Turing Instability in a 1D Neural Wave Equation

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Synaptic Processing

- Post-synaptic current:

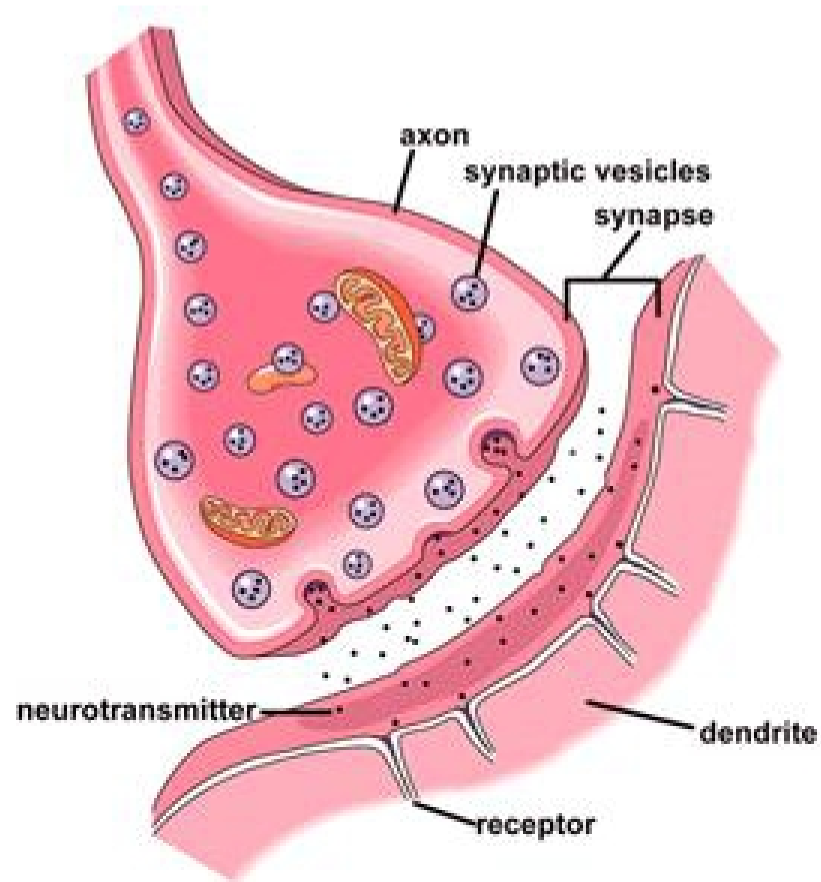
$$I_s = g(V_s - V).$$

$$V_s > 0 : \text{excitatory},$$
$$V_s < 0 : \text{inhibitory}.$$

- Conductance change:

$$g(t) = \bar{g}\eta(t - T), \quad t \geq T,$$

$$g(t) = \bar{g}\sum_m \eta(t - T_m).$$



Synaptic Processing

- Two common choices for $\eta(t)$:

$$\eta(t) = \left(\frac{1}{\alpha} - \frac{1}{\beta}\right)^{-1} [e^{-\alpha t} - e^{-\beta t}] H(t),$$

$$\eta(t) = \alpha e^{-\alpha t} H(t).$$

- Conductance change from train of APs: $$g(t) = \bar{g} \sum_m \eta(t - T_m).$$

Dendritic Processing

Basic uniform cable equation:

$$\frac{\partial V(x,t)}{\partial t} = -\frac{V(x,t)}{\tau} + D\frac{\partial^2 V(x,t)}{\partial x^2} + I(x,t), \quad x \in (-\infty,\infty)$$

Green's function:

$$G_\infty(x,t) = \frac{1}{\sqrt{4\pi D t}} \mathrm{e}^{-t/\tau} \mathrm{e}^{-x^2/(4Dt)}$$

General solution:

$$V(x,t) = \int_{-\infty}^{t} \mathrm{d}t' \int_{-\infty}^{\infty} \mathrm{d}x' G_\infty(x-x', t-t') I(x',t') + \int_{-\infty}^{\infty} \mathrm{d}x' G_\infty(x-x',t) V(x',0).$$

