Dynamic Causal Modelling for Steady State Responses

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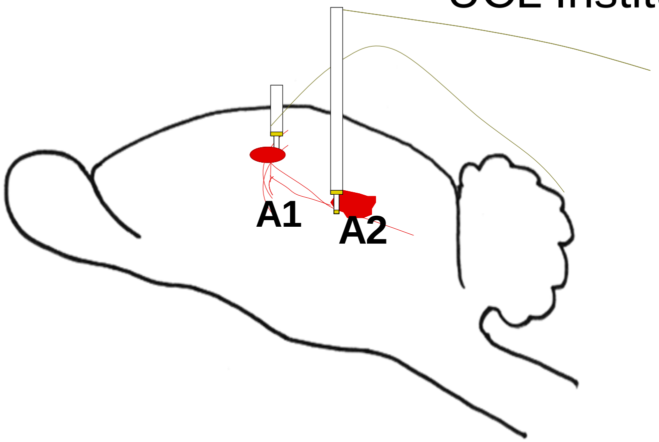
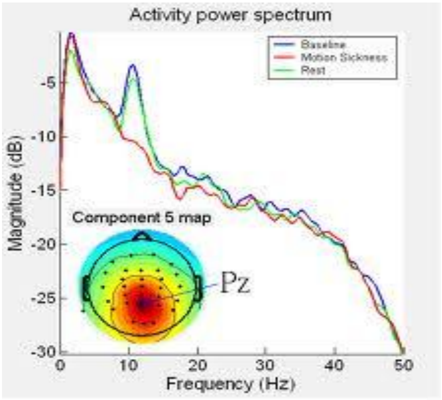
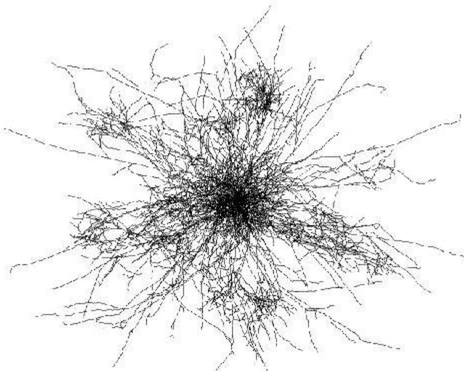


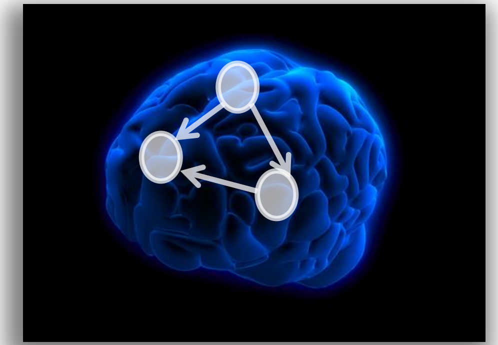


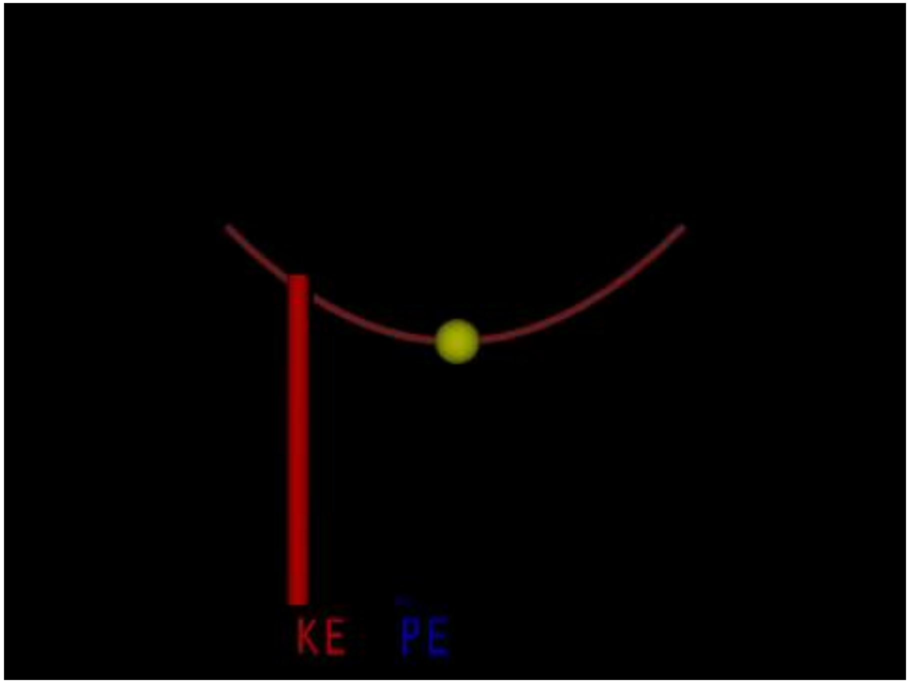


Dynamic Causal Modelling for SSR

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 ⟷ NEURAL NOISE

BALL ⟷ BRAIN REGION

RINGINGS ⟷ RESPONSES (cross spectral densities)

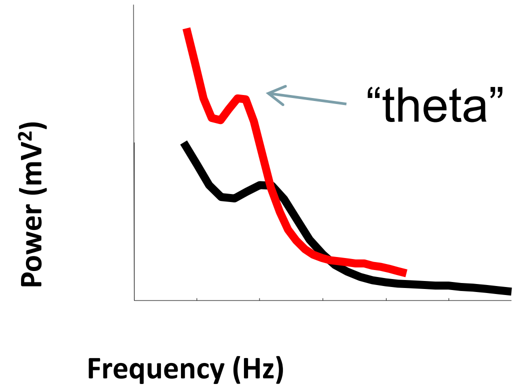
CONTAINER ⟷ MODEL (equations, parameters cf. shape/friction)

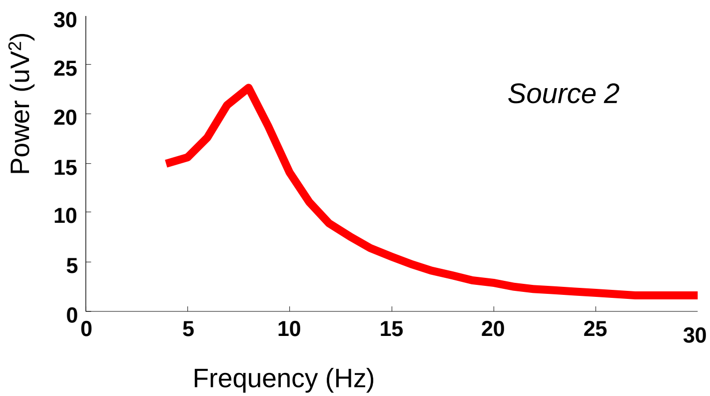
STEADY STATE PERTURBATIONS means that

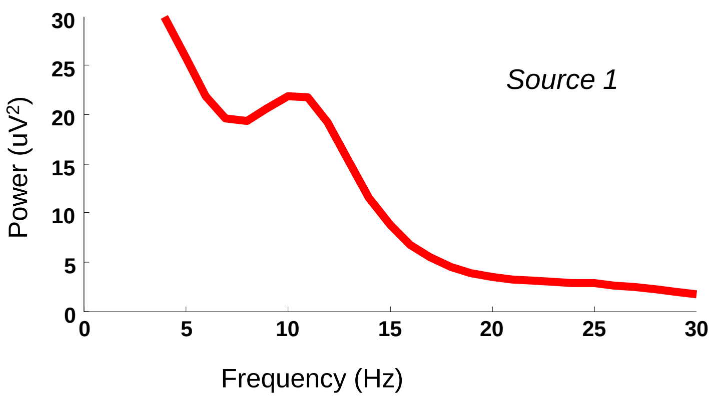
“ the ball always stays very close to the centre” (while the bowl is tilted)

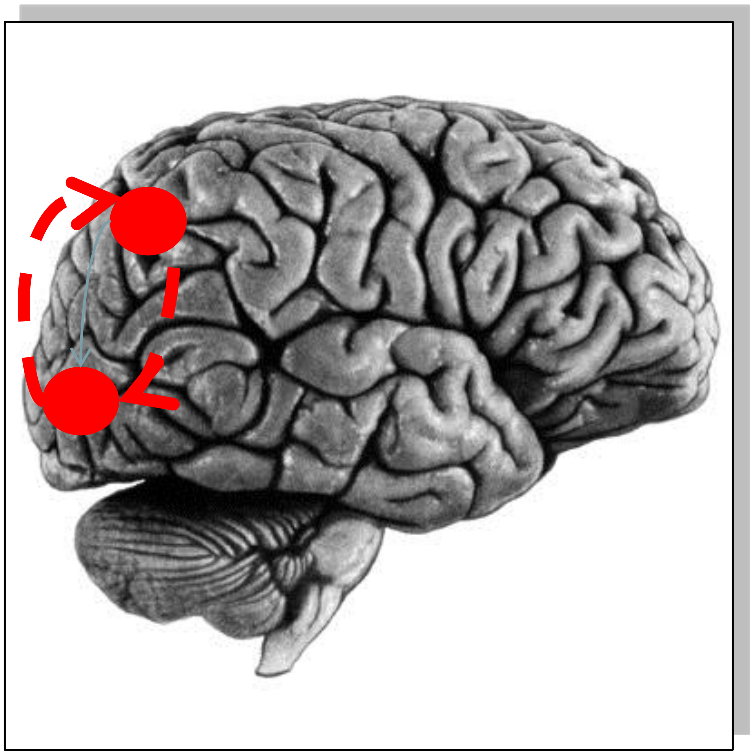
Spectral Densities

- ❑ Linearity
- ❑ Ergodicity

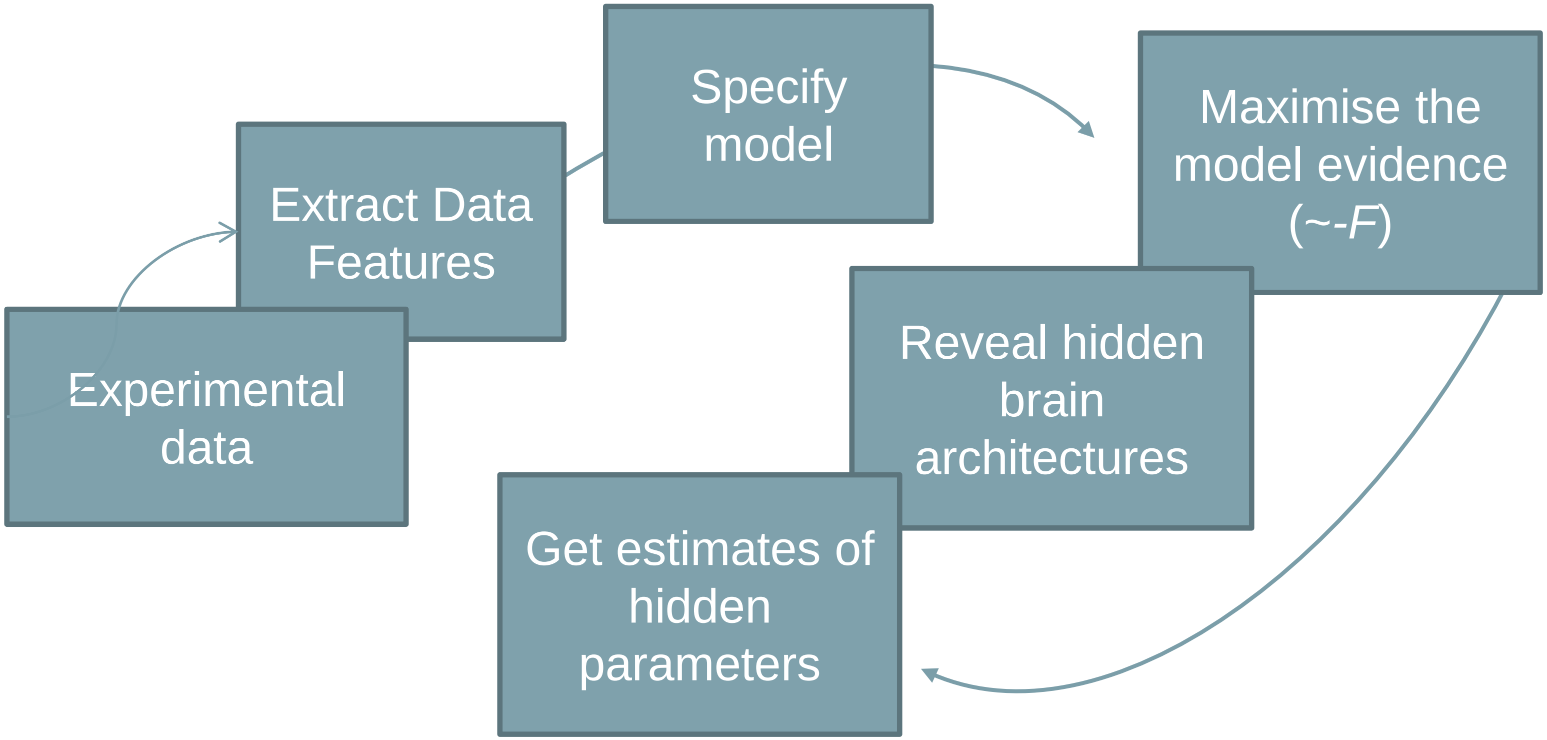








DCM Chain


Experimental data
Extract Data Features
Specify model
Maximise the model evidence (~-F)
Reveal hidden brain architectures
Get estimates of hidden parameters

