notes on efficient coding of color

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Abstract

stuff

Linear treatment

In (Atick, Li, *et al.* 1992), the authors discover red-green opponency from a treatment of the L and M channels of color vision in the linear, infinite retina approximation. Here, we rederive this result using the approach of (Jun *et al.* 2022).

We begin with the optimization objective used in (Jun *et al.* 2021). We would like to *maximize*

$$\mathbb{E}_x \log \frac{\det\left(\mathbf{G}\mathbf{W}^\top(\mathbf{C}_x + \mathbf{C}_{n_{\text{in}}})\mathbf{W}\mathbf{G} + \mathbf{C}_{n_{\text{out}}}\right)}{\det\left(\mathbf{G}\mathbf{W}^\top\mathbf{C}_{n_{\text{in}}}\mathbf{W}\mathbf{G} + \mathbf{C}_{n_{\text{out}}}\right)} + \sum_j \lambda_j \mathbb{E}_x r_j, \tag{1}$$

where the Lagrange multiplier λ_j is mean to enforce the constraint $\mathbb{E}_x r_j \leq 1$. From (Jun *et al.* 2022), the determinant in the numerator is the determinant of a matrix with entries

$$\begin{aligned} F_{ij} &= \gamma_i\gamma_j \mathbf{w}_i^\top(\mathbf{C}_x + \sigma_{\text{in}}^2 \mathbb{1})\mathbf{w}_j && (2)\\ &= \int \frac{d^2\mathbf{k}}{(2\pi)^2} e^{i\mathbf{k}\cdot(\mathbf{z}_i - \mathbf{z}_j)} |v(k)|^2 (C_x(k) + \sigma_{\text{in}}^2) && (3)\end{aligned}$$

in the continuum limit for RFs i and j located at $\mathbf{z}_i$ and $\mathbf{z}_j$, where we have assumed that $\mathbf{C}_x(\mathbf{z}, \mathbf{z}') = \mathbf{C}_x(\mathbf{z} - \mathbf{z}')$ (that is, the spectrum is translationally invariant) and we write $\mathbf{v}_i \equiv \gamma_i \mathbf{w}_i$ for the unnormalized kernel and $\mathbf{v}(k)$ for its Fourier transform (assuming rotational symmetry). In the case of color, the covariance matrix $\mathbf{C}_x$ has additional indices for color channels ($a, b = 1 \ldots 3$), and we write

$$F_{ij} = \int \frac{d^2\mathbf{k}}{(2\pi)^2} e^{i\mathbf{k}\cdot(\mathbf{z}_i - \mathbf{z}_j)} \sum_{ab} v_a^*(k)(C_{ab}(k) + \sigma_a^2 \delta_{ab}) v_b(k). \tag{4}$$

In writing this, we have dropped subscripts on C and σ^2 and assumed that noise in the inputs is uncorrelated across color channels.

Now, just as in the single channel case, we can compute the log determinant in the objective by diagonalizing $\mathbf{F}$ in its eigenbasis and performing an integral over its eigenvalues, making the first term in (1) equal to

$$\int_{G_0} \frac{d^2\mathbf{k}}{(2\pi)^2} \log \frac{\frac{\text{vol}(G_0)}{(2\pi)^2} \sum_{\mathbf{g}\in G} \sum_{ab} v_a^*(\mathbf{k}+\mathbf{g}) v_b(\mathbf{k}+\mathbf{g})(C_{ab}(\mathbf{k}+\mathbf{g}) + \sigma_a^2\delta_{ab}) + \varepsilon^2}{\frac{\text{vol}(G_0)}{(2\pi)^2} \sum_{\mathbf{g}\in G} \sum_a |v_a(\mathbf{k}+\mathbf{g})|^2 \sigma_a^2 + \varepsilon^2}, \tag{5}$$

with σ^2 the variance of input noise, ε^2 the variance of output noise, and G the dual lattice and G_0 its unit cell as in (Jun *et al.* 2022).