Firing Rates

- Spike train $Qg = \overline{g} \sum_m \delta(t - T_m).$
- Short-time average: Qg = f, the instantaneous firing rate.
- For a single population with self-feedback we get equations like

$$Qg = w_0 f(g).$$

1D Tissue Level Model

$$Qg = \int_{-\infty}^{\infty} w(x,y) f(g(y, t - D(x,y)/v)) \mathrm{d}y.$$

Voltage $V(\xi, x, t)$ at position $\xi \geq 0$ along cable:

$$\frac{\partial V}{\partial t} = -\frac{V}{\tau} + D\frac{\partial^2 V}{\partial \xi^2} + I(\xi, x, t).$$

$I =$ synaptic input, proportional to a conductance change

$$g(\xi, x, t) = \int_{-\infty}^{t} \mathrm{d}s \eta(t-s) \int_{-\infty}^{\infty} \mathrm{d}y W(\xi, x, y) f(h(y, s - D(x,y)/v)).$$

1D Tissue Level Model

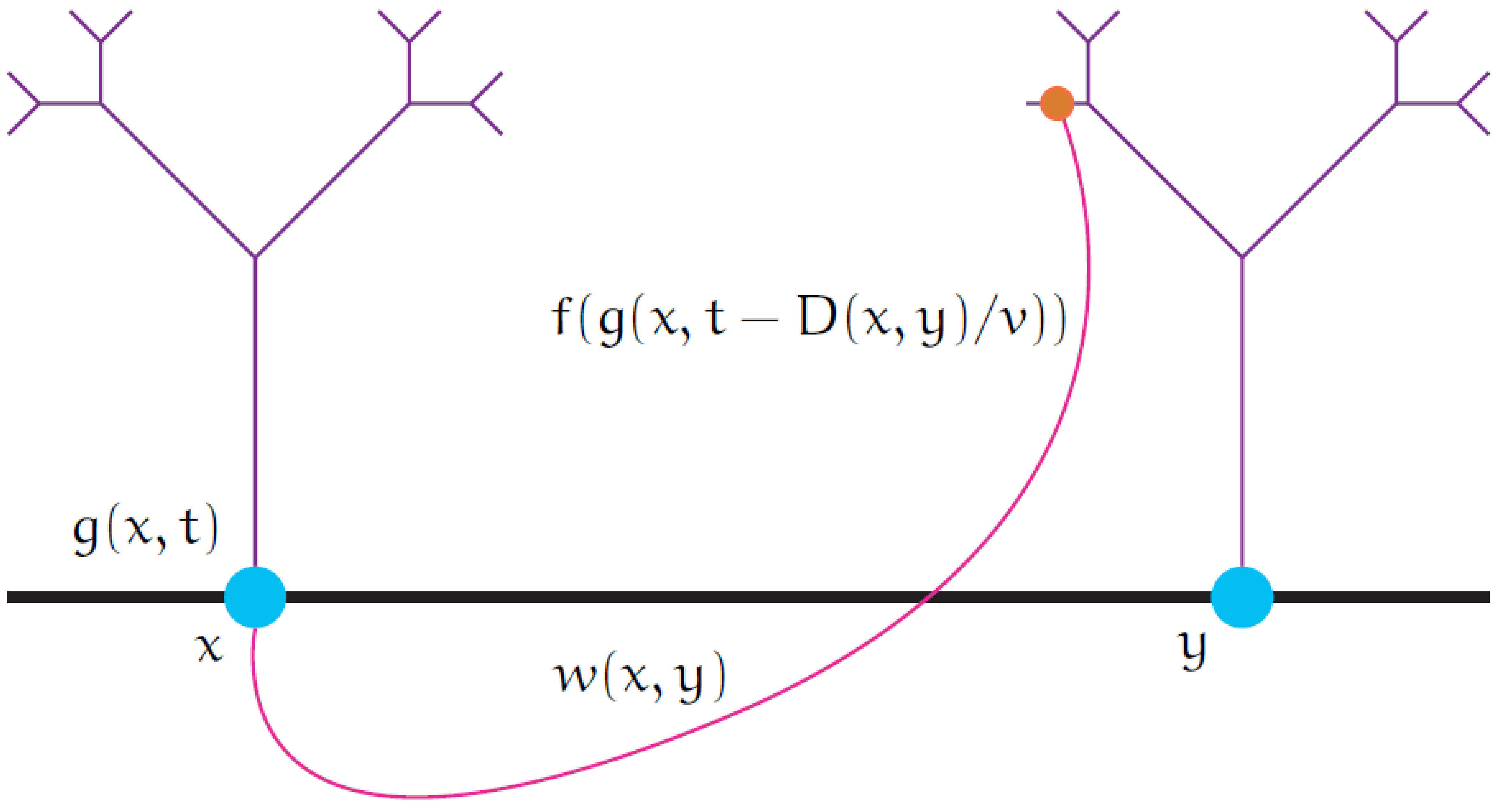
Axo-dendritic weights can be decomposed in the product form