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

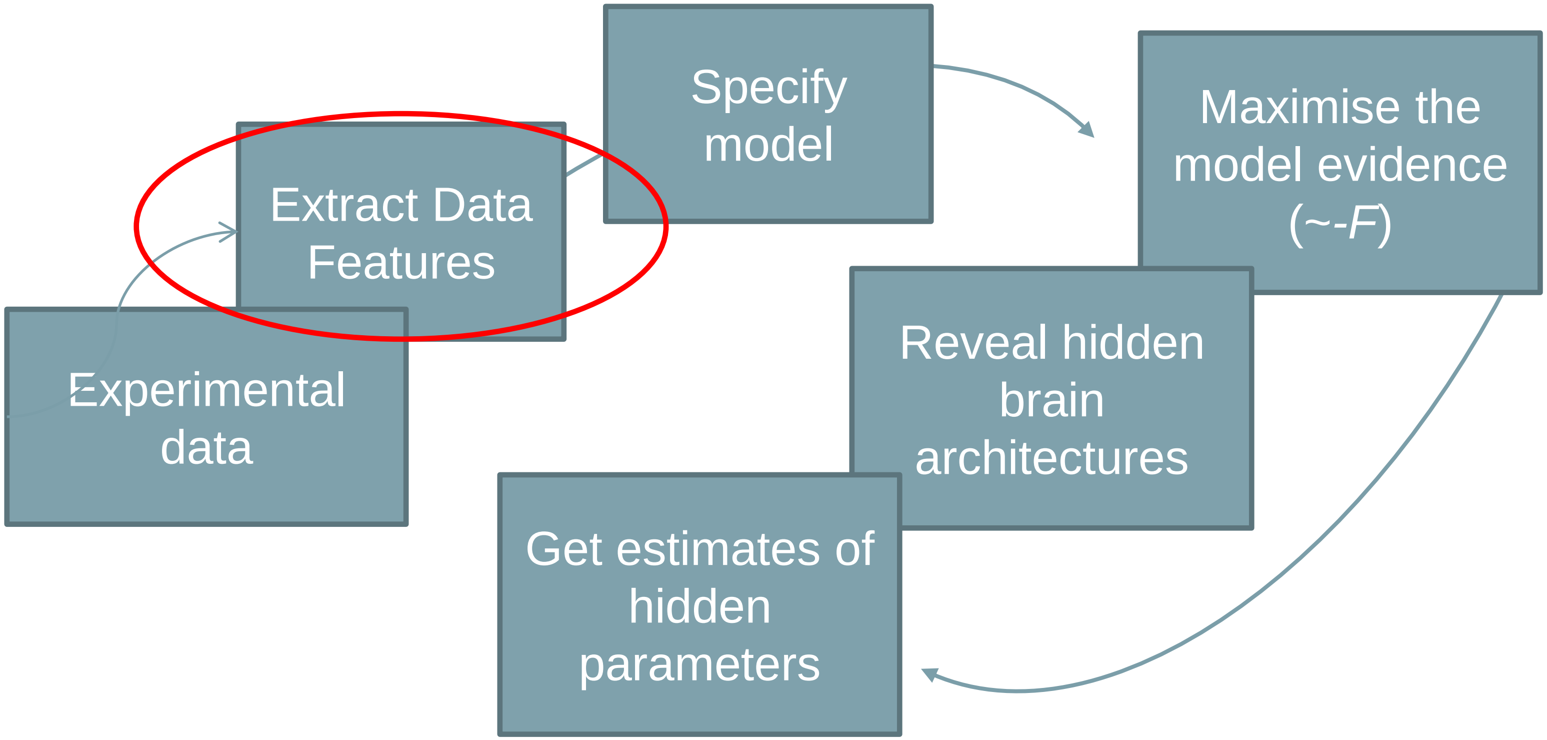
2. Generative Model

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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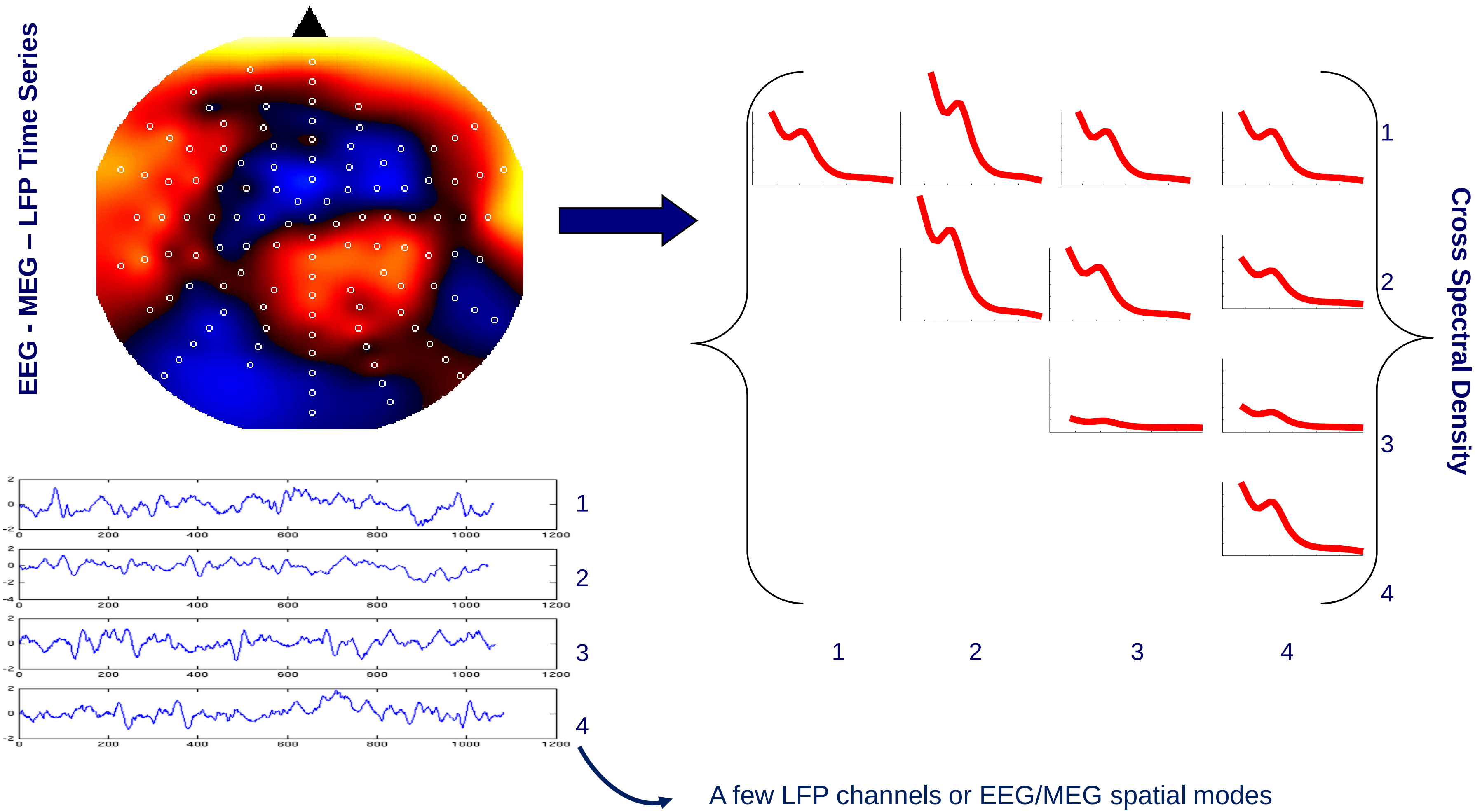
Cross Spectral Density: The Data

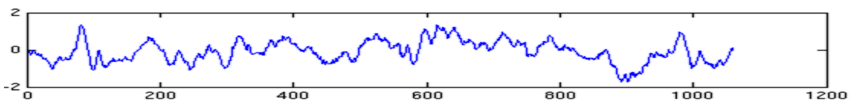


A few LFP channels or EEG/MEG spatial modes

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



$$y_n = \alpha_1 y_{n-1} + \alpha_2 y_{n-2} \dots + \alpha_p y_{n-p} + e_n$$

Resulting in *a* matrices for *c* Channels

$$\{\alpha_{1 \dots p} \in A(p) : \{c \times c\}$$

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

$$\omega = 2\pi f$$

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

$$H_{ij}(\omega) = \frac{1}{\alpha_1^{ij} e^{iw} + \alpha_2^{ij} e^{iw2} + \dots\dots + \alpha_p^{ij} e^{iwp}}$$

$$\left\{ \begin{matrix} g(\omega)_{11} & g(\omega)_{12} & .. \\ g(\omega)_{12} & .. & \\ & & \end{matrix} \right\}$$

$$g(\omega)_{ij} = H_{ij}(\omega) \prod_{ij} H(\omega)_{ij}^{*}$$

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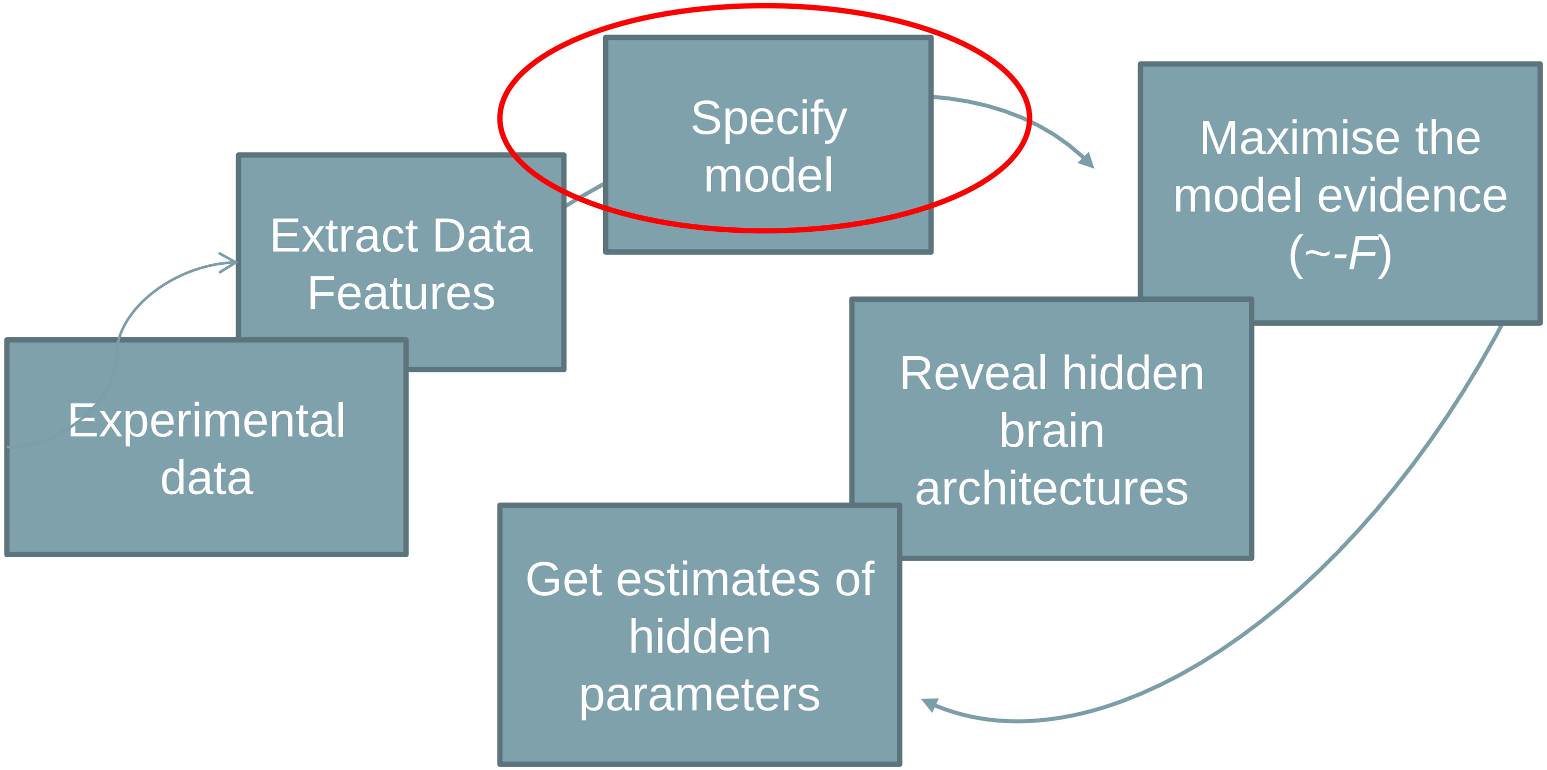
DCM Chain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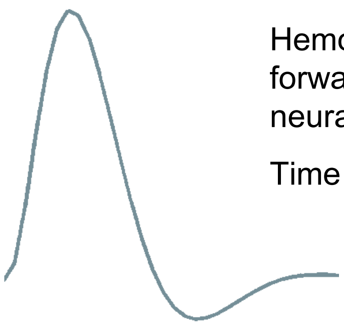
Dynamic Causal Modelling: Generic Framework

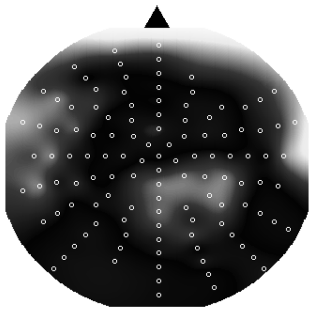


Hemodynamic
forward model:
neural activity→BOLD

Time Domain Data

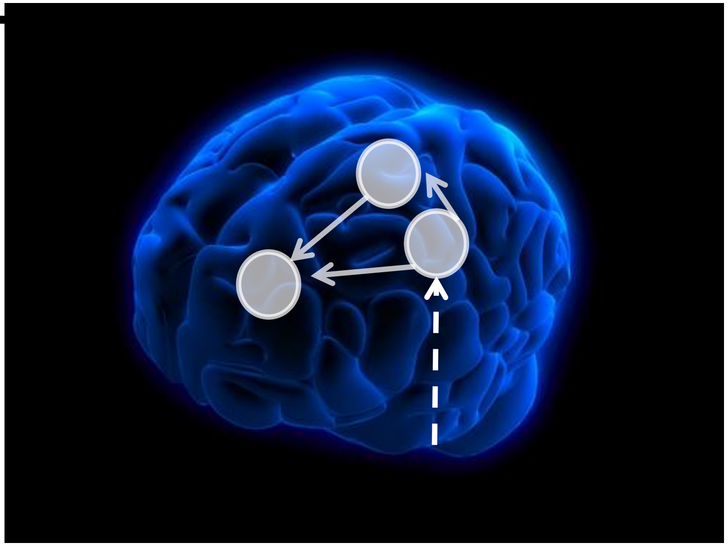
Electromagnetic
forward model:
neural activity→EEG
MEG
LFP

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



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

Neural state equation:



fMRI

simple neuronal model

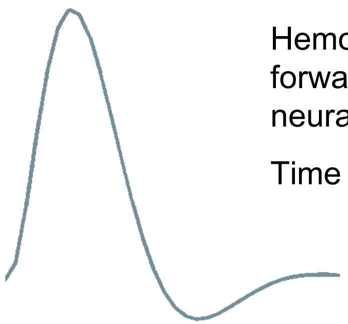
Slow time scale

EEG/MEG

complicated neuronal model

Fast time scale

Dynamic Causal Modelling: Generic Framework

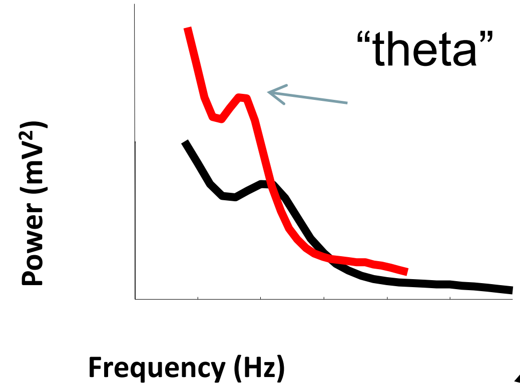


Hemodynamic forward model:
neural activity→BOLD

Time Domain Data

Electromagnetic forward model:
neural activity→EEG
MEG
LFP

Steady State Frequency Data



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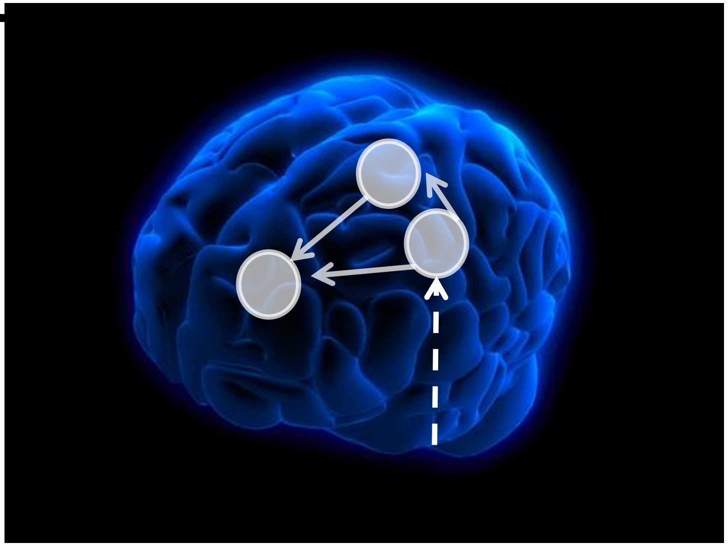
Neural state equation:



fMRI

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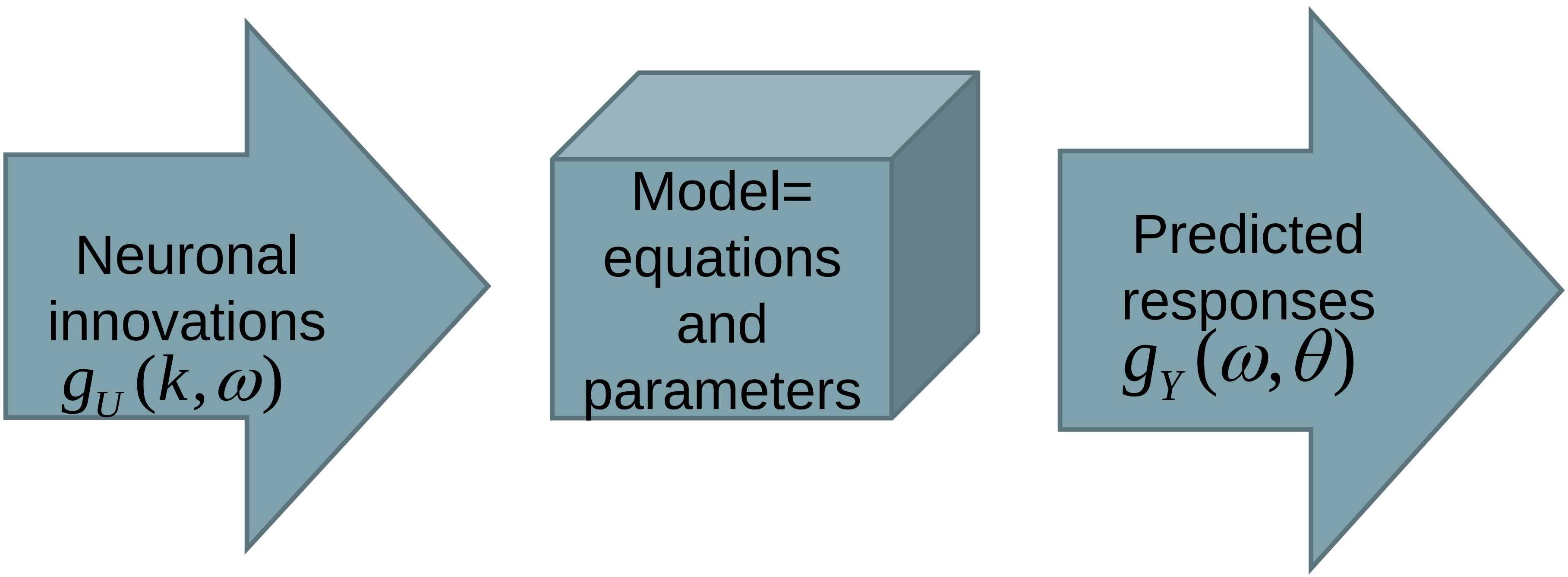
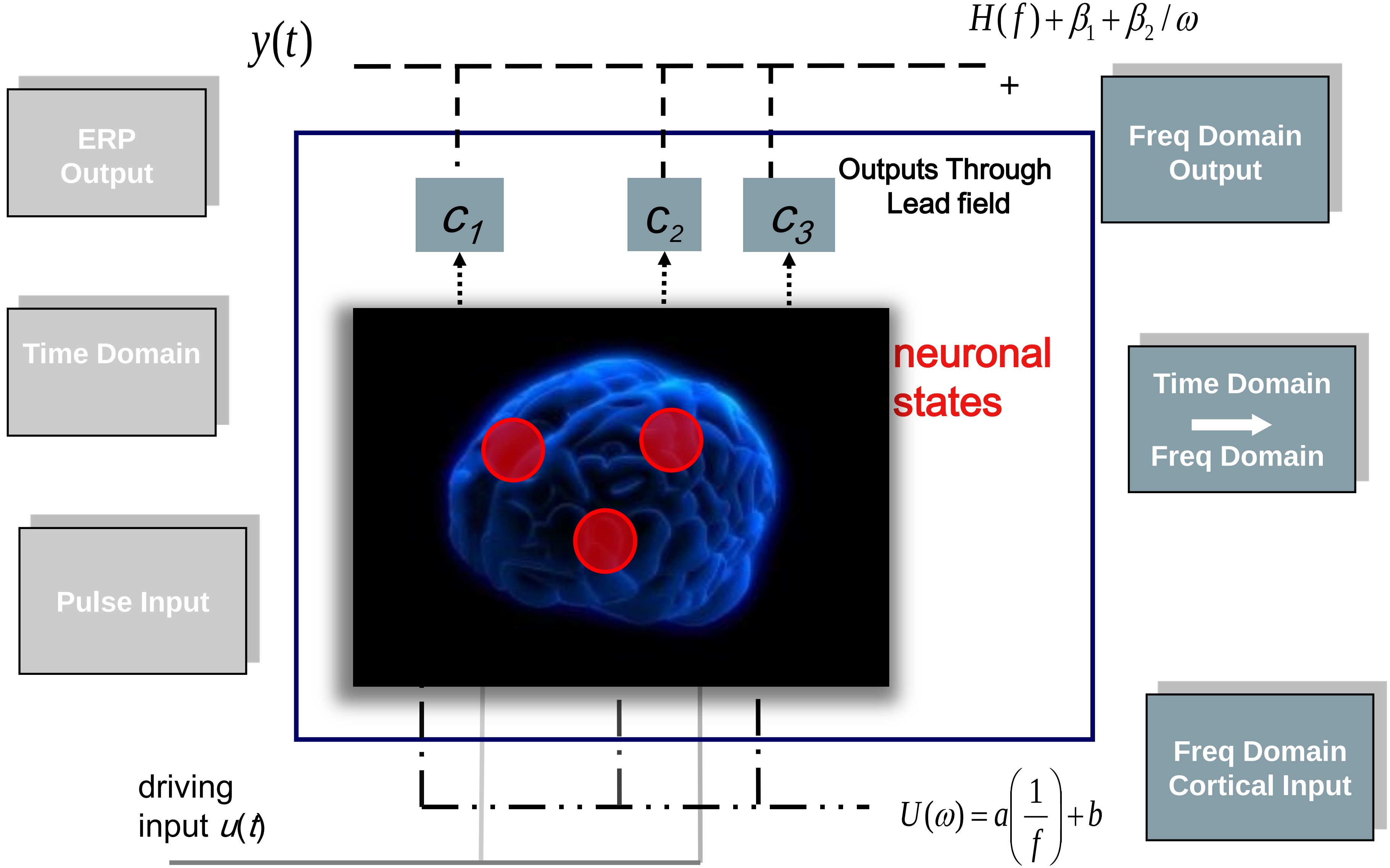
Fast time scale

