The Macroscopic Brain

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21st April 2011

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Cell Populations
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Neural Mass Model

Jansen and Rit (1995), building on the work of Lopes Da Sliva and others, developed a biologically inspired model of EEG activity. It was originally developed to explain alpha activity and Event-Related Potentials (ERPs).

It models a cortical unit with three subpopulations of cells

- Stellate cells with average membrane potential v_s and current c_s.
- Pyramidal cells with average membrane potential v_p and current c_p.
- Inhibitory interneurons with average membrane potential v_i and current c_i.

Here I describe the model as formulated in David et al. (2006).

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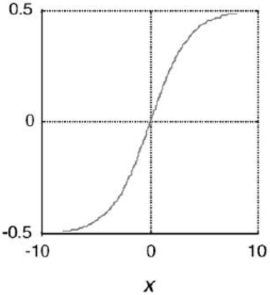
Firing Rate Curves

Membrane potentials are transformed into firing rates via sigmoidal functions (David et al 2006)

$$s(x) = \frac{1}{1+\exp(-rx)} - \frac{1}{2}$$



Negative firing rates here allow systems to have a stable fixed point at $x = 0$. All firing rates are therefore considered as deviation from steady state values. But earlier Jansen-Rit does not have 1/2.

Alpha Function Synapses

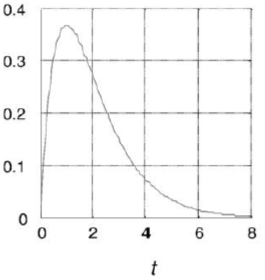
Firing rates cause postsynaptic potentials via convolutions with alpha function synaptic kernels

$$v_{out}(t) = h_e(t) \otimes s(v_{in})$$

where

$$h_e(t) = \frac{H_e}{\tau_e} t \exp(-t/\tau_e)$$

Similarly for inhibitory synapses with $h_i(t)$, H_i, τ_i.



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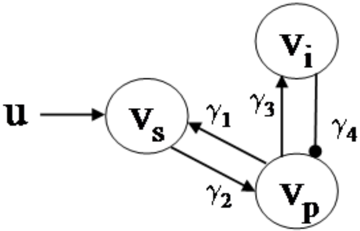
Inhibitory Interneurons

The inhibitory interneurons receive excitatory input from the pyramidal cells

$$v_i = \gamma_3 s(v_p) \otimes h_e$$



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Stellate Cells

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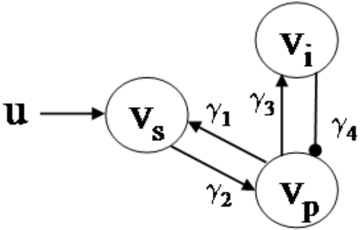
The stellate cells receive external input from thalamus or other cortical regions and excitatory feedback from pyramidal cells

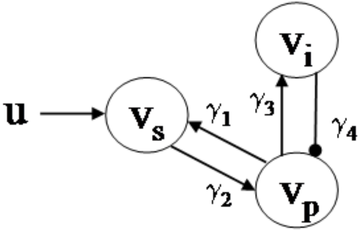
$$v_s = (s(u) + \gamma_1 s(v_p)) \otimes h_e$$



Pyramidal Cells

The pyramidal cells receive excitatory input from stellate cells and inhibitory input from interneurons. This produces both excitatory v_{pe} and inhibitory v_{pi} postsynaptic potentials. This formulation is due to David et al (2006).

$$\begin{aligned} v_{pe} &= \gamma_2 s(v_s) \otimes h_e \\ v_{pi} &= \gamma_4 s(v_i) \otimes h_i \\ v_p &= v_{pe} - v_{pi} \end{aligned}$$



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Alpha Function Synapses

Each synapse

$$\begin{aligned} v_{out}(t) &= h_e(t) \otimes s(v_{in}(t)) \\ h_e(t) &= \frac{H_e}{\tau_e} t \exp(-t/\tau_e) \end{aligned}$$

can be implemented with a second order DE or two first order DEs (Grimbert and Faugeras, 2006)

$$\begin{aligned} \dot{v}_{out} &= c_{out} \\ \dot{c}_{out} &= \frac{H_e}{\tau_e} s(v_{in}(t)) - \frac{2}{\tau_e} c_{out} - \frac{1}{\tau_e^2} v_{out} \end{aligned}$$

where c_{out} is the current flowing through the synapse. Hence each synapse gives rise to two DEs.

