An Analytical Framework for Multi-Area Balanced Networks

Symmetry and Geometry in Neural Representations

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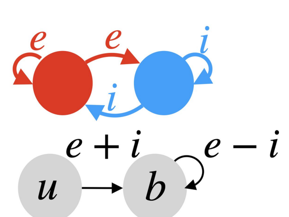
Background and methods

A hallmark of neocortical architecture is recurrent connectivity both within and between local sub-networks (cortical areas). Within an area, excitation-inhibition (E/I) balance (balanced positive and negative connections) tightly constrains neural dynamics, while across areas, dense reciprocal excitatory connections link regions into a distributed network. How does this multi-area, multi-scale recurrent architecture shape cortical neural activity dynamics? We present an analytical framework for E/I balanced multi-area networks, revealing key features of cortical computation.

Murphy and Miller 2009

Schur decomposition: Feedforward equivalent of recurrent E/I networks

$$W_{ei} = \begin{bmatrix} e & -i \\ e & -i \end{bmatrix}$$



Equivalent upper triangular connectivity

$$\widehat{W}_{ei} = \begin{bmatrix} e-i & e+i \\ 0 & 0 \end{bmatrix}$$

Schur basis

$$Q = \frac{1}{\sqrt{2}}\begin{bmatrix} 1 & 1 \\ 1 & -1 \end{bmatrix} = [\underset{\text{E/I balanced}}{b} \quad \underset{\text{E/I unbalanced}}{u}]$$

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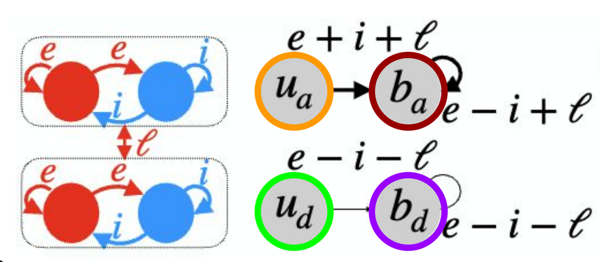
Extension to two symmetric areas



Long-range weights

$$W = \begin{bmatrix} W_{ei} & L \\ L & W_{ei} \end{bmatrix} \quad L = \begin{bmatrix} \ell & 0 \\ \ell & 0 \end{bmatrix}$$

$$\widehat{W} = \begin{bmatrix} \widehat{W}_{ei} + L^T & 0 \\ 0 & \widehat{W}_{ei} - L^T \end{bmatrix}$$

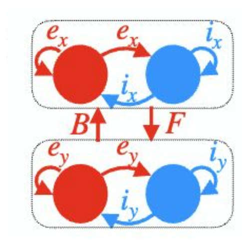
$$Q = \frac{1}{\sqrt{2}}\begin{bmatrix} \underset{\mathbf{b_a}}{\begin{matrix} b_x \\ b_y \end{matrix}} & \underset{\mathbf{u_a}}{\begin{matrix} u_x \\ u_y \end{matrix}} & \underset{\mathbf{b_d}}{\begin{matrix} b_x \\ -b_y \end{matrix}} & \underset{\mathbf{u_d}}{\begin{matrix} u_x \\ -u_y \end{matrix}} \end{bmatrix}$$

Extension to two arbitrary areas

$$W = \begin{bmatrix} W_{x,ei} & B \\ F & W_{y,ei} \end{bmatrix}$$

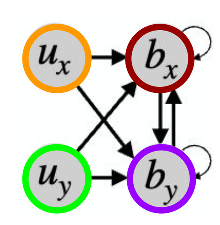
feedForward $F = \begin{bmatrix} F & 0 \\ F & 0 \end{bmatrix}$

feedBack $B = \begin{bmatrix} B & 0 \\ B & 0 \end{bmatrix}$



Single-area (quasi-Schur) basis

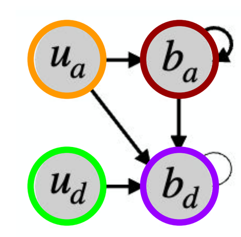
$$\widehat{W}_{single} = \begin{bmatrix} W_e - W_i & W_e + W_i \\ 0 & 0 \end{bmatrix}$$



$$W_e = \begin{bmatrix} e_x & B \\ F & e_y \end{bmatrix} \text{ and } W_i = \begin{bmatrix} i_x & 0 \\ 0 & i_y \end{bmatrix}$$

$$Q_{single} = \begin{bmatrix} b_x & 0 & u_x & 0 \\ 0 & b_y & 0 & u_y \end{bmatrix}$$

