

# Excitatory-inhibitory networks

Sebastian Seung

# Two neural populations

- “excitatory” and “inhibitory”
- interactions
  - within populations: symmetric
  - between populations: antisymmetric

The two populations of an  
excitatory-inhibitory network  
behave as if they have  
opposing goals.

# Minimax

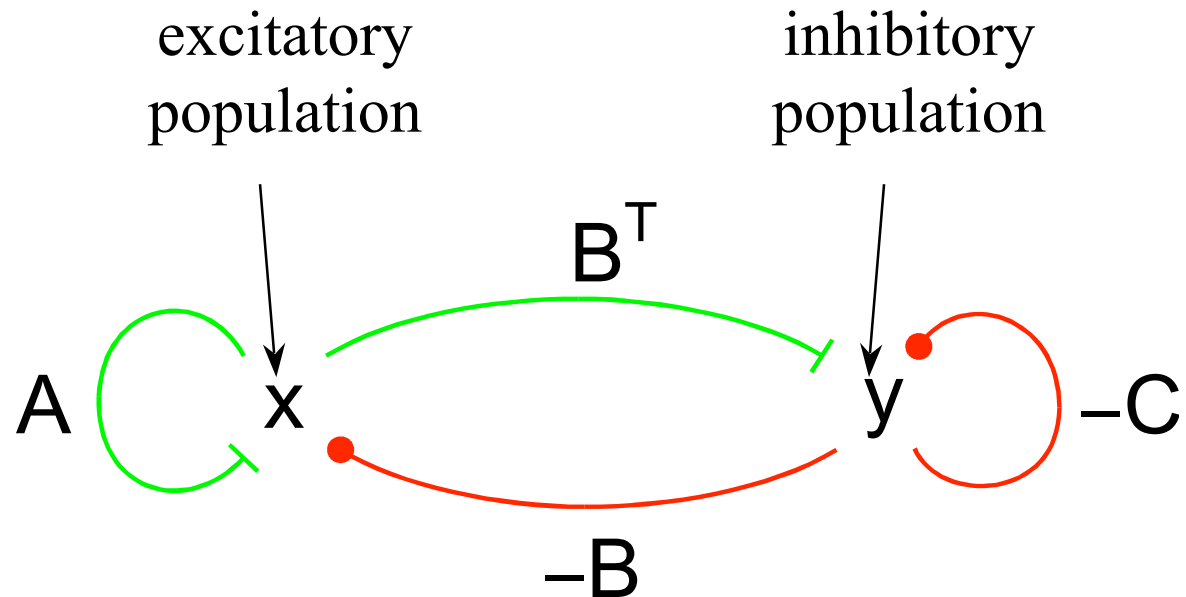
- An excitatory-inhibitory network is a method of solving a minimax problem.

$$\min_x \max_y S(x, y)$$

# Multiple goals

- Analogy to game theory
  - zero-sum game
- Equilibrium
- Oscillations
- Complex non-periodic behavior

# Synaptic interactions



- $A$  and  $C$  symmetric
- excitatory-inhibitory interpretation
  - $A$ ,  $B$ ,  $C$  nonnegative matrices

# Matrix-vector notation

$$\tau_x \dot{x} + x = f(u + Ax - By)$$

$$\tau_y \dot{y} + y = g(v + B^T x - Cy)$$

# Saddle function

- Excitatory neurons try to minimize
- Inhibitory neurons try to maximize

$$S = -u^T x - \frac{1}{2} x^T A x + v^T y - \frac{1}{2} y^T C y \\ + \mathbf{1}^T \bar{F}(x) + y^T B^T x - \mathbf{1}^T \bar{G}(y)$$

- Platt & Barr (1987)
- Mjolness & Garrett (1990)



# Saddle function gradients

$$\begin{aligned} -\frac{\partial S}{\partial x} &= u + Ax - By - f^{-1}(x) \\ &= f^{-1}(\tau_x \dot{x} + x) - f^{-1}(x) \end{aligned}$$

$$\begin{aligned} \frac{\partial S}{\partial y} &= v + B^T x - Cy - g^{-1}(y) \\ &= g^{-1}(\tau_y \dot{y} + y) - g^{-1}(y) \end{aligned}$$

# Pseudo gradient ascent-descent

$$\tau_x \dot{x} \cong -\frac{\partial S}{\partial x} \quad \text{descent}$$

$$\tau_y \dot{y} \cong \frac{\partial S}{\partial y} \quad \text{ascent}$$

- The components of these vectors have the same sign.

