Receptor Profiles and Gabor Frames

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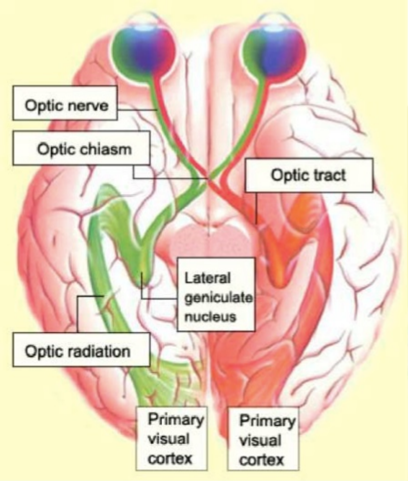
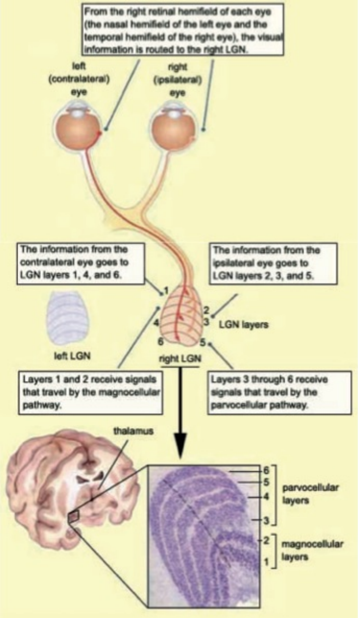
Geometry of Neuroscience

References for this lecture:

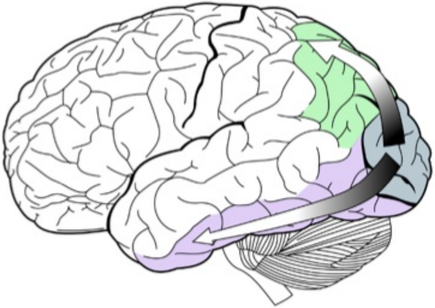
- Jean Petitot, *Neurogéométrie de la Vision*, Les Éditions de l'École Polytechnique, 2008
- D. Marr, *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information* (1982), MIT Press, 2010
- S.Marcelja, *Mathematical description of the responses of simple cortical cells*, J Opt Soc Am A 70 (1980) 1297–1300
- Karlheinz Gröchenig, *Multivariate Gabor frames and sampling of entire functions of several variables*, Appl. Comput. Harmon. Anal. 31 (2011) 218–227

Magnocellular and Parvocellular Pathways



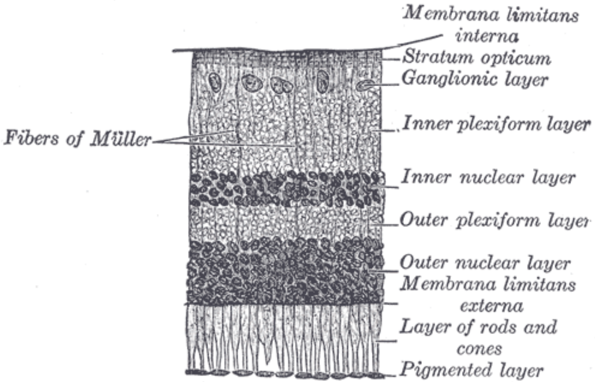


starting with the V1 cortex the magnocellular and parvocellular pathways part ways: dorsal and ventral (movement versus form recognition, where/what)

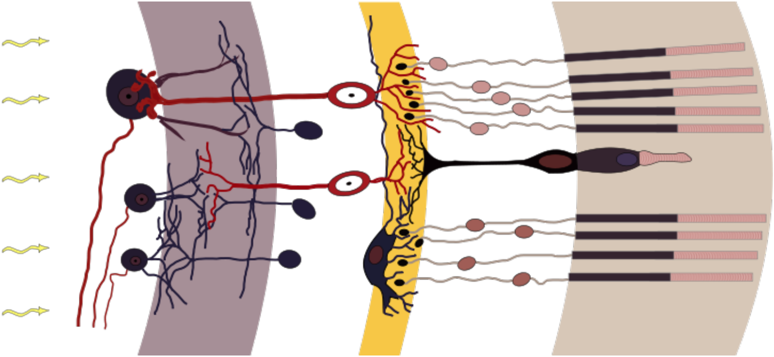


Layered structure of the retina

- ten layers of structure in the retina



- four main stages: photoreception, transmission to bipolar cells, transmission to ganglion cells containing photoreceptors (photosensitive ganglion cells), transmission along optic nerve



