

Temporal adaptation enhances efficient contrast gain control on natural images

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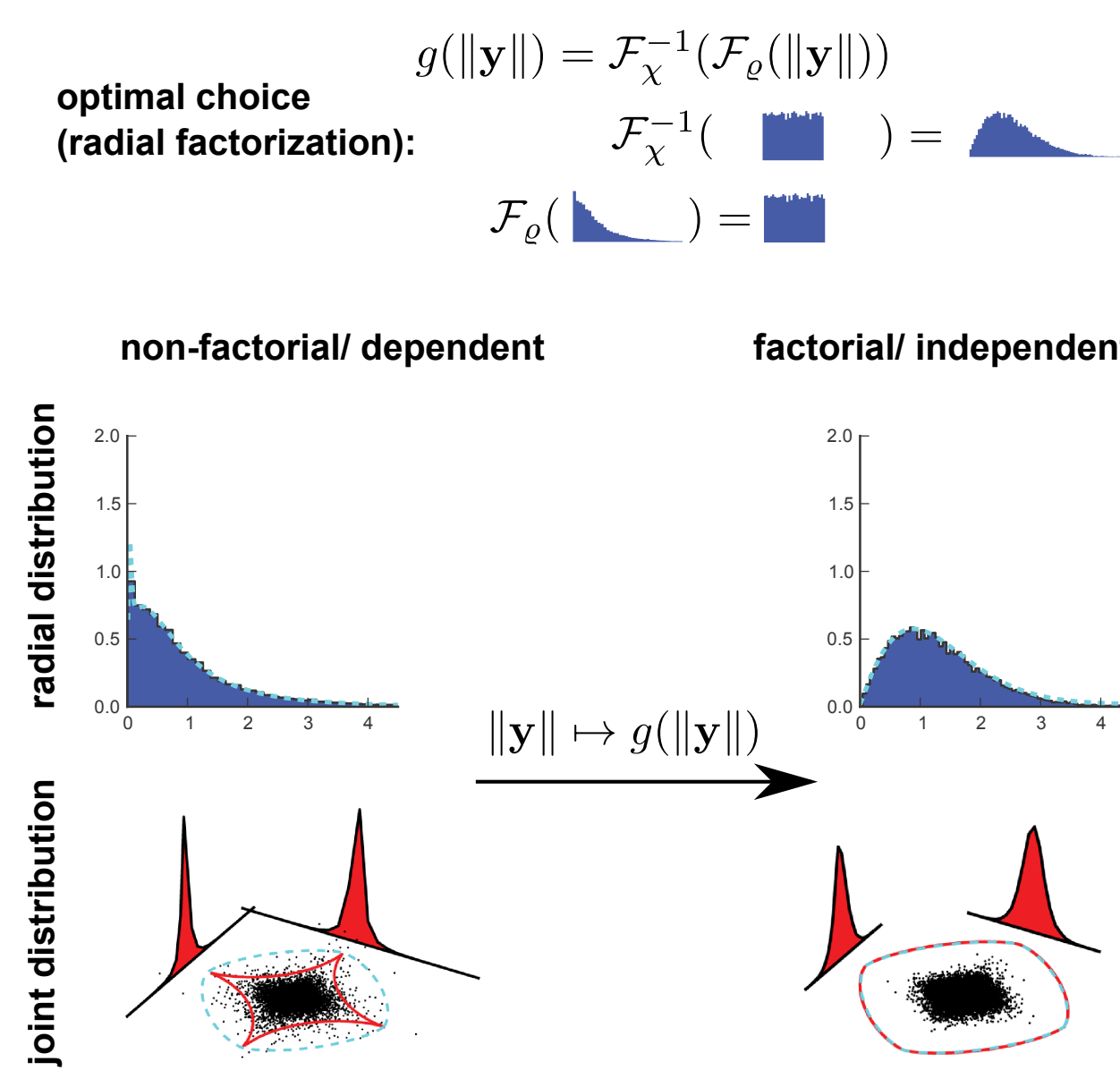
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CONTEXT