$$W(\xi, x, y) = P(\xi) w(|x - y|).$$

Then the equation for h takes the form

$$h(x,t) = \kappa \int_{-\infty}^{t} \mathrm{d}s F(t-s) \int_{-\infty}^{s} \mathrm{d}s' \eta(s-s') \int_{-\infty}^{\infty} \mathrm{d}y w(|x-y|) f(h(y, s' - D(x,y)/v))$$

$$F(t) = \int_{0}^{\infty} \mathrm{d}\xi P(\xi) G(\xi, t).$$


f(g(x, t − D(x, y)/v))
g(x, t)
x
w(x, y)
y

One-dimensional model without dendrites or axonal delays

$$h(x,t) = \kappa \int_0^\infty \eta(s) \int_{-\infty}^\infty w(|y|) f(h(x-y,t-s)) \mathrm{d}y \mathrm{d}s.$$

Spatially uniform resting state $h(x,t) = h_0$, defined by

$$h_0 = \kappa f(h_0) \int_{-\infty}^\infty w(|y|) \mathrm{d}y.$$

We linearize by letting $h(x,t) \to h_0 + h(x,t)$,

so that $f(h) \to f(h_0) + f'(h_0) h$.

Linearization around resting state

$$h(x,t) = \kappa \int_0^\infty \eta(s) \int_{-\infty}^\infty w(|y|) h(x-y, t-s) \mathrm{d}y \mathrm{d}s,$$

$$\beta = f'(h_0).$$

Solutions are of the form $e^{\lambda t} e^{ipx}$, with

$$1 = \kappa \beta \tilde{\eta}(\lambda) \hat{w}(p), \quad \hat{w}(p) = \int_{-\infty}^\infty w(|y|) e^{-ipy} dy,$$

