ringach et al. 2002; Bredfeldt and Ringach 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 regards to SF tuning, this approach has grounded the elaboration of several mechanistic hypotheses (Bredfeldt and Ringach 2002, Mazer et al. 2002; Frazor et al. 2004; Malone and Ringach 2008). 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 (Pettigrew 1979;
Nieder and Wagner 2000, 2001a,b; Baron et al. 2007; 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 stimulus 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.
Materials and 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 at 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 cycles/degree and TFs going from 0.25 to 8 Hz, both in one octave steps. Stimuli were presented in a pseudo-random, 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 nº 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 nº 02015.004197/03).

Data analysis

Isolation of recorded units was reassessed offline using a custom software developed by Dr. Nan-Hui Chen at the Max Planck Institute for Brain Research in Frankfurt, GE, 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 below. 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). Moreover, preliminary tests run in our lab using several latency estimation methods have confirmed that maximum likelihood estimation is indeed more robust. Briefly, the method assumes that the neuronal response is a stochastic process composed of three separate subprocesses: the first, going from stimulus onset \( (t = 0) \) to response latency \( (t = \theta) \), follows a Poisson \( (\lambda_1) \) distribution and corresponds to the period of spontaneous activity; the second, which has a Poisson \( (\lambda_2) \) distribution, goes from latency \( (t = \theta) \) to a cutoff value \( (t = k) \), and can be understood as the rising portion of neuronal activity; and the third, corresponding to the period of stationary response rate, goes from \( t = k \) to the end of the response and has an unknown distribution. Estimated response latency is the value of \( \theta \) that maximizes the discrete log-likelihood function calculated on the PSTH \( (f(t)) \), and given by:
where $\lambda_1$ and $\lambda_2$ are given by:

$$
\lambda_1 = \left( \sum_{t=0}^{\theta} f(t) \right) / (\theta + 1)
$$

$$
\lambda_2 = \left( \sum_{t=\theta+1}^{k} f(t) \right) / (k - \theta)
$$

(2 & 3) and $k$ is the cutoff value, which is estimated with a linear fitting procedure on the cumulative PSTH. Candidate values of $k$ ($k'$) are iteratively fixed and, for each iteration, the data sequence is segmented into two portions, one from 0 to $\theta_k$ and the other from $\theta_k$ to $k'$. Each segment is then fitted in the least squares sense with a linear function for every possible value of $\theta_k$. The chosen $\theta_k$ value is the one that maximizes the difference between the slopes of the two linear functions, and the estimated value of $k$ is the $k'$ that yields the largest slope difference. In the present study, latency was calculated on a window of 250 ms starting from stimulus onset, and had a minimum accepted value set at 20 ms.

**Time course of response rate.** To quantify the decrease in response rate as a function of stimulus presentation time, we fitted the spike-density functions from the initial response peak to the end of the stimulation period with an exponential decay function (Müller et al. 2001):

$$
R(t) = (R_{\text{max}} - R_{\text{min}}) e^{-t/\tau} + R_{\text{min}}
$$

(4) where $R_{\text{max}}$ is the peak response rate, $R_{\text{min}}$ is the asymptotic response rate and $\tau$ is the time constant, used to quantify the rate of decay. The degree of sustained response was calculated with an index given by $(R_{\text{min}} - R_{\text{spont}}) / (R_{\text{max}} - R_{\text{spont}})$, where $R_{\text{spont}}$ is the
spontaneous discharge rate (Müller et al. 2001). 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 (equations 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 1000 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:

\[
R(f) = A \times \exp \left\{ \frac{-(\log_2 f - \log_2 f_p)^2}{2(\sigma_f + \zeta(\log_2 f - \log_2 f_p))^2} \right\} - \exp \left( \frac{-1}{\zeta^2} \right)
\]

The above equation is a modified Gaussian function used by Priebe *et al.* (2006) to fit 1D
speed tuning curves, and which provided good fits for the steady-state SF and TF tuning
data in our previous study (Pinto and Baron 2009). In the equation, \( f \) is the independent
variable, i.e. the temporal frequency of the grating in Hz or its spatial frequency in
cycles/deg; \( A \) is the maximum response amplitude, \( f_p \) is the preferred frequency of the cell,
\( \sigma_f \) is the spread of the Gaussian and \( \zeta \) 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 lowpass 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 non-parametric distributions, the Wilcoxon rank-sum or Kruskal-Wallis tests were used as non-parametric equivalents of the \( t \)- and ANOVA tests, respectively. Statistical dependence between variables was measured using the non-parametric 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 ± standard error of the means (SEM).