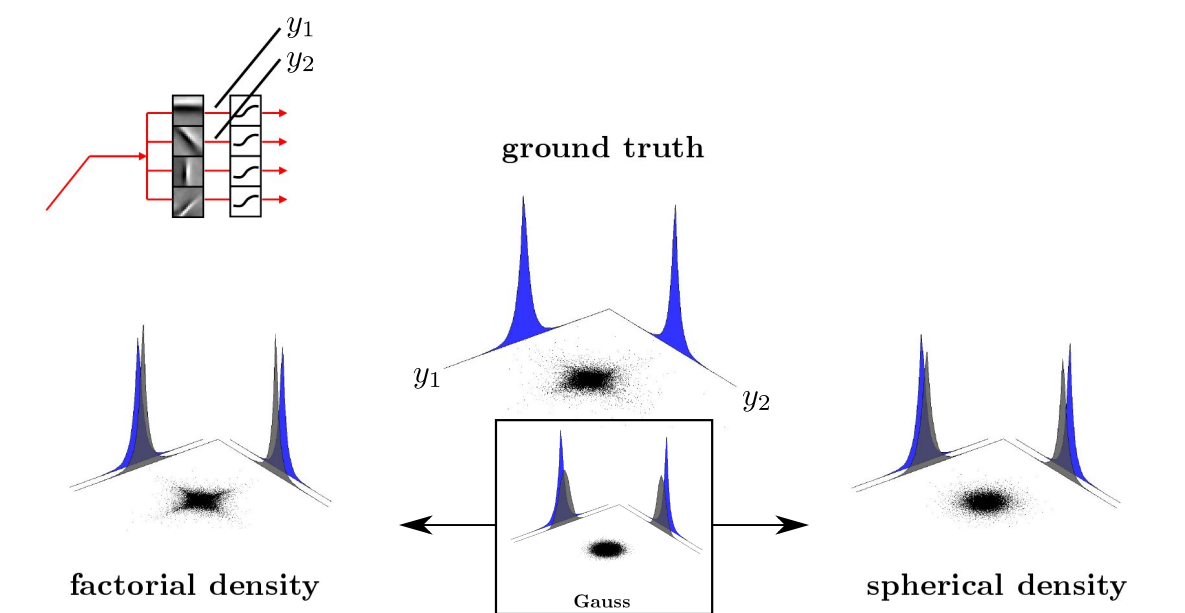
The redundancy reduction hypothesis postulates that neural representations adapt to sensory input statistics such that their responses become as statistically independent as possible. Based on this hypothesis, many properties of early visual neurons—like orientation selectivity or *divisive normalization*—have been linked to natural image statistics. *Divisive normalization* in particular models a widely observed neural response property: The divisive inhibition of a single neuron by a pool of others. This mechanism has been shown to reduce the redundancy among neural responses to typical contrast dependencies in natural images. Here, we compare a standard model of *divisive normalization* to a functionally similar, but statistically optimal mechanism called *radial factorization*.

DIVISIVE NORMALIZATION AND RADIAL FACTORIZATION

The central mechanisms of *divisive normalization* are (i) linear filtering $\mathbf{y} = W\mathbf{x}$ of an image patch \mathbf{x} and (ii) radial rescaling of the filter responses $\mathbf{z} = g(\|\mathbf{y}\|) \frac{\mathbf{y}}{\|\mathbf{y}\|}$. Whiten natural image patches \mathbf{y} still exhibit higher order dependencies. For L_p -spherically symmetric distributions, radial rescaling can remove all redundancy via *radial factorization* $\|\mathbf{y}\| \mapsto \mathcal{F}_x^{-1}(\mathcal{F}_e(\|\mathbf{y}\|))$. We compare the radial rescaling $\|\mathbf{y}\| \mapsto \kappa \|\mathbf{y}\| / \sqrt{\sigma^2 + \|\mathbf{y}\|^2}$ of *divisive normalization* to the optimal rescaling of *radial factorization*.



After whitening, the distribution of natural image patches is almost spherical and exhibits leptokurtotic marginals. Since the Gaussian is the only spherically symmetric and factorial density, it must exhibit higher order dependencies.



MATHEMATICS

Redundancy ~ Multi-Information

$$I[\mathbf{Y}] = D_{KL} \left(\rho(\mathbf{y}) \prod_{i=1}^n \rho_i(y_i) \right) = \sum_{i=1}^n H[Y_i] - H[\mathbf{Y}]$$

Multi-Information Estimation

$$A[\hat{\rho}(\mathbf{y})] := -\langle \log \hat{\rho}(\mathbf{y}) \rangle_{\mathbf{y} \sim \rho(\mathbf{y})}$$

$$= H[\mathbf{Y}] + D_{KL}(\rho(\mathbf{y}) \| \hat{\rho}(\mathbf{y}))$$

$$\hat{I}[\mathbf{Y}] = \sum_{i=1}^n \hat{H}[Y_i] - A[\hat{\rho}(\mathbf{y})]$$

$$I[\mathbf{Z}] = \sum_{i=1}^n H[\mathbf{Z}_i] - H[\mathbf{Y}] - \left\langle \log \det \left| \frac{d\mathbf{z}}{d\mathbf{y}} \right| \right\rangle_{\mathbf{Y}}$$

