Contrast response functions in the visual wulst of the alert burrowing owl: A single-unit study.

Running title: Cellular contrast responses in the owl wulst.

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Abstract
The neuronal representation of luminance contrast has not been thoroughly studied in birds. Here, we present a detailed quantitative analysis of the contrast response of 120 individual neurons recorded from the visual wulst of awake burrowing owls, *Athene cunicularia*. Stimuli were sinewave gratings presented within the cell classical receptive field and optimized in terms of eye preference, direction of drift and spatiotemporal frequency. As contrast intensity was increased from zero to near 100%, most cells exhibited a monotonic response profile with a compressive, at times saturating, nonlinearity at higher contrasts. However, contrast response functions were found to have a highly variable shape across cells. With the view to capture a systematic trend in the data, we assessed the performance of four plausible models (linear, power, logarithmic and hyperbolic ratio) using classical goodness-of-fit measures and more rigorous statistical tools for multi-model inferences based on the Akaike information criterion. From this analysis, we conclude that a high degree of model uncertainty is present in our data, meaning that no single descriptor is able on its own to capture the heterogeneous nature of single-unit contrast responses in the wulst. We further show that the generalizability of the hyperbolic ratio model established, for example, in the primary visual cortex of cats and monkeys is not tenable in the owl wulst mainly because most neurons in this area have a much wider dynamic range that starts at low contrast. The challenge for future research will be to understand the functional implications of these findings.
New & Noteworthy

In this paper, we provide the first detailed quantitative description of how neurons within a post-retinal area of the visual system of a bird respond to achromatic contrast. Using the owl visual wulst as experimental model, we show that the nonlinearities of neuronal contrast responses are not so pronounced, as they are, in V1 of mammals. Arguably, this may be taken as an indicator of a neural correlate of poor contrast sensitivity.

Introduction

The visual wulst is the part of the avian telencephalon that receives its major input from the retinothalamofugal pathway. In the owl, this area presumably plays an important role in mediating a number of visual skills such as stereopsis (Nieder and Wagner 2000, 2001a), spatial-frequency dependent detection of low-contrast oriented periodic patterns (Harmening et al. 2009; Orlowski et al. 2012), surface extraction from motion (van der Willigen et al. 2002, 2003), perception of illusory contours (Nieder and Wagner 2001b), and exogeneously-driven spatial attention (Harmening et al. 2011; Ohayon et al. 2008).

Essentially, two lines of indirect evidence support this hypothesis: first, when compared to most other birds, the visual wulst of owls is atypically large, a trait thought to be related to the large amount of binocular signals that get integrated in this structure (Iwaniuk and Hurd 2005; Iwaniuk and Wylie 2006, Iwaniuk et al. 2008; Karten et al. 1973); second, neurons in this area display a rich repertoire of response properties that seem ideally suited to extract basic attributes of a visual scene. They have small retinotopically-organized receptive fields, tuned to spatial as well as temporal frequencies and selective for orientation, direction of motion, and binocular disparity (Baron et al. 2007; Nieder and Wagner 2000, 2001a,b; Pettigrew 1979; Pettigrew and Konishi 1976a; Pinto and Baron 2009, 2010; Wagner and Frost 1993, 1994). In this respect, the owl wulst is strikingly similar to the early visual cortex of mammals, which is interesting, from a comparative
perspective, since this similarity is thought to be essentially due to a process of convergent evolution (Medina and Reiner 2000; Pettigrew 1979; Shimizu and Bowers 1999). Thus, as well as contributing to a better understanding of a neural substrate putatively important for the visual performance of owls, the functional characterization of wulst neurons in this bird is likely to provide important insights concerning the evolutionary principles governing early vision.

In line with this long-term research perspective, the present study addresses an important and yet unexplored issue of how individual neurons in the owl wulst encode luminance contrast. A neuronal representation of this physical dimension is undoubtedly the most basic requirement for extracting information about objects and surfaces in the world. It is also intrinsically linked to, and interferes with, the elaboration of receptive field properties important for encoding other spatial and motion cues. In birds, including the barn owl, contrast processing has been mainly investigated by measuring, either behaviorally or by pattern electroretinogram, contrast response thresholds as a function of spatial frequency (barn owl: Harmening et al. 2009; for other species: see Ghim and Hodos 2006 and references therein). A common and intriguing result revealed by these studies is that, despite their highly developed visual capabilities, birds have much lower contrast sensitivities than mammals. As yet, there is no obvious and satisfactory explanation for this important functional difference between birds and mammals (see Ghim and Hodos 2006). Presumably, single-unit investigations of contrast response conducted in key post-retinal areas of the visual system should provide valuable information about this issue. Unfortunately, this type of investigation is critically missing in birds. As far as we know, only two studies in the pigeon, one in the optic tectum (Jassik-Gerschenfeld and Hardy 1979), and the other one in the nucleus of the basal optic root (Wolf-Oberhollenzer and Kirschfeld 1994), have reported data on the relationship between response amplitude of individual neurons and achromatic contrast. However, because this characterization
was not the main objective of the aforementioned studies, only a few cells were analyzed such that it is difficult to make solid inferences about these data.

The situation is strikingly different with regards to the mammalian retinothalamocortical pathway for which a considerable amount of information about the contrast response properties of neurons at all stages of this pathway is available. Following the pioneering work of Kuffler (1953), the antagonistic center-surround organization of retinal ganglion cell receptive fields is thought to provide an explicit representation of local contrast, which then gets relayed by lateral geniculate nucleus (LGN) cells (reviewed in Shapley and Lam 1993). At this early processing level, neuronal contrast response functions (CRFs) typically show a monotonic increase over a relatively wide dynamic range, thereby closely matching the cumulative distribution of contrasts encountered in natural scenes (Tadmor and Tolhurst 2000). However, in visual cortex, a different representation of contrast has been shown to emerge: CRFs get steeper with more prominent response expansion and saturation at low and high contrast, respectively. This transformation is already visible at the level of the striate cortex (Albrecht and Hamilton 1982; Contreras and Palmer 2003; Dean 1981; Sclar et al. 1990), and becomes progressively more pronounced further downstream towards extrastriate cortical areas (Gegenfurtner et al. 1997; Levitt et al. 1994; Palmer et al. 2007; Sclar et al. 1990). Over the past several decades, there has been a great deal of interest in discovering the factors and biophysical mechanisms accounting for the nonlinearities that reduce the dynamic range of cortical neurons’ CRFs (for review see, for example, Albrecht et al. 2003; Carandini et al. 1999). This research goal is important given that several lines of evidence suggesting that such nonlinearities have an overall impact on the efficiency of information processing. For example, it has been shown that the expansive response profile at low contrast, also referred as “half-squaring”, may influence the tuning precision of other stimulus dimension such as orientation, direction of motion, and spatial frequency.
(Albrecht and Geisler 1991, 1994; Heeger 1992a). On the other hand, saturation at high contrast, which is thought to depend on a relatively fast-acting adaptation mechanism often referred to as “contrast gain control”, allows the maintenance of stimulus selectivity over a wide range of contrast (Albrecht and Hamilton 1982; Bonds 1991; Ferster and Miller 2000; Frazor et al. 2004; Geisler and Albrecht 1992; Heeger 1992b).

Taken together, the above considerations motivated us to undertake a detailed characterization of CRFs based on the steady-state responses of visual wulst neurons in the burrowing owl. To this end, we used sine-wave gratings, presented within the cell classical receptive field and optimized in terms of eye preference, direction of drift, and spatio-temporal frequency. The contrast-dependent responses that we find are highly variable across cells but usually monotonic and nonlinear. The extent to which such responses can be adequately described by a simple general model is assessed and contrasted with results typically encountered in the mammalian primary visual cortex (V1). Parts of these results have been reported in abstract form (Vieira et al. 2008).

Material and Methods

Animal care and recording preparation

Single-unit recordings were obtained from the visual wulst of ten adult burrowing owls (Athene cunicularia). The number of animals used in this study is large because some of the data for this study was collected sporadically during experiments performed for other, yet unpublished studies.

All experimental procedures were carried out following a method that allows us to study visual response properties of neurons in awake, non-behaving burrowing owls (Athene cunicularia). This method has been previously described in detail (Baron et al. 2007), and takes advantage of the fact that eye movements are extremely limited in owls (Knudsen 1982; Pettigrew and Konishi 1976b; Steinbach et al. 1974), reaching a
maximum estimated amplitude of 0.5° in the burrowing owl (Cooper and Pettigrew 1979). Consequently, once the head of the animal is fixed, stable receptive field properties can be obtained, without the necessity to control eye movements. Head fixation, a condition that is well accepted by burrowing owls after a positively-reinforced habituation period of about three weeks, is achieved by a device which secures a lightweight recording chamber (approximately 0.7% of animal total weight) and supports our multi-electrode holder.

The chamber was surgically implanted under general anesthesia, induced and maintained with Zoletil 50 (1:1 mixture of tiletamine and zolazepam, Virbac, Carros, France). In owls, the visual wulst forms a prominent elevation covering a large part of the dorsal telencephalon (see for example Fig 1a in Karten et al. 1973). The chamber was centered over a region known to represent the central portion of the contralateral visual field (Pettigrew 1979). Anatomically, this region is located about halfway along the anterior-posterior axis of the wulst, close to the shallow groove delimiting its lateral extent, namely, the vallecula. Implantation was performed under stereotaxic guidance, thereby maximizing the precision and reproducibility of target localization. A craniotomy (~ 5 mm in diameter) was made at the center of the recording chamber to provide brain access. The surgery lasted about one hour after which a broad-spectrum antibiotic (50 mg/kg of Terramicine®, Pfizer Laboratories, São Paulo, SP, Brazil) and an analgesic/anti-inflammatory (2 mg/kg of Ketofen® 1%, Merial, São Paulo, SP, Brazil) were administered intra-muscularly. The animals were allowed to recover for a minimum of 4 days before the beginning of the recordings.

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 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 3076223).