Single mosaic case

In the case of a single mosaic, we have a prototypical RF $v_a(k)$, which we assume to be radially symmetric. Writing $v_a(k) = v(k)u_a(k)$ with $\sum_a u^*_a(k)u_a(k) = 1$, we then have

$$\sum_{ab} v^*_a(\mathbf{k}+\mathbf{g})v_b(\mathbf{k}+\mathbf{g})C_{ab}(\mathbf{k}+\mathbf{g}) = |v(\mathbf{k}+\mathbf{g})|^2 C'(\mathbf{k}+\mathbf{g}), \tag{6}$$

where we denote by $C'(k)$ the effective one-dimensional spectrum as filtered by the normalized RF at each channel and frequency. If, in addition, we assume that the input noise is the same in every channel, we have $\sum_{ab} v^*_a(\mathbf{k}+\mathbf{g})v_b(\mathbf{k}+\mathbf{g})\sigma^2_a\delta_{ab} = |v(\mathbf{k}+\mathbf{g})|^2\sigma^2$, and we can follow the derivation in Appendix A.2 of (Jun *et al.* 2022) to reproduce the result of (Atick & Redlich 1992).

Multiple mosaics

Of course, this solution above only allows us to solve for $v(k)$ once we have fixed $u_a(k)$, the color profile of the RF at each spatial frequency. Here, we consider the case of multiple mosaics[1].

As argued in Appendix A.4 of (Jun *et al.* 2022), the optimal choice of RFs for each mosaic occurs when these RFs are as nearly as possible orthogonal to each other in the inner product defined by $C(k) + \sigma^2$. In (Jun *et al.* 2022), this was accomplished by requiring that mosaics not overlap in their spacetime frequency responses: $v^*(k,\omega)v'(k,\omega) = 0$ for v and v' in different mosaics. Here, we have another set of degrees of freedom — separate color channels — at our disposal, and the relevant conditions become

$$\int \frac{d^2\mathbf{k}}{(2\pi)^2} e^{i\mathbf{k}\cdot(\mathbf{z}_i-\mathbf{z}_j)} \sum_{ab} v^*_a(k)(C_{ab}(k) + \sigma^2_a\delta_{ab})v'_b(k) = 0 \tag{7}$$

$$\int \frac{d^2\mathbf{k}}{(2\pi)^2} e^{i\mathbf{k}\cdot(\mathbf{z}_i-\mathbf{z}_j)} \sum_{a} \sigma^2_a v^*_a(k)v'_a(k) = 0 \tag{8}$$

for all relevant off-diagonal blocks in the determinants to vanish when v and v' are in different mosaics.

To address this problem, we consider the generalized eigenvalue problem for the two matrices $\mathbf{C}(k)$ and $\mathbf{C}_{\text{in}}(k) = \text{diag}(\boldsymbol{\sigma}^\mathbf{2})$:

$$\mathbf{A}\boldsymbol{\phi}_i = \lambda_i\mathbf{B}\boldsymbol{\phi}_i \tag{9}$$

for generalized eigenvectors $\boldsymbol{\phi}_i$ (Ghojogh *et al.* 2019). Letting $\mathbf{A} = \mathbf{C}$ and $\mathbf{B} = \mathbf{C}_{\text{in}}$, we can imagine a set of eigenvectors $\mathbf{u}_i(k)$ parameterized by k satisfying

$$\mathbf{u}^*_i(k)\mathbf{C}(k)\mathbf{u}_j(k) = \lambda_j(k)\mathbf{u}^*_i(k)\mathbf{C}_{\text{in}}(k)\mathbf{u}_j(k) = \lambda_j\delta_{ij}. \tag{10}$$

That is, in matrix form (suppressing for the moment the k parameterization)

$$\mathbf{CU} = \mathbf{C}_{\text{in}}\mathbf{U\Lambda} \tag{11}$$

$$\mathbf{U}^\dagger\mathbf{C}_{\text{in}}\mathbf{U} = \mathbb{1} \tag{12}$$

$$\mathbf{U}^\dagger\mathbf{CU} = \mathbf{\Lambda}, \tag{13}$$

so that if we let the RFs for the mosaics be a linear combination of these basis vectors we have each mosaic's RF represented in the color channel basis as a column of $\mathbf{UV}$, and the matrix products in the numerator and denominator of (5) become

$$\mathbf{V}^\dagger\mathbf{U}^\dagger(\mathbf{C} + \mathbf{C}_{\text{in}})\mathbf{UV} = \mathbf{V}^\dagger\mathbf{\Lambda} + \mathbb{1})\mathbf{V} \tag{14}$$

$$\mathbf{V}^\dagger\mathbf{U}^\dagger\mathbf{C}_{\text{in}}\mathbf{UV} = \mathbf{V}^\dagger\mathbf{V}, \tag{15}$$

[1] In this linear response case, of course, each mosaic comprises both ON and OFF response types, making it equivalent to *two* mosaics in the nonlinear case.