- incoming light (left) passes through nerve layers, reaches rods and cones (right) chemical change transmits signal back to bipolar and horizontal cells (yellow) and ganglion cells (purple) and to optic nerve

Receptor Field

• the receptor field (RF) of a neuron in the visual cortex is an area D of the retina to which it responds, emitting a spike train

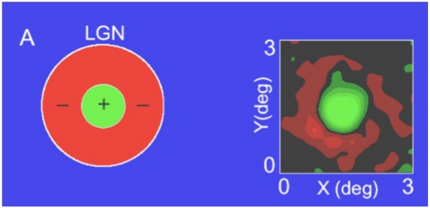
• receptor field has zones (ON) that respond positively to pointwise light stimuli and other zones (OFF) that respond negatively

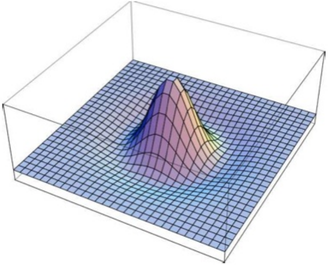
• receptive profile (RP): a function $\varphi : D \to \mathbb{R}$ that measures the response of the neuron, positive on the ON zones, negative on the OFF zones

• the neuron acts as a filter

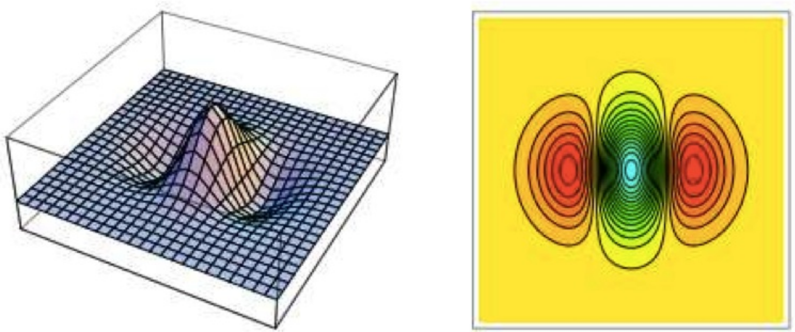
• by electrophysiology techniques it is possible to measure level sets of the receptor profiles φ of different visual neurons

Example: receptor profile of a cell in the lateral geniculate nucleus



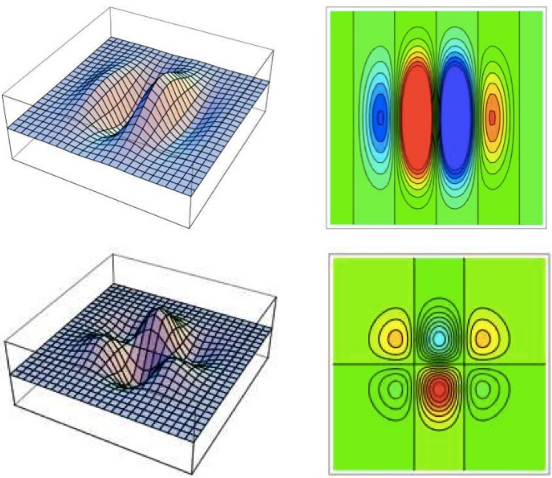


Example: typical receptor profile of a neuron in the V1 cortex



• presence of a preferred direction; modeled by directional derivatives of two-variable Gaussians