**Extracellular recording**

Spiking activity was recorded from individual neurons using quartz-isolated platinum/tungsten electrodes (Thomas Recording, Giessen, Germany) with an impedance of 0.3–0.9 MΩ at 1 kHz. A custom-built device (see Baron et al. 2007 for more details) allowed us to lower 2-3 electrodes independently into the brain using precision hydraulic microdrives (MO95, Narishige Scientific Instrument Lab, Tokyo, Japan). Readings from the latter were used to provide estimates of recording depth. The insertion point of the electrode into the brain, which was indicated by a characteristic noise in the recorded signal, provided the reference point for the coordinates of the penetration. To confirm the reliability of these coordinates, we checked whether the electrode tip exited the surface of the brain at a depth of zero when withdrawing the electrode at the end of a penetration. The search for visually responsive neurons was carried out through the entire thickness of the wulst (~3 mm in the burrowing owl). Cells isolated along the same track were spaced at 200 μm intervals or greater. In some penetrations, the first 1000 μm were ignored so that sampling biases along the dorsal-ventral axis of the wulst could be minimized.

Extracellular potentials were amplified (×1000) and bandpass filtered between 300 Hz and 7 kHz (HST/16025 headset, 32-channel Preamplifier box, Plexon, Dallas, Texas, USA), before being digitized at 32 kHz by a high-speed, 16-bit resolution A/D card with onboard trigger and timer capabilities (PCI-6259, National Instruments, Austin, Texas, USA). The A/D board was also programmed to provide a second amplification stage of ×10. Signal display, acquisition and storage were controlled through custom software written in LabVIEW (National Instruments) by Dr. Sergio Neuenschwander. Spike waveforms were detected and recorded only if they crossed a threshold of 3 to 4 standard
deviations of the voltage trace. Unit isolation and discrimination was performed online by selecting clusters formed by plotting the maximum versus minimum amplitude of action potentials. It was further refined offline with software developed by Dr. Nan-Hui Chen at the Max Planck Institute. The semi-automatic clustering algorithm implemented in this software uses a dynamic template matching procedure (for more details, see Baron et al. 2007). Quality of spike sorting was verified using several indicators, including: 1) good clustering of principal component analysis scores; 2) non violation of an absolute refractory period of 2 ms as verified from interspike interval histograms; and 3) stability of spike amplitude and width across time.

Stimulus presentation

Stimuli used for quantitative tests were sine-wave gratings displayed on a 19-inch CRT monitor (Samsung SyncMaster 955DF) at a resolution of 1024 × 768 pixels and a non-interlaced frame rate of 100 Hz. The monitor was placed 66 cm from the owl’s eyes, such that all grating stimuli had spatial frequencies below the Nyquist limit of the monitor at this resolution. An 8-bit RGB mode was used and gamma correction applied to produce a linear behavior of the displayed luminance. All gratings had a mean luminance (56.1 cd/m²) that equaled that of the background and were presented within a circular patch of 2–6 degrees diameter. Photometric measurements were made with a ColorCal colorimeter (Cambridge Research Systems, UK), and were routinely performed to verify the stability of the monitor calibration. Stimuli were prepared as sequences of bitmap images, which were then presented with timing accuracy as movies by the ActiveStim software (www.activestim.com).

Receptive field characterization and experimental protocol
We initially assessed the responses of each isolated unit by listening to its discharges on a loudspeaker and by monitoring its stability over time on our data-recording computer display. The location and extent of receptive fields were plotted as minimum response fields (Barlow et al. 1967), defined here as the area in visual space from which hand-held and mouse-controlled stimuli, such as spots and bars of varying orientation, evoked neuronal discharges at a rate exceeding that of the unit spontaneous activity. This mapping procedure was carried out separately for the ipsilateral and contralateral eyes, allowing the determination of the RF ocular dominance. The majority of cells we encountered were binocular and all of them could be driven by monocular stimuli presented to either eye alone. Following this preliminary assessment, RF measurements were then made through the eye that more effectively activated the cell (the non-dominant or non-responsive eye was covered) and with the center of the RF roughly at the center of the monitor screen.

Orientation, direction of motion, spatial frequency and temporal frequency preferences were evaluated with full-contrast sinusoidal gratings varying along these dimensions while listening to the firing rate of the cell and/or by off-line quantitative analysis. Subjective and quantitative estimation procedures were generally in good agreement. We systematically began with a protocol consisting of eight stimulus orientations, each presented in two motion directions (16 stimuli in total, 22.5 degrees steps). For the large majority of cells (109/120; ~90% of our sample), best direction estimates were derived by fitting responses with the sum of two von Mises functions (Baron et al. 2007). All subsequent tests employed gratings that drifted in the best direction. Optimal spatiotemporal frequency tuning parameters were then estimated by measuring responses to six spatial frequencies (0.25, 0.5, 1, 2, 4, 8 cycles/degree) and six temporal frequencies (0.25, 0.5, 1, 2, 4, 8 cycles/s). Roughly a quarter of our cell population had its spatiotemporal tuning profile characterized quantitatively and form part
of the dataset analyzed in Pinto and Baron (2009). For 70% of our cell sample, we also re-evaluated RF extend by expanding the size of an optimal drifting sine-wave grating until the response of the neuron stopped increasing. The stimulus-size value at peak spatial summation derived from this protocol was used thereafter.

We then proceeded to a quantitative assessment of the contrast response function (CRF) while all other parameters were held constant, in agreement with the cell preferences. Contrast was defined by the Michelson formula, \(100 \% \times \frac{L_{\text{max}} - L_{\text{min}}}{L_{\text{max}} + L_{\text{min}}}\), where \(L_{\text{max}}\) and \(L_{\text{min}}\) are the maximum and minimum luminance levels of the sinusoidal grating. The majority of neurons were tested with thirteen values of contrast (0, 2.6, 3.7, 5.0, 7.0, 9.0, 13.7, 19.0, 26.4, 36.7, 50.9, 70.0 and 98.0%). For a subset of neurons (34/120 cells; 28% of the sample) eleven steps of contrast were used (0, 1.6, 2.5, 4.0, 6.2, 9.9, 15.8, 25.0, 39.6, 62.6, 98%). Each trial started with a 1 s presentation of a uniform field of the same mean luminance as the grating test stimuli. The latter were then shown for 4 s, so that at least one full cycle of the grating was completed even at the lowest temporal frequency. An interval of 3 s between stimuli was chosen to minimize possible effects of stimulation history. Each stimulus condition was presented 10 times in a pseudo-random blockwise order.

Data analysis

Our study builds upon previous research showing a close functional analogy between V1 and the owl visual wulst. According to Pettigrew (1979), this analogy also extends to two prominent cell types extensively studied in the striate cortex, namely: simple cells, characterized by their approximately linear spatial selectivity to the contrast polarity of a stimulus; and a much more diverse population of so-called complex cells, which do not exhibit this response property. The above functional classification has provided and continues to provide an important, albeit still debated, framework to understand neuronal
mechanisms in V1. Therefore, to enable a more insightful visual wulst/V1 comparison, we decided to classify neurons as simple and complex. To do so, we relied on a linearity index of spatial summation commonly used in V1 studies (De Valois et al. 1982; Skottun et al. 1991). Accordingly, the index was computed by examining how a cell responded to a moving sinusoidal grating presented at the highest contrast and optimized in terms of spatial frequency, temporal frequency and direction of motion. More specifically, the responses of each isolated unit were converted into post-stimulus time histograms (PSTHs) with a 20 ms bin width. After removal of spontaneous activity, each histogram was then Fourier transformed to estimate responses at DC ($F_0$) and at the fundamental stimulus frequency ($F_1$) across the entire stimulus presentation period. Cells with a modulation index ($F_1/F_0$) greater than 1 for the most optimal stimulus condition were classified as simple and their response rate was calculated as the amplitude of $F_1$. All other cells were classified as complex and had their responses calculated as mean firing rate. Spontaneous activity was calculated from the mean firing rate during two ‘blank-screen’ periods: the 1000 ms before stimulus onset (for all trials and conditions) and the 4000 ms of zero-contrast stimulation.

Directional selectivity was assessed by means of the standard directional index, $DI = 1 - (R_{anti} - R_{spont})/(R_{pref} - R_{spont})$, where $R_{pref}$ and $R_{anti}$ respectively represent the responses to motion in the preferred and anti-preferred directions relative to the spontaneous activity $R_{spont}$. Based on this index, cells were classified as directional ($DI \geq 0.5$) or bidirectional ($DI < 0.5$).

Two exclusion criteria were adopted to guarantee reliable descriptions of the effect of contrast on wulst neuronal responses. We used the Kruskal-Wallis test to discard cells whose responses were not significantly modulated by the contrast intensity of the gratings. We also excluded cells for which robust evoked responses were not verified for at least two contrast conditions. This was assessed by comparing, for each contrast condition, the
firing rate in a 1000 ms window immediately before and after stimulus onset using the one-tailed Wilcoxon matched-pairs signed-rank test \( (p < 0.05) \).

Following the lead of Ledgeway et al. (2005), we quantified the degree to which neuronal responses increase monotonically as a function of contrast using a monotonicity index (MI) defined as:

\[
MI = 1.0 - \left( \frac{R_{\text{max}} - R_{\text{Cmax}}}{R_{\text{max}} - R_{\text{spont}}} \right)
\]

where \( R_{\text{max}} \) is the maximum response of the neuron, \( R_{\text{Cmax}} \) is the firing rate at the maximal contrast tested (typically 98%) and \( R_{\text{spont}} \) is the spontaneous activity of the cell. This index is inversely proportional to the degree of non-monotonic behavior (supersaturation) displayed by a cell in response to contrast, varying from unity, for cells with perfectly monotonic responses, to zero for cells that return to baseline level at the maximal contrast.

We also made use of another scalar index tailored to capture the level of response saturation at high contrast. Following Ledgeway et al. (2005), this saturation index is defined as:

\[
SI = \left( \frac{R_{\text{Cmax}} - R_{\text{C50}}}{R_{\text{max}}} \right)
\]

where \( R_{\text{C50}} \) represents the response to a grating of 50% contrast. \( SI \) takes positive values for a monotonically rising, non-saturating response and negative values for a non-monotonic response. For cells showing an asymptotic saturation, \( SI \) is zero.

