Dynamic Causal Modelling for Steady State Responses

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Dynamic Causal Modelling for SSR

A framework which uses Bayesian techniques to fit differential equations to steady – state data. It allows for comparison between competing models of brain architecture and furnishes estimates for parameters that are not measured directly by exploiting electrophysiological data.

Although it is based on sophisticated models from computational neuroscience, its application is straightforward and does not require mathematical training.
Pink line = Container (bowl)
If there is no external perturbation, the ball will stay at the centre
If there is, the container will be tilted and the ball will oscillate around the centre as shown
Now, imagine that the ball has a bell inside. If there is an external perturbation the bell will start ringing.
CAUSE of CONTAINER TILTING \(\leftrightarrow\) NEURAL NOISE
BALL \(\leftrightarrow\) BRAIN REGION
RINGINGS \(\leftrightarrow\) RESPONSES (cross spectral densities)
CONTAINER \(\leftrightarrow\) MODEL (equations, parameters cf. shape/friction)
STEADY STATE PERTURBATIONS means that “the ball always stays very close to the centre” (while the bowl is tilted)
Spectral Densities

- Linearity
- Ergodicity

**Source 1**

```
Frequency (Hz)
```

```
Power (uV^2)
```

- **Source 2**

```
Frequency (Hz)
```

```
Power (mV^2)
```

---

"theta"
Maximise the model evidence ($\sim -F$)

Specify model

Reveal hidden brain architectures

Get estimates of hidden parameters

Extract Data Features

Experimental data

DCM Chain
Examples

- Anaesthetic Depth in Rodents (Moran et al., Plos One, 2011)
- Questions of Consciousness using Anaesthesia in Humans (Boly et al., J Neuro, to appear)
- Dopamine in working memory (Moran et al., Current Biol., 2011)
- Beta oscillations in PD (Moran et al., Plos CB, 2011)
- Neural Fields (Pinotsis et al., 2011,2012)
Overview

1. Data Features
2. Generative Model
3. Bayesian Inversion: Parameter Estimates and Model Comparison
4. Example: Glutamate and GABA in Rodent Auditory Cortex
5. DCM for Current Source Density
6. DCM for Neural Fields
Extract Data Features

Experimental data

Specify model

Maximise the model evidence ($\sim -F$)

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Get estimates of hidden parameters
Cross Spectral Density: The Data

A few LFP channels or EEG/MEG spatial modes
Cross Spectral Density Data from a time series

**Vector Auto-regression $p$-order model:**

Linear prediction formulas that attempt to predict an output $y[n]$ of a system based on the previous outputs

\[ y_n = \alpha_1 y_{n-1} + \alpha_2 y_{n-2} + \ldots + \alpha_p y_{n-p} + e_n \]

Resulting in a matrices for $c$ Channels

Cross Spectral Density for channels $i,j$ at frequencies

\[ \omega = 2\pi f \]

\[
\begin{pmatrix}
  g(\omega)_{11} & g(\omega)_{12} & \cdots \\
  g(\omega)_{12} & g(\omega)_{12} & \cdots \\
\end{pmatrix}
\]

\[
g(\omega)_{ij} = f(A(p))
\]

\[
H_{ij}(\omega) = \frac{1}{\alpha_1 e^{i\omega} + \alpha_2 e^{i\omega^2} + \ldots + \alpha_p e^{i\omega^p}}
\]

\[
g(\omega)_{ij} = H_{ij}(\omega) \prod_{ij} H(\omega)_{ij}^*
\]
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6. DCM for Neural Fields
DCM Chain

- **Extract Data Features**
  - Experimental data

- **Specify model**

- **Maximise the model evidence** ($\sim F$)

- **Reveal hidden brain architectures**

- **Get estimates of hidden parameters**
Dynamic Causal Modelling: Generic Framework

Hemodynamic forward model: neural activity → BOLD

Time Domain Data

Neural state equation:

\[ \frac{dx}{dt} = F(x, u, \theta) \]

Electromagnetic forward model: neural activity → EEG, MEG, LFP

Time Domain ERP Data
Phase Domain Data
Time Frequency Data
Steady State Frequency Data

fMRI

simple neuronal model
Slow time scale

EEG/MEG

complicated neuronal model
Fast time scale
Dynamic Causal Modelling: Generic Framework

Neural state equation:
\[
\frac{dx}{dt} = F(x,u,\theta)
\]