Differential Equations

The integral equations become

$$
\begin{aligned}
v_i &= \gamma_3 s(v_p) \otimes h_e \\
v_s &= (s(u) + \gamma_1 s(v_p)) \otimes h_e \\
v_{pe} &= \gamma_2 s(v_s) \otimes h_e \\
v_{pi} &= \gamma_4 s(v_i) \otimes h_i \\
v_p &= v_{pe} - v_{pi}
\end{aligned}
$$

the differential equations

$$
\begin{aligned}
\dot{v}_i &= c_i \\
\dot{c}_i &= \frac{H_e}{\tau_e} \gamma_3 s(v_p(t)) - \frac{2}{\tau_e} c_i - \frac{1}{\tau_e^2} v_i \\
\dot{v}_s &= c_s \\
\dot{c}_s &= \frac{H_e}{\tau_e} \gamma_3 (s(u(t)) + \gamma_1 s(v_p(t)) - \frac{2}{\tau_e} c_s - \frac{1}{\tau_e^2} v_s \\
\dot{v}_{pe} &= c_{pe} \\
\dot{c}_{pe} &= \frac{H_e}{\tau_e} \gamma_2 s(v_s(t)) - \frac{2}{\tau_e} c_{pe} - \frac{1}{\tau_e^2} v_{pe} \\
\dot{v}_{pi} &= c_{pi} \\
\dot{c}_{pi} &= \frac{H_i}{\tau_i} \gamma_4 s(v_i(t)) - \frac{2}{\tau_i} c_{pi} - \frac{1}{\tau_i^2} v_{pi} \\
\dot{v}_p &= c_{pe} - c_{pi}
\end{aligned}
$$

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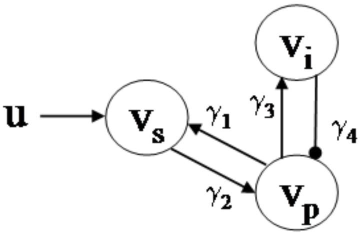
Intrinsic Connectivity

Based on the relative counts of numbers of synapses in cat and mouse visual and somato-sensory cortex Jansen and Rit (1995) determined the following connectivity values.

$$
\begin{aligned}
\gamma_1 &= C \\
\gamma_2 &= 0.8C \\
\gamma_3 &= 0.25C \\
\gamma_4 &= 0.25C
\end{aligned}
$$



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Alpha Activity

Original Jansen-Rit Model with 6 state variables produces alpha activity with $C = 135$. Input noise u was uniformly distributed between 120 and 320Hz.

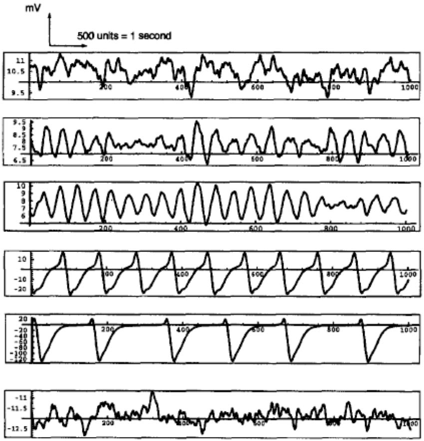
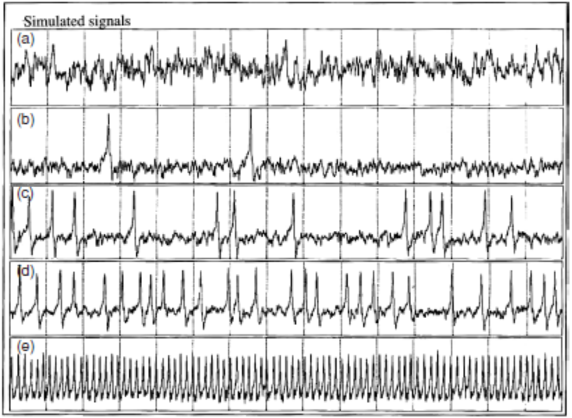


Fig. 3. Two seconds of the model's output when the lumped connectivity constant C equals (from top to bottom) 68, 128, 135, 270, 675, and 1350, respectively. The input is uniformly distributed random noise

Spike Activity

Wendling et al (2000) elicited seizure-lie spikes with lower levels of input u (gaussian noise with mean 90 and standard deviation 30 Hz).



The frequency of spike activity increases as H_e/H_i is changed.