All curves were fitted using the non-linear least-squares trust region algorithm implemented in “fit” function in Matlab (MathWorks, Natick, MA, USA). A maximum of 1000
iterations were allowed. Goodness of fit was evaluated using r-squared values and the fit F-statistics (Daniel and Wood 1980).

**Results**

**Response latency**

Fig. 1 summarizes our findings on response latency as estimated with the maximum likelihood method (see Materials and Methods). As exemplified in panel 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 (panel B). Kruskal-Wallis test confirmed that these frequency-specific latency differences were significant [Degrees of Freedom (DoF) = 5, \( P \ll 0.001 \)]. Moreover, a comparison solely between the latencies at the smallest and highest SFs tested also yielded a significant difference (58.4 ± 4.0 ms and 92.9 ± 13.9 ms for SF = 0.25 and 8 cycles/deg, 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 (Mausell and Gibson 1992; Mazer et al. 2002; Frazor et al. 2004). No significant differences were observed between response latencies for stimuli of different TFs at the neurons’ preferred SF (Kruskal-Wallis, DoF = 6, \( P = 0.19 \)). This is exemplified by the cell depicted in panel C and shown by the population results in panel D. Unfortunately, we are unaware of any studies in the mammalian visual cortex to which our results can be compared straightforwardly. A decrease in response latency as a function of speed has been reported in both V1 (Price et al. 2006) and MT (Lisberger and Movshon 1999) but the stimuli used in those studies
had a broadband SF content and consequently several embedded non-specified TF values, which makes unclear how latency is affected by specific TFs.

Fig. 1E shows the distribution of response latencies of wulst complex cells estimated at their preferred SF–TF combination. Latency values were non-normally distributed around a median of 48 ms, with a skew towards 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 Figs. 2A and B) to those with fairly sustained responses throughout the stimulation period (Figs. 2C 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 $192.9 \pm 51.6$ ms, and median was of 47.7 ms. In other words, distribution was heavily skewed towards 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 ± 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 2000 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).

Fig. 3 compares SF and TF tuning between the two epochs. Panels 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 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 to the response transient. A quantification
of these observations is presented in panels 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
panel 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 zero-median distribution: \( P = 0.09 \)). Panel
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 (Panel 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, panel F shows that TF bandwidth was not correlated
between the epochs \( \rho = 0.13, P = 0.38 \), and was significantly larger in during 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, preferred SF,
and TF and SF bandwidth decreased significantly in the later, sustained portion of the
response, as compared to the initial transient. To better understand these results, we
performed a more in-depth analysis of SF and TF tuning dynamics with finer temporal
detail, the results of which we present below.

Evaluation of the population tuning dynamics analysis
All analyses reported herein for both SF and TF tuning dynamics were performed by sliding a 10-ms window over the spike density functions with 1-ms steps and fitting mean response rates with a modified Gaussian function (see Materials and Methods for details). Only those fits with r-squared values above 0.7 were included in this analysis. As a result of this pre-selection, several data points were missing for any given time window. On average, of the 1000 SF tuning curves computed for each cell, 30% (295, range 5 – 714) did not fulfill this inclusion criterion. For TF, this proportion reached 40% (400, range 194 – 717). We did not attempt to interpolate the missing points. For each cell, the longest epochs of consecutive missing points for the computation SF tuning ranged from 4 to 225 ms with a median of 30 ms. For TF, range was 16 to 110 ms with a median value of 37 ms. With very few exceptions, these periods were found to be spread out during the sustained part of the response, minimizing the overall impact on the measures that we used to assess changes in tuning parameters (change sign index and $\Delta(w)$, see below). Another potential pitfall was that the number of cells contributing to each time window was not homogeneous throughout time (SF: mean of 63.2 ± 0.2 cells/window, range 43 – 82; TF: mean of 56.7 ± 0.2 cells/window, range 28 – 72). For SF, this number was found to be higher over the initial 200 ms after onset latency. The opposite was true for TF. 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, which 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 = 1000) and assessed how subsamples compared with the overall results reported below. 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 above 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**

Fig. 4 shows three representative examples of the temporal evolution of SF 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), while others exhibit a consistent decrease (Fig. 4A) or increase (Fig. 4C) with respect to this dimension. Second, tuning width narrows mainly due to a relative decrease of response at low frequencies, a phenomenon which appears to be more pronounced approximately within the first 50 ms. Third, no sizable changes in SF tuning profiles were observed after roughly 200 ms.