Hemodynamic forward model:
neural activity \(\rightarrow\) BOLD
Time Domain Data

Electromagnetic forward model:
neural activity \(\rightarrow\) EEG
MEG
LFP
Steady State Frequency Data

fMRI

simple neuronal model
Slow time scale

EEG/MEG

complicated neuronal model
Fast time scale

“theta”

fMRI

simple neuronal model
Slow time scale
A Brain Region as an Input - Output System

Neuronal innovations
\( g_U(k, \omega) \)

Model equations and parameters

Predicted responses
\( g_Y(\omega, \theta) \)

\[ \theta = \{ H_e, H_i, \kappa_e, \kappa_i, \kappa_a, \gamma_1, \gamma_2, \gamma_3, \gamma_4, \gamma_5, g, A_F, A_B, A_L, \lambda \} \]
ERP vs Steady State Responses

\[ y(t) = H(f) + \beta_1 + \beta_2 / \omega \]

Outputs Through Lead field

\[ U(\omega) = a \left( \frac{1}{f} \right) + b \]

Time Domain

Freq Domain

ERP Output

Freq Domain Output

Pulse Input

Freq Domain Cortical Input

Cortical Input

neuronal states

driving input \( u(t) \)
Neural Mass Model

Tens of thousands of neurons approximated by their average response. Neural mass models describe the interaction of these averages between populations and sources.

\[ \dot{x} = F(x, u, \theta) \]  

State equations
Inhibitory cells in agranular layers

\[ \dot{x}_7 = x_8 \]
\[ \dot{x}_8 = \kappa_e H_e (A^B + A^L + \gamma_3) S(x_9) - 2\kappa_e x_8 - \kappa_e^2 x_7 \]
\[ \dot{x}_{10} = x_{11} \]
\[ \dot{x}_{11} = \kappa_i H_i \gamma_5 S(x_{12}) - 2\kappa_i x_{11} - \kappa_i^2 x_{10} \]
\[ \dot{x}_{12} = x_8 - x_{11} \]

Excitatory spiny cells in granular layers

\[ \dot{x}_1 = x_4 \]
\[ \dot{x}_4 = \kappa_e H_e ((A^F + A^L) S(x_9) + Cu) - 2\kappa_e x_4 - \kappa_e^2 x_1 \]

Excitatory pyramidal cells in agranular layers

\[ \dot{x}_2 = x_5 \]
\[ \dot{x}_5 = \kappa_e H_e ((A^B + A^L) S(x_9) + \gamma_2 S(x_1)) - 2\kappa_e x_5 - \kappa_e^2 x_2 \]
\[ \dot{\mu}_3 = x_6 \]
\[ \dot{x}_6 = \kappa_i H_i \gamma_4 S(x_{12}) - 2\kappa_i x_6 - \kappa_i^2 x_3 \]
\[ \dot{x}_9 = x_5 - x_6 \]

\[ \dot{x} = f(x,u) \]
Inhibitory cells in agranular layers
\[
\begin{align*}
\dot{x}_7 &= x_8 \\
\dot{x}_8 &= \kappa_e H_e (A^B + A^L + \gamma_3) S(x_9) - 2\kappa_e x_8 - \kappa_e^2 x_7 \\
\dot{x}_{10} &= x_{11} \\
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\[\dot{x} = f(x,u)\]
Inhibitory cells in agranular layers
\[ \dot{x}_7 = x_8 \]
\[ \dot{x}_8 = \kappa_e H(A + A^L + \gamma_3)S(x_9) - 2\kappa_e x_8 - \kappa_e^2 x_7 \]
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Excitatory spiny cells in granular layers
\[ \dot{x}_1 = x_4 \]
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Excitatory pyramidal cells in agranular layers
\[ \dot{x}_2 = x_3 \]
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\[ \dot{x}_6 = \kappa_i H_i \gamma_4 S(x_{12}) - 2\kappa_i x_6 - \kappa_i^2 x_3 \]
\[ \dot{x}_9 = x_5 - x_6 \]

