notes on efficient coding of color

John Pearson[1,2,3,4*], others[1]

1 Department of Neurobiology
2 Department of Biostatistics & Bioinformatics,
3 Department of Psychology & Neuroscience,
4 Department of Electrical & Computer Engineering,
Duke University, Durham NC 27710, USA

*** Corresponding author: john.pearson@duke.edu**

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*

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

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

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

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

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

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

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

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 $\sum_{ab} v_a^*(\mathbf{k}+\mathbf{g})v_b(\mathbf{k}+\mathbf{g})\sigma_a^2\delta_{ab} = |v(\mathbf{k}+\mathbf{g})|^2\sigma^2$, 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

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

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

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 $\mathbf{C}_{\text{in}}(k) = \text{diag}(\boldsymbol{\sigma^2})$:

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

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)

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

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

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

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

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

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

[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 $\tilde{\nu}_c \equiv \sum_m \nu_m |b_{mc}|^2$ 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_{mc}, 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: $\mathbf{V} = \mathbf{A}\boldsymbol{\Upsilon}\mathbf{B}^\dagger = \sum_i \upsilon_i \mathbf{a}_i \mathbf{b}_i^\dagger$ 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 (cp. Eqs. 29 and 30 in (Jun *et al.* 2022))

$$\mathcal{I}_c = \int_{G_0} \frac{d^2\mathbf{k}}{(2\pi)^2} \log \frac{p_c(k;\tilde{\nu}_c) + \varepsilon^2}{\frac{1}{\lambda_c R(k)+1} p_c(k;\tilde{\nu}_c) + \varepsilon^2}. \tag{23}$$

Clearly, if $R(k) \xrightarrow[k\to\infty]{} 0$, then $\mathcal{I}(k) \to 0$ in the same limit, and there are diminishing returns to information as we increase power.

We can also get some intuition for the geometry of the problem by rewriting the constraints in matrix form:

$$\mathrm{diag}(\tilde{\boldsymbol{\nu}}) = \mathbf{B}^\dagger \mathrm{diag}(\boldsymbol{\nu}) \mathbf{B} \tag{24}$$

$$P\mathbf{1} \geq \mathrm{diag}\left(\mathbf{B}\,\mathrm{diag}(\mathbf{p})\mathbf{B}^\dagger\right) \tag{25}$$

$$p_c(\tilde{\nu}_c) \equiv \int_{G_0} \frac{d^2\mathbf{k}}{(2\pi)^2} p_c(k;\tilde{\nu}_c). \tag{26}$$

Note a few things here:

- In both cases, the transformation on the right-hand side is that of a covariance matrix under coordinate rotations specified by $\mathbf{B}$.
- For the Lagrange multipliers, the fact that $\mathbf{B}$ is Hermitian means that we also have $\mathrm{diag}(\boldsymbol{\nu}) = \mathbf{B}\,\mathrm{diag}(\tilde{\boldsymbol{\nu}})\mathbf{B}^\dagger$, which means that $\mathrm{diag}(\boldsymbol{\nu})$ is the representation of $\mathrm{diag}(\tilde{\boldsymbol{\nu}})$ in the new coordinates specified by $\mathbf{B}$.
- This also means that any possible $\tilde{\boldsymbol{\nu}} \geq \mathbf{0}$ corresponds to a feasible choice of Lagrange multipliers $\boldsymbol{\nu} \geq \mathbf{0}$, since the original diagonal matrix is positive-definite, and that is preserved under a Hermitian transformation. This means that we can dispense with $\boldsymbol{\nu}$ and think instead in terms of $\tilde{\boldsymbol{\nu}}$, which will be easier.
- A similar thing is true for the inequality constraint, except that the constraint is only applied to the *diagonal* entries of the $\mathrm{diag}(\mathbf{p})$ matrix transformed into the new coordinates.
- Since the Hermitian transformation cannot alter the trace of a matrix it transforms, $\mathrm{tr}(\mathbf{B}\,\mathrm{diag}(\mathbf{p})\mathbf{B}^\dagger) = \sum_c p_c$, and the diagonal elements of the transformed matrix that end up being constrained are necessarily just a reapportionment of power in the eigenchannels.

Together, these lead us to the following solution for $\mathbf{B}$: For a given choice of $\tilde{\boldsymbol{\nu}}$, we have a relationship $\mathbf{p}(\tilde{\boldsymbol{\nu}})$ that yields the total power in each eigenchannel. That is, specifying $\tilde{\nu}_c$ is the same as specifying the power in its corresponding eigenchannel. The matrix $\mathbf{B}$ then rotates the diagonal matrix $\mathrm{diag}(\mathbf{p})$ into a new basis, where we constrain its diagonal elements to each be less than P, though the sum of these diagonal elements cannot change. Clearly, the optimal solution in this case is to use the rotation to *balance* the allocation, such that $\mathrm{diag}\left(\mathbf{B}\,\mathrm{diag}(\mathbf{p})\mathbf{B}^\dagger\right) \propto \mathbf{1}$.[4] That is, the power carried by each mosaic (a combination of eigenchannels) is *equal*.

Thus, given $\tilde{\boldsymbol{\nu}}$ (and thus $\mathbf{p}$), we can always calculate the optimal $\mathbf{B}$. But how do we choose $\tilde{\boldsymbol{\nu}}$? The answer lies in (23), which calculates the information carried by each eigenchannel.[5] As a result, the total information carried by all mosaics is just a sum of this quantity, and the optimal allocation will be the point at which total information is maximized subject to the power constraint. If the power constrain is P in each mosaic, and there are M mosaics, then we must have $\sum_c p_c(\tilde{\nu}_c) = PM$, since, as we've

[4]Proof: Assume we have an optimal solution in which the rotated power matrix does not have equal diagonals. If none of the constraints is tight, we can, by (23), increase the information encoded by further increasing power to one or more eigenchannels. If some but not all of the constraints are tight, we can redistribute power from tight constraints to loose ones by choosing a different $\mathbf{B}$, loosening all constraints and allowing us to add more power (and thus more information). Thus, the original solution was not optimal. ■

[5]It may seem odd that we are concerned with the power carried by the actual mosaic but that information can be calculated by eigenchannels. The resolution is that, in our linear setup, the mosaics are a linear combination of eigenchannels, and linear transformations do not change information.

seen, the rotation by $\mathbf{B}$ does not change the trace of the matrix diag($\mathbf{p}$), and the optimal solution is to distribute this power equally across mosaics. As a result, if we could invert the (monotonic) relationship between $\tilde{\nu}_c$ and p_c to yield $\tilde{\nu}_c(p_c)$, then we could write

$$\mathcal{I}(\mathbf{p}) = \sum_c \mathcal{I}_c(p_c) \tag{27}$$

and we are looking for the highest contour of this quantity in $\mathbf{p}$ space that lies inside the hyperplane $\mathbf{p} \cdot \mathbf{1} = PM$. In (Jun *et al.* 2022), it was found that for $p_c \sim \tilde{\nu}_c^{-1}$ initially and $p_c \sim \tilde{\nu}_c^{-1/2}$ for larger values of p_c when $C(k) \simeq 1/k^{\alpha}$.

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

stuff goes here