A Brain Region as an Input - Output System

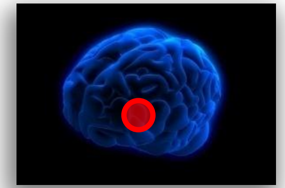


$$\theta = \{H_e, H_i, \kappa_e, \kappa_i, \kappa_a, \gamma_1, \gamma_2, \gamma_3, \gamma_4, \gamma_5, g, A_F, A_B, A_L, \lambda\}$$

ERP vs Steady State Responses

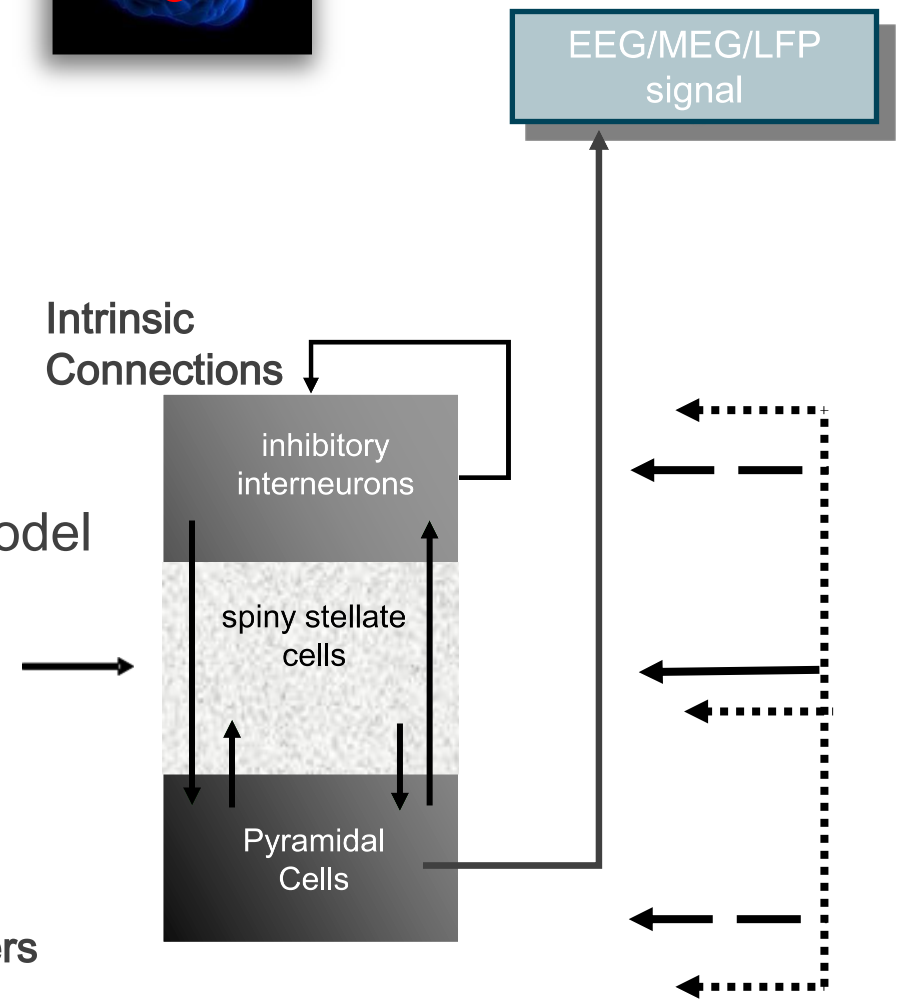


Neural Mass Model



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

neuronal (source) model



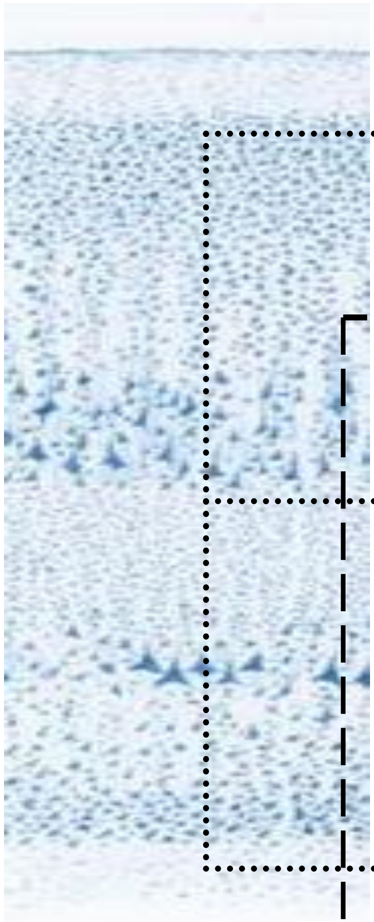
Internal Parameters

Extrinsic Connections

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

State equations

Neural Mass Model



Intrinsic connections

γ_5

Inhibitory cells in agranular layers

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

γ_4 γ_3

Excitatory spiny cells in granular layers

$$\dot{x}_1 = x_4$$
$$\dot{x}_4 = \kappa_e H_e ((A^F + A^L + \gamma_1) S(x_9) + Cu) - 2\kappa_e x_4 - \kappa_e^2 x_1$$

γ_1 γ_2

Excitatory pyramidal cells in agranular layers

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

Extrinsic Connections:

Forward

Backward

Lateral

$$\dot{x} = f(x,u)$$

Neural Mass Model

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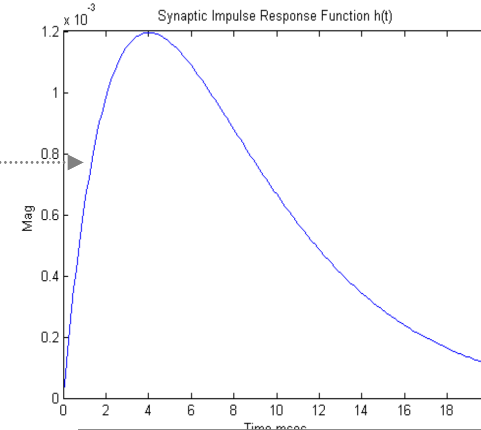
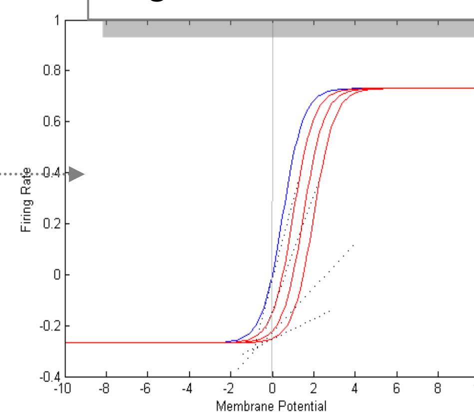


Synaptic 'alpha' kernel

Sigmoid function



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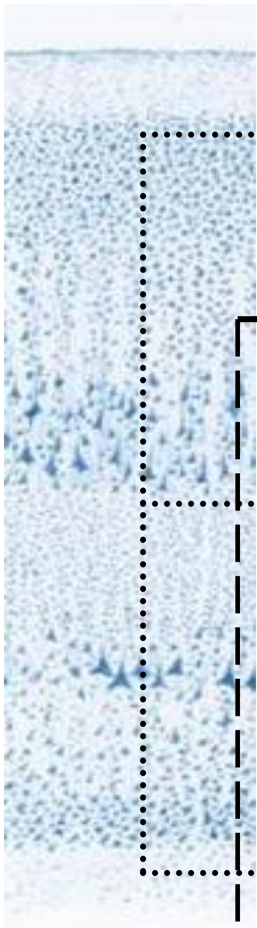

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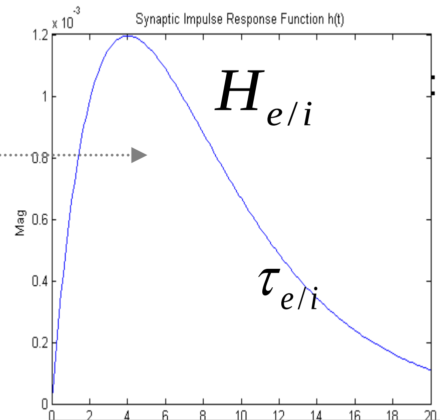
Extrinsic Connections:

Forward

Backward

Lateral

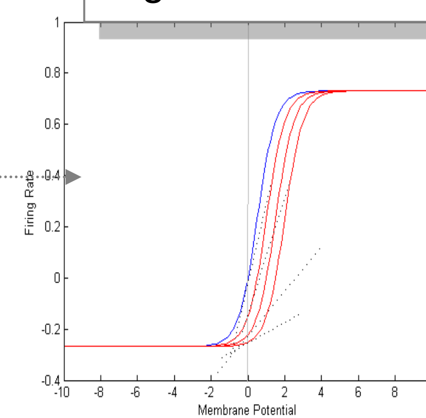


$H_{e/i}$: Receptor Density

Synaptic 'alpha' kernel

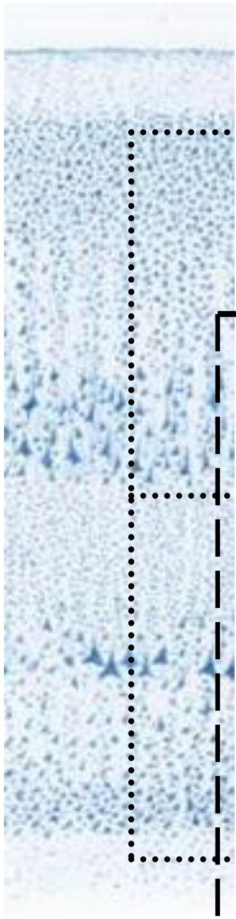
$$v = r \otimes h$$

Sigmoid function



Neural Mass Model

Intrinsic connections



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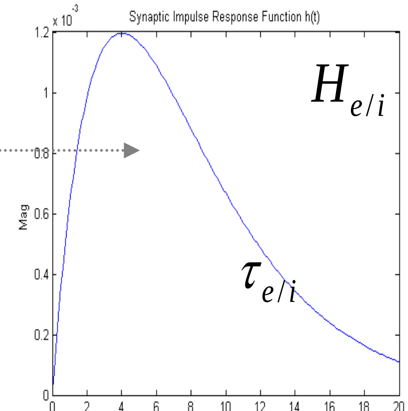
$$\dot{x} = f(x,u)$$

Extrinsic Connections:

Forward →

Backward - - →

Lateral ····→



: Receptor Density

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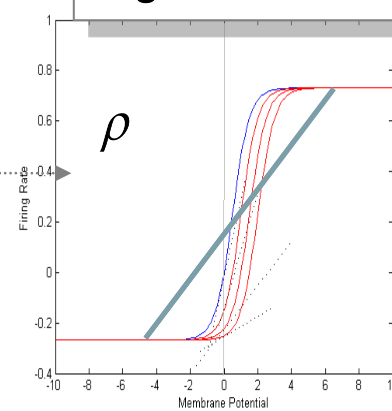


: Firing Rate

$$r = S(v)$$

Frequency Domain Generative Model
(Perturbations about a fixed point)

Time Differential Equations

$$\dot{x} = f(x) + Bu$$
$$y = l(x)$$

→

State Space Characterisation

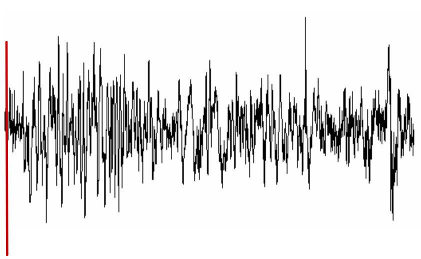
$$\dot{x} = Ax + Bu$$
$$y = Cx$$

→

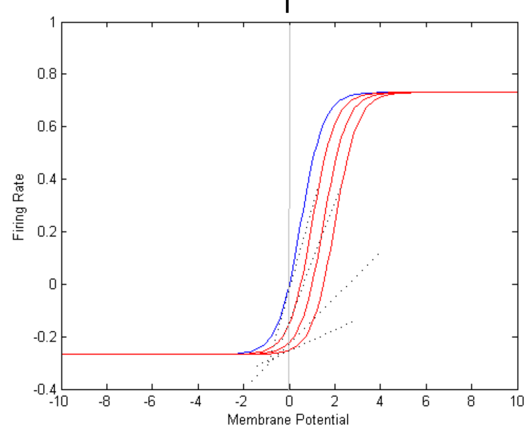
Transfer Function Frequency Domain

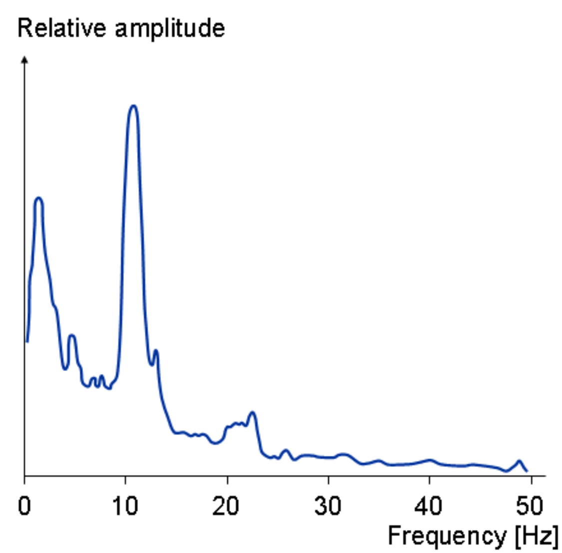
$$H(s) = C(sI - A)B$$

mV



Linearise





Frequency Domain Generative Model
(Perturbations about a fixed point)

Transfer Function Frequency Domain

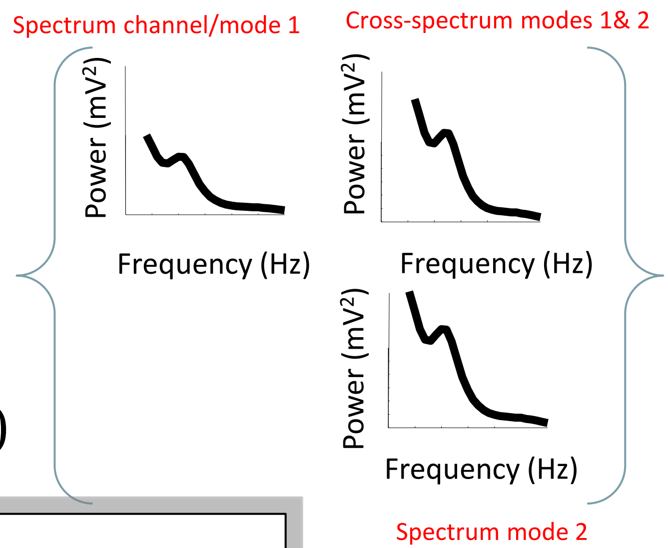
$$H1(\omega) = f(\theta : H_{e/i}, \tau_{e,i} ..)$$

