

Supporting Information

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SI Text

Estimation of Linear–Nonlinear Models

Standard linear–nonlinear (LN) models with no position invariance were fitted using maximum likelihood with a flexible nonlinear function (1, 2) relating the neural firing to stimulus components along the maximally informative dimensions. The method begins by computing the spike-triggered average. After that the profile of the relevant stimulus feature is refined to increase predictive power of the model (either according to the mutual information between the stimuli and the neural responses or the likelihood of the model given the data). The optimization is based on a combination of simulated annealing and gradient descent following the procedure described in ref. 1. As a result, all stimulus correlations that are not associated with the neural response are removed, because they do not provide additional information about the neural response.

LN models with partial invariance can be estimated by a two-step maximum likelihood optimization (3) that iteratively updated both the relevant features and the locations that were most likely to have triggered a spike. Because of the large number of models that needed to be estimated for each neuron (12 ranges of position invariance at two different scales, each computation repeated for different jackknife estimates; see below), we have simplified the second step in the calculation by estimating the locations that were most likely to have triggered a spike just once, using the image frame that elicited the maximal number of spikes as the relevant feature. In cases in which more than one image elicited the maximal firing rate, these images were aligned to each other to maximize their dot product and averaged, producing an estimate of the “optimal image.” This simplification of the method is similar to the “dejittering” technique that was previously developed to minimize the effects of time and spatial jitter on the estimates of neural feature selectivity (4). We found that this simplified approach produced models with statistically the same predictive power (Fig. S8) compared with models obtained by full two-step likelihood optimization.

Models with unlimited range of invariance were fitted using the same maximum likelihood approach as models without translation invariance (1, 2), but with respect to the amplitudes of the 2D Fourier transform applied to stimulus frames (5).

Four jackknife estimates (6) were generated for each type of model using different subsets of the unrepeated dataset. This choice of the number of jackknives was motivated by the need to balance the size of the “training” and “validation” datasets. Larger numbers of jackknives reduce the size of the validation set, leading to greater overfitting biases in model estimation. At the same time, reasonable estimates of variance in receptive field estimates can be obtained with four jackknives. Results are reported as averages across jackknife estimates (in the case of models with limited range of position invariance, individual jackknives for each neuron were realigned to maximize correlation with each other). The (signed) signal-to-noise was computed as a SD scaled by a factor of 3 according to the jackknife correction (6).

Computation of Information Explained by an LN Model

The amount of information accounted for by an LN model with two relevant features, \vec{v}_1 and \vec{v}_2 , was computed by projecting all stimuli onto the relevant stimulus features and forming the probability distributions of these projections x_1 and x_2 , respectively, both across all of the presented stimuli $P_{\vec{v}_1, \vec{v}_2}(x_1, x_2)$ and across stimuli that elicited a spike $P_{\vec{v}_1, \vec{v}_2}(x_1, x_2 | spike)$. For the latter, conditional distribution, the contribution of each stimulus is proportional to the number of spikes it elicited (there is no need to binarize the spike trains; one can work with spike counts obtained in each bin of the spike train). The Kullback–Leibler distance between these two probability distributions $I(\vec{v}_1, \vec{v}_2) =$

$$\int dx_1 dx_2 P_{\vec{v}_1, \vec{v}_2}(x_1, x_2 | spike) \log_2 \left[\frac{P_{\vec{v}_1, \vec{v}_2}(x_1, x_2 | spike)}{P_{\vec{v}_1, \vec{v}_2}(x_1, x_2)} \right]$$

yields the amount of information per spike that is accounted for by the reduced model.

Both the overall information and the information accounted by different estimated models contain a positive bias, which decreases as more data are collected (7–9). To correct for this bias, we followed procedures described in ref. 7. Specifically, we computed information values based on different fractions of repeats (80–100%) and then used a linear extrapolation to find values predicted if an infinite number of repetitions could be obtained. The linear dependence is expected on theoretical grounds in the asymptotic regime of sufficiently large dataset sizes (7–9). This procedure was used to correct for bias in both the information per spike and the information accounted for by each type of model.