Other Examples: more receptor profiles of neurons in the V1 cortex

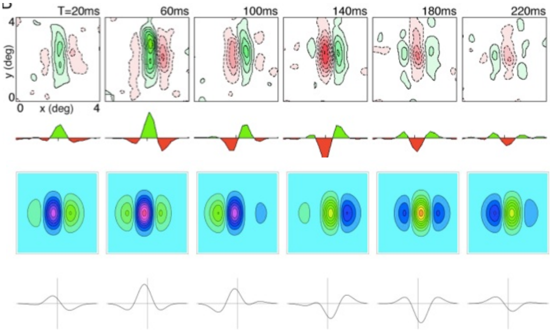


Spatio-temporal separability

• certain receptor profiles do not change their spatial pattern with time, only the intensity:

$$\varphi(x, y, t) = \varphi_{\text{spatial}}(x, y) \cdot \varphi_{\text{temporal}}(t)$$

• other receptor profiles do not have this kind of space/time dependence separation



Gaussian derivatives and Hermite polynomials

$$G_\sigma = G(x,\sigma) = \frac{1}{\sqrt{2\pi}\,\sigma} \exp\left(-\frac{x^2}{2\sigma^2}\right)$$

$$\frac{d^n}{dx^n} \exp\left(-\frac{x^2}{2\sigma^2}\right) = (-1)^n\, H_{n,\sigma}(x)\, \exp\left(-\frac{x^2}{2\sigma^2}\right)$$

$$H_{n,\sigma}(x) = (\sqrt{2}\,\sigma)^{-n}\, H_n(\frac{x}{\sigma\sqrt{2}})$$

- Hermite polynomials $H_n(x)$

$$\frac{d^n}{dx^n} e^{-x^2} = (-1)^n H_n(x)\, e^{-x^2}$$

$$H_0(x) = 1,\ H_1(x) = 2x,\ H_2(x) = 4x^2 - 2,\ H_3(x) = 8x^3 - 12x, \cdots$$

- recursion relation

$$H_{n+1}(x) = 2x\, H_n(x) - H_n'(x)$$

- explicit form

$$H_n(x) = n! \sum_{m=0}^{\lfloor \frac{n}{2} \rfloor} \frac{(-1)^m}{m!(n-2m)!} (2x)^{n-2m}$$

- orthogonality: $L^2(\mathbb{R}, w(x)dx)$ with $w(x) = e^{-x^2}$

$$\int_{\mathbb{R}} H_n(x) H_m(x)\, w(x) dx = n! 2^n \sqrt{2}\, \delta_{n,m}$$

complete orthogonal basis

- generating function

$$\exp(2xs - s^2) = \sum_{n=0}^{\infty} H_n(x) \frac{s^n}{n!}$$

Fourier transform and power spectra

- Fourier transform

$$\mathcal{F}(f)(\omega) = \hat{f}(\omega) = \frac{1}{\sqrt{2\pi}} \int_{\mathbb{R}} f(x)\, e^{-ix\omega} dx$$

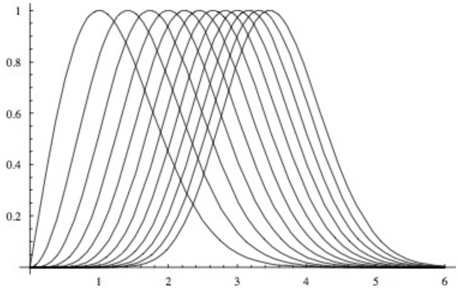
$$\mathcal{F}(G_\sigma)(\omega) = \frac{1}{\sqrt{2\pi}} \exp(-\frac{\sigma^2\omega^2}{2})$$

$$\mathcal{F}(D^n G_\sigma)(\omega) = (-i\omega)^n \mathcal{F}(G_\sigma), \quad \text{with } D^n = \frac{d^n}{dx^n}$$

Gaussian derivatives, when used as kernel operators (acting by convolution) act as bandpass filters