Extrinsic Connections:
- Forward
- Backward
- Lateral

Intrinsic connections

\[ \gamma_5 \]

\[ \gamma_4 \]

\[ \gamma_3 \]

\[ \gamma_2 \]

\[ \gamma_1 \]

\[ \dot{x} = f(x,u) \]
Neural Mass Model

Inhibitory cells in agranular layers
\[ \dot{x}_7 = x_8 \]
\[ \dot{x}_8 = \kappa_e H_e (A^B + A^L + \gamma_3) S(x_6) - 2\kappa_e x_8 - \kappa_e x_7 \]
\[ \dot{x}_{10} = x_{11} \]
\[ \dot{x}_{11} = \kappa_i H_i \gamma_5 S(x_{12}) - 2\kappa_i x_{11} - \kappa_i^2 x_{10} \]
\[ \dot{x}_{12} = x_8 - x_{11} \]

Excitatory spiny cells in granular layers
\[ \dot{x}_1 = x_4 \]
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Excitatory pyramidal cells in agranular layers
\[ \dot{x}_2 = x_3 \]
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Extrinsic Connections:
- Forward
- Backward
- Lateral

Intrinsic connections
\[ \gamma_1 \]
\[ \gamma_2 \]
\[ \gamma_3 \]
\[ \gamma_4 \]
\[ \gamma_5 \]

Extrinsic Connections:
- Forward
- Backward
- Lateral

Intrinsic connections

\[ \dot{x} = f(x,u) \]

Synaptic ‘alpha’ kernel
\[ \nu = r \otimes h \]

Sigmoid function
\[ r = S(\nu) \]

: Receptor Density

: Firing Rate

\[ H_{e/i} \]

\[ \tau_{e/i} \]

\[ \rho \]

\[ S(x) \]
Frequency Domain Generative Model
(Perturbations about a fixed point)

Time Differential Equations
\[ \dot{x} = f(x) + Bu \]
\[ y = l(x) \]

State Space Characterisation
\[ \dot{x} = Ax + Bu \]
\[ y = Cx \]

Transfer Function Frequency Domain
\[ H(s) = C(sI - A)B \]
Frequency Domain Generative Model
(Perturbations about a fixed point)

Transfer Function
Frequency Domain

\[ H_1(\omega) = f(\theta : H_{el_i}, \tau_{e,i}..) \]

Cross-Transfer Function
Frequency Domain

\[ H_{12}(\omega) = f(\theta : H_{el_i}, \tau_{e,i}..) \]

Transfer Function
Frequency Domain

\[ H_2(\omega) = f(\theta : H_{el_i}, \tau_{e,i}..) \]
Overview

1. Data Features

2. Generative Model

3. Bayesian Inversion: Parameter Estimates and Model Comparison

4. Example: Glutamate and GABA in Rodent Auditory Cortex

5. DCM for Cross Spectral Density

6. DCM for Neural Fields
Bayesian Inversion

1. Extract Data Features
   - Experimental data

2. Specify model

3. Maximise the model evidence ($\sim -F$)

4. Reveal hidden brain architectures

5. Get estimates of hidden parameters

Mathematical Formulas:

\[ U(\omega) = a \left( \frac{1}{f} \right) + b \]
Roadmap

Generative model
- predicted responses
- parameters
- hyperparameters

Priors
- variance

Bayesian Inference
- Model Evidence
- Posteriors

\[ g_Y(\omega) = g_Y(\omega, \theta) + g_N(\omega, \theta) + \varepsilon(\omega) \]

\[ g_N(\omega, \theta) = \alpha_N + \frac{\beta_N}{\omega} \]

\[ \text{Re}(\varepsilon) \sim N(0, \Sigma(\omega, \lambda)) \quad \text{Im}(\varepsilon) \sim N(0, \Sigma(\omega, \lambda)) \]

\[ p(G \mid \theta, m) = N(g_Y(\omega), \Sigma(\omega, \lambda)) \]

\[ p(G \mid m) = \int p(G \mid \theta, m) p(\theta) d\theta \]

\[ p(\theta \mid G, m) = \frac{p(G \mid \theta, m) p(\theta, m)}{p(G \mid m)} \]
Bayesian Model Inversion

**Variational Laplace Algorithm**

Maximize a free energy bound to model evidence:

\[
F = \log p(y|m) - D(q(\theta) \| p(\theta|y,m))
\]

\[
= \log p(y|\theta,m) >_q - D(q(\theta) \| p(\theta|m))
\]

**Iterative procedure:**

1. Compute model response using current set of parameters and hyperparameters
2. Compare model response with data
3. Improve parameters and hyperparameters