Naka-Rushton Distribution

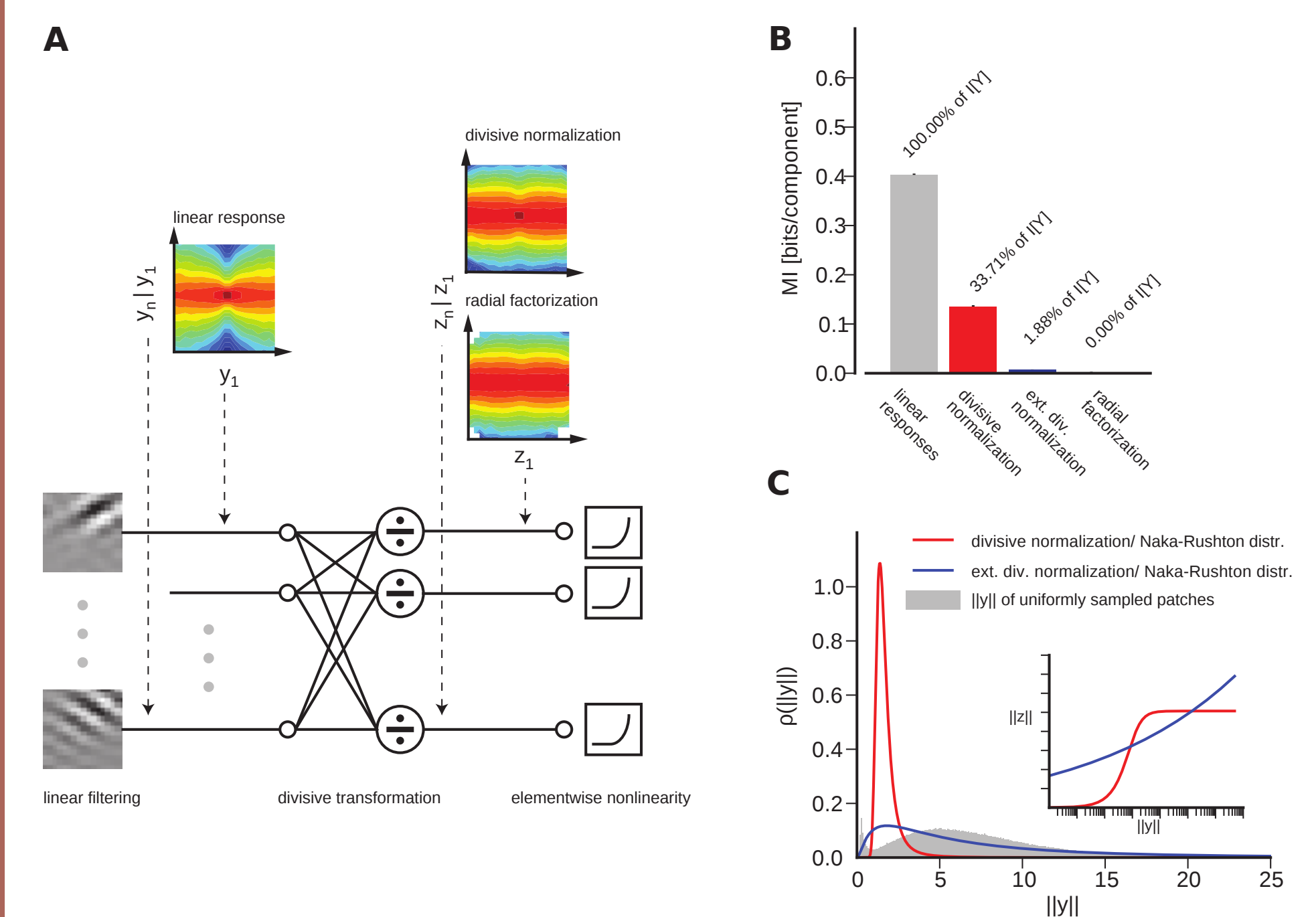
$$r \sim \nu(r | \kappa, \sigma, s) \Rightarrow \frac{\kappa r}{\sqrt{\sigma^2 + r^2}} = \zeta \sim \chi_{\perp \kappa}(\zeta | s)$$

$$\nu(r | \kappa, \sigma, s) = \frac{2\kappa^n \sigma^2 r^{n-1} \exp\left(-\frac{\kappa^2 r^2}{2s(\sigma^2 + r^2)}\right)}{\mathfrak{G}\left(\frac{n}{2}, \frac{\kappa^2}{2s}\right) \Gamma\left(\frac{n}{2}\right) (2s)^{\frac{n}{2}} (\sigma^2 + r^2)^{\frac{n+2}{2}}}$$