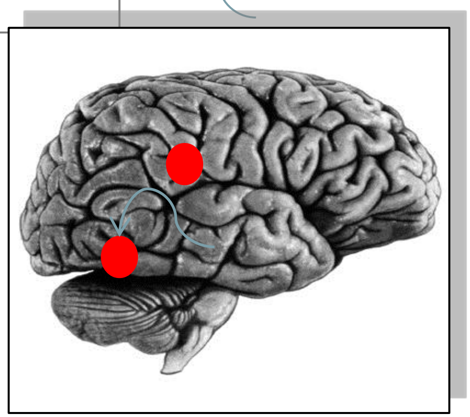
Cross-Transfer Function Frequency Domain

$$H12(\omega) = f(\theta : H_{e/i}, \tau_{e,i} ..)$$

Transfer Function Frequency Domain

$$H2(\omega) = f(\theta : H_{e/i}, \tau_{e,i} ..)$$





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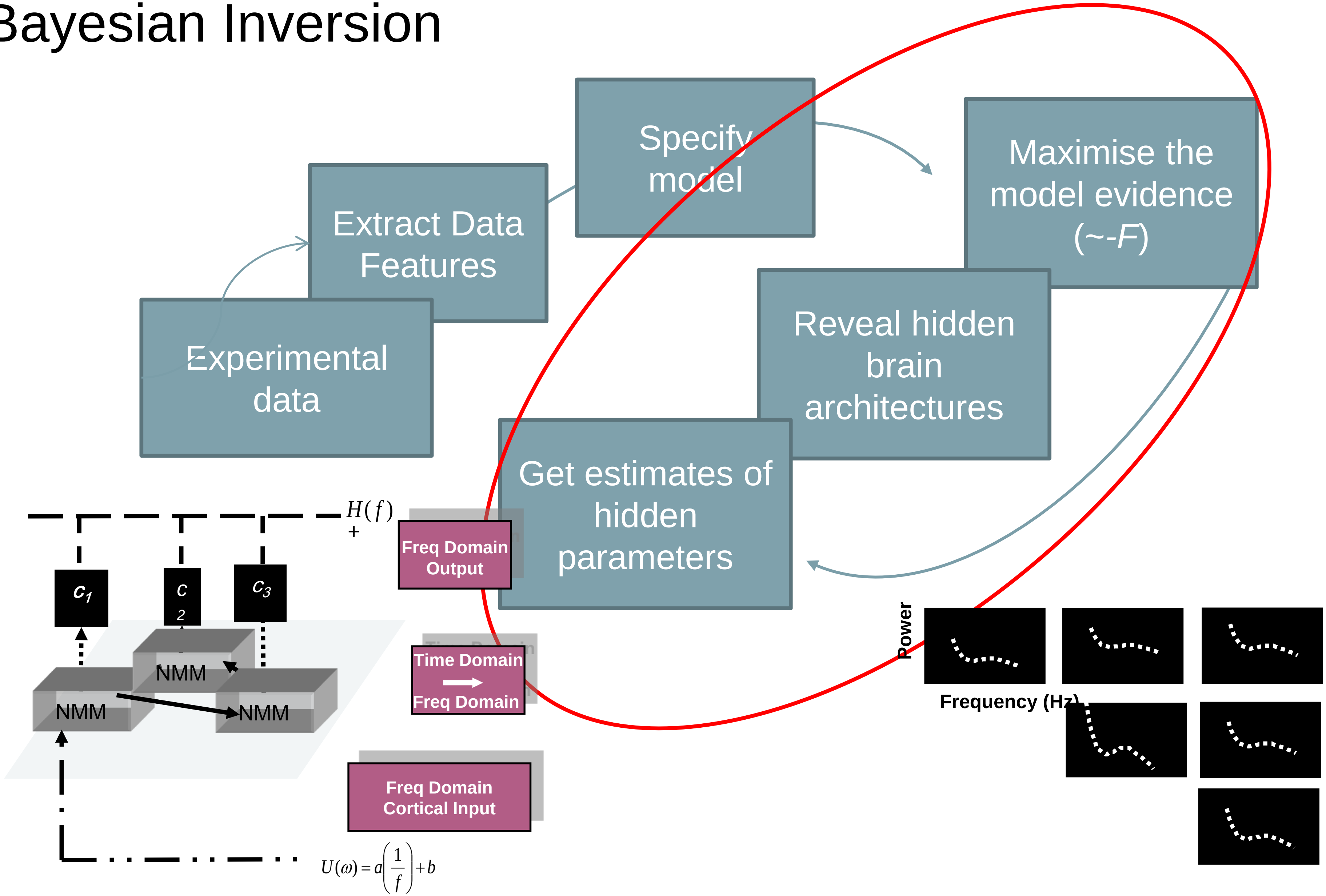
Bayesian Inversion



Roadmap

Generative model
- predicted responses
- parameters
- hyperparameters

Priors
- variance

Bayesian Inference
- Model Evidence
- Posteriors

$$\mathbf{g}_Y(\omega) = g_Y(\omega,\theta) + g_N(\omega,\theta) + \varepsilon(\omega)$$

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

$$\mathrm{Re}(\varepsilon) \sim \mathrm{N}\,(0, \Sigma(\omega,\lambda)) \qquad \mathrm{Im}(\varepsilon) \sim \mathrm{N}\,(0, \Sigma(\omega,\lambda))$$

+

$$p(\theta, m) = N(\mu_\theta, \Sigma_\theta)$$

=

$$p(G \mid \theta, m) = N(\mathbf{g}_Y(\omega), \Sigma(\omega,\lambda))$$

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

$$p(\theta \mid G, m) = \frac{p(G \mid \theta, m)\, p(\theta, m)}{p(G \mid m)}$$

Measured data

Specify generative forward model (with prior distributions of parameters)

Variational Laplace Algorithm

Maximize a free energy bound to model evidence :

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

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

<u>Iterative procedure:</u>

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:

$$BF = \frac{p(y \mid m_1)}{p(y \mid m_2)}$$

$$q(\theta) \approx p(\theta|y,m)$$

Maximum accuracy over complexity constraints

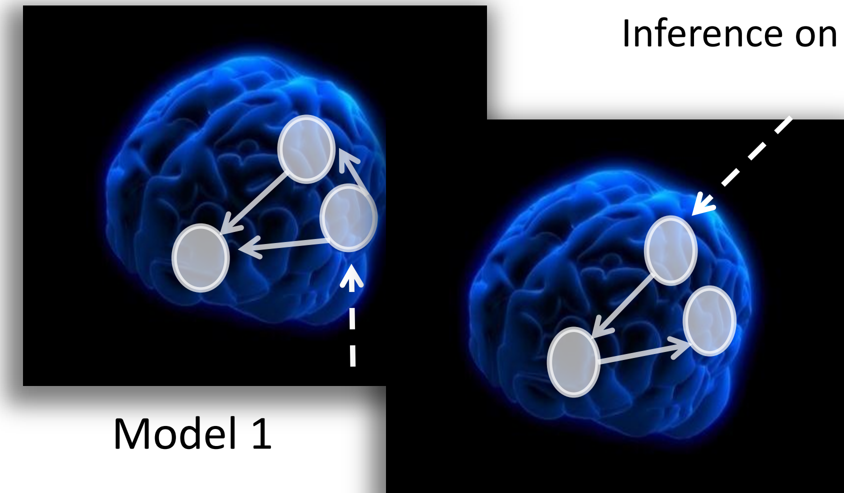
Bayes' rules: $p(\theta \mid y,m) = \dfrac{p(y \mid \theta, m)\, p(\theta \mid m)}{p(y \mid m)}$

Bayesian Inversion

Free Energy: $\underset{\max}{F} = \ln p(y|m) - D(q(\theta) \| p(\theta|y,m))$

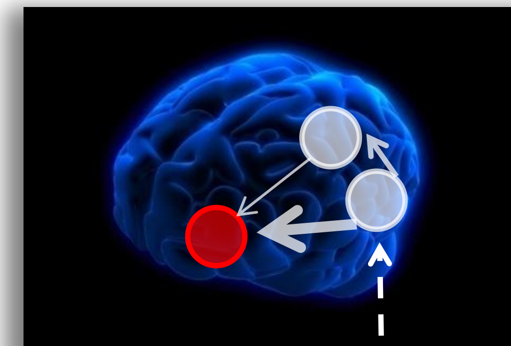
Inference on parameters

Inference on models



Model 1

Model 2

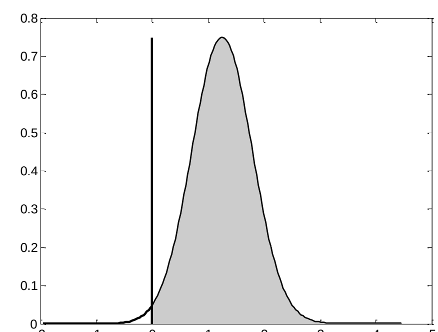


Model 1

Model comparison via Bayes factor:

$$BF = \frac{p(y \mid m_1)}{p(y \mid m_2)}$$

$$q(\theta) \approx p(\theta|y,m)$$



- accounts for both accuracy and complexity of the model
- allows for inference about structure (generalisability) of the model

Overview

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4. Example: Glutamate and GABA in Rodent Auditory Cortex

5. DCM for Cross Spectral Density

6. DCM for Neural Fields

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

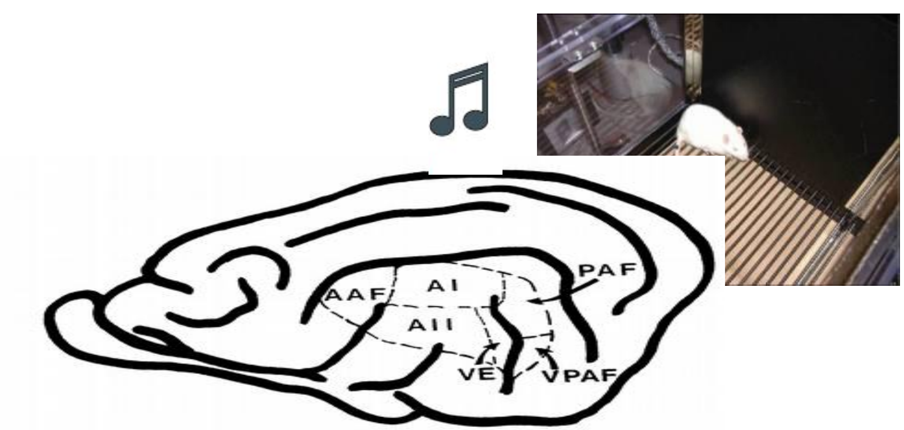
Moran, Tetsuya, Jung, Endepols, Graf, Dolan, Friston, Stephan, Tittgemeyer, *PLoSONE, 2011*

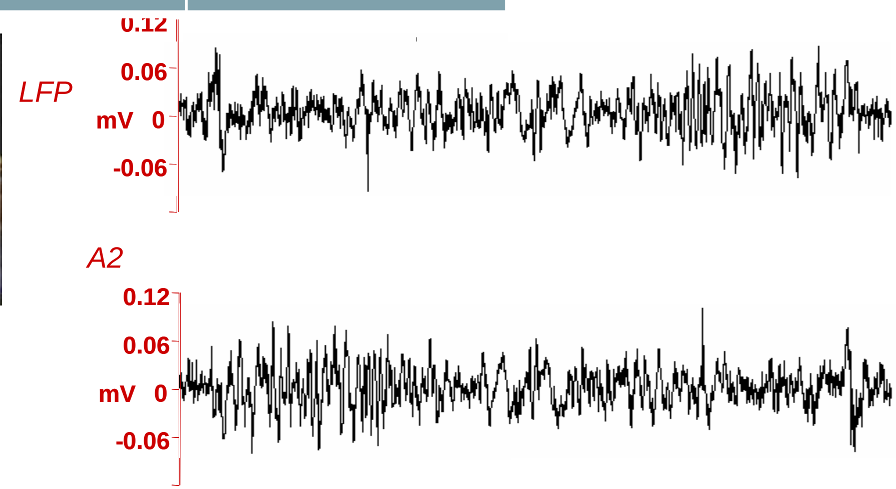
Pharmacological Manipulation of Glutamate and GABA

- 4 levels of anaesthesia: each successively decreasing glutamate and increasing GABA

  (Larsen *et al* Brain Research 1994; Lingamaneni *et al* Anesthesiology 2001; Caraiscos *et al* J Neurosci 2004 ; de Sousa *et al* Anesthesiology 2000)
- LFP recordings from primary auditory cortex (A1) & posterior auditory field (PAF)
- White noise stimulus & Silence

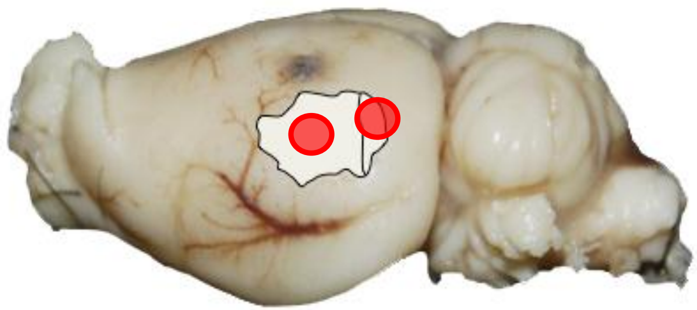
1.4 % Isoflurane	1.8 % Isoflurane	2.4 % Isoflurane	2.8 % Isoflurane