Multi-area (Schur) basis

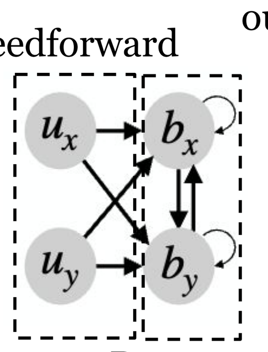


$$\widehat{W}_{multi} = \begin{bmatrix} -\sqrt{FB} & \frac{\alpha N_1}{N_2} & B-F & \frac{\beta}{N_1 N_2} \\ 0 & 0 & \sqrt{FB} & \frac{N_2}{N_1} \end{bmatrix} \otimes \begin{bmatrix} 1 \\ 0 \end{bmatrix}$$

$$Q_{multi} = \begin{bmatrix} \underset{\mathbf{b_d}\ \text{(generalized)}}{\begin{matrix} \frac{\sqrt{B}}{N_1} b_x \\ -\frac{\sqrt{F}}{N_1} b_y \end{matrix}} & \underset{\mathbf{u_d}}{\begin{matrix} \frac{\sqrt{B}E}{N_2} u_x \\ -\frac{\sqrt{F}G}{N_2} u_y \end{matrix}} & \underset{\mathbf{b_a}}{\begin{matrix} \frac{\sqrt{F}}{N_1} b_x \\ \frac{\sqrt{B}}{N_1} b_y \end{matrix}} & \underset{\mathbf{u_a}}{\begin{matrix} \frac{\sqrt{F}G}{N_2} u_x \\ \frac{\sqrt{B}E}{N_2} u_y \end{matrix}} \end{bmatrix}$$

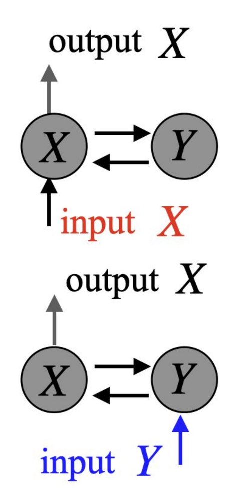
$$N_1 = \sqrt{F+B},\ N_2 = \sqrt{BE^2 + FG^2}$$
$$E = y + \sqrt{FB},\ G = e_x + \sqrt{FB}$$
$$\alpha = (e_x e_y - FB)$$
$$\beta = \sqrt{FB}(e_x^2 + B^2 - e_y^2 - F^2) + (B-F)(e_x F + e_y B)$$

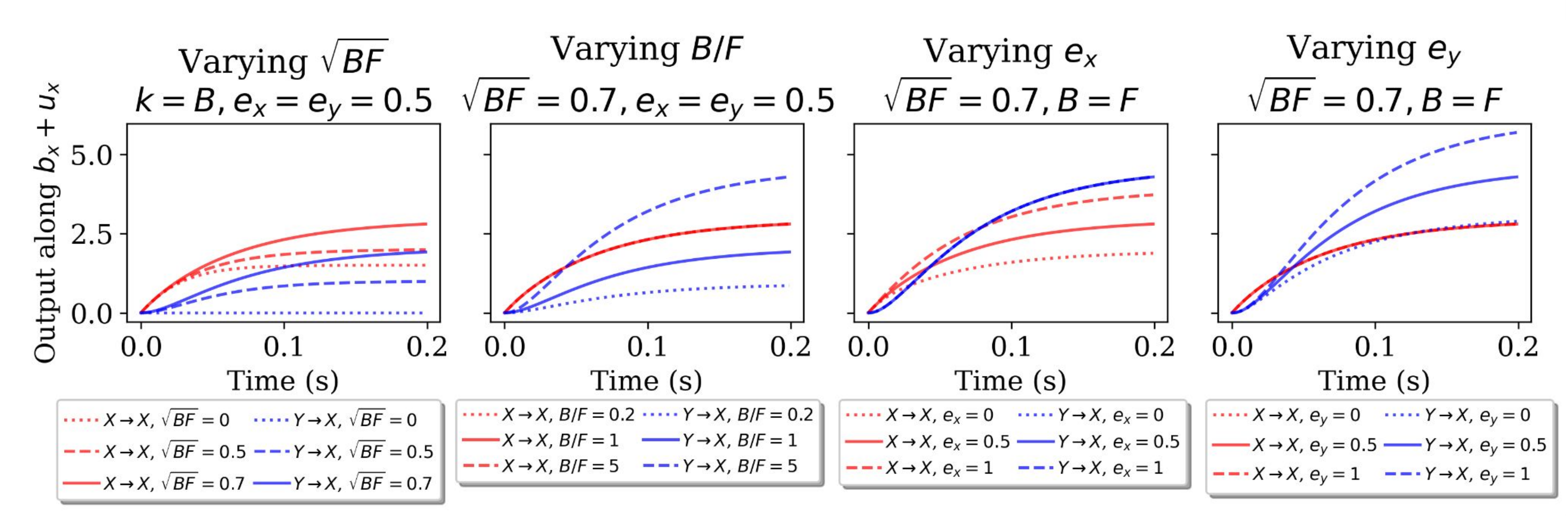
Local dynamics are recruited only via direct inputs and are not sustained