respectively. This then gives rise to a new objective in the multi-mosaic case:

$$\int_{G_0} \frac{d^2\mathbf{k}}{(2\pi)^2} \sum_m \left[\log \frac{\sum_{\mathbf{g}\in G} (\upsilon_m^2(\lambda_m + 1))(\mathbf{k}+\mathbf{g}) + \varepsilon^2}{\sum_{\mathbf{g}\in G} \upsilon_m^2(\mathbf{k}+\mathbf{g}) + \varepsilon^2} \right], \tag{16}$$

where the υ_m are eigenvalues of $\mathbf{V}^\dagger\mathbf{V}$[2] and, as in (Jun *et al.* 2022) we have chosen units in which $\mathrm{vol}(G_0) = (2\pi)^2$.

Moreover, the constraints on total power can be written as constraints on the column norms of $\mathbf{V}$ (one per mosaic):

$$P \geq (\mathbf{V}^\dagger\mathbf{V})_{mm} = \sum_k |v_{km}|^2 = \sum_k \left| \sum_i \upsilon_i a_{ki} b_{mi} \right| \tag{18}$$

$$= \sum_{ijk} \upsilon_i \upsilon_j^* a_{ki} b_{mi} a_{kj}^* b_{mj}^* = \sum_{ijk} \upsilon_i \upsilon_j^* \delta_{ij} b_{mi} b_{mj}^* \tag{19}$$

$$= \sum_i |\upsilon_i|^2 |b_{mi}|^2 \tag{20}$$

where we have implicitly summed over $\mathbf{k}$ and used the SVD: $\mathbf{V} = \mathbf{A}\boldsymbol{\Upsilon}\mathbf{B}^\dagger$ and $\mathbf{A}^\dagger\mathbf{A} = \mathbf{A}\mathbf{A}^\dagger = \mathbb{1}$. Of course, $\mathbf{B}$ is also unitary, so $\sum_i |b_{mi}|^2 = 1$. Taken together, this gives a combined optimization objective

$$\int_{G_0} \frac{d^2\mathbf{k}}{(2\pi)^2} \left[\sum_c \left[\log \frac{\sum_{\mathbf{g}\in G} (\upsilon_c^2(\lambda_c + 1))(\mathbf{k}+\mathbf{g}) + \varepsilon^2}{\sum_{\mathbf{g}\in G} \upsilon_c^2(\mathbf{k}+\mathbf{g}) + \varepsilon^2} \right] \right.$$
$$\left. - \sum_m \nu_m \sum_{\mathbf{g}\in G} \sum_c \upsilon_c^2(\mathbf{k}+\mathbf{g}) |b_{mc}(\mathbf{k}+\mathbf{g})|^2 + \sum_{\mathbf{g}\in G} \sum_c \alpha_c(\mathbf{k}+\mathbf{g}) \upsilon_c^2(\mathbf{k}+\mathbf{g}) \right], \tag{21}$$

which is equivalent to the optimization problem in (Jun *et al.* 2022) provided we identify υ_c^2 here with $|v|^2$ there and define an effective $\tilde{\nu}_c \equiv \sum_m \nu_m |b_{mi}|^2$ to be identified with ν in that earlier work. Clearly, the frequency-space shapes of the filters for the different m, which correspond to different generalized eigenvalues of $\mathbf{C}(k)$, will then have the same form as derived in (Jun *et al.* 2022), that of (Atick & Redlich 1992), while the b_{mi}, which are constrained for each m to lie on a sphere, apportion the power budget among these eigenvalue channels (which are *not* necessarily color channels). Indeed, these channels are equivalent to the eigenspectra $R_\pm(\mathbf{f})$ in (Atick, Li, *et al.* 1992)[3] that give rise to $M_\pm(f)$ and $K_\pm(f)$, resulting in per-eigenspectrum filters like those in (Atick & Redlich 1992). In addition, in (Atick, Li, *et al.* 1992), several additional assumptions further simplify this treatment. There, it was assumed that $C_{ab}(k) = c_{ab}R(k)$ (correlations among photoreceptors are independent of frequency, and the power spectrum of each photoreceptor is the same). Symmetry among channels then suggests we take $b_{mc}(\mathbf{k}+\mathbf{g}) = b_{mc}$ (mosaics mix eigenchannels independent of frequency) and $\lambda_c(\mathbf{k}+\mathbf{g}) = \lambda_c R(k)$ (again, eigenchannel vectors are the same at each frequency).