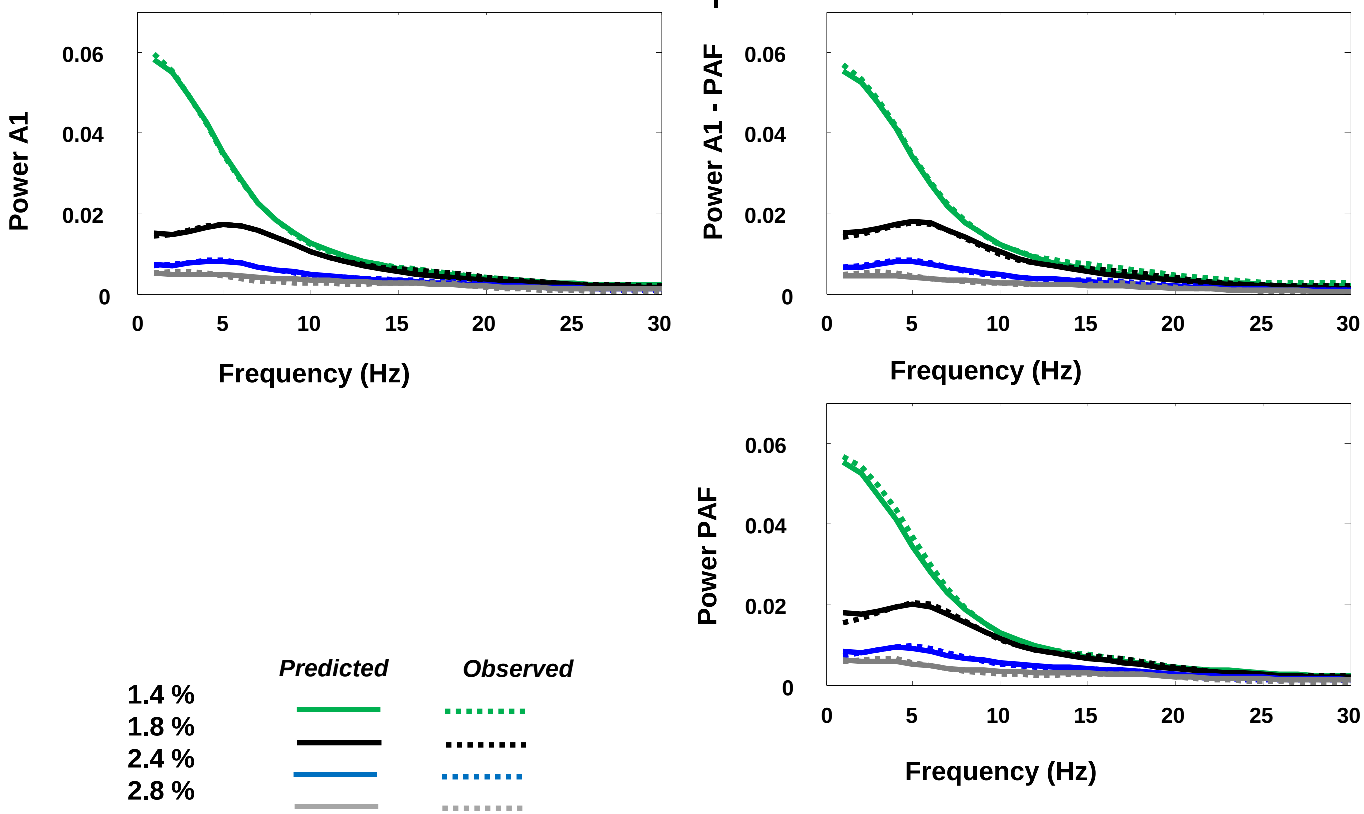


Pharmacological Manipulation of Glutamate and GABA

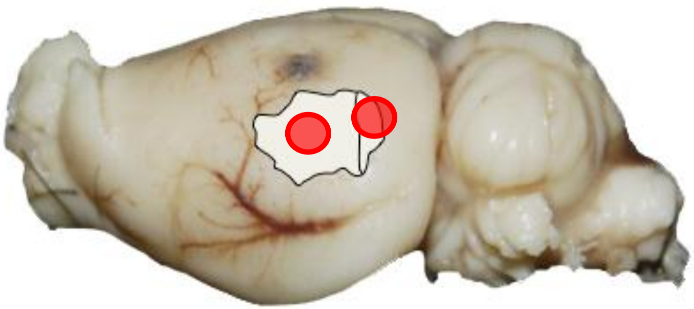
Data

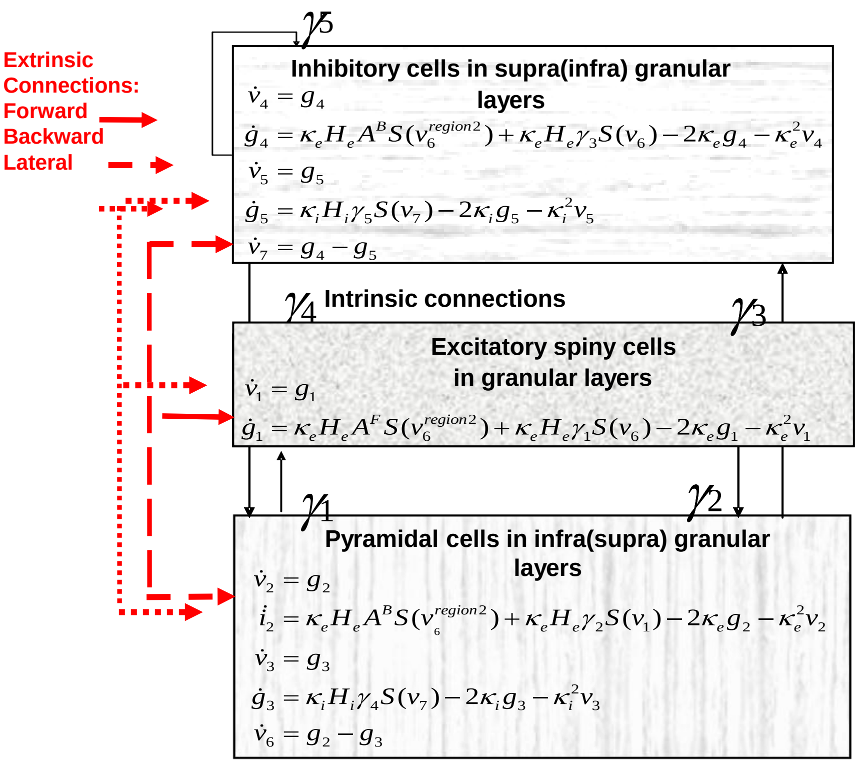


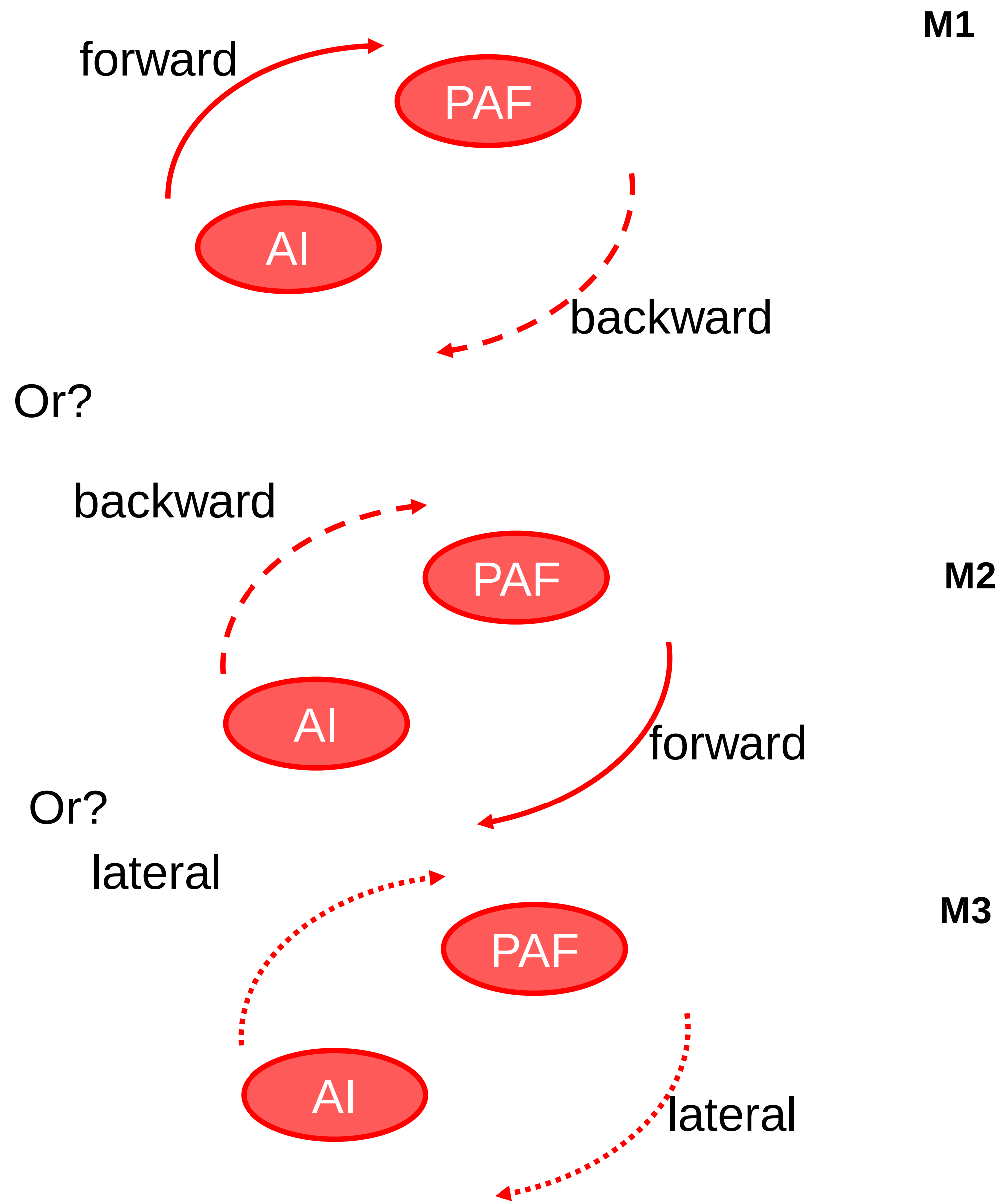
Cross-spectra white noise



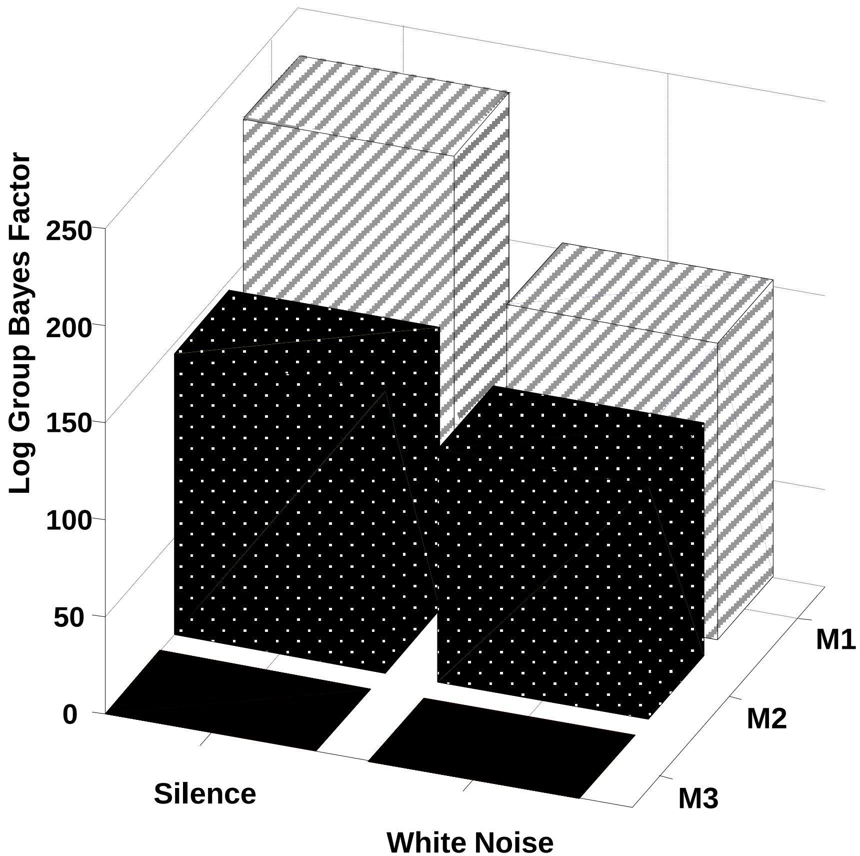
Model

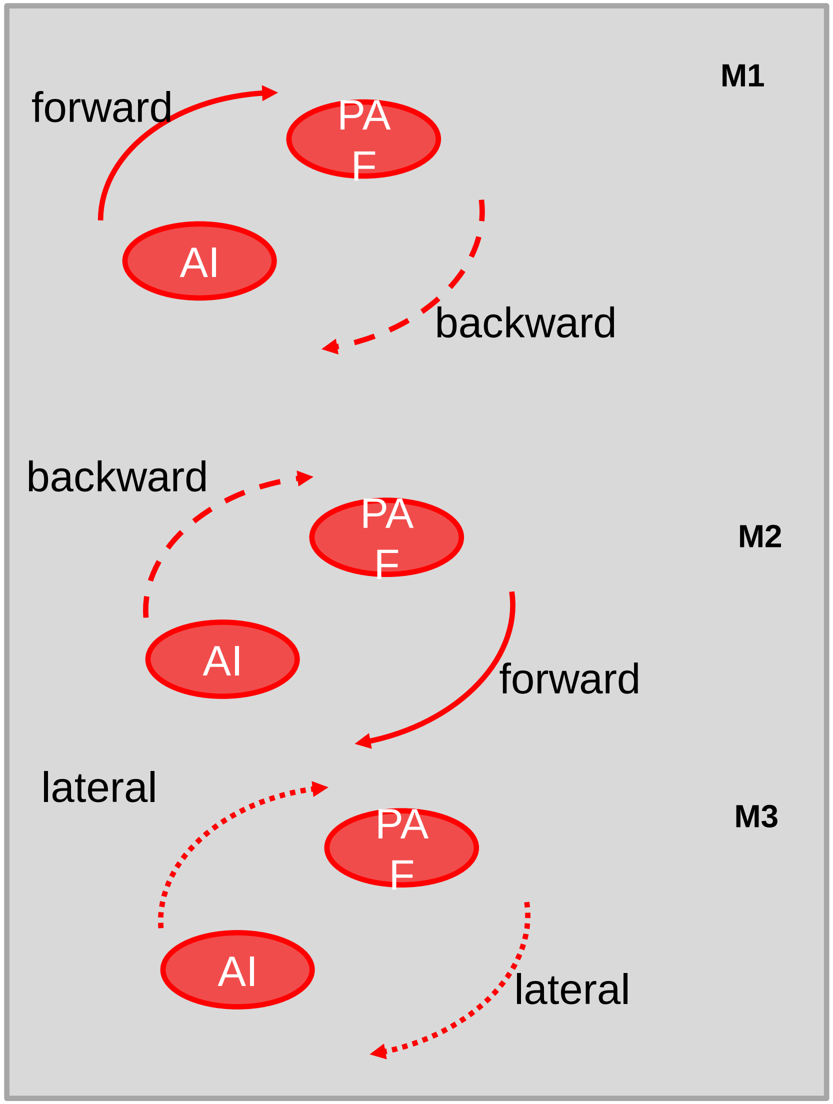



Extrinsic Connections:
Forward
Backward
Lateral
γ_5
Inhibitory cells in supra(infra) granular layers
$\dot{v}_4 = g_4$
$\dot{g}_4 = \kappa_e H_e A^B S(v_6^{region2}) + \kappa_e H_e \gamma_3 S(v_6) - 2\kappa_e g_4 - \kappa_e^2 v_4$
$\dot{v}_5 = g_5$
$\dot{g}_5 = \kappa_i H_i \gamma_5 S(v_7) - 2\kappa_i g_5 - \kappa_i^2 v_5$
$\dot{v}_7 = g_4 - g_5$
γ_4
Intrinsic connections
γ_3
Excitatory spiny cells in granular layers
$\dot{v}_1 = g_1$
$\dot{g}_1 = \kappa_e H_e A^F S(v_6^{region2}) + \kappa_e H_e \gamma_1 S(v_6) - 2\kappa_e g_1 - \kappa_e^2 v_1$
γ_1
γ_2
Pyramidal cells in infra(supra) granular layers
$\dot{v}_2 = g_2$
$\dot{i}_2 = \kappa_e H_e A^B S(v_6^{region2}) + \kappa_e H_e \gamma_2 S(v_1) - 2\kappa_e g_2 - \kappa_e^2 v_2$
$\dot{v}_3 = g_3$
$\dot{g}_3 = \kappa_i H_i \gamma_4 S(v_7) - 2\kappa_i g_3 - \kappa_i^2 v_3$
$\dot{v}_6 = g_2 - g_3$


M1
forward
PAF
AI
backward
Or?
backward
PAF
M2
AI
forward
Or?
lateral
PAF
M3
AI
lateral

Model


Log Group Bayes Factor
0
50
100
150
200
250
Silence
White Noise
M1
M2
M3

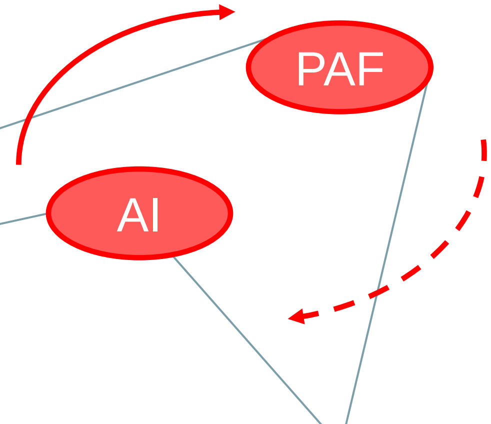

M1
forward
PA
F
AI
backward
backward
PA
F
M2
AI
forward
lateral
PA
F
M3
AI
lateral