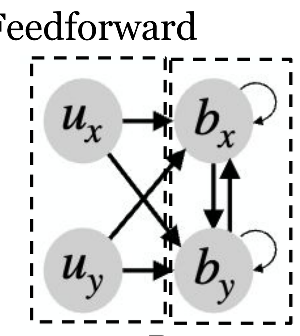
Steady-state balanced output of area x

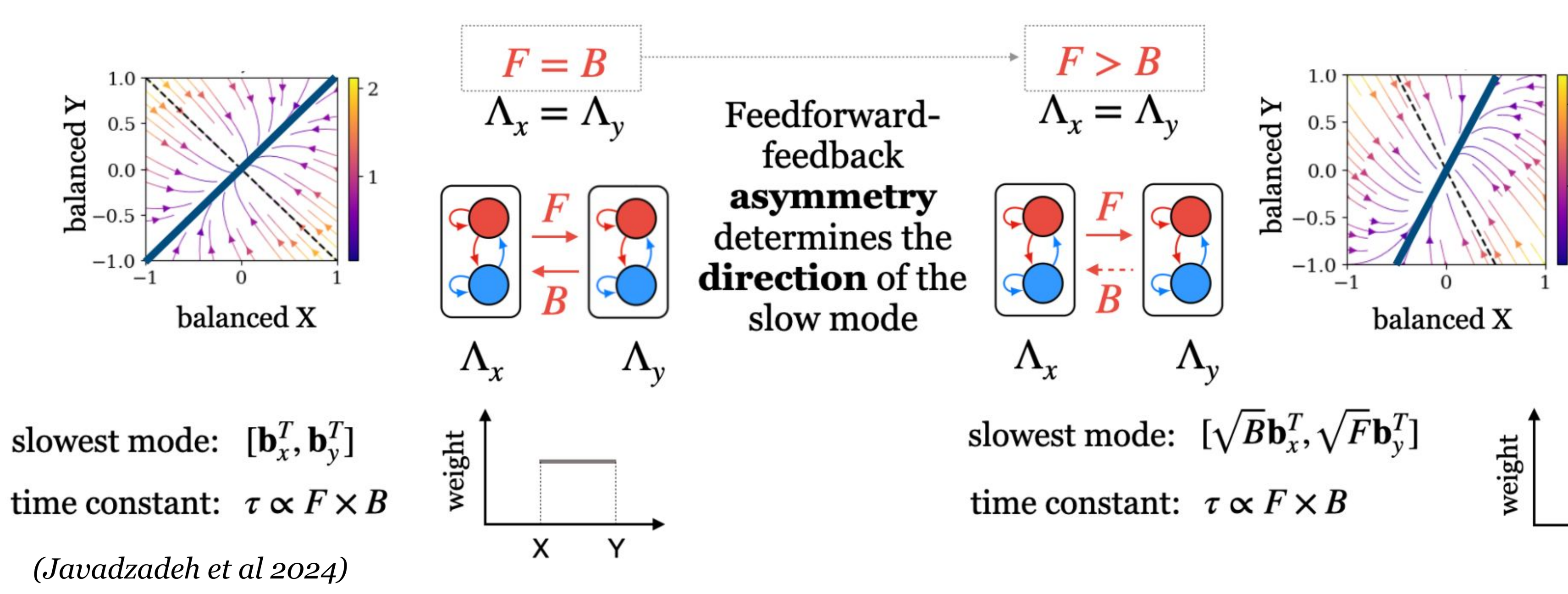
$$b_x = \left(\underbrace{\frac{1}{1-FB} s_{b,x}}_{\text{Balanced input to area x}} + \frac{\overbrace{2e_x}^{\text{Local weights of area x}} + FB}{1-FB} \underbrace{s_{u,x}}_{\text{Unbalanced input to area x}}\right) + \left(\underbrace{\frac{B}{1-FB} s_{b,y}}_{\text{Balanced input to area y}} + \frac{B(1+\overbrace{2e_y}^{\text{Local weights of area y}})}{1-FB} \underbrace{s_{u,y}}_{\text{Unbalanced input to area y}}\right)$$