Fig. 5 shows population results for SF tuning dynamics. Plots on the left (panels A, C, E, G) show the temporal evolution of the mean population values of several tuning parameters. Right-hand side panels (B, D, F, 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, 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 1000-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 $\Delta_{(w)}$ number which 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 Materials and 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 1000 ms (median: 0.08, $P = 0.17$). Accordingly, neither $\Delta_{(100)}$ nor $\Delta_{(1000)}$ were statistically different from a 0-mean distribution (mean $\Delta_{(100)} = 0.12 \pm 0.15$ octaves, $P = 0.55$; mean $\Delta_{(1000)}= 0.39 \pm 0.18$ 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 greater than 0.5 (more than 75% of ‘+’ counts), we find an expressive sub-population of 30%. This sub-population has a $\Delta_{(100)}$ 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 1000 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, $P << 0.001$, median(100) = -0.85 and
median(1000) = -0.47]. The opposite behavior was seen in the distributions of $\Delta_{(100)}$ and
$\Delta_{(1000)}$: whilst both were different from 0-median distributions (Wilcoxon rank sum, $P = 0.03$
and $P << 0.01$, respectively), the negative shift in tuning bandwidth had greater magnitude
when assessed over the entire 1000-ms period [median($\Delta_{(100)}$) = 0.13 octaves,
median($\Delta_{(1000)}$) = -0.37 octaves; Wilcoxon rank sum, $P = 0.05$], which confirms that fully
fledged SF bandwidth reduction requires more than 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 $\Delta_{(100)}$ = -
0.09 ± 0.03, mean $\Delta_{(1000)}$ = -0.20 ± 0.05, both significantly smaller than zero – Student’s t
test, $P \leq 0.01$; but not significantly different from each other, Student’s t test, $P = 0.10$).
Moreover, change sign indices computed for both the 100- (median: -0.14) and the 1000-
ms (median: -0.39) periods differed significantly from zero (Wilcoxon rank sum, $P << 0.01$),
and were also different between themselves. Notably, LSFS and bandwidth were
significantly correlated both in terms of $\Delta$ and sign index, measured at both time periods,
strongly suggesting that reduction in bandwidth may be explained at least partly by relative
response suppression at low frequencies [BW vs. LSFS, Spearman correlation, $\Delta_{(100)}$: $\rho$
= 0.59 (Fig. 8A), $\Delta_{(1000)}$: $\rho = 0.49$, index(100): $\rho = 0.44$, index(1000): $\rho = 0.53$, $P <<$
0.01 for all]. In contrast to LSFS, no significant changes were detected in high-frequency
suppression in either analyzed period [median($\Delta_{(100)}$) = median($\Delta_{(1000)}$) = 0.00;
median(index(1000)) = median(index(100)) = 0.00; Wilcoxon rank sum $P > 0.5$ for all]. The
relatively slow development of low-frequency suppression, and its concurrent time course
with SF bandwidth narrowing, suggest that such processes are taking place at least partly
within the wulst. According to the model developed by Bredfeldt and Ringach (2002), the
effect of lagged low-frequency suppression on preferred SF would be to shift it towards
higher values. If this mechanism is at work in the wulst, one would should detect a
correlation between the magnitude of suppression at low SFs and of the shift in optimal
SF. A significant negative correlation was found between $\Delta_{(100)}$ (LSFS) and $\Delta_{(100)}$ (preferred
SF) (Fig. 8B, $\rho = -0.42$, $P < 0.001$). As we have shown above, 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 non-significant 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 $\Delta_{(100)}$ (mean: $1.57 \pm 0.48$ octaves) and sign change index(100) (mean:
$0.32 \pm 0.11$) 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 $\Delta_{(100-1000)} = -1.25 \pm 0.45$
octaves, Student’s t test, $P < 0.01$; median index(100-1000): -0.67, Wilcoxon test, $P <<$
0.001). When one looks at the whole 1000-ms period, the upward and downward shifts
cancel out, resulting in no significant net changes in preferred TF (mean index: $-0.08 \pm$
0.09; mean $\Delta_{(1000)}= -0.05 \pm 0.31$; 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, 
$\Delta_{(1000)}$: $\rho = 0.36$, $P = 0.05$; $\Delta_{(100)}$: $\rho = 0.41$ (Fig. 8C), $P = 0.01$; sign index (100-1000): $\rho = 0.30$, $P = 0.02$]. 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, $\Delta_{(100)}$ (mean: $-1.13 \pm 0.30$) and $\Delta_{(1000)}$ (mean: $-1.07 \pm 0.36$) 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 1000 ms (median: -0.69) (Wilcoxon test, $P << 0.01$), and both had 
distributions that differ statistically from a 0-median 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 non-significant 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; $\Delta_{(100)}$: $\rho = 
0.50$ and $P = 0.001$, $\Delta_{(1000)}$: $\rho = 0.82$ and $P << 0.001$ (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 ± 0.05) and \( \Delta_{(1000)} \) (mean = -0.24 ± 0.06), and sign index 100 (median
= -0.09) and 1000 (median = -0.71) are significantly different from each other \( (P << 0.05 \)
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, \( \Delta_{(100)} \): \( P = 0.14 \), \( \Delta_{(1000)} \): \( P << 0.01 \); Wilcoxon test, sign index(100): \( P = 0.52 \), sign index(1000): \( P << 0.001 \)]. 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, which 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 which 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.