$$\tilde{\eta}(\lambda) = \int_0^\infty \eta(s) e^{-\lambda s} ds.$$

Instability Analysis

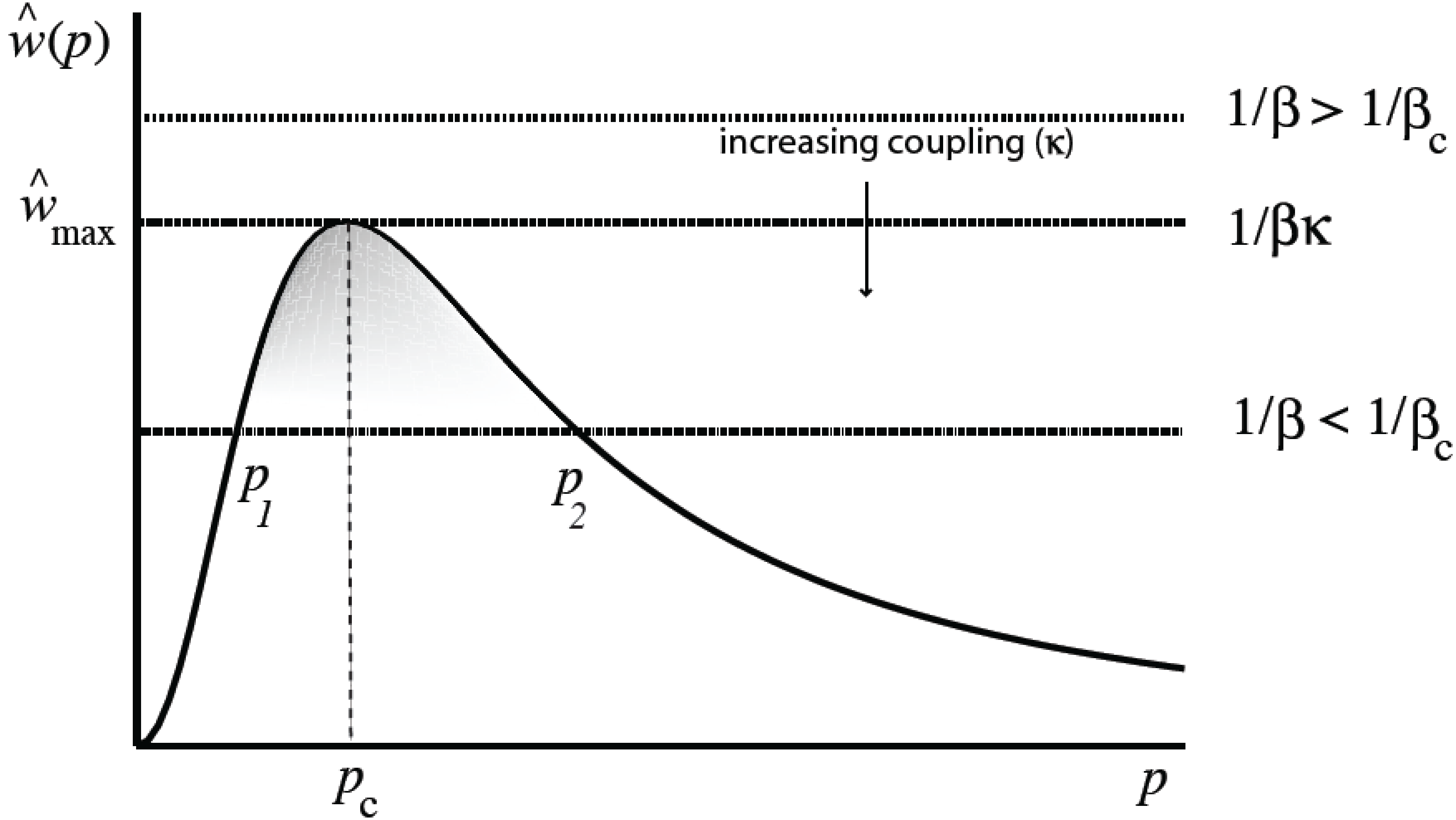
The uniform steady state is linearly stable if

$\mathrm{Re}(\lambda(p)) < 0 \quad \forall p \in \mathbb{R}\backslash 0.$

Chosing $\eta(t) = \alpha e^{-\alpha t} H(t),$ we get $\tilde{\eta}(t) = (1 + \lambda/\alpha)^{-1},$

so that $1 = \kappa\beta(1 + \lambda/\alpha)^{-1}\hat{w}(p),$

$$\begin{aligned}
\lambda &= \alpha(\hat{w}(p)\kappa\beta - 1),\\
\hat{w}(p)\kappa\beta &< 1,\\
\hat{w}(p) &< \frac{1}{\kappa\beta}.
\end{aligned}$$


$\hat{w}(p)$
$1/\beta > 1/\beta_c$
increasing coupling (κ)
$\hat{w}_{max}$
$1/\beta\kappa$
$1/\beta < 1/\beta_c$
p_1
p_2
p_c
p

- For $\beta < \beta_c$ we have $\kappa\widehat{w}(p) \leq \kappa\widehat{w}_{\max} < 1/\beta$ for all p and the resting state is linearly stable.
- At the critical point $\beta = \beta_c$ we have $\beta_c\kappa\widehat{w}(p_c) = 1$ and $\beta_c\kappa\widehat{w}(p) < 1$ for all $p \neq p_c$. Hence, $\lambda(p) < 0$ for all $p \neq p_c$, but $\lambda(p_c) = 0$. This signals the point of a *static* instability due to excitation of the pattern $\mathrm{e}^{\pm ip_c x}$.
- Beyond the bifurcation point, $\beta > \beta_c$, $\lambda(p_c) > 0$ and this pattern grows with time. In fact there will typically exist a range of values of $p \in (p_1, p_2)$ for which $\lambda(p) > 0$, signalling a set of growing patterns. As the patterns grow, the linear approximation breaks down and nonlinear terms dominate behaviour.
- The saturating property of $f(u)$ tends to create patterns with finite amplitude, that scale as $\sqrt{\beta - \beta_c}$ close to bifurcation and have wavelength $2\pi/p_c$.
- If $p_c = 0$ then we would have a *bulk instability* resulting in the formation of another homogeneous state.