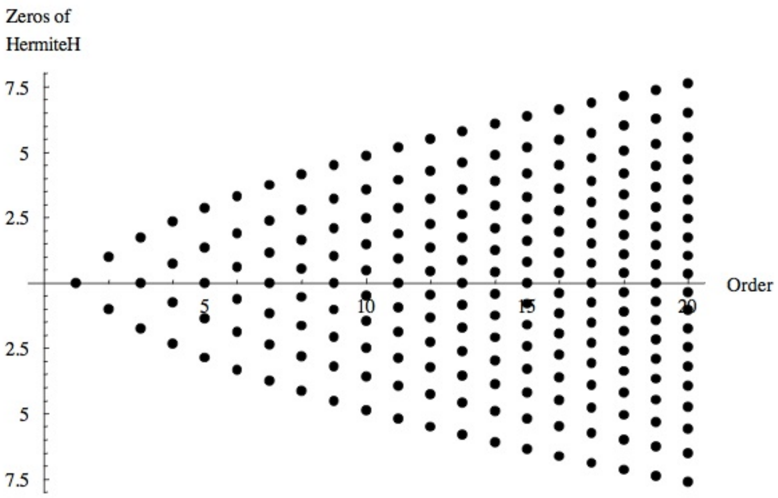
- maximum amplitude for $\mathcal{F}(D^n G_\sigma)$ at $\omega = \sqrt{n}$

shape of normalized power spectra $|\mathcal{F}(D^n G_\sigma)(\omega)/\mathcal{F}(D^n G_\sigma)(\sqrt{n})|$

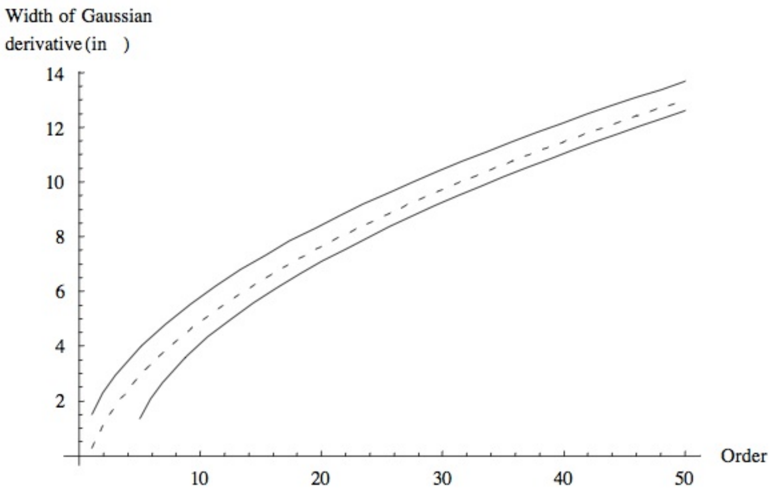


for $n = 1, \ldots, 12$ (left to right) with $\sigma = 1$

• width of a Gaussian derivative $D^n G_\sigma(x)$ is largest distance between zeros (zeros of Hermite polynomials): zeros of second derivatives $x = \pm\sigma$ one standard deviation from $x = 0$


Zeros of
HermiteH
7.5
5
2.5
2.5
5
7.5
5
10
15
20
Order

• no exact close formula for largest zero, but Zernicke and Szego estimates (above and below in plot)



Correlation between Gaussian Derivatives

$$r_{n,m} = \frac{\langle D^n G_\sigma, D^m G_\sigma \rangle}{\|D^n G_\sigma\| \cdot \|D^m G_\sigma\|}$$

Note: inner product and norm in $L^2(\mathbb{R}, dx)$ (non-weighted)

- $r_{n,n} = 1$ and $r_{n,m} = 0$ if $n - m$ odd
- for $n - m$ even, suppose $n > m$, after integrations by parts

$$\langle D^n G_\sigma, D^m G_\sigma \rangle = (-1)^{\frac{n-m}{2}} \|D^{\frac{n-m}{2}} G_\sigma\|^2$$