**Model comparison via Bayes factor:**

\[
BF = \frac{p(y|m_1)}{p(y|m_2)}
\]

\[
q(\theta) \approx p(\theta|y,m)
\]

Maximum accuracy over complexity constraints
Bayesian Inversion

Bayes’ rules:
\[ p(\theta \mid y, m) = \frac{p(y \mid \theta, m) p(\theta \mid m)}{p(y \mid m)} \]

Free Energy:
\[ F = \max_{\theta} \ln p(y \mid m) - D(q(\theta) \mid \mid p(\theta \mid y, m)) \]

Inference on models

Model comparison via Bayes factor:
\[ BF = \frac{p(y \mid m_1)}{p(y \mid m_2)} \]

Inference on parameters

Model comparison via Bayes factor:
- accounts for both accuracy and complexity of the model
- allows for inference about structure (generalisability) of the model
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Pharmacological Manipulation of Glutamate and GABA

Aim:
- Can we differentiate different connection types in the brain?
- Are our estimates of excitation and inhibition veridical, e.g. $H_e, H_i$?

Approach:
- Use animal LFP recordings from a small two-region auditory network
- Manipulate neurotransmitter processing via anaesthetic agent Isoflurane

- 4 levels of anaesthesia: each successively decreasing glutamate and increasing GABA
- LFP recordings from primary auditory cortex (A1) & posterior auditory field (PAF)
- White noise stimulus & Silence

<table>
<thead>
<tr>
<th>Isoflurane</th>
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<tbody>
<tr>
<td>1.4 %</td>
<td>1.8 %</td>
<td>2.4 %</td>
<td>2.8 %</td>
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</table>

LFP

A2
Pharmacological Manipulation of Glutamate and GABA

Data

Cross-spectra white noise

Predicted

Observed

1.4 %
1.8 %
2.4 %
2.8 %
Model

Extrinsic Connections:
Forward
Backward
Lateral

Inhibitory cells in supra(infra) granular layers
\[ \dot{v}_4 = g_4 \]
\[ g_4 = \kappa_4 H_4 A^B S(v_6) + \kappa_3 H_4 y_3 S(v_6) - 2\kappa_2 g_4 - \kappa_2^2 v_4 \]
\[ \dot{v}_3 = g_3 \]
\[ \dot{g}_3 = \kappa_3 H_4 y_3 S(v_7) - 2\kappa_2 g_3 - \kappa_2^2 v_3 \]
\[ \dot{v}_2 = g_4 - g_3 \]

Intrinsic connections

Excitatory spiny cells in granular layers
\[ \dot{v}_1 = g_1 \]
\[ g_1 = \kappa_1 H_1 A^F S(v_6^{region2}) + \kappa_2 H_1 y_2 S(v_6) - 2\kappa_2 g_1 - \kappa_2^2 v_1 \]

Pyramidal cells in infra(supra) granular layers
\[ \dot{v}_2 = g_2 \]
\[ i_2 = \kappa_2 H_2 A^B S(v_6^{region2}) + \kappa_3 H_2 y_3 S(v_6) - 2\kappa_2 g_2 - \kappa_2^2 v_2 \]
\[ \dot{v}_3 = g_3 \]
\[ \dot{g}_3 = \kappa_3 H_2 y_3 S(v_7) - 2\kappa_2 g_3 - \kappa_2^2 v_3 \]
\[ \dot{v}_6 = g_2 - g_3 \]

Forward

Backward

Or?

PAF

Or?

PAF

PAF

PAF
Pharmacological Manipulation of Glutamate and GABA

Model

- Log Group Bayes Factor
- Forward
- Backward
- Lateral

- Silence
- White Noise

- M1
- M2
- M3
Physiological Parameters

Decreased Glutamate Release

Increased gabaergic transmission

Inhibitory cells in agranular layers

Excitatory spiny cells in granular layers

Excitatory pyramidal cells in agranular layers

Synaptic ‘alpha’ kernel

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Pharmacological Manipulation of Glutamate and GABA
Pharmacological Manipulation of Glutamate and GABA

Parametric Effect of Isoflurane

Inhibitory cells in agranular layers

Excitatory spiny cells in granular layers

Excitatory pyramidal cells in agranular layers
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5. DCM for Cross Spectral Density

6. DCM for Neural Fields
1. Interface Additions
2. New CSD routines, similar to SSR
3. SPM_NLSI_GN accommodates imag numbers, slopes, curvatures
4. A host of new results features, in channel and source space!