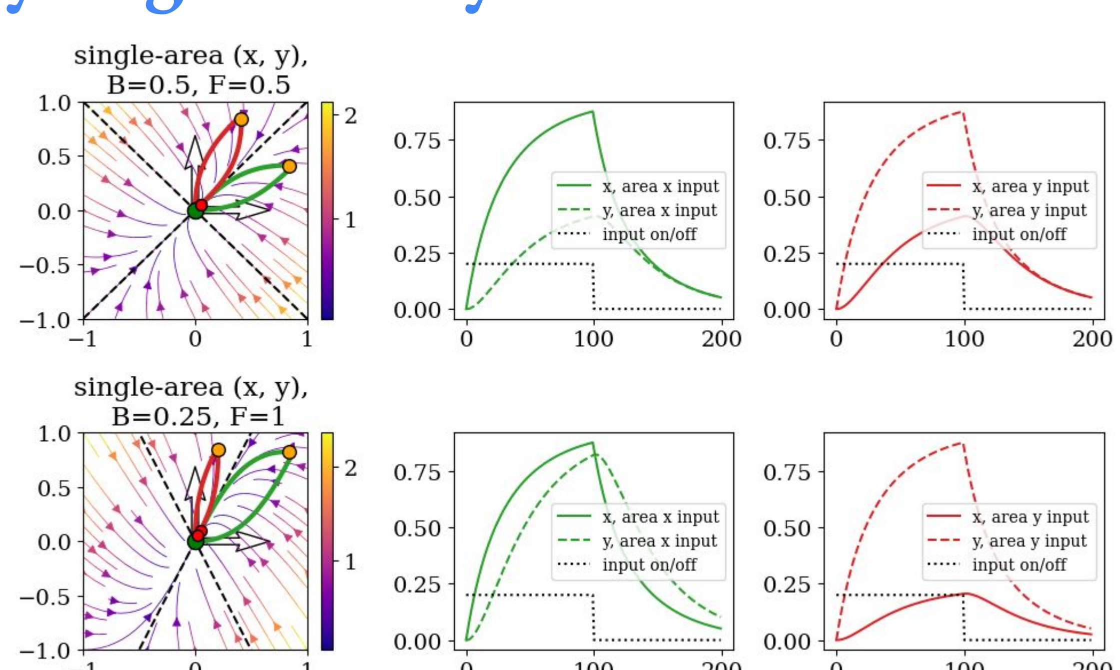




Inter-area connections give rise to slow dynamics that gradually align activity across areas







Composition into cortical-like architectures

Balanced cortical hierarchies form **tridiagonal connections** between balanced agree modes