- Parseval identity (Plancherel theorem): Fourier transform preserves L^2-norm

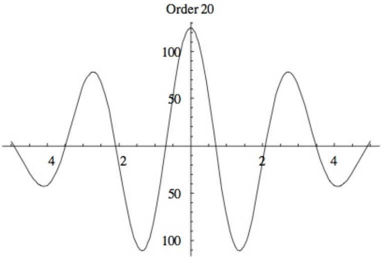
$$= (-1)^{\frac{n-m}{2}} \|(i\omega)^{\frac{n-m}{2}} \mathcal{F}(G_\sigma)(\omega)\|^2 = \frac{(-1)^{\frac{n-m}{2}}}{2\pi\sigma^{n+m+1}} \int_{\mathbb{R}} \omega^{n+m} e^{-\omega^2} d\omega$$

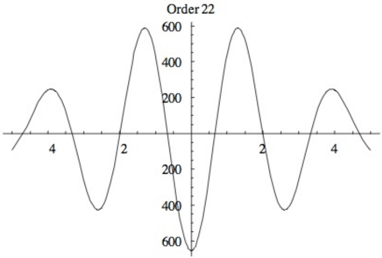
- last integral explicitly in terms of Γ-function

$$\int_{\mathbb{R}} x^{n+m} e^{-x^2} dx = \frac{1 + (-1)^{m+n}}{2} \Gamma(\frac{m+n+1}{2})$$

- resulting correlations:

$$r_{n,m} = \frac{(-1)^{\frac{n-m}{2}} (2\pi\sigma^{n+m+1})^{-1} \Gamma(\frac{m+n+1}{2})}{\sqrt{(2\pi\sigma^{2n+1})\Gamma(\frac{2n+1}{2})}\sqrt{(2\pi\sigma^{2m+1})\Gamma(\frac{2m+1}{2})}} = \frac{(-1)^{\frac{n-m}{2}} \Gamma(\frac{m+n+1}{2})}{(\Gamma(\frac{2n+1}{2})\Gamma(\frac{2m+1}{2}))^{1/2}}$$



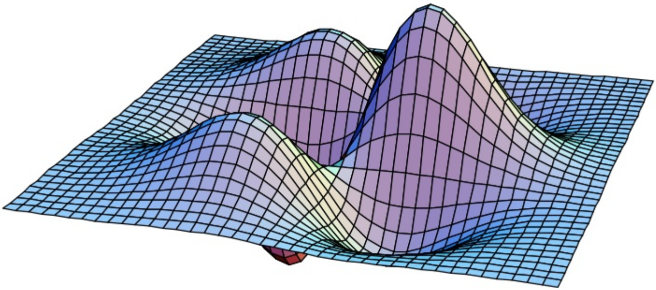


with $|n-m| = 2$ anticorrelation while very similar with large overlap when $|n-m| = 4$

- higher dimensional Gaussian Derivatives filters

$$G_\sigma(x,y) = G_{\sigma_x}(x) \cdot G_{\sigma_y}(y)$$

$$D_x^n D_y^m G_\sigma(x,y)$$



Gaussian Derivative filter $D_x D_y^2 G_\sigma(x,y)$ with $\sigma_x = \sigma_y = 2$

anisotropic if $\sigma_x \neq \sigma_y$ with anisotropy ratio σ_x/σ_y

Gabor Frames for Modulation

• if want filters tuned to waves at certain specific frequencies better use the Gabor functions

$$\mathcal{G}_{n,m}(a, b, \sigma; x) = e^{2\pi imbx} G_\sigma(x - na)$$

parameters $a, b, \sigma > 0$, and $n, m \in \mathbb{Z}$

• trigonometric functions $\sin(2\pi mbx)$ and $\cos(2\pi mbx)$ instead of Hermite polynomials:

- infinite number of zeros
- amplitude bounded by the Gaussian shape (Gaussian window)

• can approximate Gaussian Derivatives well by Gabor functions

• Gabor function model of cortical receptive fields (Marcejia, 1980)
S.Marcelja, *Mathematical description of the responses of simple cortical cells*, J Opt Soc Am A 70 (1980) 1297–1300