SUMMARY

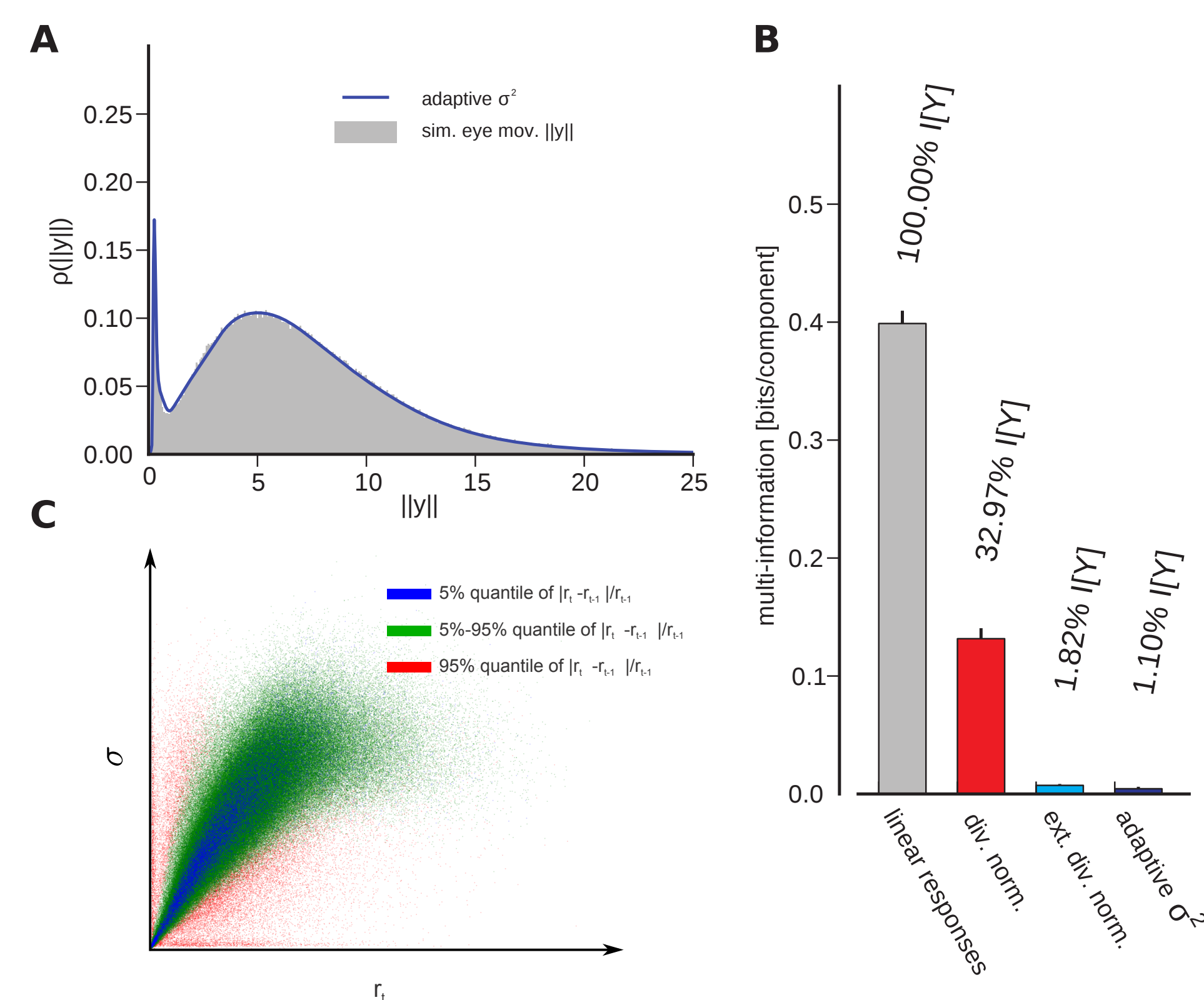
- ➔ : *Divisive normalization* has been shown to reduce higher order dependencies on natural images.
- ⬆ & ➔ : The central mechanisms of *divisive normalization* are (i) linear filtering $\mathbf{y} = W\mathbf{x}$ of an image patch \mathbf{x} and (ii) radial rescaling of the filter responses $\mathbf{z} = g(\|\mathbf{y}\|) \frac{\mathbf{y}}{\|\mathbf{y}\|}$.
- ⬆ : *Radial factorization* is an optimal redundancy reduction transform for these two mechanisms.
- ⬅ & ➔ : We compared the amount of the redundancy removed by *divisive normalization* and *radial factorization*.
- ➔ : *Divisive normalization* performs suboptimally.
- ⬅ & ➔ : We analyze why by deriving the distribution for which *divisive normalization* would perform optimal.
- ➔ : Results demonstrate that *static divisive normalization* cannot easily be improved without becoming biologically implausible.
- ⬇ : We propose a *dynamic divisive normalization* model that adapts to the ambient contrast level under naturalistic viewing conditions (simulated eye movements) which substantially improves the redundancy reduction performance.
- ⬇ : Our results indicate that experimentally observed temporal dynamics of *divisive normalization* might be critical for redundancy reduction.