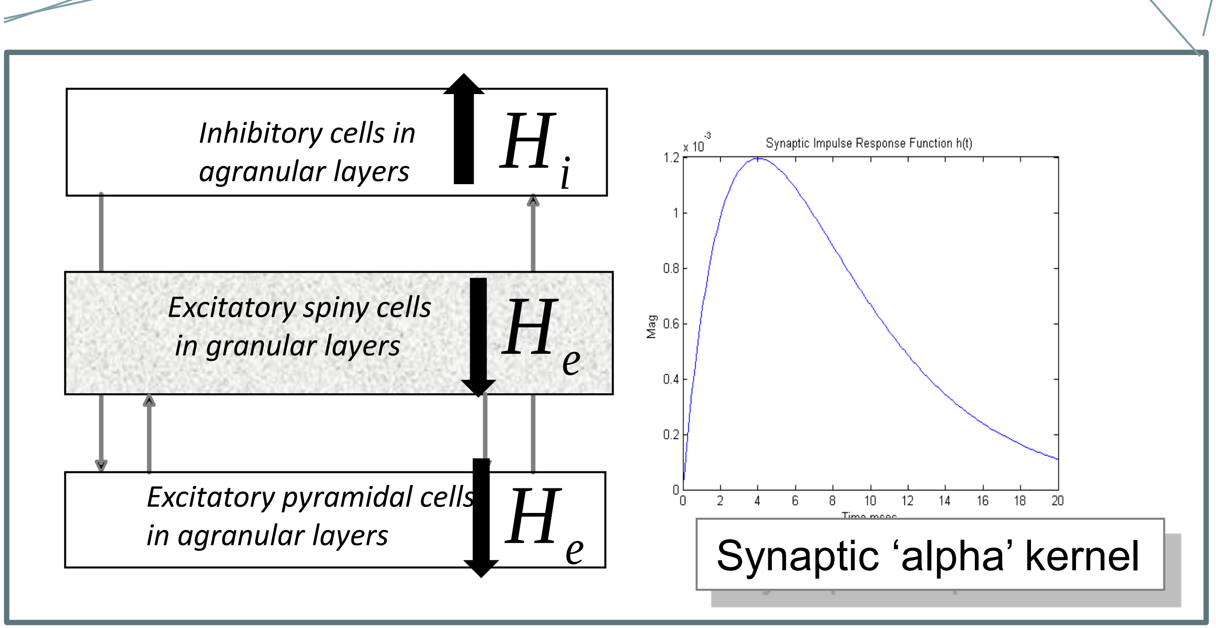
Physiological Parameters

1.4 % Isoflurane	1.8 % Isoflurane	2.4 % Isoflurane	2.8 % Isoflurane

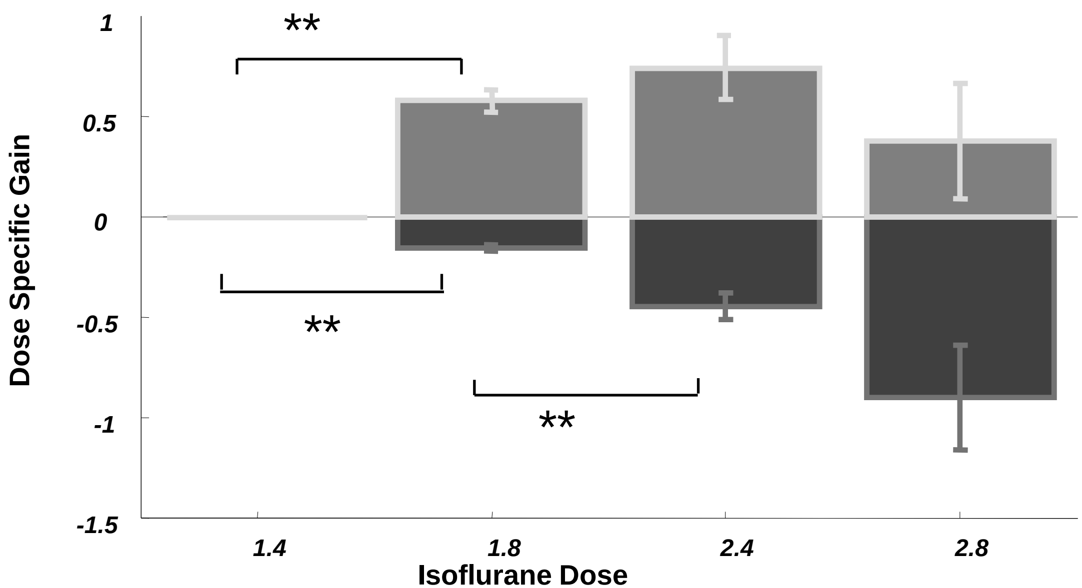
Decreased Glutamate Release

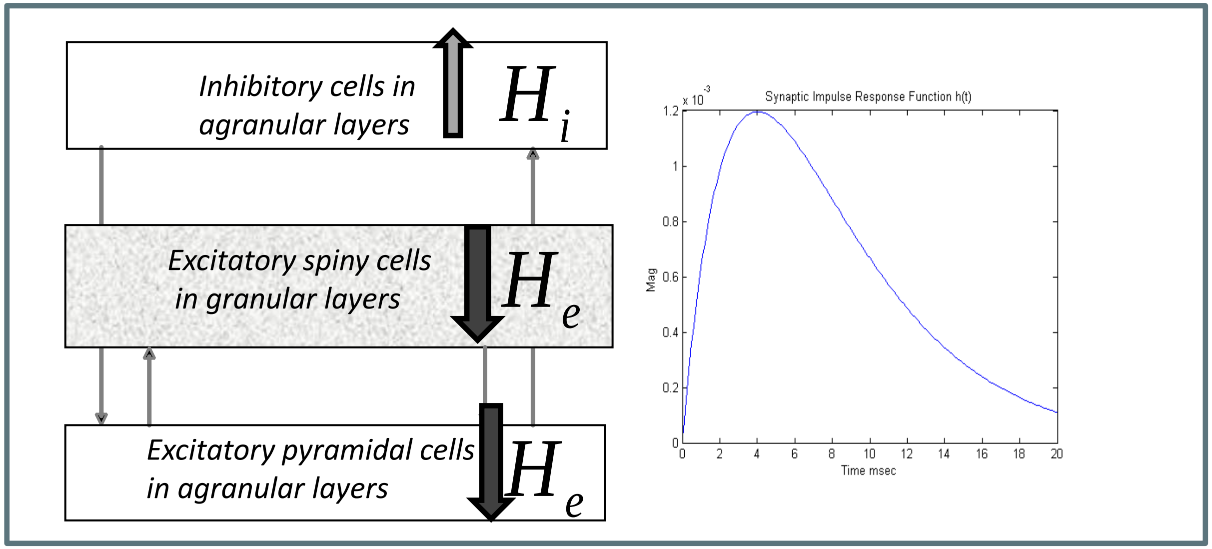
Increased gabaergic transmission





Parametric Effect of Isoflurane





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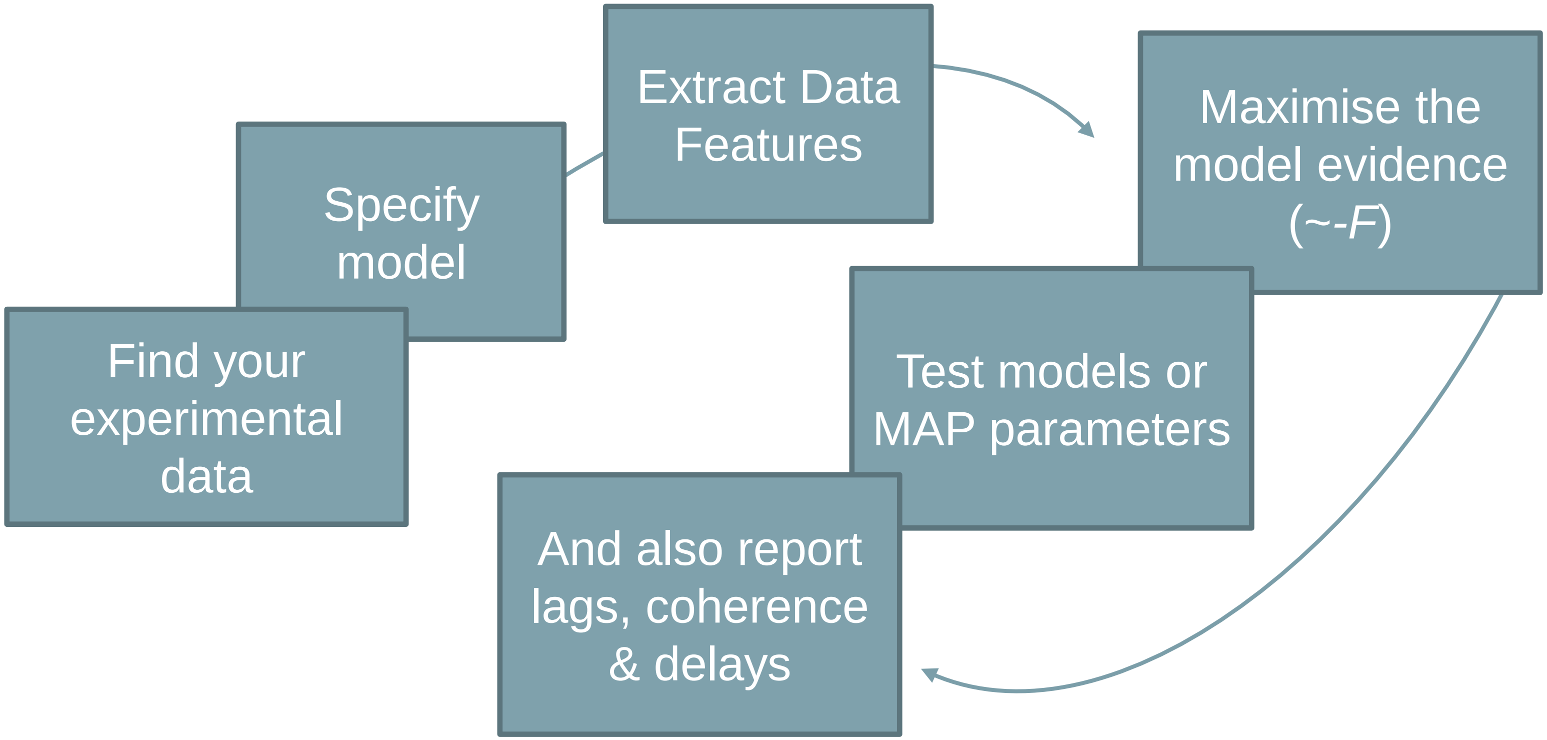
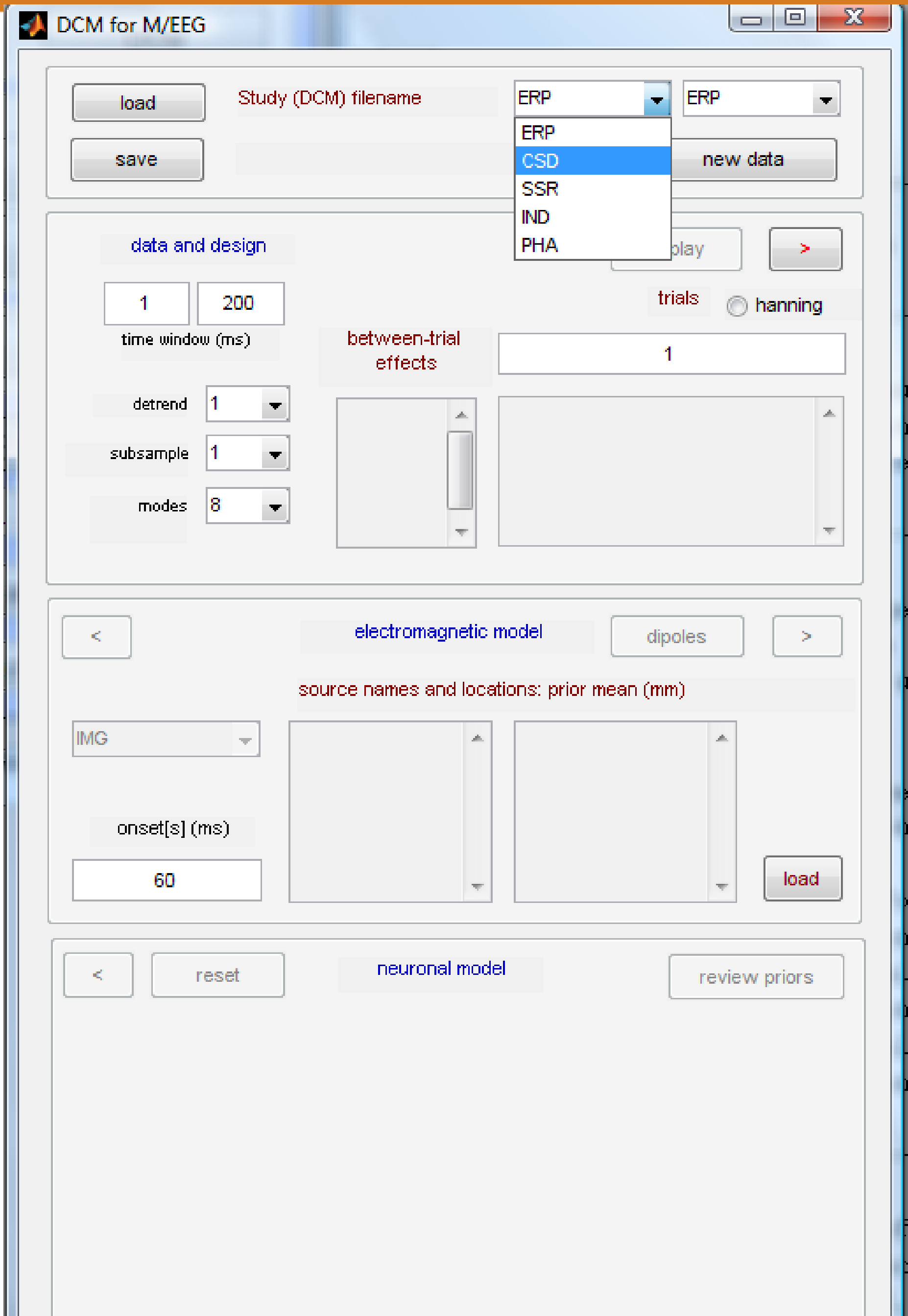
DCM Chain

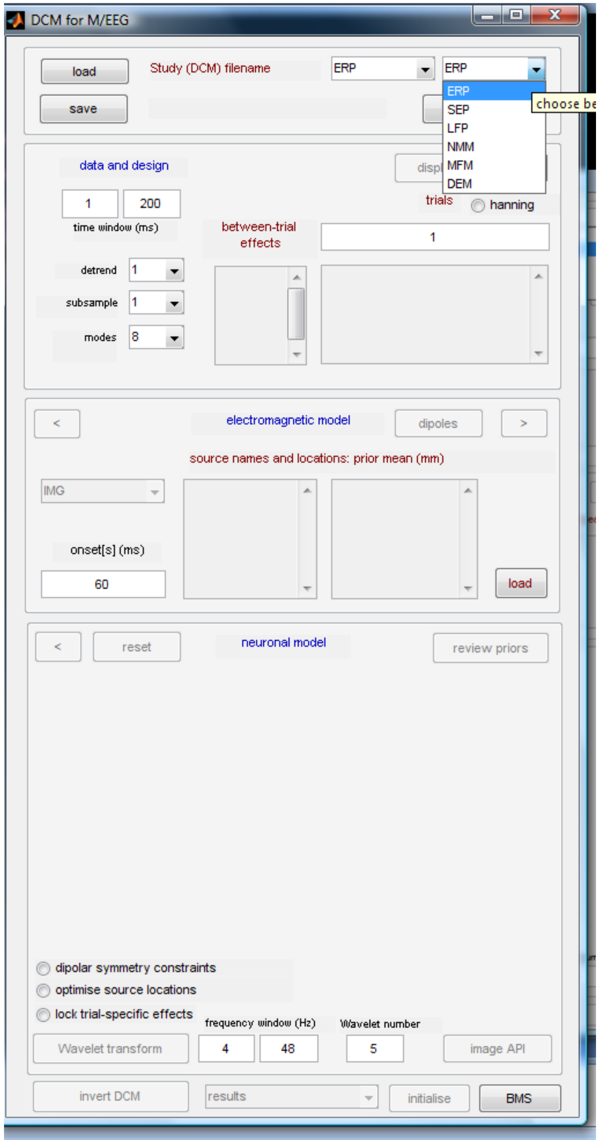


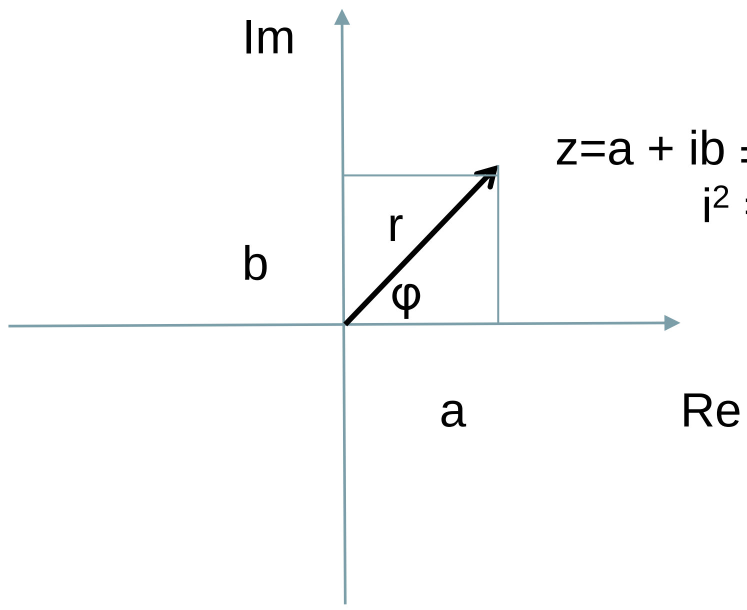
1. Interface Additions
2. New CSD routines, similar to SSR
3. SPM_NLSI_GN accommodates imag numbers, slopes, curvatures
4. A host of new results features, in channel and source space!

Friston, Bastos, Litvak, Stephan, Fries, Moran, *Neuroimage, 2012*

Interface Additions





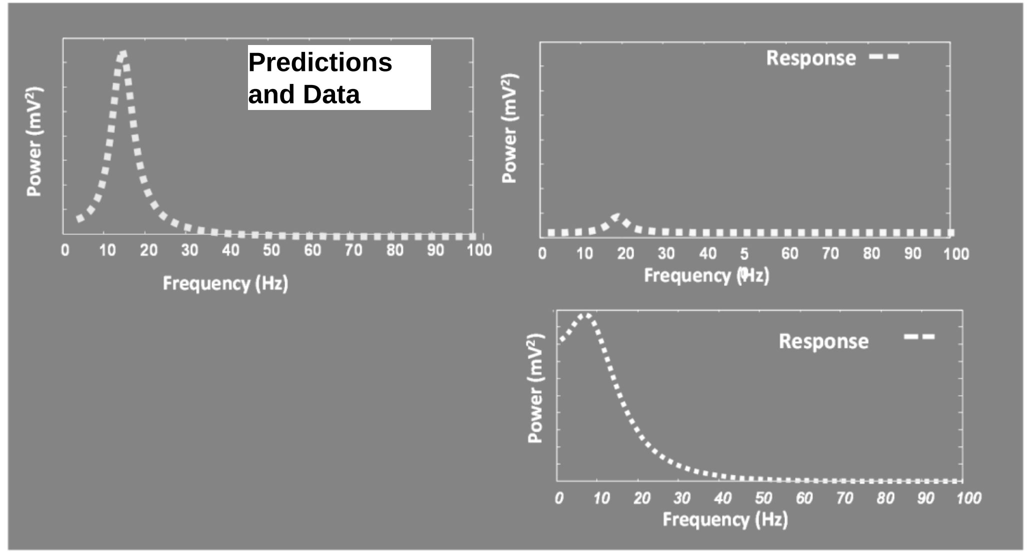


$$z = a + ib = r(\cos\varphi + i\sin\varphi) = re^{i\varphi}$$

$$i^2 = -1$$

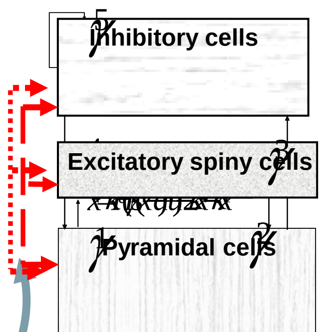
$$H(\omega) = \mathbb{F}(f) = \int_{-\infty}^{\infty} f(t) e^{-2\pi\omega i t}\, dt$$

The Fourier transform of a signal is a continuous complex function

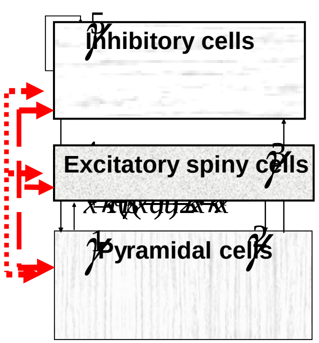


Model Inversion using absolute value (modulus)