Frames and non-orthonormal overcomplete expansions

- usual setting: Hilbert space $\mathcal{H}$, complete orthonormal system $\{\phi_n\}$, expansion $f = \sum_n c_n \phi_n$ with unique $c_n = \langle \phi_n, f \rangle$
- more generally Banach space $\mathcal{B}$, complete system $\{\phi_\alpha\}$ if every element $f \in \mathcal{B}$ can be approximated arbitrarily well in norm by linear combinations of ϕ_α
- system $\{\phi_\alpha\}_{\alpha \in \mathcal{J}}$ is overcomplete if it is a redundant complete set, namely it is complete and for some $j \in \mathcal{J}$ the set $\{\phi_\alpha\}_{\alpha \in \mathcal{J} \smallsetminus \{j\}}$ is also complete
- a set $\{\phi_\alpha\}$ in a Hilbert space $\mathcal{H}$ is a frame if there are constants $A, B > 0$ such that for all $f \in \mathcal{H}$

$$A\|f\|^2 \leq \sum_{\alpha \in \mathcal{J}} |\langle \phi_\alpha, f \rangle|^2 \leq B\|f\|^2$$

- non-orthogonal overcomplete expansion in a frame: frame $\{\phi_\alpha\}$, every $f \in \mathcal{H}$ has expansion $f = \sum_\alpha c_\alpha \phi_\alpha$ with $c = (c_\alpha) \in \ell^2(\mathcal{J})$ with $\|c\|_{\ell^2} \leq C\|f\|_{\mathcal{H}}$

Gabor frames (Lyubarskii, Seip)

- Gabor frame in dimension $d = 1$: set $\{\mathcal{G}_\lambda\}_{\lambda\in\Lambda}$ of Gabor functions

$$\mathcal{G}_\lambda(x) = e^{2\pi i \lambda_2 x} G(x - \lambda_1)$$

with $\lambda = (\lambda_1, \lambda_2) \in \Lambda \subset \mathbb{R}^2$ a lattice and with $G(x) = e^{-\pi x^2}$ is a frame if and only if lower Beurling density

$$\delta^-(\Lambda) > 1$$

- lower and upper Beurling density (or uniform densities) of a lattice $\Lambda \subset \mathbb{R}^2$

$$\delta^-(\Lambda) = \liminf_{r\to\infty} \frac{n_\Lambda^-(r)}{r^2}, \quad \delta^-(\Lambda) = \limsup_{r\to\infty} \frac{n_\Lambda^+(r)}{r^2}$$

where $n_\Lambda^\pm(r)$ are the largest and smallest number of points of Λ contained in the set $r\mathcal{I}$ where $\mathcal{I} \subset \mathbb{R}^2$ is a fixed compact set of measure 1 (and measure zero boundary: e.g. unit square)

Higher dimensional Gabor frames

• Gabor functions in d dimensions: lattice $\Lambda \subset \mathbb{R}^{2d}$

$$\mathcal{G}_\lambda(x) = \exp(2\pi i \lambda_2 \cdot x)\, G(x - \lambda_1)$$

$$G(x) = \exp(-\pi x \cdot x), \quad x \in \mathbb{R}^d$$

for $\lambda = (\lambda_1, \lambda_2) \in \Lambda$, with $\lambda_1 \in \mathbb{R}^d$

• Karlheinz Gröchenig, *Multivariate Gabor frames and sampling of entire functions of several variables*, Appl. Comput. Harmon. Anal. 31 (2011) 218–227

• lattice $\Lambda = A\mathbb{Z}^{2d}$ some $A \in \mathrm{GL}(2d, \mathbb{R})$

$$s(\Lambda) = |\det(A)|$$

$s(\Lambda)^{-1}$ measures lattice points per unit cube, gives density

• adjoint lattice $\Lambda^o = J(A^T)^{-1}\mathbb{Z}^{2d}$, with A^T transpose and

$$J = \begin{pmatrix} 0 & I \\ -I & 0 \end{pmatrix}$$

• Wexler-Raz biorthogonality: if know $\{\mathcal{G}_\lambda\}_{\lambda\in\Lambda}$ satisfies

$$\sum_\lambda |\langle \mathcal{G}_\lambda, f\rangle|^2 \leq B\|f\|^2$$

for all $f \in L^2(\mathbb{R}^d)$ (Bessel sequence) then also frame iff there is another Bessel sequence

$$\mathcal{L}_\lambda(x) = \exp(2\pi i \lambda_2 \cdot x)\, L(x - \lambda_1)$$

where $L \in L^2(\mathbb{R}^d)$ satisfying biorthogonality

$$\langle L, \mathcal{G}_\mu\rangle = s(\Lambda)\cdot \delta_{\mu,0}, \quad \mu \in \Lambda^o$$