REDUNDANCY MEASUREMENTS



A: *Divisive normalization* model used in this study: Natural image patches are linearly filtered and nonlinearly transformed by *divisive normalization* or *radial factorization*. Linear filter responses still exhibit dependencies in the form of variance correlations (bow-tie plots). These dependencies are decreased by *divisive normalization* and *radial factorization*. **B:** Redundancy measured via multi-information after *divisive normalization*, *extended divisive normalization*, and *radial factorization*: *divisive normalization* leaves a substantial amount of residual redundancy. **C:** Radial distributions for which *divisive normalization* (red) and its extended version $\|\mathbf{y}\|^{\frac{\gamma}{2} + \delta} / \sqrt{\sigma^2 + \|\mathbf{y}\|^2}^{\gamma}$ (blue) would be optimal. *Extended divisive normalization* achieves good redundancy reduction, but leads to a physiologically implausible shape of the contrast response.

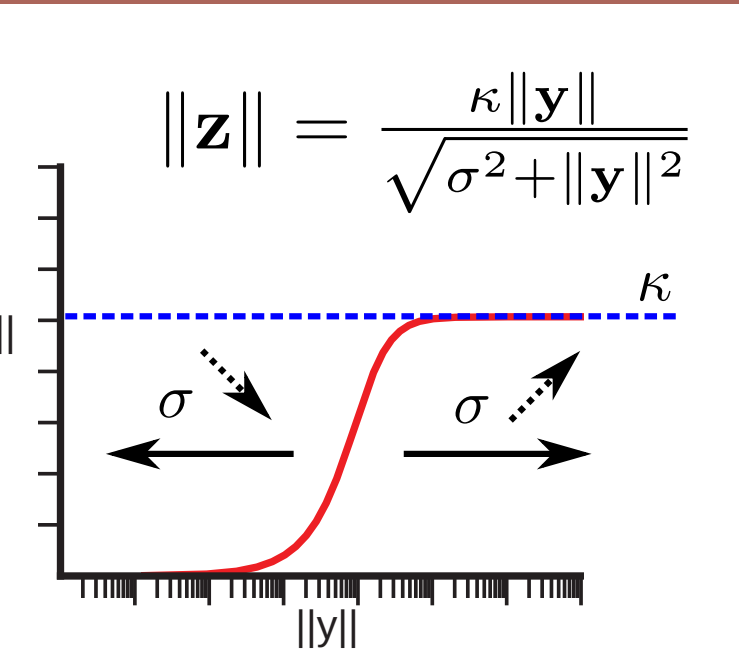
DYNAMIC MODEL



A: Histogram of $\|\mathbf{y}\|$ for natural image patches sampled with simulated eye movements: The dynamically adapting σ^2 predicts a mixture of Naka-Rushton distributions for $\|\mathbf{y}\|$, which closely matches the empirical distribution. **B:** Redundancy reduction performance for simulated eye movement data. The dynamically adapting σ^2 achieves an almost optimal redundancy reduction performance. **C:** Dynamics of the adaptive σ : values of $r_t = \|\mathbf{y}_t\|$ plotted against its σ_t adapted to r_{t-1} . The correlated values indicate that the shift of the contrast response curve (controlled by σ) tracks the ambient contrast level.

CONTRAST ADAPTATION

Shifts of the (individual) contrast response function are realized by changes in σ^2 . Neurophysiological measurements have demonstrated that individual neurons shift the steepest region of their contrast response curve towards the ambient contrast level.



FURTHER INFORMATION

Code and papers are available at <http://www.bethgelab.org>