**Model fitting**

An important objective of our study was to seek out a simple general descriptive model of neuronal contrast responses in the visual wulst of the burrowing owl. Inspired by previous similar studies in the mammalian primary visual cortex (Albrecht and Hamilton 1982;
Contreras and Palmer 2003) and encouraged by the largely monotonic response behavior of our cell sample, we decided to consider four different models defined as:

**Linear:** \[ R(C) = a + b\cdot C; \]

**Logarithmic:** \[ R(C) = a + b\cdot \log_{10}(C); \]

**Power:** \[ R(C) = a\cdot C^b; \]

**Hyperbolic ratio** \[ R(C) = R_{\text{max}}\cdot C^n/(C_{50}^{-n} + C^n). \]

where \( R(C) \) refers to response as a function of luminance contrast. More detailed information about these models can be found in the Result section. Note that the hyperbolic ratio model is also known as the Naka-Rushton function.

Models were fitted to the data from each neuron by means of a nonlinear least-square minimization procedure using the trust region algorithm, implemented in the Matlab Curve Fitting Toolbox (MathWorks, Natick, MA, USA). Curve fitting was carried out on median values, computed over all trials associated with each condition. This choice was motivated by the fact that the majority of cells showed significant positive correlation between spike count variance and mean contrast response (data not shown), thereby violating an important condition for regression analysis, namely the homogeneity of variance (heteroscedasticity). In addition, normal distribution of trial responses across all conditions was satisfied for only 33% of our cell sample. For the rest of the dataset, departure from normality was typically due to one or two outliers associated with a maximum of three conditions per cell (except for one instance of five conditions). Although the removal of these outliers caused very mild effects on the overall shape of trial-based fits, their inclusion would contravene the assumption of independent, Gaussian-distributed residuals and would therefore weaken, at least in principle, the robustness of our non-linear regression analysis. Given the above, and under the reasonable assumption that central tendency in our dataset is overall better captured by the medians, our approach can be viewed as more conservative. Moreover, for most cells in our sample, this
approach yielded residuals with zero-mean, normally distributed residuals, which is a prerequisite for the model selection analysis we employed subsequently (see below).

Fitting started with a specific set of initial parameter values for each tested model. These values were estimated on the basis of pilot analysis and data reported in the literature, and were maintained unchanged for all cells. After an initial run of successive interactions (600 maximum) of the fitting algorithm, fits were checked to ensure that they had converged and their adjusted parameter values lay within acceptable bounds. In the rare cases when either of these conditions was not satisfied, we re-fitted the data with other starting parameter values until satisfactory convergence solutions representing global minima were obtained. To gain an accessible assessment of the quality of the fits provided by a model, we computed the percentage of the variance across conditions explained by this model:

\[
R^2 = 100 \left(1 - \frac{SS_{fit}}{SS_{total}}\right)
\]

where \(SS_{fit}\) is the sum of squares extracted from the fit and \(SS_{total}\) is the sum of squares obtained from a flat line formed by the mean of the fitted residuals. The \(F\)-test was also used to evaluate the statistical reliability of \(R^2\) values obtained for each fitted curves. This statistics served as rejection criterion only when the null hypothesis could not be rejected for the four models under investigation.

Model selection

A shortcoming of relying solely on goodness-of-fit measures as a means to compare multi-model performance is that such measures do not establish a trade-off between fitting accuracy and model complexity (i.e., number of free parameters). This trade-off is especially important when the models that are being compared have different numbers of parameters, as it is the case in our study (\(n=2\) for the linear, power and logarithmic
models; n=3 for the hyperbolic model). While adding parameters to a model tends to improve its data-fitting abilities, it may also diminish its predictive power (generalizability). This is because, instead of approximating the true underlying process, an overlying complex model exaggerates the representation of sampling errors (noise) that are specific to one dataset and not necessarily reproducible across datasets, a classical statistical problem known as overfitting.

To circumvent this potential pitfall, we assessed the relative performance of each fitted model by using a model selection approach based on the Akaike Information Criterion (AIC, Akaike 1974). Detailed information about the theoretical concepts and mathematical formalisms underlying this information criterion are provided in Burnham and Anderson (2002). In essence, AIC implements a form of complexity-penalization to balance the trade-off between model complexity and fitting accuracy, thereby incorporating the statistical principle of parsimony according to which the best model is the one with the highest information content but least complexity. Given the number of data points being modeled N, and the number of estimated parameters K included in a model, AIC is defined as:

$$AIC = N \ln \left( \frac{SS_{fit}}{N} \right) + 2K$$

where $SS_{fit}$ is the root-mean-square error of the model fit. The first term rewards descriptive accuracy, while the second term penalizes the lack of model parsimony. Although this equation is very simple, it is important to emphasize that its derivation is founded on solid information-theoretic concepts according to which the smaller the AIC value the better the model has performed. This is because the model with the lowest AIC value is asymptotically equivalent to choosing that with lowest expected information loss as estimated by the Kullback-Leibler discrepancy. In the present study, we used a derivate
of AIC for small-size sample which is recommended whenever $N/K < 40$ (see Burnham and Anderson 2002). This derivate takes the form:

$$AIC_c = AIC + \frac{2K(K+1)}{N-K-1}$$

$AIC$ or $AIC_c$ values, on their own, have no meaning: they vary on a relative scale and are much affected by sample size. By taking the differences to the minimal value $\min(AIC_c)$ within the model set $M = \{M_i, i = 1, 2, ..., m\}$ under consideration:

$$\Delta AIC^i_c = AIC_c^i - \min(AIC_c)$$

we therefore ranked the models according to their Akaike weights ($w_i$), which is a normalized measure of relative model likelihoods, and is defined as:

$$w_i = \frac{\exp\left(-\frac{\Delta AIC^i_c}{2}\right)}{\sum_{m=1}^{M} \exp\left(-\frac{\Delta AIC^m_c}{2}\right)}$$

In other words, $w_i$ can be interpreted as the relatively probability of each model be the best one among the whole set of candidate models (the sum of $w_i$ of all models are equal to 1).

The above procedure was carried out on a cell-by-cell basis.

**General statistical analysis**

Several standard statistical tests were also computed. We used the Lilliefors modification of the Kolmogorov-Smirnov test to check normality of datasets. If normality was verified we applied a t-test to compare the means of two populations or an ANOVA test if comparisons were made between more than two populations. Otherwise, the Wilcoxon rank-sum or Kruskal–Wallis tests were used, as nonparametric equivalents of the t- and ANOVA tests, respectively. Significance of differences in categorical properties was assessed with either
the Fisher’s exact test (for sample size < 5) or the chi-square test (for sample size > 5).

Spearman’s rank correlation test was used to evaluate the relationship between groups.

The significance level used for all the tests was $p < 0.05$. 
Results

The results presented in this study are based on quantitative data obtained from 120 well-isolated neurons recorded from a total of 97 sites and 63 vertical penetrations in the visual wulst of ten burrowing owls. The number of cells for each animal is 21, 11, 17, 5, 5, 9, 3, 22, 14, and 8. The responses of 156 neurons were initially screened, but 36 of these neurons were eliminated after application of our exclusion criteria (see Materials and Methods). Reliable estimates of recording depths were obtained for 78% of the remaining neurons (94/120). The distribution of these estimates ranged from 60 to 2850μm but was not uniform, yielding a median value of 870μm (25th and 75th percentiles = 350 - 1714μm). Recording site locations were not confirmed histologically and cannot, therefore, be accurately assigned to specific regions of the wulst. Nevertheless, what we can safely infer from the above result is that more neurons (around 70%) were sampled from the superficial layer, namely the hyperpallium apicale (HA), than from the three other layers altogether, namely, the nucleus interstitialis hyperpallii apicale (IHA), the hyperpallium intercalatum (HIS) and the hyperpallium densocellulare (HD).

Neuronal response properties were studied quantitatively using patches of sine-wave drifting gratings carefully centered on the cell’s receptive field. This spatial co-registration was stable throughout the recording period, as revealed by systematic verifications of receptive field position before and after each quantitative protocol. Minimum response field size estimates ranged from approximately 1° to 5°, confirming that the area of the wulst devoted to the central visual field had been effectively targeted by our electrode penetrations. In line with this finding, the median peak value of area summation curves obtained for 70% of the 120 cells filtered out for further contrast response analysis was 3.0° (25th - 75th percentiles: 2.0 - 3.6). Given the foregoing description, the small and sporadic eye movements seen in the burrowing owl (Cooper and Pettigrew 1979), are unlikely to have a significant impact on the physiological measurements we report in the
Cells were classified according to their level of response modulation (simple or complex) and directional selectivity (directional, bidirectional and omnidirectional), thereby allowing the investigation of possible differences in contrast response profiles with respect to these cell categories. Seventeen per cent of the neurons (20/120) were classified as simple on the basis of the $F_1/F_0$ modulation index (mean $F_1/F_0$: 1.66, SD 0.53), while the large majority (100/120, 83%) was classified as complex (mean $F_1/F_0$: 0.51, SD 0.22). Bimodality of $F_1/F_0$ value distribution was not supported by the Hartigan’s dip test ($p > 0.05$, Hartigan and Hartigan 1985). With respect to directional selectivity, the proportion of directional, bidirectional and omnidirectional cells in our sample was 59%, 36% and 2%, respectively. Only 4 cells out 120 were not significantly modulated by the grating direction of motion and were therefore left unclassified. Overall, these classification results are similar to those encountered in our two previous studies (Baron et al. 2007; Pinto and Baron 2009).

To assess the CRF of each cell, we typically used thirteen, at times eleven, contrast intensity values that increased in an exponential rather than linear fashion, so that the majority of values fell within the lower half of the contrast range (see Material and Methods). As it will become apparent further below, this stimulation protocol allowed us to define more accurately the part of the contrast response functions that changed most dynamically while covering the whole range of contrast intensities.