# True gradient ascent-descent

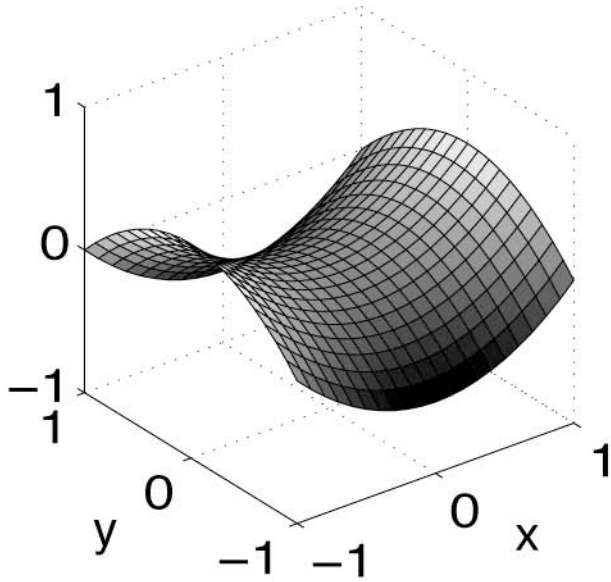
$$\dot{x} = -\frac{\partial S}{\partial x} \quad \text{descent}$$

$$\dot{y} = \frac{\partial S}{\partial y} \quad \text{ascent}$$

- When does this dynamics converge to the solution of the minimax problem?