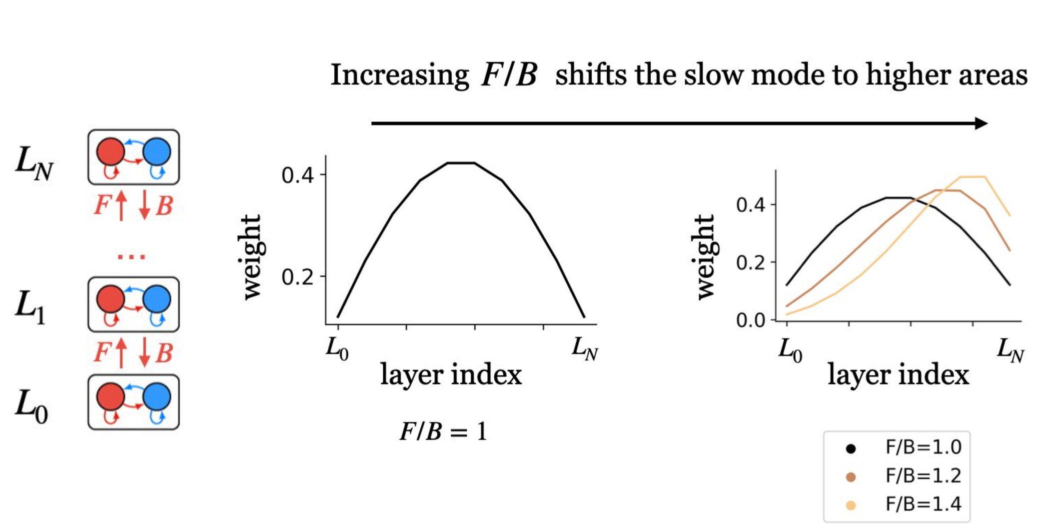
$$T = \begin{bmatrix} L^{(0)} & B & 0 & \dots & 0 \\ F & L^{(1)} & B & \dots & 0 \\ 0 & F & L^{(2)} & \ddots & 0 \\ \vdots & \vdots & \ddots & \ddots & B \\ 0 & 0 & 0 & F & L^{(n-1)} \end{bmatrix}$$

Eigenvalues and eigenvectors:

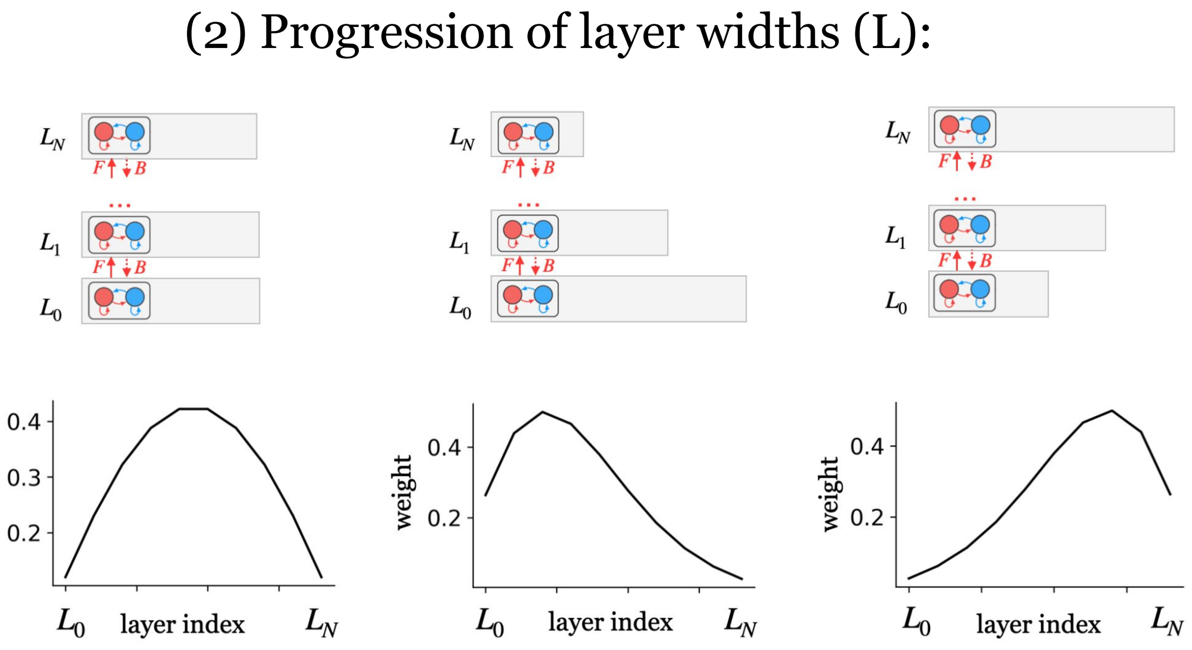
$$\lambda_k = L + 2\sqrt{FB}\cos\left(\frac{k\pi}{n+1}\right)\ \forall k \in \{1, \dots, n\}$$

$$v_j^{(k)} = \sin\left(\frac{jk\pi}{n+1}\right)\sqrt{\frac{F}{B}}^{\,j-1},\ \forall j \in \{1, \dots, n\}$$