Figure 1 displays typical responses profiles of simple (Fig. 1A) and complex (Fig. 1B) cells as a function of contrast. Responses are presented in the form of peri-stimulus time histograms (PSTHs), binned at 20 ms resolution and averaged across 10 repetitions of the same contrast. Visual inspection of these PSTHs reveals several key features of neuronal response dependency on contrast in the wulst. To start with, clear evoked sustained responses can be observed even at relatively low contrast levels. The complex
The cells in figure 1 are a good example of this feature. For these cells, a grating contrast of 2.5% (Fig. 1B) was actually sufficient to elicit a significant increase in firing rate (one-tailed Wilcoxon matched-pairs signed-rank test, $p < 0.003$). In the case of the simple cells, a higher contrast was actually necessary to evoke a response above baseline (9.9%) according to our statistical analysis, $p = 0.001$), notwithstanding the fact that this difference between simple and complex cells was not a general trend in our data set. A more robust difference between these two cell classes, exemplified in figure 1, is that simple cells tended to increase their firing rate throughout the whole contrast range whereas complex cells tended to show response increments over a more limited contrast range, usually showing little or no changes in firing at higher contrast values. This characteristic is readily noticeable when looking at the steady-state response component of complex cells, which largely contributes to the results presented in this study as our quantitative analysis is based on spike frequency averaged over the whole stimulation period. However, it is important to mention that contrast-specific changes in the temporal evolution of neuronal activity, like the appearance of onset transients in the response at higher contrast of the complex cell in figure 1B, may represent important coding strategies and would therefore be interesting to be evaluated in the future.

As a preliminary quantitative assessment of the contrast response behavior of our cell sample, we calculated two scalar indices (see Material and Method): one designed to capture the degree of response monotonicity ($MI$), and other one tailored to estimate the level of response saturation ($SI$). As shown in figure 2A, the population histogram of $MI$ has a pronounced negative skewness with a median value of one, indicating that the large majority of cells (72% - 86/120) respond monotonically to increasing contrast intensities. The nonmonotonic behavior observed in the remaining cell subset was weak with $MI$ values concentrated around 0.8. Note that $MI$ was calculated on median raw data and therefore does not consider the statistical reliability of the difference in amplitude between
the two quantities from which it is derived, namely the maximum response ($R_{\text{max}}$) and the response at the maximum contrast level ($R_{c_{\text{max}}}$). Such difference was actually confirmed for only 2 out of the 34 cells that had an $MI$ below 1, reinforcing the notion that single-unit contrast responses in the owl wulst are largely monotonic.

The population histogram of $SI$ plotted in figure 2B was normally distributed around a mean of 0.18 ($SD$: 0.19), indicating that most of our sampled neurons also exhibit some degree of response compression or even saturation at higher contrast levels. The mean $SI$ of simple cells was 0.26 ($SD$: 0.19) and that of complex cells was 0.16 (SD: 0.19). The difference between these two means was however not statistically significant (t-test, $p = 0.052$). Similarly, no difference in $SI$ between directional (mean: 0.17, $SD$ 0.22) and bidirectional (mean: 0.20, $SD$ 0.18) cells was observed (t-test, $p = 0.396$). Negative $SI$ values, indicative of supersaturation (nonmononic) behavior, characterized 14% of our cell population. However, when statistically comparing the two terms that render this index negative ($R_{C_{\text{max}}}$ and $R_{C_{50}}$), significance was reached for only two cells. This argues that supersaturation in our data is mainly due to small inherent trial-trial variability in our measurements and do not represent a robust behavior.

**Contrast response functions**

Although the above analysis indicates that single-unit contrast response functions (CRFs) in the owl wulst are mostly nonlinear and monotonic, a great deal of cell-to-cell variability was observed with respect to the shape of CRFs. This is exemplified for eight representative neurons in figure 3. To account for this variability, we chose four simple mathematically defined shape descriptors (linear, power, logarithmic and hyperbolic ratio) that emphasize different contrast-response profiles. Albrecht and Hamilton (1982) as well as Contreras and Palmer (2003) performed a detailed comparison of those four functions within the primary visual cortex of cats and monkeys, and concluded that the hyperbolic
ratio function was the most adequate and general model to describe the CRF of cells at
this level of cortical processing. Testing whether this would also apply to the owl wulst is
sound given the functional analogy between this area and early visual cortex. Interest in
considering the logarithmic and power models also stem from the fact that they formalize
two long-standing psychophysical laws (the Weber-Fechner and Stevens’ law,
respectively) of how subjective intensity co-varies with stimulus strength. Thus, their
adequacy in fitting our data may offer the possibility to connect neural observables to
classic theories in psychophysics.

For each cell, we assessed the fitting quality provided by the four models using a
least-square optimization approach, and computed the percentage of the variance
explained by each model ($R^2$) as an initial estimate of the goodness-of-fit. For the two cells
shown in figure 3A and B, the linear fit yielded a higher $R^2$. However, according to this
criterion, most cells in our sample were better described by either a logarithmic (Fig. 3C –
D), power (Fig. 3E – F) or hyperbolic ratio (Fig. 3G – H) function. An important point
illustrated in figure 3 is that a substantial degree of variability in fitting parameters values
was observed across cells sharing the same model as 'best' fit. Take, for example, the
three-fold difference in $C_{50}$ between the two cells shown at the bottom of the figure, which
is indicative of a marked shift in the dynamic range of the response along the contrast axis.
A more detailed analysis of parameter values will be provided further below in the section
analysis of model parameter values.

For the four models under investigation, the distribution of $R^2$ values departed from
normality with a prominent skew towards higher values. We therefore used medians
(together with the 25th - 75th percentile) as a measure of central tendency and obtained,
for each model, the following results: linear 79% (65 - 88%); logarithmic 83% (73 - 0.90%);
power 88% (78 – 92%); and hyperbolic ratio 91% (84 – 95%). From these results, it can be
inferred that although the hyperbolic model seems to provide an overall better description
of the CRF, considerable overlap in distribution of $R^2$ values also exists among models. To test for the statistical reliability of the $R^2$ values obtained for each model, we performed an $F$-test, which essentially tests the null hypothesis that all regression coefficient values are equal to zero versus the alternative that at least one of them does not. For only one cell in our sample, the null hypothesis could not be rejected at a 5% significance level, for all the models tested. This cell was, therefore, excluded for further analysis. Model-specific non-validation of the $F$-test was detected for only seven cells. It occurred mainly for the linear (4 cells) and hyperbolic (2 cells) models, except for one instance in which this non-validation occurred for a family of models (power, log and hyperbolic). To verify whether a given cell class was more likely to be better fitted by a particular function, we applied a fisher exact test on a 2 (cell category) by 4 (models) contingency table. According to this analysis, the linear model was found to be more adequate for simple cells, whereas all three nonlinear models accounted equally better for complex cells (Fisher exact test, $DoF = 3, p < 0.001$). Dependency for nonlinear models was also verified for the population of directional selective neurons (Fisher exact test, $DoF = 3, p = 0.013$).

To get a better appreciation of the difference in fitting quality between the hyperbolic model and the three other models, we constructed scatter plots where each point represents a pair of $R^2$ values, one obtained from the hyperbolic model and other from one of the three other models. Figure 4 shows the results of this analysis.

As predicted by our preliminary analysis, which indicates that the response for the vast majority of the cells in our sample tend to compress to some extent at higher contrast values, the performance of the linear model was overall substantially worse than that exhibited by the hyperbolic model. The extent of this difference in performance can be appreciated by noting that the majority of data points in figure 4A fall below the straight line of the scatter plot. $R^2$ statistics indeed favored the linear model for only 21 out of 119 cells considered in this analysis, and often did so in a markedly fashion. However, it is worth
mentioning that 30% of the data set displayed reasonable and approximately similar fitting qualities ($R^2 > 80\%$, $R^2$ model differences < 5%) for both linear and hyperbolic models. This reflects the fact that compressive nonlinearity is fairly mild for a sizable fraction of wulst neurons.

Figure 4B and C makes it clear that, when compared with the linear model, the logarithmic and power models not only allow a substantial improvement in fitting quality, but also show an increased overlap with the hyperbolic model. The proportion of logarithmic and power fits with $R^2 > 80\%$ and that differed from the hyperbolic model by only 5% was 49% and 56%, respectively. This result is not surprising given that logarithmic, power and hyperbolic models are all able to account for a wide range of response compression and inflexion points where such compression begins to occur along the contrast axis. These models also predict the relatively linear contrast-response relationship before compression. The small improvement in performance of the power model over the logarithmic model is likely due to the fact that the former accommodate a wider range of response profiles than the latter. Indeed, depending on the value of its exponent, a power function may describe a strictly linear response profile (exponent ~ 1), a linear followed by a compressive / saturating profile (0 < exponent < 1) or an expansive nonlinear profile followed by a linear increase (exponent > 1), though this last type of profiles was encountered for only two cells in our sample.

Why is the fitting quality obtained with the hyperbolic model overall superior to that of other models, and can we infer from this that the hyperbolic model provide a general and ideal description of single-unit CRF in the owl wulst?

### Model selection uncertainty

As a first step towards addressing the aforementioned related issues, it is important to bear in mind that because of its additional parameter, the hyperbolic model has an
inherent predisposition to yield better fits than other competing models. Is this extra flexibility truly necessary to characterize a large proportion of our cell sample or is it prone to overfit the data? This question is particularly important given that the generalizability of a model depends intimately on its parsimony. We therefore decided to re-estimate the performance of our model set on the basis of AICc scores that implement a principled trade-off between model descriptive accuracy and model complexity (see Material and Methods).

Table 1 compares the proportion of cells, broken-down according to their respective classes, for which a particular model scored best according to $R^2$ or AICc measurements. Remember that for AICc scoring the model yielding the lowest value was selected as it provides the minimum Kullback-Leibler information loss and adequately filters out noise (or entropy) in the data from the information provided by the model parameters. The most striking result evident in table 1 is that the performance of the hyperbolic model drops substantially when assessed by the AIC method, which implies that the extra variance explained by this model reflects a certain degree of overfitting, and has therefore poor predictive power. The table also indicates that this conclusion applies indiscriminately to all cell categories. It is also interestingly to note that the vast majority of cells no longer supported by the hyperbolic model on the basis of AICc scores instead admit the logarithmic model as best fit. We initially found this result curious, as we expected this transfer in model support to impact equally the logarithmic and power models. Visual inspection of our dataset revealed that in fact this did not occur because the CRFs in these particular instances had a rather rapidly accelerating compression that was more accurately described by both logarithmic and hyperbolic models.