Example: Mexican Hat Function

Biologically motivated choice for $w(x)$:

$$w(x) = \Lambda \left[e^{-\gamma_1 |x|} - \Gamma e^{-\gamma_2 |x|} \right].$$

$\Lambda = 1,$ short-range excitation and long-range inhibition,

$\Lambda = -1,$ short-range inhibition and long-range excitation.

$$\widehat{w}(p) = 2\Lambda \left[\frac{\gamma_1}{\gamma_1^2 + p^2} - \Gamma \frac{\gamma_2}{\gamma_2^2 + p^2} \right],$$

$$p_c^2 = \frac{\gamma_1^2 \sqrt{\Gamma \gamma_2 / \gamma_1} - \gamma_2^2}{1 - \sqrt{\Gamma \gamma_2 / \gamma_1}}.$$

Full Model

$$h(x,t) = \kappa \int_{-\infty}^{t} \mathrm{d}s F(t-s) \int_{-\infty}^{s} \mathrm{d}s' \eta(s-s') \int_{-\infty}^{\infty} \mathrm{d}y w(|x-y|) f(h(y, s' - D(x,y)/v)),$$

with $D(x,y) = |x-y|$.

The homogenous steady state $h(x,t) = h_0$ is

$$h_0 = \kappa f(h_0) \int_0^{\infty} F(s)\mathrm{d}s \int_{-\infty}^{\infty} \mathrm{d}y w(|y|),$$ so that we obtain

$$1 = \kappa \beta \widehat{w}(p,\lambda) \widetilde{\eta}(\lambda) \widetilde{F}(\lambda),$$

$$\widehat{w}(p,\lambda) = \int_{-\infty}^{\infty} \mathrm{d}y w(|y|) \mathrm{e}^{-ipy} \mathrm{e}^{-\lambda |y|/v}, \qquad \beta = f'(h_0).$$

Full Model

In the limit $v \to \infty$, $\hat{w}(p, \lambda) \to \hat{w}(p)$.

Then, for $\eta(t) = \alpha e^{-\alpha t} H(t)$, we have

$$1 + \lambda/\alpha = \kappa\beta\hat{w}(p)\tilde{F}(\lambda).$$

For a dynamic instability to occur, we must have

$\mathrm{Re}(\lambda) = 0$ and $\mathrm{Im}(\lambda) \neq 0$, i.e. there must be a pair $\omega, p \neq 0$ s.t. $\lambda = i\omega$ and

$$1 + i\omega/\alpha = \kappa\beta\hat{w}(p)\tilde{F}(i\omega).$$

Full Model

Defining $C(\omega) = \ \mathrm{Re}(\tilde{F}(i\omega)), S(\omega) = \ \mathrm{Im}(\tilde{F}(i\omega))$, where

$$C(\omega) = \int_0^\infty \mathrm{ds} F(s)\cos(\omega s) \leq |C(0)|.$$

Equating the real and imaginary parts, we get

$$1 = \kappa\beta\hat{w}(p)C(\omega), \quad \omega/\alpha = \kappa\beta\hat{w}(p)S(\omega).$$

Dividing the second equation by the first gives

$$\frac{\omega}{\alpha} = \mathcal{H}(\omega), \text{ with } \mathcal{H}(\omega) := \frac{S(\omega)}{C(\omega)}.$$

Instability Analysis

Bifurcation condition $\beta = \beta_d$ for a dynamic instability

$$\beta_d \kappa \hat{w}(p_{\min}) = \frac{1}{C(\omega_c)}.$$

Bifurcation condition $\beta = \beta_s$ for a static instability

$$\beta_s \kappa \hat{w}(p_{\max}) = \frac{1}{C(0)}.$$

Assuming $\hat{w}(p_{\min}) < 0 < \hat{w}(p_{\max})$,

dynamic Turing instability if $\beta < \beta_s$ and $p_{\min} \neq 0$,

static Turing instability if $\beta_s < \beta$ and $p_{\max} \neq 0$.

Instability Analysis

Mexican hat with $\Lambda = 1$:

No Turing instability because $p_{\min} = 0$.