Taken together, our results indicate that the spatiotemporal frequency tuning of complex cells in the owl visual wulst evolve over a relatively fast time scale, supporting the general notion that receptive fields should not be viewed as ‘static’ filters but as genuinely dynamic entities. Using a different methodological approach based on white noise and reverse correlation techniques, this notion has in fact been recognized for many years by several investigators working in the retino-thalamo-cortical pathway of mammals (for
review see DeAngelis et al. 1995; Ringach 2004). Our study may therefore be regarded as a piece of evidence which suggests that receptive field dynamics is an evolutionary conserved aspect of central visual pathways of vertebrates. Important considerations for further investigations should address the mechanisms underlying spatiotemporal tuning dynamics in the owl wulst and its functional implications for visual perception. As we discuss below, our findings, together with other available evidence, are compatible with the idea that such dynamics might be achieved through the concerted action of feedforward and intratelencephalic circuits.

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 stimulus SF, a finding which has been interpreted as evidence for the convergence of LGN parvo and magno inputs onto a single V1 neuron (Mazer et al. 2002; Frazor et al. 2004). According to this explanation, tuning to higher SFs is characteristic of LGN parvocellular neurons, which have lower conduction velocities than magnocellular neurons (Schiller and Malpeli 1978; Kaplan and Shapley 1982). 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 vs 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, which 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 cells’ preferred SF, one would expect to see decreasing latencies for increasing TFs, as parvocellular LGN neurons tend to respond better to lower TFs (Hicks et al. 1983; Derrington and Lennie 1984). 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. Mausell and Gibson 1992; Schmolesky et al. 1998; Mazer et al. 2002; Frazor et al. 2004). 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. Müller et al. 2001; Palanca and DeAngelis 2003; Hegdé and Van Essen 2003, 2004; Zhang et al. 2008). Most notably, the distribution of \( \tau \) 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 (Maunsell 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 been typically performed with stationary stimuli (Müller et al. 2001; Palanca and DeAngelis 2003; Hegdé and Van Essen 2003, 2004; Zhang et al. 2008). In our study, moving gratings were used, which may have favored higher sustained response rates. This in turn would imply that responses of wulst neurons could be even more transient than what the present results indicate, which would be in agreement with the findings by Pettigrew (1979) that the majority of owl GLd neurons are of the Y type.

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 intratelencephalic mechanisms. A finer-grained analysis of the temporal dynamics of SF and TF tuning further supports this notion, as discussed below.

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; Mazer et al. 2002; Frazor et al. 2004; Nishimoto et al. 2005; Malone and Ringach 2008). 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 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 octaves), 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 which 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 which 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 non-negligible 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 feedforward 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 et al. 1973), they do display a wide repertoire of head movements, including saccades, fixations, translations and rotations (Knudsen et al. 1995; Ohayon et al. 2006).
Acknowledgements

We would like to thank Pedro G. Vieira for assistance with the preliminary tests on response latency estimation methods, as well as Sergio Neuenschwander for providing the SPASS data acquisition software and Nan-hui Chen for allowing us to use his spike-sorting software. We are also grateful to Michaela Klinkmann for manufacturing the recording electrodes.