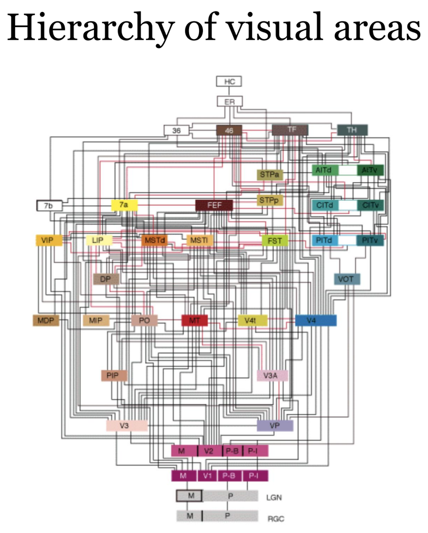
(1) F/B asymmetry:



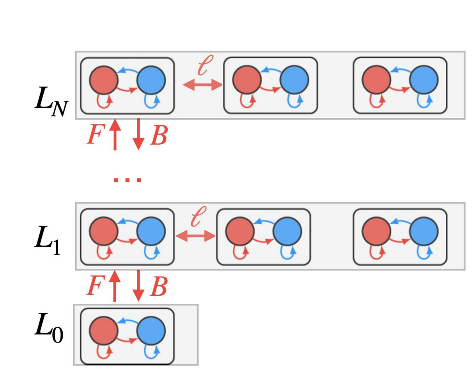
(2) Progression of layer widths (L):



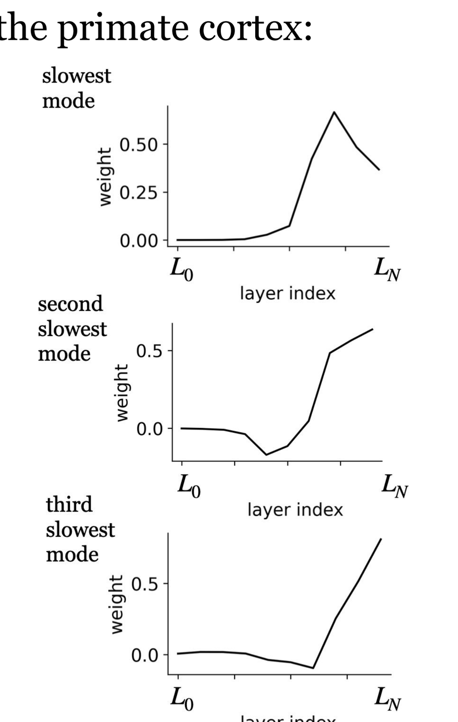
Hierarchy of visual areas in the primate cortex:

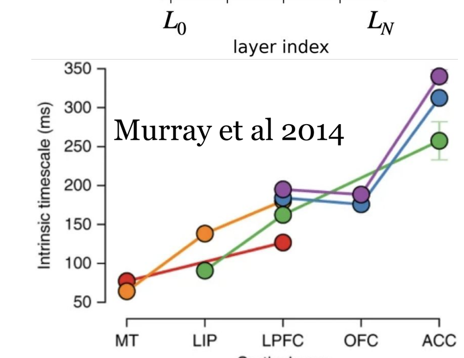


Felleman & Van Essen (1991)



(10 layers, 2-7 areas per layer, F/B >1)





Summary

We present an analytical framework for balanced multi-area networks, revealing key features of cortical computation:

(1) Local connectivity determines the area's response to inputs received locally (extra-cortical), but not to inputs relayed from other cortical areas. Local responses to these relayed inputs are instead primarily driven by long-range inter-area connections.

(2) Slow modes of the network dynamics are determined by long-range connections: The overall strength of long-range loops determines the slowest time constant and the feedforward/feedback asymmetry determines the direction of the slow mode (contribution of areas to slow activity).

(3) Applying these principles to cortical-like architectures predicts participation in slow dynamics to be biased towards higher areas, consistent with empirically observed progression of intrinsic timescales across the cortex.