• density result: if $\{\mathcal{G}_\lambda\}_{\lambda\in\Lambda}$ is a frame then $s(\Lambda) < 1$ (based on Poisson summation formula, with $G \in \mathcal{S}(\mathbb{R}^d)$)

• open condition: if for $\Lambda = A\mathbb{Z}^{2d}$ the set $\{\mathcal{G}_\lambda\}_{\lambda\in\Lambda}$ is a frame, then there is an open neighborhood $\mathcal{V}$ of A in $\mathrm{GL}(2d,\mathbb{R})$ where also a frame

Gabor frames via complex analysis (Gröchenig)

- Gabor frames question (with Gaussian window) related to sampling and interpolation in Bargmann-Fock spaces

$$\|F\|^2_{\mathcal{F}} = \int_{\mathbb{C}^d} |F(z)|^2 e^{-\pi|z|^2} dz < \infty$$

F entire function $z = (z_1, \dots, z_d) \in \mathbb{C}^d$, with $|z|^2 = \sum_i z_i \bar{z}_i$

$$\langle F_1, F_2 \rangle_{\mathcal{F}} = \int_{\mathbb{C}^d} \overline{F_1(z)} F_2(z) e^{-\pi|z|^2} dz$$

- Bargmann transform unitary $\mathcal{B} : L^2(\mathbb{R}^d) \to \mathcal{F}$

$$(\mathcal{B}f)(z) = 2^{d/4} e^{-\pi z^2/2} \int_{\mathbb{R}^d} f(x) e^{-\pi x\cdot x} e^{2\pi x\cdot z} dx$$

- frames and sampling: $\{\mathcal{G}_{\bar\lambda}\}_{\bar\lambda \in \bar\Lambda}$ frame iff

$$\sum_{\lambda\in\Lambda} |F(\lambda)|^2 e^{-\pi|\lambda|^2} \asymp \|F\|^2_{\mathcal{F}}$$

for all $F \in \mathcal{F}$: Λ is a sampling of $\mathcal{F}$

because $|\langle f, \mathcal{G}_{\bar z}\rangle| = |\mathcal{B}f(z)| e^{-\pi|z|^2/2}$ and $F = \mathcal{B}f$

• sampling and interpolation: frame condition equivalent to sampling condition as above; by Wexler-Raz biorthogonality frame condition also equivalent to interpolation condition:

$$\exists F_o \in \mathcal{F} : \quad F_o(\mu) = \delta_{\mu,0}, \quad \forall \mu \in \Lambda^o$$

taking $F_o = \mathcal{B}L$ with L in biorthogonality

• addressing frame question by constructing solutions of the interpolation problem: entire functions with controlled growth and with zeros at all points of a given lattice

• in one dimension $d = 1$ lattices $\Lambda \subset \mathbb{C}$ a version of the Weierstrass sigma-function

$$\sigma_\Lambda(z) = \left(z \prod_{\lambda \in \Lambda \smallsetminus \{0\}} \left(1 - \frac{z}{\lambda}\right) e^{\frac{z}{\lambda} + \frac{z^2}{2\lambda^2}} \right) e^{az^2}$$

parameter $a \in \mathbb{C}$ can be fixed so that $|\sigma_\Lambda(z)| e^{-\frac{\pi}{2s(\Lambda)}|z|^2}$ is Λ-periodic, so get vanishing and growth: $\sigma_\Lambda(\mu) = 0 \ \forall \mu \in \Lambda$ and

$$|\sigma_\Lambda(z)| \leq C\, e^{\frac{\pi}{2s(\Lambda)}|z|^2}$$

Higher dimensional interpolation solutions

• restrict to complex lattices $\Lambda = A(\mathbb{Z}^d + i\mathbb{Z}^d) \subset \mathbb{C}^d$ with $A \in \mathrm{GL}(d,\mathbb{C})$: can also write as $\Lambda = A(\oplus_{j=1}^d L_j)$ with $L_j \subset \mathbb{C}$ normalized lattice $s(L_j) = 1$; size $s(\Lambda) = |\det(A)|^2$