The preceding analysis relied on selecting the model with the lowest raw AICc value as an indication of its performance, making it impossible to intuit the extent to which this particular model differs from the other three models. Note, however, that when AICc
differences among models are small for a given cell, the acceptance of a single model may lead to a false sense of confidence. Although classical statistical reasoning based on hypothesis testing induces one to believe that valid inferences implies, at best, the rejection of all but one candidate model (and is formally limited to do so for nested models only), the AIC-based approach pursues a radically different philosophy. It emphasizes multi-model inferences, and provides a practical and mathematically well-founded methodology to do so. The latter essentially relies on Akaike weights (see Material and Methods). These are computed by ranking the fitted models from best to worst, based on the differences in AICc values, and then by deriving the relative probability of each model to be the best one, which in the AIC sense means that it minimizes the Kullback–Leibler discrepancy, given the data and the set of candidate models.

The frequency histogram plotted in figure 5 compiles the Akaike weights obtained for each cell and each model considered in our study. Probability values were largely concentrated between 0 and 0.1, indicating that, for most cells, no strong evidence exists in favor of one particular model. Using a 95% confidence interval (as recommended by Burnham and Anderson 2002), satisfactory inferential properties (i.e. small bias and good precision) was embodied by a single model for only 19% of our cell sample. Most often (43%), three models (usually, the three nonlinear ones) were necessary to make up a confidence set; the inclusion of two and four models was necessary for 25% and 13% of the cells, respectively. In agreement with what we have already shown, the linear model had less inferential coverage across cells (42%) than the nonlinear models, whose coverage ranged between 65% and 76%.

The main conclusion we draw from the above analysis is that there is a substantial degree of model uncertainty in our dataset, implying that the notion of a single general descriptor of neuronal contrast response profiles may not be applicable to the owl wulst, at least with respect to the models we chose to compare. To fully understand why the
hyperbolic function does not serve as a general model in the wulst, as reported in the primary visual cortex (e.g. Albrecht and Hamilton 1982; Contreras and Palmer 2003; Sclar et al. 1990), we proceeded with an analysis of its parameter values.

Analysis of hyperbolic ratio model parameter values

The hyperbolic ratio model derives its nonlinear properties through the interaction of three parameters: \( C_{50} \), that is the contrast necessary to reach 50% of the maximum response, also called semi-saturation contrast; \( n \), the exponent, which determines the slope of the curve as well as the sharpness of the nonlinearities at low and high contrasts; and \( R_{\text{max}} \), which is the spike rate at which the response saturates.

Starting with the distribution of \( C_{50} \) (Fig. 6A), it is important to emphasize that a considerable number of cells (49/119, 41%) assumed incompatible values for this parameter, being higher than the maximum theoretically possible contrast (i.e. with \( C_{50} > 100\% \)). This occurred when a cell exhibited very little or no sign of response saturation at high contrast, as exemplified in Fig. 3A, B, E and F. Thus, for these cells, the hyperbolic function had good fitting capabilities (median \( R^2 = 0.89 \)), but loses its descriptive relevance, and data for this cell group is therefore shown separately as figure insets. The high incidence of incompatible hyperbolic ratio fits is a key piece of evidence for rejecting the hyperbolic function as a general contrast response descriptor of the owl wulst, and constitutes a major difference between this model system and the striate (as well as extrastriate) cortex of cats and monkeys in which such incompatible fits are rare.

Notwithstanding, the distribution of semi-saturation contrast values of wulst neurons with compatible hyperbolic ratio fits (i.e. with \( C_{50} < 100\% \)) resembled that reported for the striate cortex: both were rather broad, indicating a great deal of variability in contrast sensitivity, and peaked below 1.3 of log contrast unit. However, the central tendency of our \( C_{50} \) distribution was lower than that reported for mammals. Note that, for this analysis,
simple and complex cells were grouped together because only very few simple cells (5/70) had compatible hyperbolic fits and their $C_{50}$ values were not statistically different from those of complex cells. We interpret this result as being consistent with the overall tendency of simple cells to respond more linearly to contrast than complex cells.

Examining figure 6B, we observe that the large majority of cells yielding compatible hyperbolic ratio fits have estimated exponent $n$ values between 1 and 2. This is characteristic of contrast–response curves having a gentle, close-to-linear incline until approaching their $C_{50}$. In fact, only a small proportion of cells (17%, 12/70) have a rather steep slope ($n > 2$) as typically encountered in the striate cortex where the average value of $n$ is around 2.5 (Sclar et al. 1990). The parameter $n$ of the hyperbolic model also captures a nonlinear property that the other models considered herein do not, namely the ability to predict an expansive nonlinearity at low contrast at the same time as a compressive profile at high contrasts. For $n > 1$, this property is evidenced; for $n \leq 1$, it is not. The latter scenario was found for 57% of our sampled neurons. Most of these had incompatible hyperbolic ratio fits (Fig. 6B, inset). However, a lack of expansive nonlinearity was also found in 30% of the population of cells with compatible fits (Fig. 6B, main histogram). Moreover, for the remaining 70% of this population, the contrast range over which an expansive power-law profile occurred was fairly restricted. This is evident when looking at the distribution of inflexion points $C_i$ (Fig. 6C) that determine the contrast at which the power-law profile ends and give way to a linear increase. Analytically, it is calculated as follows (see Duong and Freeman 2008):

$$C_i = C_{50}^{n} \sqrt{\frac{n-1}{n+1}} \quad n > 1$$

If one considers the total cell sample, only a minority of cells (20/119, 17%) had a marked response expansion over 1.0 log unit contrast when stimulated with low contrast gratings. The opposite is true in the mammalian primary visual cortex (Albrecht and Hamilton 1982;
Sclar et al. 1990), and in part explain the superiority of the hyperbolic ratio function over
the linear, logarithmic and power models in this area.

The distribution of $R_{\text{max}}$ values is presented in figure 6D, but provides little
explanatory power for understanding the lack of generalizibility of the hyperbolic function in
the wulst. We note however that this distribution approximates that reported for single-
units in the striate cortex of cats (Contreras and Palmer 2003) and monkeys (Sclar et al.
1990).

Limiting the contrast range

Many studies that have characterized contrast-response relationships in the mammalian
visual system have either under-sampled or ignored the top half of the contrast scale. For
example, Albrecht and Hamilton (1982) considered contrast values up to 56%. This
methodological bias may be justified by the fact that, although local contrast in the natural
world varies considerably, its distribution is highly skewed towards lower values (Balboa
and Grzywacz 2003; Brady and Field 2000; Clatworthy et al. 2003; Frazor and Geisler
2006; Laughlin 1981; Tadmor and Tolhurst 2000). Thus, finding a good match between
this distribution and neuronal responses is presumably a strong indicator of an efficient
coding scheme for luminance contrast under photopic conditions (see for example
Laughlin 1981; Tadmor and Tolhurst 2000).

Considering the above, we decided to examine whether our CRF characterization
established over the full contrast range (98%) would be altered by restricting our analysis
to 50% and 70% contrast. For this, we considered only the 84 cells that had been probed
with 13 contrast levels (see Materials and Method). All the quantitative assessments
described before were repeated for the reduced-contrast-range groups, and the results
obtained for the three groups (50%, 70% and 98% contrast range) were compared using
Kruskal–Wallis and chi-squared tests. No statistical differences were found in the amount
of cells better adjusted by a given model, despite small variations in the percentage of
cells better fitted by the hyperbolic ratio and power functions. This result was confirmed
both in terms of model fitting accuracy ($R^2$ analysis) and model predictive power (AIC
analysis). From this finding, we conclude that the neuronal representation of contrast in the
wulst is fully specified within the lower half of the contrast scale, which is compatible with
the aforementioned notion of a contrast coding efficiency scheme in this area.

**Stability of CRF over time**

Our recordings were performed in non-anesthetized owls, trained to accept head-
restriction while being presented with a battery of test stimuli. Visual monitoring inclines us
to believe that owls remained in a steady state of active wakefulness during the
experimental sessions, which presumably contributed to the good recording stability that
we obtained here and in previous studies (Baron et al. 2007; Pinto and Baron 2009).
Nonetheless, a drawback of our preparation is that it does not permit to control possible
non-observable fluctuations in internal behavioral states such as attention, arousal and
motivation. A question therefore arises concerning the extent to which the receptive field
characteristics reported in this study correspond to intrinsic properties of wulst cells and
are independent of other factors, such as uncontrolled behavioral variables.

To investigate this issue, we used a similar approach to that described by Nieder
and Wagner (2000), which basically consists in cross-correlating tuning profiles obtained
from two consecutive recording periods in order to evaluate the stability of these profiles
over time. Our stimulation protocols lasted about 15 minutes, during which the entire set of
contrast levels was repeated 10 times in an internally randomized block design. For each
cell, we computed two CRFs, one derived from the first five blocks of trials, the other one
derived from the remaining five blocks. The mean temporal difference between trials from
the first and second evaluation period was therefore around 7 minutes.
Figure 7A-C shows examples of these bipartite CRFs for three cells together with their respective Spearman’s rank correlation coefficients. Clearly, a relatively high degree of similarity in the contrast response between the first and second evaluation period was found for most cells independently of their response profile. The distribution of correlation coefficients for all 120 analyzed CRF pairs was skewed towards higher values (Kolmogorov-Smirnov test, $p << 0.001$) with a median coefficient of 0.85 (Fig. 7D). Only 17% of pairs (20/120) yielded correlation coefficients below statistical significance ($\rho < 0.61$) as it is the case for the cell shown in figure 7C. For this subset of pairs, there was no obvious trend in the data indicative of consistent effects over time, which inclines us to believe that lower correlation coefficients were mostly due to inherent noise in the measurements.