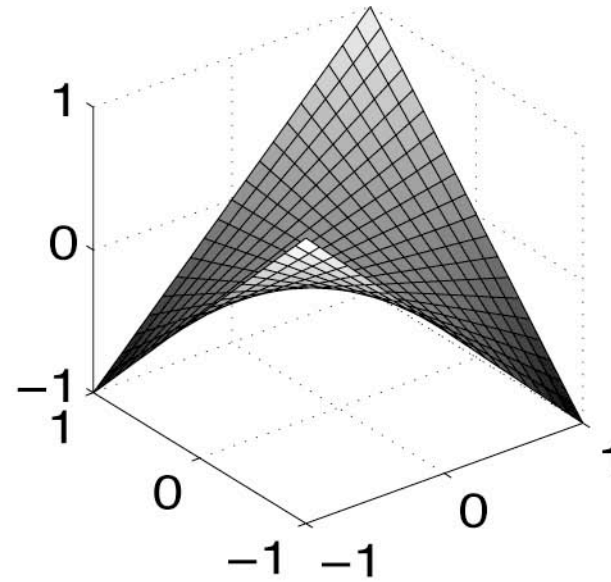
$$\min_x \max_y S(x, y)$$

# It depends



$$S = \frac{x^2}{2} - \frac{y^2}{2}$$

steady state



$$S = xy$$

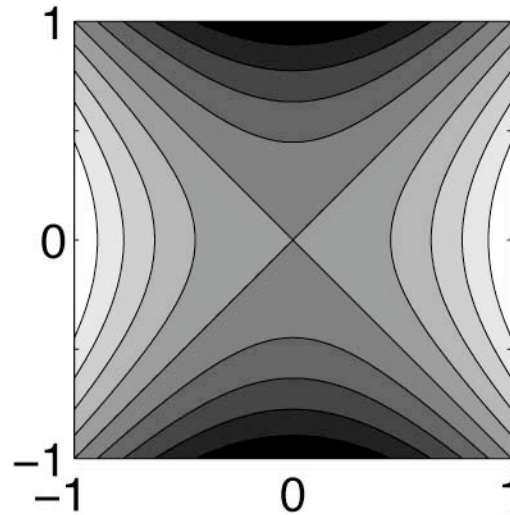
oscillations

# Steady state

$$S = \frac{x^2}{2} - \frac{y^2}{2}$$

$$\dot{x} = -\frac{\partial S}{\partial x} = -x$$

$$\dot{y} = \frac{\partial S}{\partial y} = -y$$

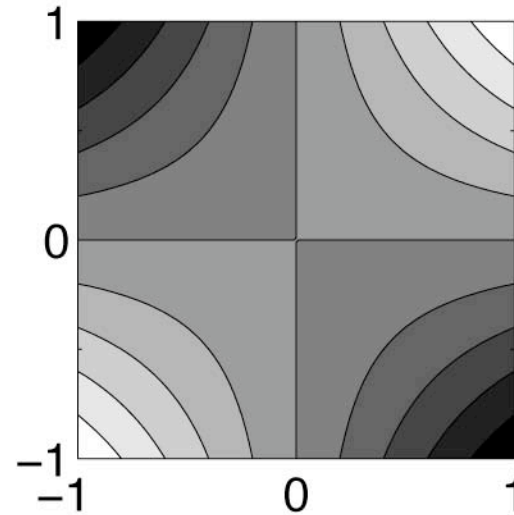


# Periodic behavior

$$S = xy$$

$$\dot{x} = -\frac{\partial S}{\partial x} = -y$$

$$\dot{y} = \frac{\partial S}{\partial y} = x$$



# Kinetic energy

$$T = \frac{\dot{x}^2}{2} + \frac{\dot{y}^2}{2} \qquad \dot{T} = -\dot{x}^T \frac{\partial^2 S}{\partial x^2} \dot{x} + \dot{y}^T \frac{\partial^2 S}{\partial y^2} \dot{y}$$

- lower bounded
- nonincreasing if

$\frac{\partial^2 S}{\partial x^2}$  positive definite

$\frac{\partial^2 S}{\partial y^2}$  negative definite

# Proof

$$\dot{x} = -\frac{\partial S}{\partial x} \longrightarrow \ddot{x} = -\frac{\partial^2 S}{\partial x^2} \dot{x} - \frac{\partial^2 S}{\partial x \partial y} \dot{y}$$

$$\dot{y} = \frac{\partial S}{\partial y} \longrightarrow \ddot{y} = \frac{\partial^2 S}{\partial x \partial y} \dot{x} + \frac{\partial^2 S}{\partial y^2} \dot{y}$$

$$\dot{T} = \dot{x}\ddot{x} + \dot{y}\ddot{y}$$

$$= -\frac{\partial^2 S}{\partial x^2} \dot{x}^2 + \frac{\partial^2 S}{\partial y^2} \dot{y}^2$$



The saddle function could either increase or decrease

$$\frac{dS}{dt} = \dot{x}^T \frac{\partial S}{\partial x} + \dot{y}^T \frac{\partial S}{\partial y} = -\dot{x}^T \dot{x} + \dot{y}^T \dot{y}$$

# Lyapunov function

$$L = T + rS$$

$$\dot{L} = -\dot{x}^T \left( \frac{\partial^2 S}{\partial x^2} + rI \right) \dot{x} + \dot{y}^T \left( \frac{\partial^2 S}{\partial y^2} + rI \right) \dot{y}$$

$$\frac{\partial^2 S}{\partial x^2} + rI \text{ positive definite}$$

$$\frac{\partial^2 S}{\partial y^2} + rI \text{ negative definite}$$

choose  $r$  to satisfy these conditions  
and keep  $L$  lower bounded

# Legendre transform pairs

$$F \xleftrightarrow{\text{Legendre transformation}} \bar{F}$$

$$F'(x) = f(x) \quad \bar{F}'(x) = f^{-1}(x)$$

$$\bar{F}(x) = \max_p \{px - F(p)\}$$

$$\Phi(p, x) = \mathbf{1}^T F(p) - p^T x + \mathbf{1}^T \bar{F}(x)$$

# Generalized kinetic energy

$$\tau_x \dot{x} + x = f(u + Ax - By)$$

$$\frac{1}{2} \tau_x \dot{x}^2 \longrightarrow \tau_x^{-1} \Phi(u + Ax - By, x)$$

$$\Phi(p, x) = \mathbf{1}^T F(p) - p^T x + \mathbf{1}^T \bar{F}(x)$$

$$\Phi(p, x) \geq 0$$

$$\Phi(p, x) = 0 \text{ for } f(p) = x$$

$$\text{likewise, } \Gamma(q, x) = \mathbf{1}^T G(q) - q^T x + \mathbf{1}^T \bar{G}(x)$$