Now, using these conventions, we can write the total power in each eigenchannel as (cf. A.5 in (Jun *et al.* 2022))

$$P_c = \int dk\, p_c(k) = \int_{G_0} \frac{d^2\mathbf{k}}{(2\pi)^2} \varepsilon^2 \left[\frac{1}{2}\lambda_c R(k) \left(\sqrt{1 + \frac{1}{\varepsilon^2} \frac{4}{\tilde{\nu}_c \lambda_c R(k)}} - 1 \right) - 1 \right]_+ \tag{22}$$

[2]One can show this by using the SVD: $\mathbf{V} = \mathbf{A}\mathbf{S}\mathbf{B}^\dagger = \sum_i s_i \mathbf{a}_i \mathbf{b}_i^\dagger$ gives

$$\mathbf{V}^\dagger(\boldsymbol{\Lambda} + \mathbb{1})\mathbf{V} = \sum_{ij} \upsilon_i^* \upsilon_j \mathbf{b}_i \mathbf{a}_i^\dagger (\lambda_i + 1) \delta_{ij} \mathbf{a}_j \mathbf{b}_j^\dagger = \sum_i |\upsilon_i|^2 (\lambda_i + 1) \mathbf{b}_i \mathbf{b}_i^\dagger \tag{17}$$

with $\mathbf{b}_i$ the eigenvectors of $\mathbf{V}^\dagger\mathbf{V}$.

[3]Under the factorizing assumption the spectra are identical as a function of frequency: $C_{ab}(k) = c_{ab}R(k)$.

and the information in each eigenchannel as

$$\mathcal{I}_c = \int_{G_0} \frac{d^2\mathbf{k}}{(2\pi)^2} \log \frac{p_c(k) + \varepsilon^2}{} \tag{23}$$

Information as a function of power

We can now try to get an intuition for the solutions of (21): maximizing the sum of log terms will incentivize whitening among the eigenchannels, such that we want to equate $\upsilon_c^2(\lambda_c + 1)$ as much as possible across them within our power budget, and each eigenchannel carries roughly equal information. This power budget, in turn, is allocated to each eigenchannel based on $\mathbf{B}$, a Hermitian matrix, and in considering its effect, it will help us to define $(\mathbf{B}^2)_{mc} = |b_{mc}|^2 = (\mathbf{B}^\dagger \odot \mathbf{B})_{mc}$. Now the fact that $\mathbf{B}$ is Hermitian implies $\mathbf{B}^\dagger\mathbf{B} = \mathbf{B}\mathbf{B}^\dagger = \mathbb{1}$, and both the columns and the rows are orthonormal. This means that

$$\sum_m |b_{mc}|^2 = 1 \qquad \sum_c |b_{mc}|^2 = 1 \qquad \mathbf{B^2} \cdot \mathbf{1} = \mathbf{1} \qquad \mathbf{1}^\top \mathbf{B^2} = \mathbf{1}^\top, \tag{24}$$

and $\mathbf{B^2}$ is a doubly stochastic matrix. This lets us rewrite things more simply as:

$$\tilde{\boldsymbol{\nu}}^\top \equiv \boldsymbol{\nu}^\top \mathbf{B^2} \tag{25}$$

$$\mathbf{B^2} \cdot \mathbf{p} \leq P\mathbf{1} \qquad p_c \equiv \sum_k \upsilon_c^2(k; \tilde{\nu}_c) \tag{26}$$

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References

1. Atick, J. J., Li, Z. & Redlich, A. N. Understanding retinal color coding from first principles. *Neural computation* **4,** 559–572 (1992).
2. Atick, J. J. & Redlich, A. N. What does the retina know about natural scenes? *Neural computation* **4,** 196–210 (1992).
3. Ghojogh, B., Karray, F. & Crowley, M. Eigenvalue and generalized eigenvalue problems: Tutorial. *arXiv preprint arXiv:1903.11240* (2019).
4. Jun, N. Y., Field, G. & Pearson, J. Efficient coding, channel capacity, and the emergence of retinal mosaics. *Advances in neural information processing systems* **35,** 32311–32324 (2022).
5. Jun, N. Y., Field, G. D. & Pearson, J. Scene statistics and noise determine the relative arrangement of receptive field mosaics. *Proceedings of the National Academy of Sciences* **118,** e2105115118 (2021).

Supplemental Material

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