Discussion

The primary goal of this study was to characterize the steady-state responses of neurons in the owl visual wust as a function of contrast intensity. The originality of this work may be appreciated by considering the fact that, to our knowledge, this is the first detailed study on the relationship between neuronal response and contrast ever done in birds (see Introduction). Our findings and the inferences drawn from them may be summarized as follows: 1) As contrast intensity was increased from zero to near 100%, most cells exhibited a monotonic response profile with a compressive, at times saturating, nonlinearity at higher contrasts; 2) Despite this general trend, the shape of CRFs was highly variable across cells; 3) With the view to capture a systematic trend in the data, we initially applied conventional goodness-of-fit measures to assess the performance of four plausible models – linear, power, logarithmic and hyperbolic ratio – and found that the latter provided an overall improvement, albeit weak, in fitting quality over the other candidate models; 4) Nonetheless, using a more rigorous statistical method for multi-
model inferences based on Akaike’s information criterion, we demonstrated that a high degree of model uncertainty is present in our data, meaning that no single descriptor is able on its own to capture the heterogeneous nature of single-unit contrast representation in the wulst; 5) We further showed that the generalizability of the hyperbolic ratio model is not tenable in the owl wulst, as it may be in the primary visual cortex of cats and monkeys, essentially because most neurons in this area have a much wider dynamic range that starts at low contrast; 6) Finally, the fact that CRF profiles were found to be quite stable over the entire recording session of a cell suggests that such profiles are shaped, to a large extent, by hardwired circuit properties of the system.  

In the remainder of this section, we start by addressing some methodological issues that are inherent to our animal recording preparation and which may have influenced our results. We then discuss the benefit of considering multi-model selection methods such as the one we used here in order to compare the support provided by each model within a set of promising candidates. Finally, we compare our results with those reported in the mammalian retinothalamocortical pathway, and consider their functional implications with respect to the owl wulst.  

**Awake versus anaesthetized recording preparation**  
Current understanding of contrast coding in the mammalian visual system is primarily based on experimental studies performed on animals that have been anesthetized and immobilized with a variety of pharmacological agents. Here, single-cell data were obtained in alert owls, leaving open the possibility that some discrepancies between our study and others are in fact due to differences in recording preparation. Though meager, available evidence is indeed consistent with this hypothesis. In the mammalian visual cortex, several basic receptive field properties have been shown to alter depending on whether the animal is awake or anesthetized (Guo et al. 2004; Lamme et al. 1998; Pack et al. 2001), and what
kind or dose of anesthesia is used (Ikeda and Wright 1974; Solomon et al. 1999; Villeneuve and Casanova 2003). More specifically with respect to contrast, there is evidence that anesthesia can lead to a reduction in sensitivity threshold, as well as a decrease in neuronal response levels for high values of contrast (Ikeda and Wright 1974; Solomon et al. 1999). In line with such findings, the $C_{50}$ parameter of the hyperbolic ratio function, which is inversely related to contrast sensitivity, is typically lower in awake behaving monkeys (7% in Palmer et al. 2007; between 11% and 17% in Thiele et al. 2009) than in anesthetized monkeys (24% in Albrecht and Hamilton 1982; 33% in Sclar et al. 1990). It is interesting to note, however, that a more recent study by Alitto et al. (2011) in the primate LGN found a reduction in neuronal firing rate associated with anesthesia but no significant difference in contrast sensitivity between anesthetized and alert animals. Altogether, the above evidences thus indicate that caution needs to be exercised before assuming a straightforward correspondence between data obtained from different recording preparations, even when basic receptive field properties such as luminance contrast are being considered. To clarify this complex issue, studies such as that reported by Leopold et al. (2002) and Greenberg et al. (2008), in which neuronal responses are compared as the same animal is pharmacologically brought in and out of consciousness, would certainly be useful.

It is also important to bear in mind that our awake recordings were carried out in head-restrained burrowing owls that were not required to perform any particular behavioral task. It was possible to do so because eye movements are negligible in this owl species (Cooper and Pettigrew 1979). However, a limitation of this approach is that it provides no direct means of controlling for potential influences of covert behavioral states on neuronal activity. Single-unit recordings in awake behaving macaque monkey have shown that attention, for example, can significantly modulate CRFs in at least three different ways: it may increase the overall contrast sensitivity of the curve (contrast-gain model, Martinez-
Trujillo and Treue 2002; Reynolds et al. 2000), amplify neuronal responses as contrast is increased (response-gain model, Williford and Maunsell 2006), or add a fixed amount to the response for all visible contrast values (additive gain model, Thiele et al. 2009). Our analysis of CRF stability (see Fig. 7) suggests that attention-dependent effects, if any, remained stable throughout a recording protocol. However, it does not allow us to discard the presence of such effects in our experiments, especially if these were exerted in a stimulus-dependent manner. For example, the appearance of high-contrast gratings may have systematically attracted the owl’s attention to that location and increased firing as a result, thereby reducing the degree of saturation of CRFs. Clearly, the foregoing discussion highlights the need for further work to investigate the extent to which attention and other related brain states such as alertness exert an influence in the wulst, an issue that has not been addressed yet.

Consideration on stimulus luminance

We assessed the dependence of wulst neuronal responses on contrast using sine-wave gratings as test stimuli. Contrast was varied from 0 to 98%, thereby practically covering the entire Michelson contrast scale. As conventionally done in single-unit studies with a similar goal, all grating parameters other than contrast were maintained at a constant value defined according to the preference of each cell, except for mean luminance which was always fixed at 56 cd/m² across all recording sessions. Three reasons motivated us to choose this level of luminance. First, the latter is comparable to luminance values most frequently used in neurophysiological (e.g. Albrecht and Hamilton, 1982; Alitto and Usrey, 2004; Busse et al. 2011; Contreras and Palmer, 2003) and bird psychophysical (e.g. Harmening et al. 2009; Hirsch 1982; Jarvis et al. 2009) studies on contrast sensitivity. Second, according to measurements from Frazor and Geisler (2006), 56 cd/m² is well within the range of luminance typically encountered in natural photopic environments. Third, given the cathemerality of burrowing owls (Berger and Walker 1972; Haug and
Oliphant 1990; Levey et al. 2004; Sissons et al. 2001; Thomsen 1971), it is most probable that most visually guided tasks performed by these birds will occur at luminance levels around or below the one we used in this study. Note that testing the influence of mean luminance levels on contrast-response profiles was beyond the scope of this study. Therefore, we cannot discard the possibility that our choice of luminance intensity was sub-optimal for some cells in our sample to reach saturation at higher contrasts. However, current evidences suggest that this hypothesis is unlikely. In V1, CRFs are known to be largely independent of photopic luminance levels (Geisler et al., 2007; Dai and Wang, 2012). That is, luminance scales CRFs without changing their overall profile. Given that this coding strategy is presumably adapted to the statistical properties of natural images (Mante et al., 2005), it is thus reasonable to expect that such a strategy is also operational in the owl wulst.

**Model uncertainty**

The present study was motivated by the tantalizing attempt to find a simple mathematical function capable on its own to describe the response profiles of all the cells in our dataset. As discussed by Albrecht et al. (2002, 2003), this research objective is critical for further quantitative elaborations of functional or mechanistic models. In this context, the need for appropriate methods for model selection is clearly mandatory. Naively, it may be argued that choosing the ‘best’ model among competing candidates consists in identifying the model that fits more tightly the data at hands according to some indices of goodness-of-fit (e.g. $R^2$, root-mean-square). This is in fact the approach taken by the vast majority of electrophysiological studies in visual neuroscience. In this paper, we tried to overcome some of the drawbacks associated with this rather conventional approach by using a sample-size-corrected version of the Akaike information criterion (AIC, Burnham and Anderson 2002). This well-established and simple statistical procedure formalizes the
importance of choosing a model according to its predictive power by weighting the fitting performance of each model against its respective complexity (i.e. number of free parameters). In contrast to goodness-of-fit measures for which no formal standards exist for their comparison, the AIC-based method determines the strength of evidence for each evaluated model according to an objective, mathematically well-grounded framework. In addition, as exemplified in the present study, this method can be applied to non-nested models and considers all models at once without the need to perform pairwise comparisons and significant tests with arbitrarily chosen critical values for rejecting or accepting the null hypothesis. Despite their considerable advantages over hypothesis-testing methods, AIC and other information criterion approaches (see Burnham and Anderson 2002; Zucchini 2000) have been used in only a limited number of neurophysiological studies (Averbeck and Lee 2003; Schall et al. 2004; Vladusich et al. 2006).

In our work, the application of the AIC method revealed two important and related features. The first one was that the improvement in fitting quality provided by the hyperbolic function is not sufficient to justify the use of this three-parameter model for describing the response pattern of most cells in our sample. A subsequent analysis of the fitted model parameter values showed that this is mainly related to the fact that little expansive non-linearity at low contrast is present in our data, thereby making the hyperbolic fit somehow redundant with the other two-parameter models we evaluated. Second, by calculating the evidence ratio of Akaike weights for one model to be preferred over its competitors, we were able to demonstrate that none of the models examined herein was overwhelmingly better than the others. We interpret this finding as indicating that a great deal of contrast response heterogeneity exists in the visual wulst of the burrowing owl at the single cell level (see Fig. 8). This characteristic has also been often reported by V1 contrast-response studies (see for example Albrecht and Hamilton 1982;
Girman et al. 1999; Niell and Stryker 2008; Van den Bergh et al. 2010), but never rigorously quantified as we did here. Interestingly, it has been shown that the combined output of a population of neurons heterogeneously encoding a particular stimulus attribute improves the accuracy with which such attribute is being represented (Chelaru and Dragoi 2008; Shamir and Sompolinsky 2006; Tripathy et al. 2013). Therefore, rather than conceptualizing neuronal response heterogeneity as an epiphenomenon of biological variability, its existence should be more thoroughly investigated. In our view, the holistic approach implemented by AIC-like strategies provides an ideal way to do so.