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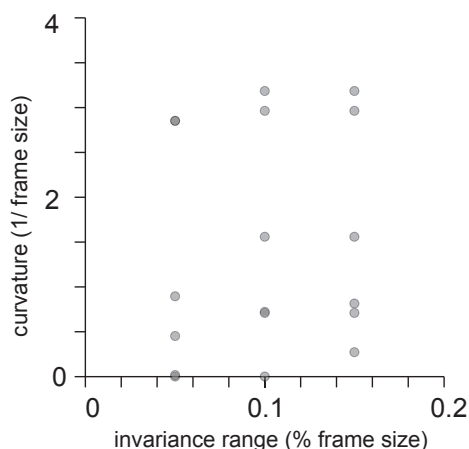


Fig. S3. Control analysis showing that the trade-off between curvature tuning and position invariance is not due to the estimation procedure. We analyzed a set of model cells that had the same preferred curvature regardless of the range of invariance. These model spike trains were subjected to identical analysis to how V4 data were analyzed, from receptive field estimation to receptive field fitting with curved Gabor models. The derived curvature values show no dependence on the range of position invariance ($P = 0.58$, linear correlation). The curvature index 1 is parameter ρ (*Materials and Methods*) normalized such that the frame size equals 1.

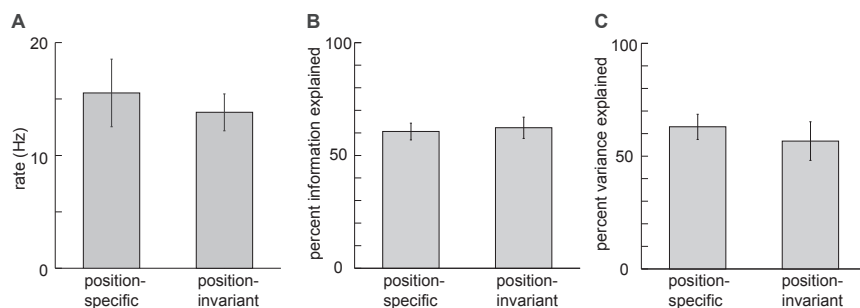


Fig. S4. There were no significant differences in the mean firing rate (A) for neurons best described by either a position-specific or position-invariant model ($P = 0.59$). These models also yielded similar percentages of information explained (B) and variance (C), with corresponding P values of 0.91 and 0.34 (Mann–Whitney test).

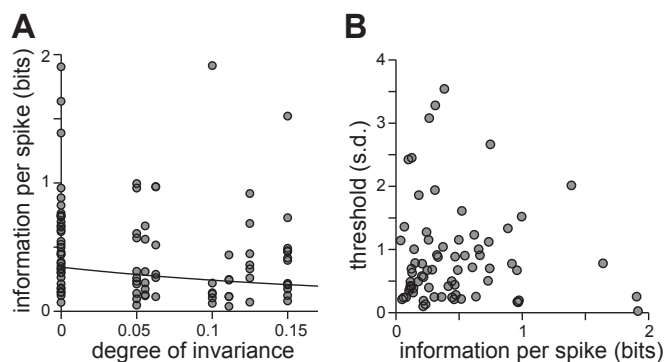


Fig. S5. Using information per spike as another measure of sparseness in neural responses. Both the dependence on threshold (A) and threshold (B) mirror those obtained with sparseness quantified as normalized variance in the firing rate (Fig. 2). (A) The information per spike was lower for neurons exhibiting position invariance compared with neurons with partial position invariance (from 5% to 15%, $P = 0.0037$, Mann–Whitney test). The dependence of information per spike on invariance range was better described by an inverse quadratic function than a linear function: $I_{\text{spike}} \sim (x+c)^{-2}$, where x is the invariance range and c is a constant (solid line shows the best fit, $P = 0.039$, correlation between x and I_{spike}). (B) There was no correlation between threshold and information per spike ($P = 0.65$).