Bulk oscillations instead of static patterns when

$$\hat{w}(p_c) < -\frac{C(\omega_c)}{C(0)}|\hat{w}(0)|, \qquad p_c^2 = \frac{\gamma_1^2\sqrt{\Gamma\gamma_2/\gamma_1} - \gamma_2^2}{1 - \sqrt{\Gamma\gamma_2/\gamma_1}}.$$

Mexican hat with $\Lambda = -1$:

$p_{\min} = p_c$ and $p_{\max} = 0$. Turing instability when

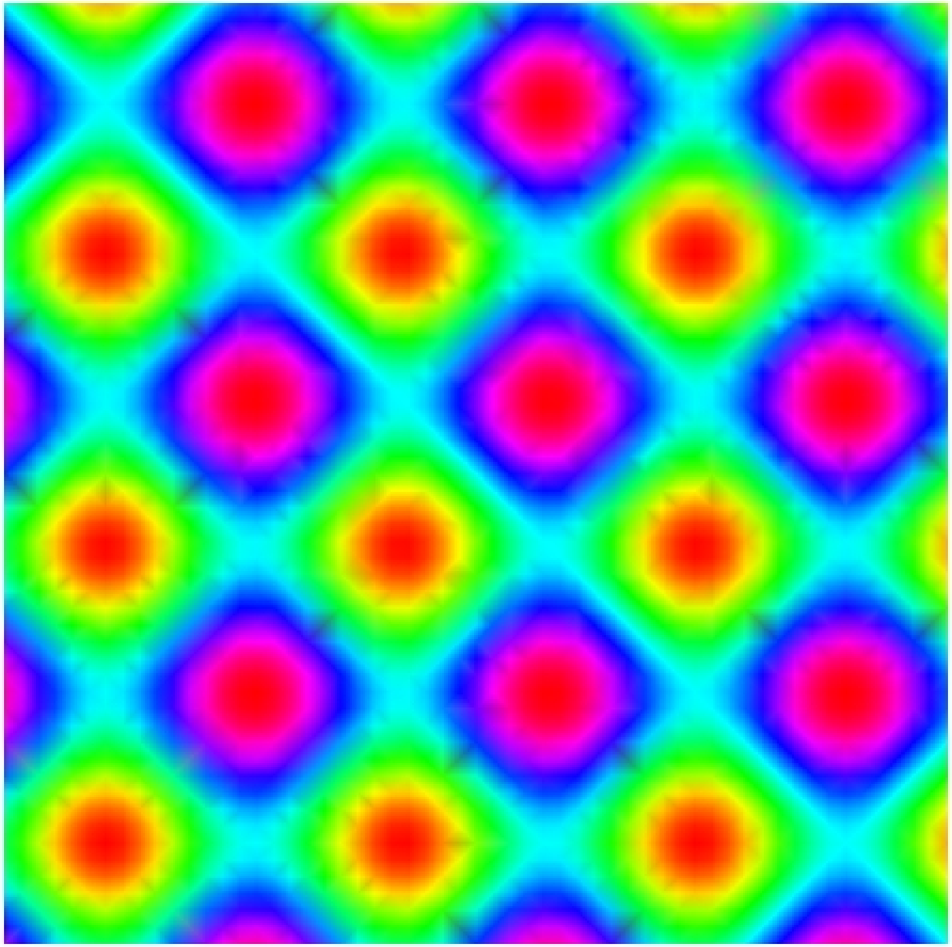
$$\hat{w}(0) < -\frac{C(\omega_c)}{C(0)}|\hat{w}(p_c)|.$$

Doubly Periodic Square Function

$$h(\mathbf{r}) = \sum_j A_j e^{ip_c \mathbf{R}_j \cdot \mathbf{r}}$$

$$\mathbf{R}_1 = \begin{bmatrix} 1 \\ 0 \end{bmatrix}, \mathbf{R}_2 = \begin{bmatrix} 0 \\ 1 \end{bmatrix},$$

$$A_1 \in [0, 2], A_2 = 1.$$



Doubly Periodic Hexagonal Function

$$h(\mathbf{r}) = \sum_j A_j e^{ip_c \mathbf{R}_j \cdot \mathbf{r}}$$

$$\mathbf{R}_1 = \begin{bmatrix} 1 \\ 0 \end{bmatrix},$$

$$\mathbf{R}_2 = \frac{1}{2}\begin{bmatrix} -1 \\ \sqrt{3} \end{bmatrix},$$

$$\mathbf{R}_3 = \frac{1}{2}\begin{bmatrix} 1 \\ \sqrt{3} \end{bmatrix}.$$