$| H_2(\omega) . H_2^*(\omega) |$

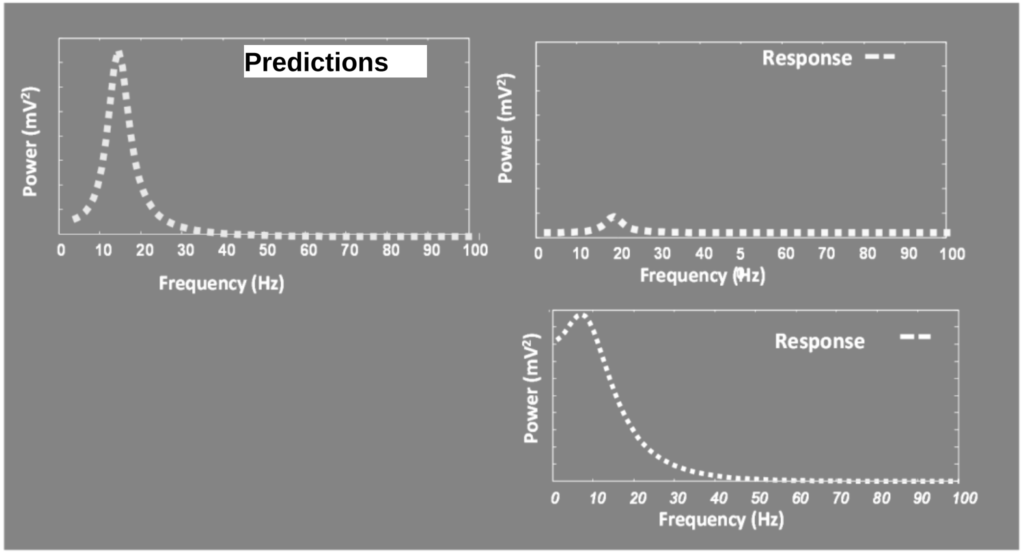


$| H_1(\omega) . H_1^*(\omega) |$



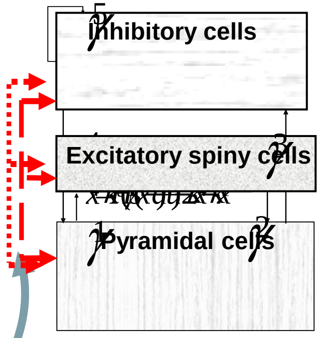
$| H_1(\omega) . H_2^*(\omega) |$

DCM for Cross Spectral Density

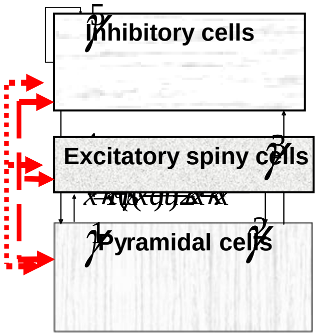


Generative Model

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

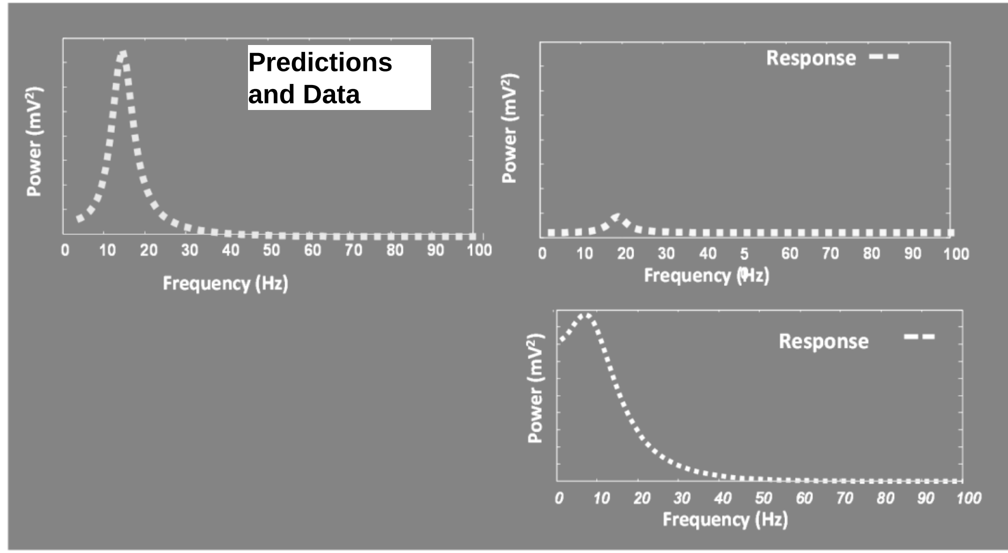


$H_1(\omega)\ .\ H_1^*(\omega)$



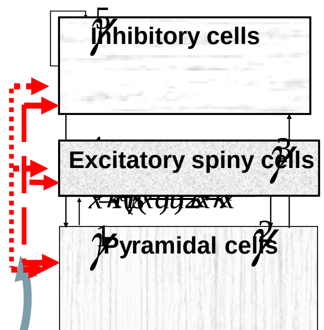
$H_1(\omega)\ .\ H_2^*(\omega)$

DCM for Cross Spectral Density

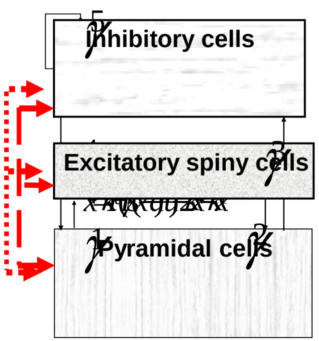


Model Inversion using full complex signal

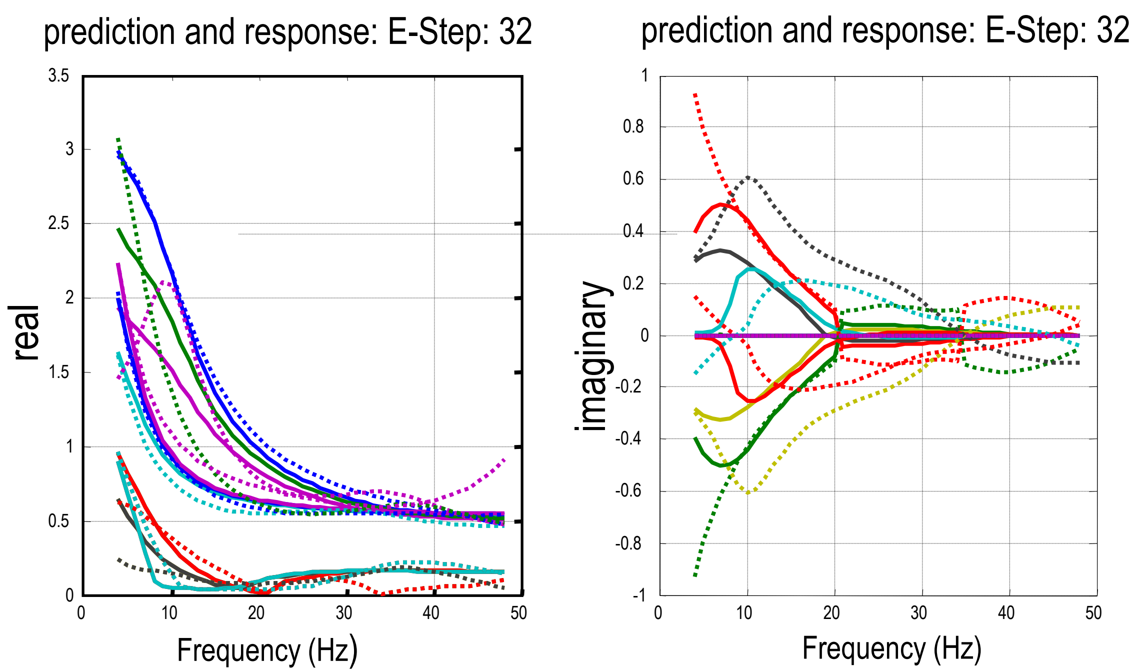
$H_2(\omega) \,.\, H_2^*(\omega)$



$H_1(\omega) \,.\, H_1^*(\omega)$



$H_1(\omega) \,.\, H_2^*(\omega)$


prediction and response: E-Step: 32
real
Frequency (Hz)
prediction and response: E-Step: 32
imaginary
Frequency (Hz)

Spectra $\mathrm{Abs}(H_1(\omega) \,.\, H_1^*(\omega))$, $\mathrm{Abs}(H_1(\omega) \,.\, H_2^*(\omega))$ …

Coherence $|(H_1(\omega).H_2^*(\omega))|^2 \,/\, \{ (H_1(\omega).H_1^*(\omega)) + (H_2(\omega).H_2^*(\omega))\}$

Delay at particular frequencies $\arg(H_1(\omega).H_2^*(\omega))/2\pi f$

Covariance (lags over time, collapsed across frequencies) $\mathrm{Real}(\mathbb{F}^{-1}(H_1(\omega).H_2^*(\omega)))$

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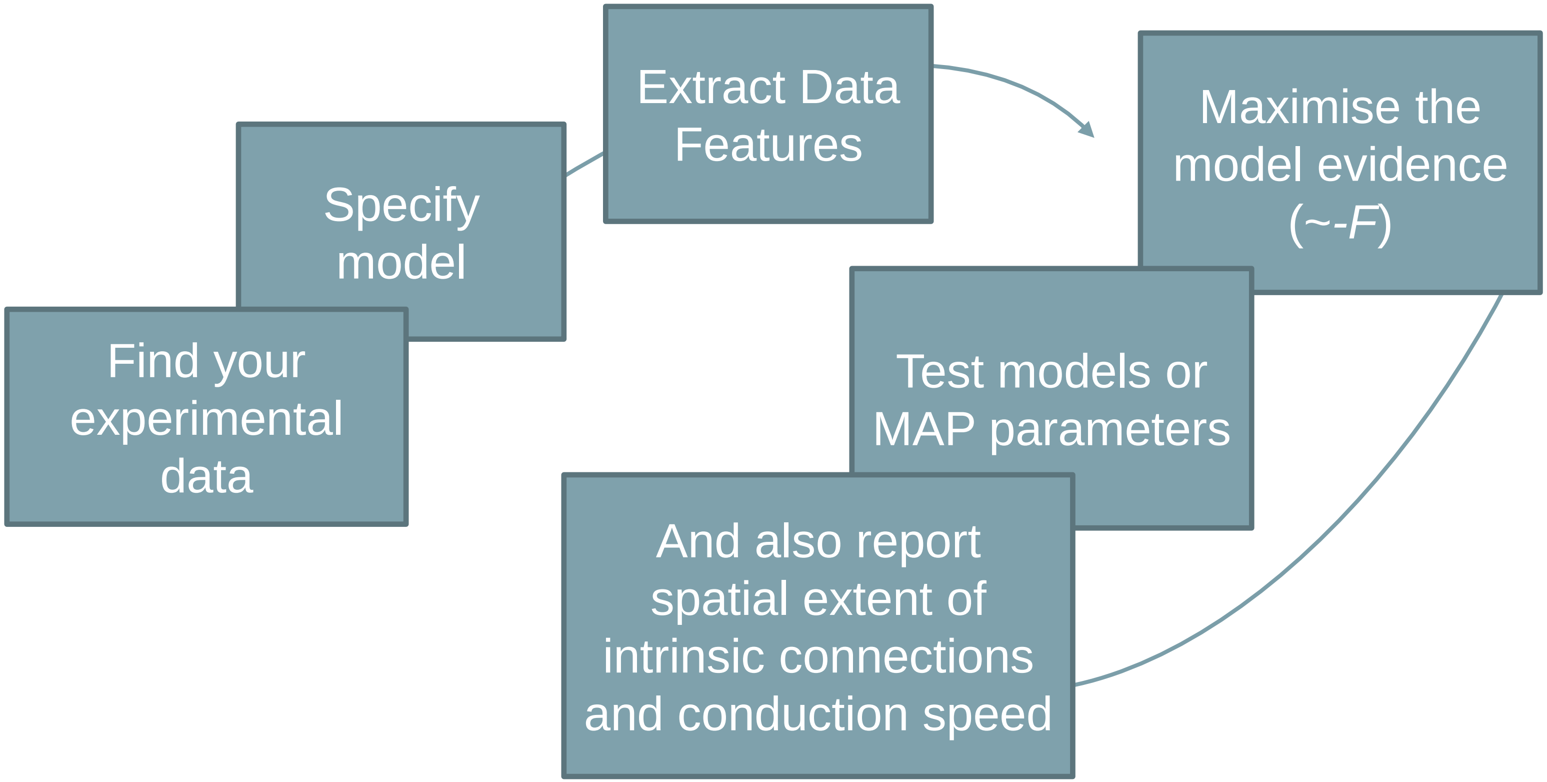
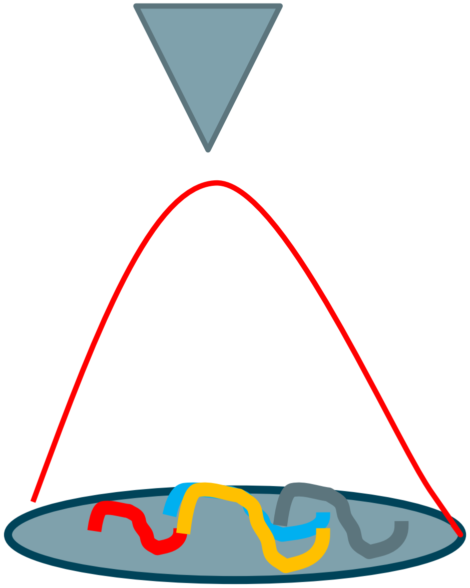
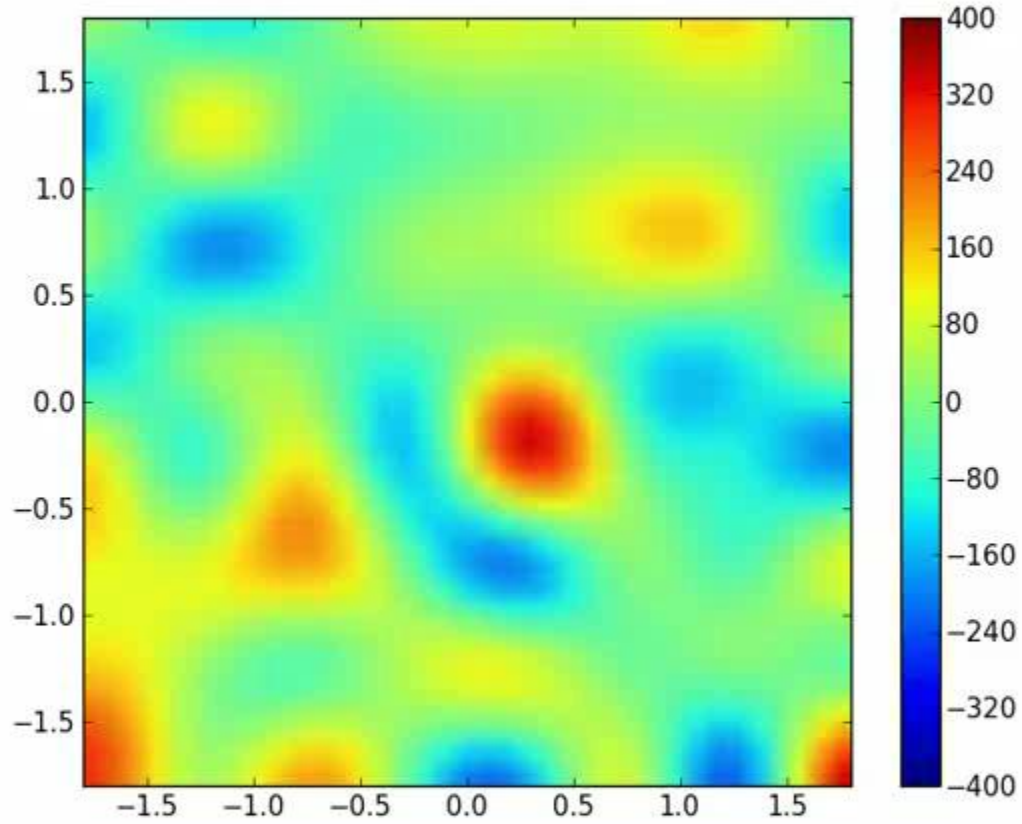