The Fourier transform of a signal is a continuous complex function.

\[ H(\omega) = F(f) = \int_{-\infty}^{\infty} f(t) e^{-2\pi i \omega t} \, dt \]

The Fourier transform of a signal is a continuous complex function.
Model Inversion using absolute value (modulus)

\[ |H_1(\omega) \cdot H_1^*(\omega)| \]

\[ |H_2(\omega) \cdot H_2^*(\omega)| \]

DCM for SSR

Predictions and Data
Predictions

$H_1(\omega) \cdot H_1^*(\omega)$

$H_2(\omega) \cdot H_2^*(\omega)$

Excitatory spiny cells

Pyramidal cells

Inhibitory cells

Excitatory spiny cells

Pyramidal cells

DCM for Cross Spectral Density
$$H_1(\omega) \cdot H_1^*(\omega)$$

$$H_2(\omega) \cdot H_2^*(\omega)$$

Model Inversion using full complex signal

DCM for Cross Spectral Density

Predictions and Data

Power (mV^2)

Frequency (Hz)

Response
prediction and response: E-Step: 32

real

Frequency (Hz)

imaginary

Frequency (Hz)
Spectra \[ \text{Abs}(H_1(\omega) \cdot H_1^*(\omega)), \text{Abs}(H_1(\omega) \cdot H_2^*(\omega)) \ldots \]

Coherence \[ |(H_1(\omega) \cdot H_2^*(\omega))|^2 / \{ (H_1(\omega) \cdot H_1^*(\omega)) + (H_2(\omega) \cdot H_2^*(\omega)) \} \]

Delay at particular frequencies \[ \text{arg}(H_1(\omega) \cdot H_2^*(\omega)) / 2\pi f \]

Covariance (lags over time, collapsed across frequencies) \[ \text{Real}(F^{-1}(H_1(\omega) \cdot H_2^*(\omega))) \]
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New NFM routines

Specify model

Find your experimental data

Extract Data Features

Maximise the model evidence ($\sim F$)

Test models or MAP parameters

And also report spatial extent of intrinsic connections and conduction speed

Pinotsis, Moran, Friston, *Neuroimage* 2012
\[ L(x, \varphi) = \varphi_1 \exp \left( -\frac{x^2}{\varphi_2} \right) \]
Connections in V1

\[ K(|x|) = ae^{-cx} \]

- \( a \) intrinsic connection strength
- \( c \) spatial decay rate \( \leftrightarrow \) connection extent
Inference on Model Parameters

(A) Neural field model

(B) Neural mass model

(Spectral density vs. Frequency (Hz))

(Conditional mean vs. Model Parameter)
New peaks appear:
- as intrinsic speed decreases
- as connectivity extent increases
Summary

• DCM is a generic framework for asking mechanistic questions of neuroimaging data

• Neural mass models parameterise intrinsic and extrinsic ensemble connections and synaptic measures

• DCM for SSR and CSD is a compact characterisation of multi-channel LFP or EEG data in the frequency domain

• Bayesian inversion provides parameter estimates and allows model comparison for competing hypothesised architectures

• Neural field models incorporate propagation of activity on a cortical patch, so one can distinguish between spatial effects due and other factors such as cortico-thalamic interactions or intrinsic cell properties

• Neural field models yield estimates of parameters related to topographic properties of the sources such as spatial decay rate of synaptic connections and intrinsic conduction speed
Thanks to

Rosalyn Moran       Vladimir Litvak       Will Penny       Klaas Stephan

... and thank you !
Field Power Spectra

\[ L(x, \varphi) = \varphi_1 \exp\left(-\frac{x^2}{\varphi_2}\right) \]

\[ g_Y(\omega) = g_Y(\omega, \theta) + g_N(\omega, \theta) + \varepsilon(\omega) \]

\[ g_Y(\omega, \theta) \approx \frac{\pi}{\ell} \sum_j L\left(\frac{j\pi}{\ell}\right) T_m\left(\frac{j\pi}{\ell}, \omega\right) g_U\left(\frac{j\pi}{\ell}, \omega\right) T_{m'}\left(\frac{j\pi}{\ell}, \omega\right) L\left(\frac{j\pi}{\ell}\right) \]