• interpolation solution for complex Λ: entire function F_Λ

$$F_\Lambda(\lambda) = \delta_{\lambda,0}, \ \forall \lambda \in \Lambda, \quad \text{and} \quad |F_\Lambda(z)| \leq C e^{\pi \|A^{-1}\|_{op}^2 \frac{|z|^2}{2}}$$

• construction for $\Lambda = \oplus_j L_j$

$$\sigma_0(z_1, \ldots, z_d) = \prod_{j=1}^d \frac{\sigma_{L_j}(z_j)}{z_j}, \quad \text{and} \quad F_\Lambda(z) = \sigma_0(A^{-1} z)$$

previous properties of the Weierstrass sigma-functions σ_{L_j} determine vanishing and growth conditions for F_Λ

Frame Conditions: for a complex lattice $\Lambda = A(\oplus_j L_j)$

- adjoint lattice: for complex lattices $\Lambda^o = (A^*)^{-1}(\oplus_j L_j)$
- decompose $A = US$, unitary U (unitaries do not change frame/sampling/interpolation property) and S upper diagonal with characteristic numbers γ_j on diagonal
- then enough to check $\Lambda = S(\oplus_j L_j)$ with $\Lambda^o = (S^*)^{-1}(\oplus_j L_j)$
- assume $\gamma_j < 1$ for $j = 1, \ldots, d$
- entire function

$$F_\Lambda(z) = \prod_{j=1}^{d} \frac{\sigma_{L_j}(\gamma_j z_j)}{z_j}$$

$$|F_\Lambda(z)| \leq C \prod_j e^{\pi \gamma_j^2 |z_j|^2/2}$$

because $\gamma_j < 1$ entire function $F_\Lambda \in \mathcal{F}$

- also vanishing on $\mu = (S^*)^{-1}\lambda \in \Lambda^o$

Conclusions on Gabor Frames

• for Λ complex lattice with characteristic indices $0 < \gamma_j < 1$ the set $\{\mathcal{G}_\lambda\}_{\lambda\in\Lambda}$ is a frame for $L^2(\mathbb{R}^d)$

• Note: condition $\gamma_j < 1$ is sufficient but not necessary: there are lattices without this condition that give rise to frames

• for modeling of visual receptor fields especially interested in the case $d = 2$

$$\Lambda = A(L_1 \oplus L_2), \quad A = \begin{pmatrix} \gamma_1 & b \\ 0 & \gamma_2 \end{pmatrix}$$

1. $\gamma_1 < 1$ and $\gamma_2 < 1$: Gabor frame
2. $\gamma_2 \geq 1$: not Gabor frame
3. $\gamma_1 \geq 1$, $\gamma_2 < 1$ and $\gamma_1\gamma_2 < (\gamma_2^2 + |b|^2)^{1/2} < 1$: Gabor frame
4. $\gamma_1 \geq 1$, $\gamma_2 < 1$ and $\gamma_1\gamma_2 \geq (\gamma_2^2 + |b|^2)^{1/2}$: not Gabor frame
5. $\gamma_1 \geq 1$, $\gamma_2 < 1$ and $\gamma_1\gamma_2 < 1 \leq (\gamma_2^2 + |b|^2)^{1/2}$: not known

Conclusions about Reception Fields

• Receptor Profiles described accurately by Gabor functions in dimension $d = 2$

• Gabor functions act as a filters at specific frequencies, shaped with preferred directions

• if Gabor frame: good non-orthogonal overcomplete expansions for signal processing

• Question: when are the $d = 2$ Gabor frame conditions satisfied in the neuron receptor fields case?