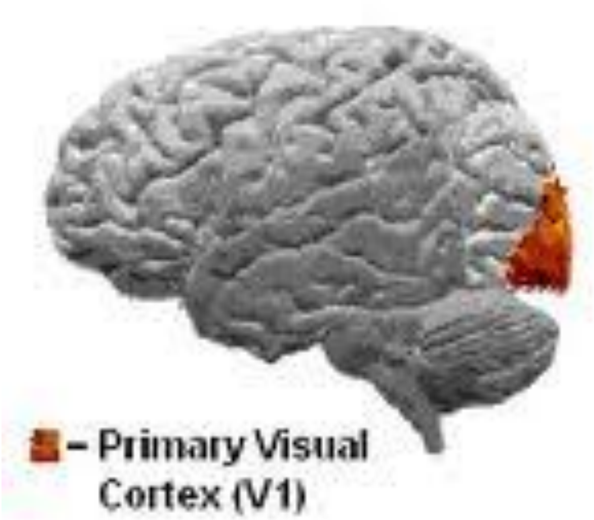
New NFM routines

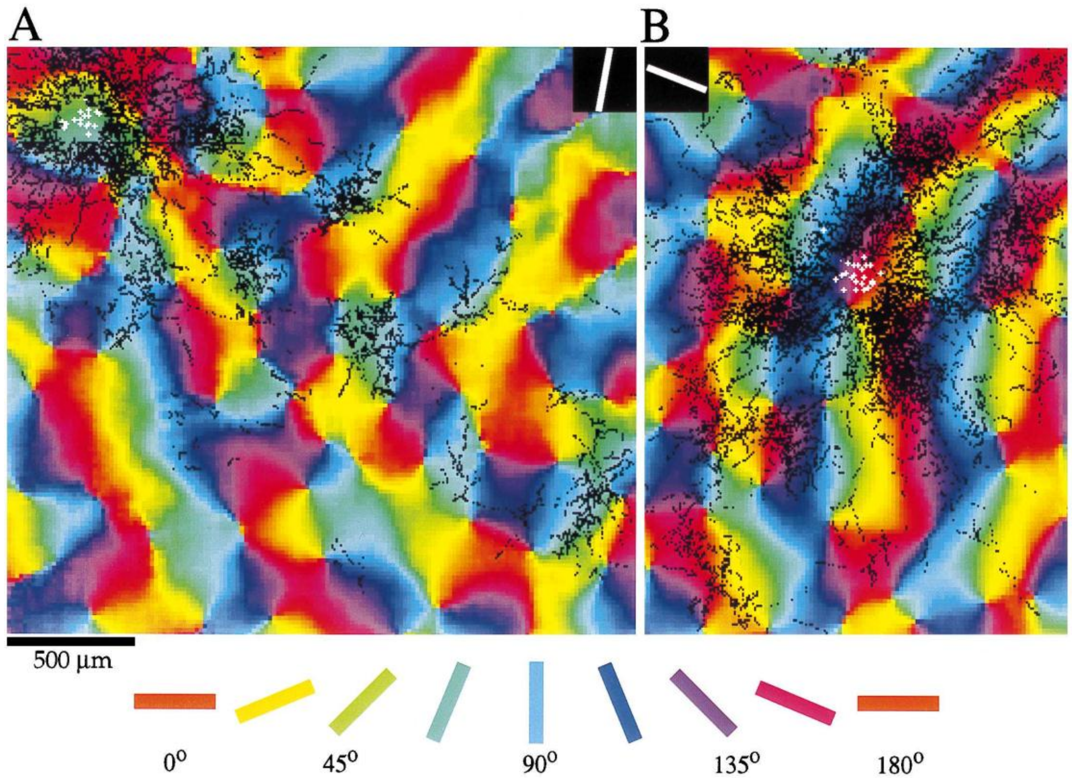
Pinotsis, Moran, Friston, *Neuroimage 2012*

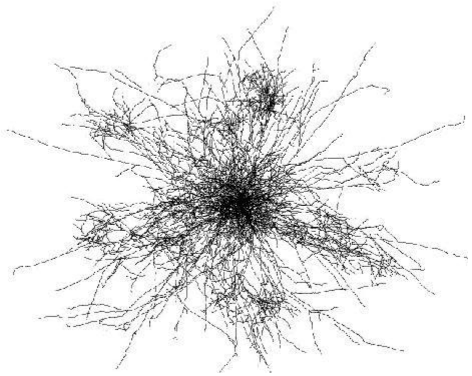




$$L(x,\varphi) = \varphi_1 \exp\left(-\frac{x^2}{\varphi_2}\right)$$





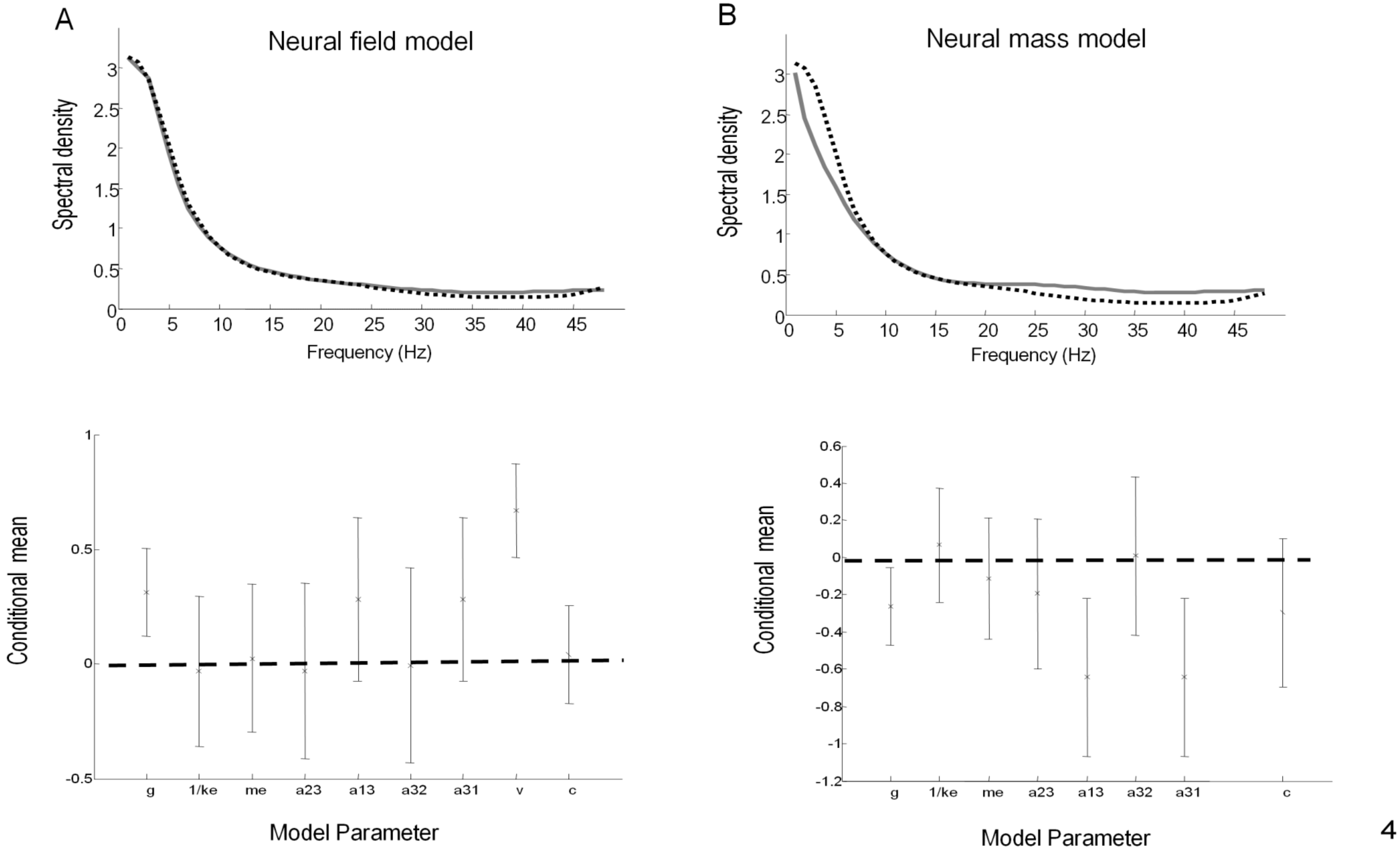


$$K\left(|x|\right) = ae^{-c|x|}$$

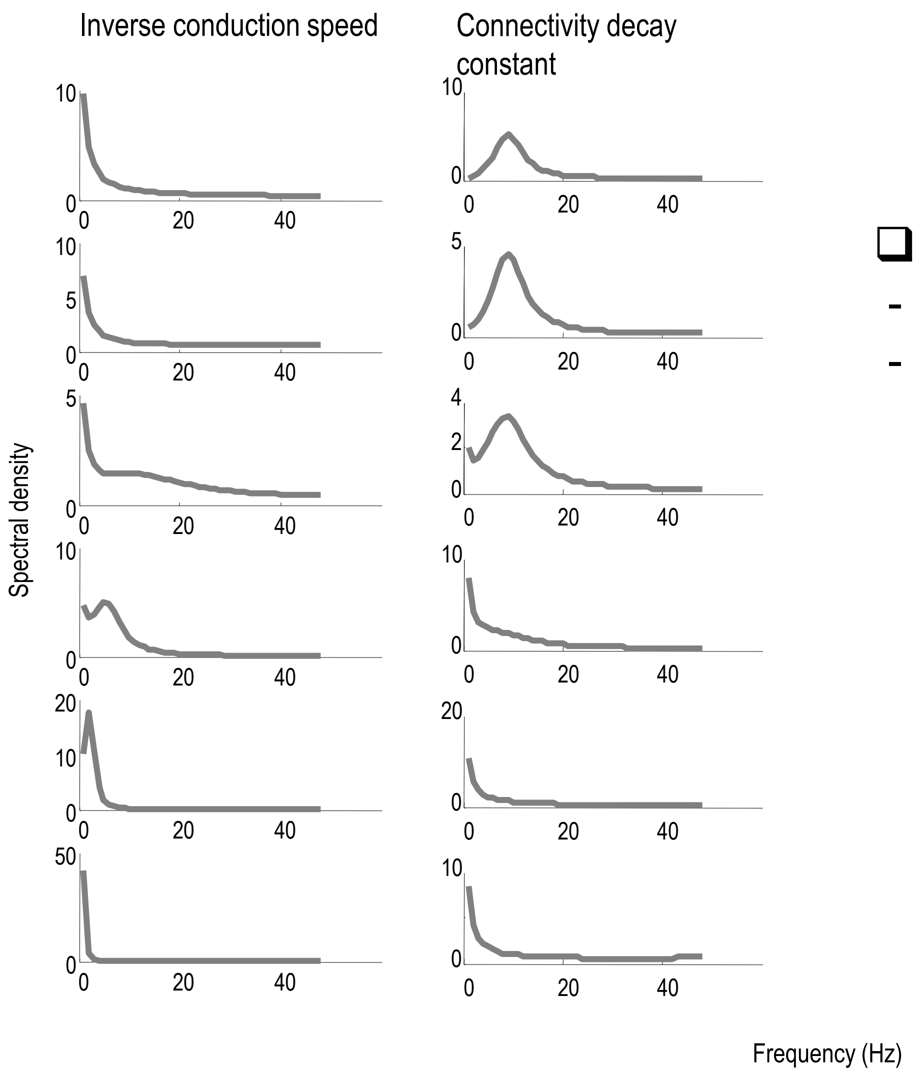
a intrinsic connection strength

c spatial decay rate $\leftrightarrow$ connection extent

Inference on Model Parameters



Changing model parameters



- New peaks appear:
  - as intrinsic speed decreases
  - as connectivity extent increases

Pinotsis, Moran, Friston, *Neuroimage 2012*

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

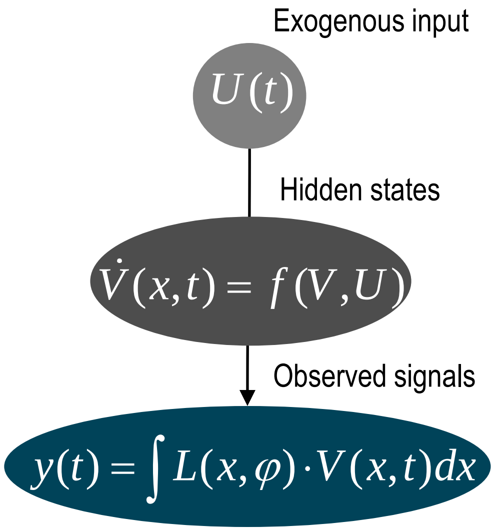
Thanks to

Rosalyn Moran   Vladimir Litvak   Will Penny   Klaas Stephan

… and thank you !

Field Power Spectra

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



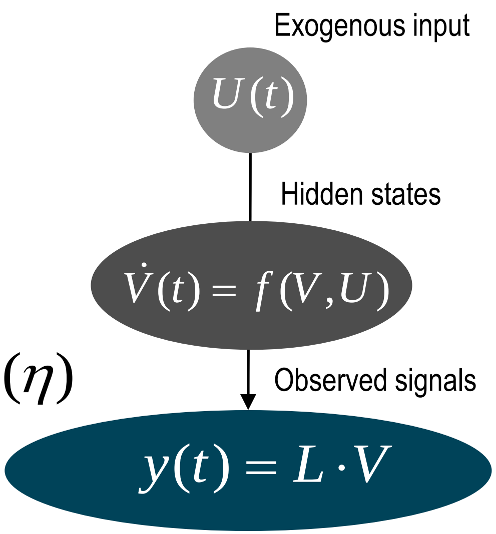
$$\mathbf{g}_Y(\omega)=g_Y(\omega,\theta)+g_N(\omega,\theta)+\varepsilon(\omega)$$

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

$$g_N(\omega,\theta)=\alpha_N+\frac{\beta_N}{\omega} \qquad g_U(k,\omega)=\alpha_U+\frac{\beta_U}{\omega}$$

$$\mathrm{Re}(\varepsilon)\sim\mathrm{N}(0,\Sigma(\omega,\lambda)) \qquad \mathrm{Im}(\varepsilon)\sim\mathrm{N}(0,\Sigma(\omega,\lambda))$$

Mass Power Spectra



$$\mathbf{g}_Y(\omega) = g_Y(\omega,\theta) + g_N(\omega,\theta) + \varepsilon(\omega)$$

$$L(x,\varphi) = L(\eta)$$

$$g_Y(\omega,\theta) \approx \sum_k L(\eta) T_m^k(\omega,\theta) g_U(\omega) T_{m'}(\omega,\theta)^* L(\eta)^*$$

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

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

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

$$\kappa_m^k(t,\theta) = \frac{\partial g}{\partial x} e^{\Im\tau} \Im^{-1} \frac{\partial f}{\partial u_k}$$

$$\mathrm{Re}(\varepsilon) \sim \mathrm{N}(0, \Sigma(\omega,\lambda)) \qquad \mathrm{Im}(\varepsilon) \sim \mathrm{N}(0, \Sigma(\omega,\lambda))$$

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

Neural Field

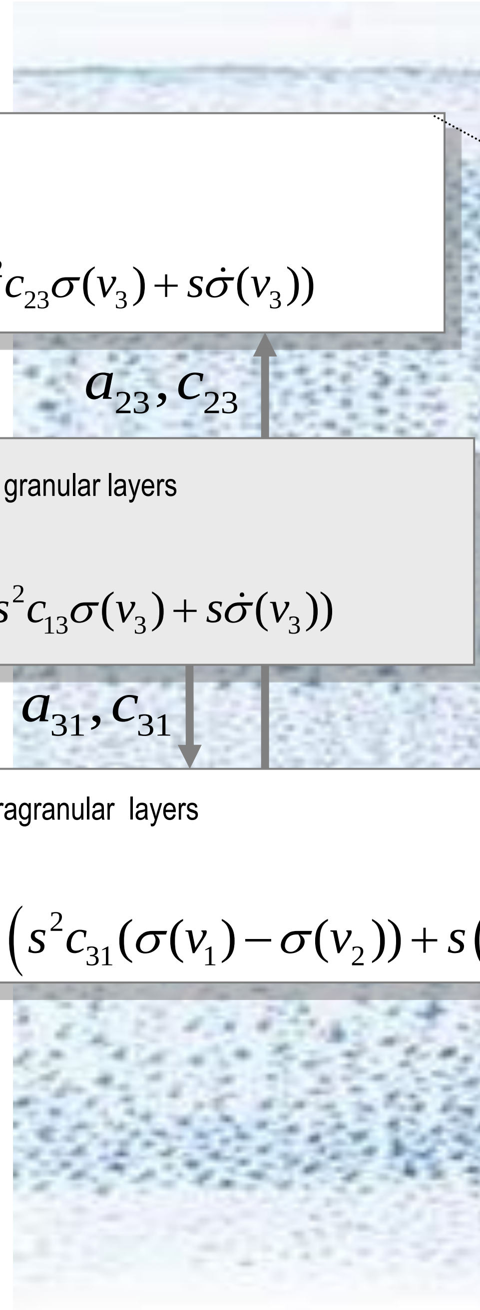
$U(t)$ — Exogenous input — $U(t)$

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

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

$$D \otimes Q = \iint D\left(x - x', t - t'\right) \cdot Q(x', t')dx'dt'$$

Jansen and Rit Neural Field Models



Inhibitory cells in supragranular layers

$$\ddot{v}_2 + 2\kappa_i \dot{v}_2 + \kappa_i^2 v_2 = \kappa_i m_i \mu_2$$

$$\ddot{\mu}_2 + 2sc_{23}\dot{\mu}_2 - s^2(\mu_{2xx} - c_{23}^2 \mu_2) = \alpha_{23}(s^2 c_{23}\sigma(v_3) + s\dot{\sigma}(v_3))$$

a_{32}, c_{32} $\quad$ a_{23}, c_{23}

$U(t)$ →

Excitatory spiny cells in granular layers

$$\ddot{v}_1 + 2\kappa_e \dot{v}_1 + \kappa_e^2 v_1 = \kappa_e m_e(\mu_1 + U)$$

$$\ddot{\mu}_1 + 2sc_{13}\dot{\mu}_1 - s^2(\mu_{1xx} - c_{13}^2 \mu_1) = \alpha_{13}(s^2 c_{13}\sigma(v_3) + s\dot{\sigma}(v_3))$$

a_{13}, c_{13} $\quad$ a_{31}, c_{31}

Excitatory pyramidal cells in supra- and infragranular layers

$$\ddot{v}_3 + 2\kappa_e \dot{v}_3 + \kappa_e^2 v_3 = \kappa_e m_e \mu_3$$

$$\ddot{\mu}_3 + 2sc_{31}\dot{\mu}_3 - s^2(\mu_{3xx} - c_{31}^2 \mu_3) = \alpha_{31}\left(s^2 c_{31}(\sigma(v_1) - \sigma(v_2)) + s\left(\dot{\sigma}(v_1) - \dot{\sigma}(v_2)\right)\right)$$

$v_3(t)$

Endogenous output

Exogenous input

$U(t)$

Hidden states

$$\dot{V}(x,t) = f(V,U)$$

Observed signals

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

s conduction velocity