\[ g_N(\omega, \theta) = \alpha_N + \frac{\beta_N}{\omega} \]

\[ g_U(k, \omega) = \alpha_U + \frac{\beta_U}{\omega} \]

\[ \text{Re}(\varepsilon) \sim N\left(0, \Sigma(\omega, \lambda)\right) \quad \text{Im}(\varepsilon) \sim N\left(0, \Sigma(\omega, \lambda)\right) \]
\[ g_Y(\omega) = g_Y(\omega, \theta) + g_N(\omega, \theta) + \varepsilon(\omega) \]

\[ L(x, \varphi) = L(\eta) \]

\[ y(t) = L \cdot V \]

\[ g_Y(\omega, \theta) \approx \sum_k L(\eta)T_m^k(\omega, \theta) g_U(\omega)T_m^*(\omega, \theta)^* L(\eta)^* \]

\[ g_N(\omega, \theta) = \alpha_N + \frac{\beta_N}{\omega} \]

\[ T_m^k(\omega, \theta) = \int \kappa_m^k(t, \theta)e^{-j\omega t} dt \]

\[ \kappa_m^k(t, \theta) = \frac{\partial g}{\partial x} e^{3\tau} \mathcal{S}^{-1} \frac{\partial f}{\partial u_k} \]

\[ \text{Re}(\varepsilon) \sim \mathcal{N}(0, \Sigma(\omega, \lambda)) \quad \text{Im}(\varepsilon) \sim \mathcal{N}(0, \Sigma(\omega, \lambda)) \]
Maximum postsynaptic depolarization
8, 32 (mV)

Postsynaptic time constants
1/4, 1/28 (ms⁻¹)

Amplitude of intrinsic connectivity kernels
2000, 8000, 2000, 1000

Intrinsic connectivity decay constant
0.32 (mm⁻¹)

Sigmoid parameters (post synaptic firing rate function)
0.54, 0, 0.135

Conduction velocity
3 m/s

Radius of cortical source
50 (mm)
Neural Mass vs Neural Field

Difference in predicted spectra $g_Y(\omega, \theta)$ because of difference in underlying model:

**Neural Mass**

- **Exogenous input**
  - $U(t)$

- **Hidden states**
  - $V = -B^2V - 2BV + ABF \circ V + GU$

- **Observed signals**
  - $y(t) = L \cdot V$

**Neural Field**

- **Exogenous input**
  - $U(t)$

- **Hidden states**
  - $\dot{V} = -B^2V - 2BV + ABD \otimes F \circ V + GU$

- **Observed signals**
  - $y(t) = \int L(x, \varphi) \cdot V(x, t) dx$

$$D \otimes Q = \iint D(x - x', t - t') \cdot Q(x', t') dx' dt'$$
Inhibitory cells in supragranular layers
\[
\dot{v}_2 + 2\kappa_i \dot{v}_2 + \kappa_i^2 v_2 = \kappa_i m_i \mu_2 \\
\dot{\mu}_2 + 2sc_{23} \dot{\mu}_2 - s^2 (\mu_{2xx} - c_{23}^2 \mu_2) = \alpha_{23} (s^2 c_{23} \sigma(v_3) + s \dot{\sigma}(v_3))
\]

Excitatory spiny cells in granular layers
\[
\dot{v}_1 + 2\kappa_e \dot{v}_1 + \kappa_e^2 v_1 = \kappa_e m_e (\mu_1 + U) \\
\dot{\mu}_1 + 2sc_{13} \dot{\mu}_1 - s^2 (\mu_{1xx} - c_{13}^2 \mu_1) = \alpha_{13} (s^2 c_{13} \sigma(v_3) + s \dot{\sigma}(v_3))
\]

Excitatory pyramidal cells in supra- and infragranular layers
\[
\dot{v}_3 + 2\kappa_e \dot{v}_3 + \kappa_e^2 v_3 = \kappa_e m_e \mu_3 \\
\dot{\mu}_3 + 2sc_{31} \dot{\mu}_3 - s^2 (\mu_{3xx} - c_{31}^2 \mu_3) = \alpha_{31} \left( s^2 c_{31} (\sigma(v_1) - \sigma(v_2)) + s (\dot{\sigma}(v_1) - \dot{\sigma}(v_2)) \right)
\]

\( s \) conduction velocity

\( y(t) = \int L(x, \varphi) \cdot V(x, t) \, dx \)