Comparison with V1

Over the last few decades, comparative neurobiologists have provided a large body of evidence suggesting that homologous relationships exist between different pallial domains of birds and reptiles and specific sectors of the mammalian neocortex (Butler et al. 2011; Jarvis et al. 2005; Karten 1969; Reiner et al. 2005). In particular, it is now of consensual acceptance that the visual wulst, the major subdivision of the avian dorsal pallium, is, in many ways, homologically related to the striate cortex of mammals. A central argument in favor of this hypothesis is that both structures are primary telencephalic projection areas of the retinothalamofugal pathway (Karten et al. 1973; Medina and Reiner 2000; Shimizu and Bowers 1999). Additional support for this hypothesis comes from morphological, neurochemical, developmental, genetic and physiological data (reviewed in Medina 2009 and Butler et al. 2011). At this point, it is perhaps worth emphasizing that most of what we know about the functional organization of the visual wulst is derived from electrophysiological studies done in the owl. Ever since the pioneering work of Pettigrew and colleagues in the late seventies (Pettigrew 1979; Pettigrew and Konishi 1976a,b), the response properties of visual wulst neurons in this bird have indeed been the subject of several complementary investigations (Baron et al. 2007; Liu and Pettigrew 2003; Nieder
and Wagner 1999, 2000, 2001a,b; Pinto and Baron 2009, 2010). The general consensus emerging from all this work is that the owl visual wulst bears astonishing functional similarities with the early visual cortex of mammals, especially V1 and, to a lesser extent, V2.

Our study reveals a quite distinct pattern of results with regards to contrast. Under steady-state stimulation using optimal drifting gratings, V1 neurons typically respond in a sigmoidal fashion over a relatively limited range of contrast. This overall response profile appears to be present in a wide variety of mammalian species. When one analyzes the parameters of the best fitting hyperbolic function, which, following the lead of Albrecht and Hamilton (1982), has been standardly applied in V1 studies, notable differences with the owl wulst can be readily identified. These differences are rendered visually more explicit in figure 9, where the average CRF of all our hyperbolic ratio fits is compared with similar data reported in key mammalian studies. Note that, in V1, contrast-response relationships do not seem to vary significantly across layers. Their mean profiles were therefore computed using the reported mean values of the hyperbolic ratio fit parameters ($C_{50}$ and $n$). Note also that a large proportion of cells (41%) in our study yielded $C_{50}$ values higher than 100% contrast, meaning that these cells did not show response saturation at high contrast levels. Therefore, figure 9A and B contain two distinct mean curves derived from our study: (i) one resulting from compatible hyperbolic ratio curves (black solid line), i.e. the ones with $C_{50}$ lower than the maximal theoretical value; and (ii) one obtained from the incompatible hyperbolic ratio fits ($C_{50} > 100%$; gray solid line). The number of incompatible fits already indicates a striking difference with V1, where non-saturating cells are rare (e.g. 9% in cats and monkeys, Albrecht and Hamilton 1982). With respect to compatible fits, we find a median $C_{50}$ of 12.6% which is lower than the central tendency typically reported for this parameter in the striate cortex of mammals, including cats (Albrecht and Hamilton 1982, mean $C_{50} = 15.5%$; Contreras and Palmer 2003, mean $C_{50} = 25.9%$), macaque...
monkeys (Albrecht and Hamilton 1982, mean $C_{50} = 24.0\%$; Sclar et al. 1990, median $C_{50} = 33.0\%$; Van den Bergh et al. 2010, mean $C_{50} = 24.6\%$), marmoset monkeys (Persi et al. 2011, median $C_{50} = 25.5\%$), owl monkeys (O'Keefe et al. 1998, median $C_{50} = 42.0\%$), ferrets (Alitto and Usrey 2004, median $C_{50} = 16.7\%$); squirrels (Heimel et al. 2005, median $C_{50} = 35.0\%$); rats (Girman et al. 1999, mean $C_{50}$ around 50%, see Fig. 7D) and mice (Busse et al. 2011, median $C_{50} = 35.0\%$; Niell and Stryker 2008, median $C_{50} = 19.8\%$; Van den Bergh et al. 2010, mean $C_{50} = 42.5\%$).

The slope of CRFs that we estimated on the basis of the hyperbolic model exponent is also different from that usually reported in V1 studies. In the cortex, exponent values are typically higher than 2.5 (Albrecht and Hamilton 1982; Contreras and Palmer 2003; Heimel et al. 2005; Niell and Stryker 2008; Sclar et al. 1990; Van der Bergh et al. 2010; Zheng et al. 2007). In the visual wulst of burrowing owls, considering compatible fits, we obtained a central tendency of approximately 1.2. The exponent values for incompatible fits were even lower, ranging from 0.13 to 1.0 (median = 0.47). Altogether, these results indicate that the response expansion at low contrast values is much less pronounced in the wulst than in V1. To better visualize this difference, we replotted, in figure 9B, the same data as shown in figure 9A, but on a logarithmic contrast scale.

It is also interesting to note that smoothly graded responses over an extended range of contrast were a prominent feature of cells we classified as simple on the basis of $F_1/F_0$ ratio. In fact, our analysis reveals that, on the whole, simple cells ($F_1/F_0 > 1$) tend to be better fitted by a strictly linear model, whereas complex cells ($F_1/F_0 < 1$) are better described by the nonlinear models. This behaviour constitutes another major difference with mammalian V1 wherein simple cells, although quasi-linear in many aspects, exhibit a clear sigmoidally shaped contrast-response, much like complex cells (for review see Carandini et al. 1999). It may be that, in the wulst, simple and complex cells contribute differently to contrast sensitivity and, as a result, to the enhancement of neuronal
selectivity. In V1, this distinction does not seem to be tenable (Albrecht and Hamilton 1982; Contreras and Palmer 2003). But for now, it is unclear whether the aforementioned hypothesis is plausible, in view of the fact that the small proportion of simple cells together with the non-bimodal distribution of $F_1/F_0$ values we encountered in this study argue against the notion that simple and complex cells represent two distinct functional classes in the owl wulst.

Another notable difference between wulst and striate cortex neurons refers to the monotonicity of CRFs. In the primary visual cortex of monkeys and cats, several studies have reported that, at high contrast, the firing rate of a non-negligible proportion of cells drop instead of plateauing, a phenomenon also referred to as supersaturation (Albrecht and Hamilton 1982; Bonds 1991; Ledegeway et al. 2005; Li and Creutzfeldt 1984; Peirce 2007; Somers et al. 1998). As discussed by Peirce (2007), the existence of this phenomenon has not been widely recognized in the cortical literature, in part due to the fact that most studies have dedicated little or no attention in probing high contrast values. This is not the case of the present study, since our stimulation protocol included at least two and most often three points falling within the top half of the contrast scale. Yet, we found no robust evidence of supersaturation in the owl’s wulst. For now, it would be premature to speculate on the functional implications of this finding, especially so because even in V1, supersaturation is not at all well understood, neither with regards to its potential contribution for visual perception (although see Peirce 2007, 2011 and May and Zhaoping 2011, 2013 for interesting hypothesis), nor in terms of how it may be mediated by neuronal circuits (on this point, see Li and Creutzfeldt 1984; Somers et al. 1998).
Evidence for LGN-like response profiles?

Standing back and looking at our results from a broad phylogenetic perspective, it may be argued that contrast-dependent steady-state responses of wulst neurons resemble more closely those reported for the mammalian LGN. Even though there are clear species differences in this area (see for example Van Hooser et al. 2003), geniculate CRFs are overall more linear and less steep than in V1. This feature is often quantified in the LGN by the ratio between $R_{\text{max}}$ and $C_{50}$, also referred to as contrast gain (Croner and Kaplan 1995; Kremers et al. 1997; Solomon et al. 1999; Van Hooser et al. 2003). Calculating this ratio, we found that 61% (73/119) of our cells yielded values equal to or smaller than 1 Hz/\%contrast, very much like, for example, primate parvocellular cells (Croner and Kaplan 1995; Kremers et al. 1997; Solomon et al. 1999) and grey squirrel X-/Y-cells (Van Hooser et al. 2003). Only 25% (30/119) of cells we sampled showed contrast gain higher than 2 Hz/\%contrast and, in this respect, are more similar to feline geniculate X- and Y-cells as well as primate magnocellular cells (typical range: from 2 to 10 Hz/\%contrast; Benardete et al. 1992; Croner and Kaplan 1995; Kaplan and Shapley 1986; Shapley and Perry 1986; Solomon et al. 1999). Interestingly, directly comparing our data with those from Sclar et al. (1990), who reported $C_{50}$ and $n$ values for both P- and M-cells, suggests a bipartite trend for contrast processing in the owl remarkable similar to the one found in monkey LGN. This correspondence can be verified in figure 9C and D, where we compare our average CRF derived from compatible hyperbolic fits with the contrast-response of monkey M-cells, as well as our average incompatible hyperbolic fit curve with monkey P-cells. Moreover, the absence of response supersaturation we found in the wulst, which also typifies mammalian LGN neurons, again reinforces the functional resemblance of these two areas with respect to contrast processing.
Although no psychophysical assessment of contrast sensitivity has been performed in the burrowing owl, it is most unlikely that this bird species would stray away from what has been consistently found in birds when behaviorally evaluating their contrast sensitivity as a function of spatial frequency using stationary gratings at photopic light levels. That is, an inverted U-shape curve peaking at average values below 20 (barn owl: 13, Harmening et al. 2009; Budgerigars: 10, Lind and Kelber 2011; Chicken: 12, Jarvis et al. 2009; Pigeon: 12, Hodos et al. 2002; Wedge-tailed eagle: 14, Reymond and Wolfe 1981). To date, the American kestrel is the only avian species known to have a contrast-sensitivity maximum of about 30 (Hirsch 1982). However, this exceptional case does not fundamentally modify the general observation that birds perform on the whole much worse than many mammals, especially primates, on contrast-discrimination tasks (see Ghim and Hodos 2006; Souza et al. 2011; Uhlrich et al. 1981 and references therein). This difference in performance is surprising given that birds rely heavily on vision for their survival success, although it is possible that in the case of nocturnal birds, such a discrepancy may not be so pronounced under scotopic conditions, as shown recently in the barn owl (Orlowski et al. 2012).