# Lyapunov function

$$F'(x) = f(x) \quad \bar{F}'(x) = f^{-1}(x) \quad G'(x) = g(x) \quad \bar{G}'(x) = g^{-1}(x)$$

kinetic

$$\Phi(p, x) = \mathbf{1}^T F(p) - p^T x + \mathbf{1}^T \bar{F}(x)$$

energy

$$\Gamma(q, x) = \mathbf{1}^T G(q) - q^T x + \mathbf{1}^T \bar{G}(x)$$

saddle  
function

$$S = -u^T x - \frac{1}{2} x^T A x + v^T y - \frac{1}{2} y^T C y \\ + \mathbf{1}^T \bar{F}(x) + y^T B^T x - \mathbf{1}^T \bar{G}(y)$$

Lyapunov  
function

$$L = \frac{1}{\tau_x} \Phi(u + Ax - By, x) + \frac{1}{\tau_y} \Gamma(v + B^T x - Cy, y) + rS$$

Need to verify that  $L$  is lower bounded

# Sufficient conditions for stability

$$\dot{L} = \dot{x}^T A \dot{x} - \dot{y}^T C \dot{y} - (\tau_x^{-1} + r) \dot{x}^T [f^{-1}(\tau_x \dot{x} + x) - f^{-1}(x)] \\ + (r - \tau_y^{-1}) \dot{y}^T [g^{-1}(\tau_y \dot{y} + y) - g^{-1}(y)]$$

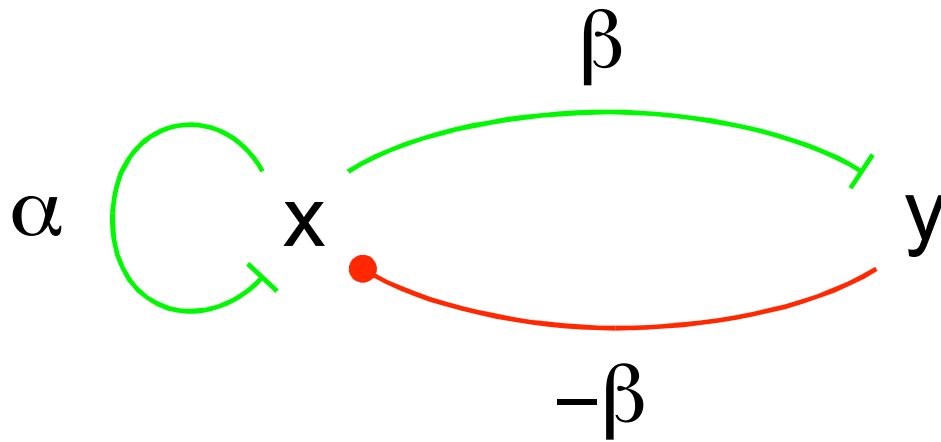
sufficient condition for  $\dot{L} \leq 0$

$$\max_{a,b} \frac{(a-b)^T A (a-b)}{(a-b)^T (f^{-1}(a) - f^{-1}(b))} \leq 1 + r\tau_x$$