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Grants

This work was supported by the Research Support Foundation of the State of Minas Gerais (FAPEMIG) and the FINEP research grant “Rede Instituto Brasileiro de Neurociência (IBN-Net)” # 01.06.0842-00; L.P. received a graduate (MSc) scholarship from the Brazilian National Council for Scientific and Technological Development (CNPq).
References


Figure Legends

Figure 1. Frequency-specific response latency of owl visual wulst neurons. A) Initial 100 ms following stimulus onset of spike-density functions of a representative neuron responding to different SFs (0.25, 1, 2 and 4 cycles/degree) at the preferred TF (2 Hz), with respective latencies indicated in parenthesis and with the open circles. B) Mean population latencies for each SF tested (black circles), with error bars indicating ± SEM. C) Representative example of neuronal responses to several TFs (1, 2, 4 and 8 Hz) at the preferred SF (1 cycle/degree), using the same conventions as panel A. D) Mean population latencies for each TF tested, with conventions as in panel B. E) Histogram showing the population distribution of response latency values at the optimal SF-TF combination, where the white arrow head indicates population median (n = 80).

Figure 2. Time course of neuronal responses to gratings of optimal SF and TF. A – D) Examples of spike density functions with overlying best-fitting curves of exponential decay (gray lines) from which time constant ($\tau$) values were extracted. Gray bars above the plots indicate the duration of stimulation. E) Population distribution of $\tau$. White arrow head indicates population median. F) Distribution of sustained response ratio. White arrow heads indicate population arithmetic mean. Distributions shown in E and F were derived from the responses of 78 neurons.

Figure 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 two periods, conventions as in panel 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 values 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: cycles/deg; rho: Spearman’s rank correlation coefficient.

Figure 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, B and C). The black dots correspond to mean response and the bars
indicate S.E.M. The gray arrows indicate the location of preferred frequency as assessed
on the first temporal window.

Figure 5. Fine- and large-scale temporal evolution of SF tuning parameters. Plots on the
left (A, C, E, G) show the mean population values for each time window (black line), with
gray lines indicating ± SEM (n = 90). Histograms on the right (B, D, F, H) show the
population distribution of the change sign index (see Materials and Methods) (n = 82),
computed for the initial 100 ms (white bars) and the whole 1000-ms analysis period (black
bars). Arrow heads of corresponding colors indicate population median. Note that the
differences in sample size in different panels of this figure is a result of different inclusion
criteria for each analysis (see Evaluation of the population tuning dynamics analysis in the
Results section). For example, the change sign index compares the sign of change of
each window in relation to the first ones, such that missing points in the beginning of the
response do not allow for the calculation of the index. BW: bandwidth, LSFS: low spatial
frequency suppression, HSFS: high spatial frequency suppression.
**Figure 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.

**Figure 7.** Fine- and large-scale temporal evolution of TF tuning parameters. For panels on the left, n = 90; for histograms on the left, n = 44. As in Fig. 5, this difference in sample size reflects different inclusion criteria (see Evaluation of the population tuning dynamics analysis in the Results section). Conventions are the same as in Figure 5. BW: bandwidth, LTFS: low temporal frequency suppression, HTFS: high temporal frequency suppression.

**Figure 8.** Examples of significant correlations in the analysis of SF and TF tuning dynamics. A) $\Delta_{(100)}$ SF BW vs. $\Delta_{(100)}$ LSFS (n = 79). B) $\Delta_{(100)}$ LSFS vs. $\Delta_{(100)}$ preferred SF (n = 77). C) $\Delta_{(100)}$ preferred TF vs. $\Delta_{(100)}$ HTFS (n = 37). D) $\Delta_{(1000)}$ TF BW vs. $\Delta_{(1000)}$ LTFS (n = 36). On each scatter plot, dashed gray lines indicate slopes of linear fits. BW: bandwidth, HTFS: high TF suppression, LSFS: low SF suppression, LTFS: low TF suppression, pref.: preferred; $\rho$: Spearman’s rank correlation coefficient.
A. Preferred SF (cycles/deg)

B. Preferred TF (Hz)

C. Preferred SF (cycles/deg)

D. SF BW (octaves)

E. Preferred TF (Hz)

F. TF BW (octaves)
A

Preferred SF (c/deg)

Pref. SF (c/deg) − change sign index

Proportion of cells

B

Preferred SF − change sign index

Proportion of cells

C

BW (octaves)

BW − change sign index

Proportion of cells

D

Pref. SF − change sign index

Proportion of cells

E

LSFS

LSFS − change sign index

Proportion of cells

F

LSFS − change sign index

Proportion of cells

G

HSFS

HSFS − change sign index

Proportion of cells

H

HSFS − change sign index

Proportion of cells
A. $\rho = 0.59$, $P << 0.001$

B. $\rho = -0.42$, $P < 0.001$

C. $\rho = 0.41$, $P = 0.01$

D. $\rho = 0.82$, $P < 0.001$