To date, the neuronal mechanisms underlying the poor photopic contrast sensitivity of birds remain without explanation. Several theoretical models have demonstrated the importance of considering the combined contribution of the optical properties of the eye, receptor sampling and retinal lateral inhibition in order to explain the overall band-pass profile of contrast sensitivity functions (Barten 1999; Rovamo et al. 1993, 1994 and 1999). More recently, an expanded version of these earlier models has been successfully applied to predict the behavioral results obtained experimentally in a wide range of vertebrate species, including birds (Jarvis and Wathes 2007, 2008; Jarvis et al. 2009). However, the fact that these models are not explicitly constrained by post-retinal mechanisms makes them difficult to reconcile with a bunch of evidence obtained in mammals, which suggests
an important role of early visual cortex, especially V1, in mediating frequency-dependent contrast discrimination. For example, using optogenetic manipulations in mice, a recent study by Glickfeld et al. (2013) has elegantly demonstrated a causal link between neuronal activity in V1 and behavioral performance. This study is actually consistent with a previous lesion work performed in the same species (Prusky and Douglas 2004). In monkeys, chemical lesions in V1 seem to generate even more severe impairments on contrast sensitivity (Merigan et al. 1993). Furthermore, response properties in V1 are compatible with the idea that the latter plays a key role for this perceptual function. The evidence backing up this claim comes not only from numerous single-unit studies (Busse et al. 2011; Geisler and Albrecht 1997; Hawken and Parker 1990; Hua et al. 2010; Meng et al. 2013; Tolhurst et al. 1983), but also from investigations based on visual evoked potential (Berkley and Watkins 1973; Campbell et al. 1973; Souza et al. 2007) and fMRI bold signals (Boynton et al. 1999; Leguire et al. 2011).

On the basis of our results and in the light of the foregoing discussion, we think it is reasonable to hypothesize that behavioral contrast sensitivity in birds is also compromised, at least in part, by central mechanisms which limit the emergence of marked neuronal contrast-response nonlinearities (exponentiation at low contrast and saturation at higher contrast) in visual areas of critical importance for perceptual discrimination. Presumably, candidate areas need to contain neurons with relatively small receptive fields tuned to orientation and spatial frequency (Blakemore and Campbell 1969; Campbell and Robson 1968; De Valois and De Valois 1988; Graham 1989; Graham and Nachmias 1971). In owls, visual wulst neurons are known to possess such properties (Baron et al. 2007; Pettigrew 1979; Pettigrew and Konishi 1976a; Pinto and Baron 2009, 2010). It is therefore an ideal model system to evaluate further our hypothesis. To do so, it will be important to assess whether the neuronal representation of contrast gets significantly transformed as it ascends the owl retinothalamofugal pathway. Our null hypothesis is that no such
transformation occurs, at least not in the same pronounced manner as in mammals (Sclar et al. 1990). Clearly, another important set of actions to validate our hypothesis will be to demonstrate that behavioral contrast sensitivity deteriorates as neuronal activity in the owl visual wulst is reversibly or permanently silenced.

**Concluding remarks**

The overwhelming majority of neurons in the early visual cortex of mammals exhibit a clear sigmoidal response curve as stimulus contrast is increased. It would have been reasonable to expect a similar result in the owl visual wulst given available evidence indicating a close functional resemblance of this area with V1. Yet, interestingly, the data reported in this study do not support this conjecture. Though monotonic, CRFs are highly variable across visual wulst neurons and often lack a pronounced exponentiation and saturation at low and high contrasts, respectively. A direct consequence of this overall trend towards more linear, gradual contrast responses is that the hyperbolic ratio (Naka-Rushton) model, conventionally used in the cortex, proved to be inappropriate as a single overarching CRF descriptor in the wulst. These results are especially significant because they provide the groundwork for future studies seeking to understand how seemingly different neural encoding schemes of contrast information have emerged in visual telencephalic areas that are evolutionary distant but presumably homologous. The present work also lends support to the untapped idea that the visual wulst may have an important role in mediating the low contrast-sensitivity typically observed in birds at the psychophysical level.

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Figure Legends

Figure 1. Responses of a simple and complex cell to 4s of stimulation with sinusoidal gratings of various contrast levels. On the left hand side are the eleven stimulus contrast levels used to elicit the neuronal responses shown on the right hand side. (A) Peri-stimulus time histograms for the simple cell. This cell class tends to increase its response throughout the whole contrast range. For this particular neuron, a minimum contrast level of 9.9% was required to evoke a significant response (one-tailed Wilcoxon matched-pairs signed-rank test, p = 0.001). (B) Peri-stimulus time histograms for the complex cell. The
latter tends to increase its firing rate over a more limited contrast range, generally with little response changes associated with high contrasts. For this cell, a 2.5% stimulus contrast value was sufficient to elicit a significant response (one-tailed Wilcoxon matched-pairs signed-rank test, $p = 0.003$).

**Figure 2.** Distribution of monotonicity and saturation indices for our population of wulst neurons. (A) For the monotonic index, a value of one indicates a monotonic response behavior; a value of zero indicates a nonmonotonic profile, for which the response at maximum contrast is the same as that of the baseline. In general, the majority of wulst neurons are monotonic. (B) Neurons with a saturation index above zero have a monotonic response profile and a progressively lower degree of response saturation as the values of this index increase. Values equal to zero indicate an asymptotic saturation response. Negative values signal a nonmonotonic profile. The mean (not the median) of the saturation index distribution (white arrow) was used as an indicator of central tendency because normality was verified for this distribution.

**Figure 3.** Contrast response function of eight representative neurons recorded from the visual wulst. Responses are plotted against a linear scale of contrast. Each data point indicates the cell’s median firing rate over trials, with 1st and 3rd quartiles represented by error bars. The smooth curve through the responses of each cell is the best fit of four candidate models. It may be either linear (A,B), logarithmic (C,D), power (E,F), or hyperbolic ratio (G,H). Here, fitting performance was assessed on the basis of the percentage of the variance explained by a given model ($R^2$). For each selected model, the values of its free parameters are specified at the lower right of its respective plot. The dotted lines drawn in the two bottom plots (cells with hyperbolic ratio as best fit) indicates $C_{50}$, that is the contrast required to produce 50% of the cell’s maximum response. The
difference between the two cells with respect to this parameter is illustrative of the large variation in the dynamic range of the responses along the contrast axis that is present across our cell sample. Cells shown in panels A, B and E are simple cells; the other five are complex cells. SF = spatial frequency; TF = temporal frequency; DI = directional index; SI = saturation index.

**Figure 4.** Comparison of fitting quality between the hyperbolic model and the linear (A), logarithmic (B), or power (C) model as estimated by $R^2$ statistics. Each circle represents a pair of $R^2$ values, one obtained from the hyperbolic and other from the other function under comparison. A circle below the straight line of the scatter plots (y=x) indicates that a better fit was obtained with the hyperbolic function. Although the latter displayed an overall better performance than the linear model, a substantial improvement of fitting quality, with an increased overlap, may be seen with respect to the logarithmic and power models.

**Figure 5.** Model comparison for each cell of our sample using the Akaike’s information criterion (AIC). Probability values between 0.9 and 1.0 indicate, for a given cell, relatively strong evidence in favor of a particular model. Probability values between 0 and 0.1 mean that no strong evidence exists in favor of a single model. Clearly, single model support was not frequent in our dataset.

**Figure 6.** Distribution of the hyperbolic ratio model parameter values: (A) $C_{50}$ that is the semi-saturation contrast; and (B) the exponent $n$, responsible for the steepness of the CRF as well as the non-linearities at low (expansion; for $n > 1$) and high (compression / saturation) contrasts. (C) $C_i$ is derived from the hyperbolic model (see main text) and corresponds to the contrast at which the expansion ends, and give way to a linear response increase. (D) $R_{max}$ which indicates the firing rate at the saturation point. The
main histograms show the distribution of parameter values for cells whose hyperbolic fits were compatible (n = 70); the inset panels show the distribution of values for incompatible hyperbolic ratio fits (n = 49; see text). Note the broad distribution of $C_{50}$ indicative of the relatively high degree of variability in contrast sensitivity of wulst neurons. The small number of cells with higher $n$ values indicates that an expansive profile is rare in the CRF. The white arrows specify the median of the distributions.

Figure 7. Reproducibility of contrast responses over time. (A–C) Examples of unit contrast response profiles obtained during the early (tuning part 1, solid lines) and late (tuning part 2, dotted lines) period of stimulation. Total stimulation time was about 15 minutes, resulting in a mean temporal difference between the two evaluation periods of 7 minutes. Correlation coefficients of the curves are shown at the bottom right corner of each panel. (D) Distribution of correlation coefficients computed for the whole population of wulst neurons (n = 120). Coefficients to the right of the vertical dotted line are statistically significant (Spearman’s rank correlation, $p = 0.05$).

Figure 8. Contrast response functions of all dataset, highlighting response heterogeneity. Each gray line represents the best-fitted model normalized for each isolated cell in our sample. Black line corresponds to the mean curve. n=119.

Figure 9. Comparison between contrast responses derived from burrowing owl and mammals. (A) Mean CRF estimated for cells in owl wulst and mammalian primary visual cortex. The graph shows two curves related to owl wulst: the black solid line is the mean curve from compatible hyperbolic ratio fits (n = 70), while the gray solid line is the mean curve from incompatible hyperbolic ratio fits (n = 49). (B) Same as A, but with contrast
values plotted in logarithm scale to highlight the small response expansion at low contrast values and the gentle slope of the owl CRF, when compared to mammals. (C-D)

Comparison between owl CRF curves (black and gray solid lines are the same as A and B) and CRF derived from monkey parvo- and magnocellular streams, both plotted in a linear-linear scale (C) and with contrast values in logarithm scale (D). Note the similarity between owl wulst and monkey LGN. Mammalian curves were derived from: cat (Contreras and Palmer 2003), macaque monkey (Sclar et al. 1990), marmoset (Persi et al. 2011), mouse (Van den Bergh et al. 2010) and squirrel (Heimel et al. 2005).

Table 1. Proportion of cells ‘best fitted’ by one of the four candidate models according to $R^2$ and AICc measurements and cell classes.
A

Monotonicity index

Number of cells

Median = 1

B

Saturation index

Number of cells

Mean = 0.18
SD = 0.19
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