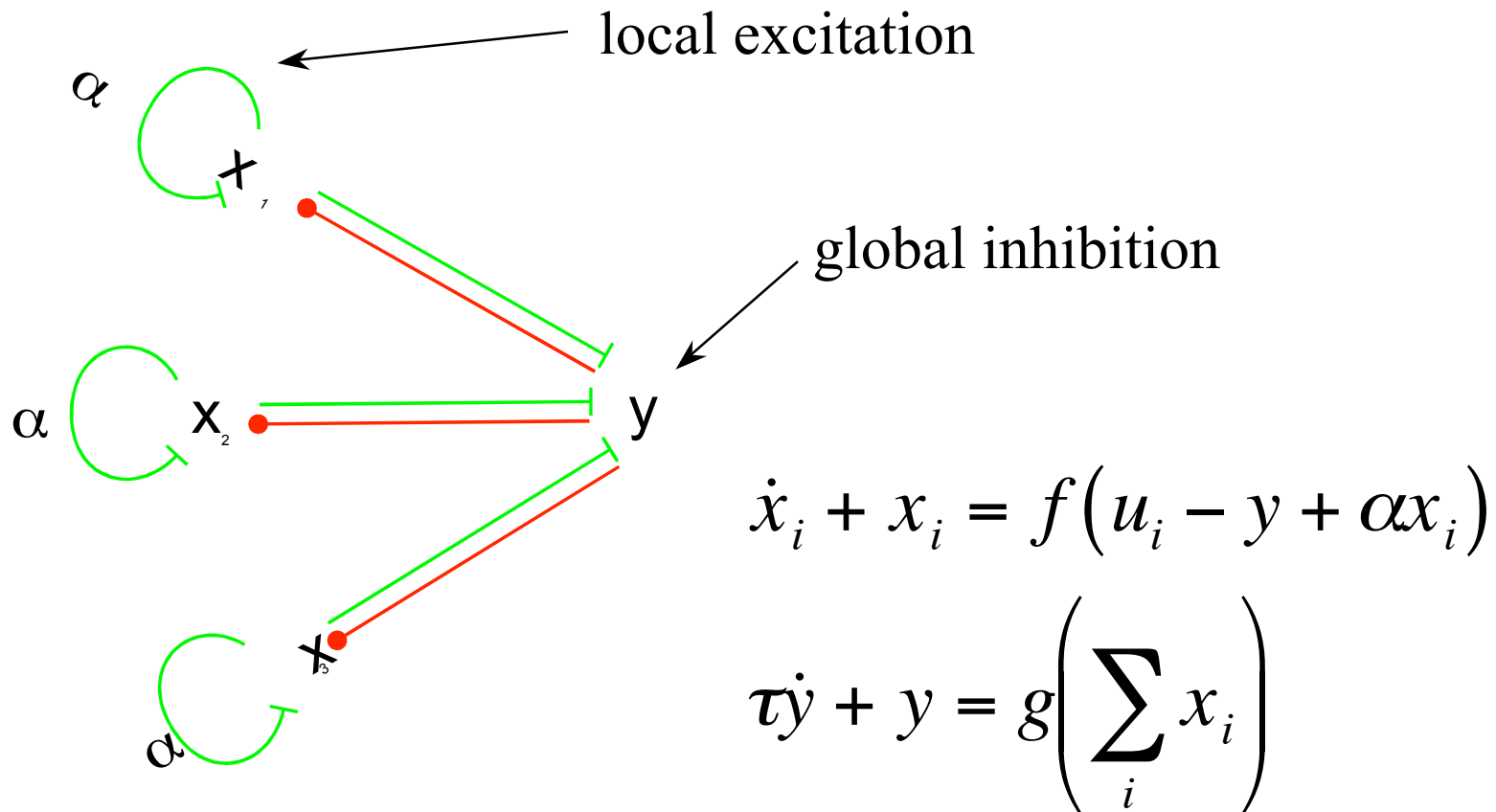
$$\min_{a,b} \frac{(a-b)^T C (a-b)}{(a-b)^T (g^{-1}(a) - g^{-1}(b))} \geq r\tau_y - 1$$

# Excitatory-inhibitory pair

- inhibitory feedback causes oscillations
- self-excitation required to sustain them



# Competitive network





# Sufficient conditions

$$T = \sum_i \left[ F(u_i + \alpha x_i - y) - (u_i + \alpha x_i - y)x_i + \bar{F}(x_i) \right]$$

$$V = \sum_i \left[ -u_i x_i - \frac{1}{2} \alpha x_i^2 + \bar{F}(x_i) + G\left(\sum_i x_i\right) \right]$$

$$L = T + V/\tau$$

$$\dot{L} = \sum_i \left\{ \alpha \dot{x}_i^2 - (\tau^{-1} + 1) \dot{x}_i \left[ f^{-1}(\dot{x}_i + x_i) - f^{-1}(x_i) \right] \right\}$$

# Conclusion

- excitatory-inhibitory network
- dynamics on a saddle
  - gradient ascent/descent
  - shape of saddle determines behavior