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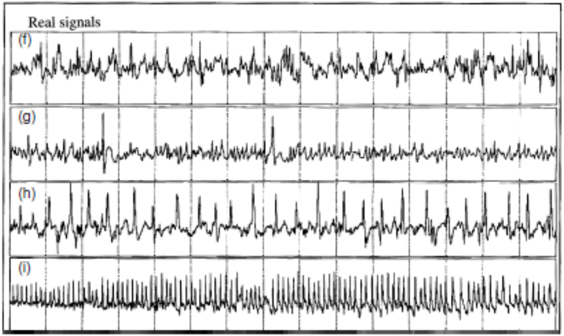
Spike Activity

This figure from Wendling et al. (2000) shows spike activity from mid-temporal gyrus (MTG) of epileptic patients before (f,g) and during a seizure (h,i).



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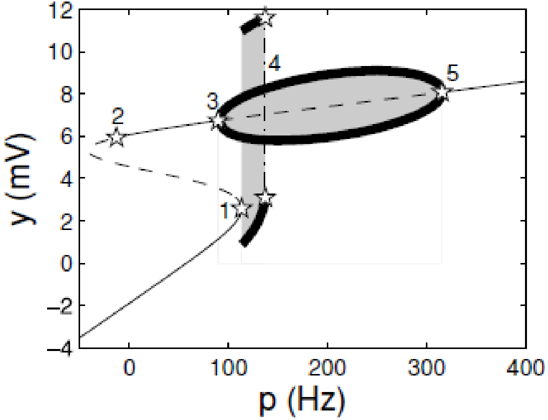
Bifurcation Analysis

Grimbert and Faugeras (2006) provide a bifurcation analysis of the standard Jansen-Rit model.



The figure shows pyramidal cell PSP, y (previously v_p) as a function of input to the cortical unit, p (previously u), with stable fixed points marked as solid lines and unstable FPs as dashed lines.

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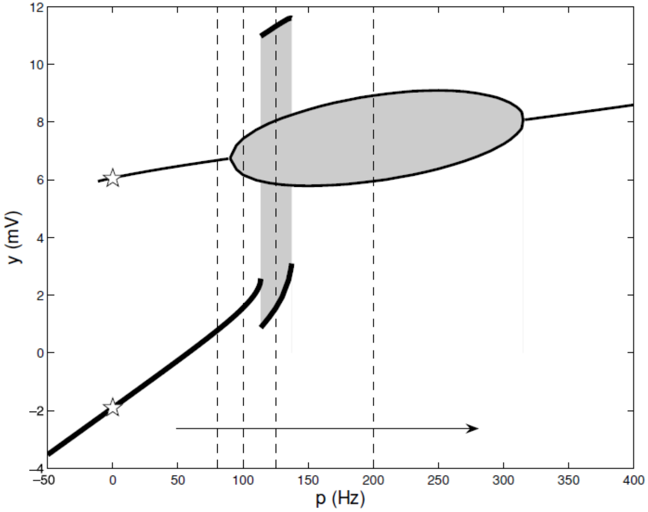
Bifurcation Analysis



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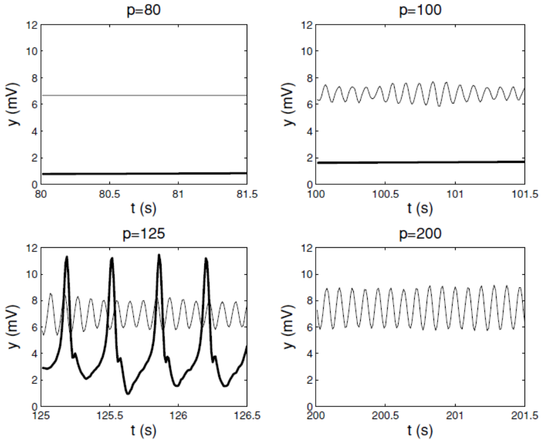
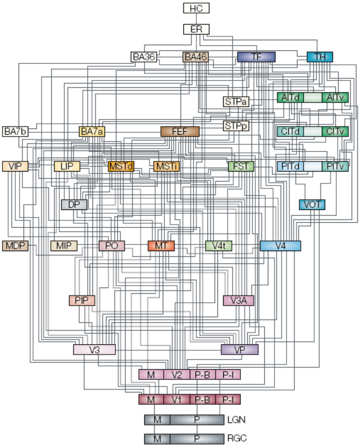


Figure 6: Activities produced by Jansen's neural mass model for typical values of the input parameter p (see the text). The thin (resp. thick) curves are the time courses of the output y of the unit in its upper (resp. lower) state. For $p > 137.38$, there is only one possible behavior of the system. In the case of oscillatory activities, we added a very small amount of noise to p (a zero mean gaussian noise with standard deviation 0.05).

Macroscopic Models

Cortex is organised hierarchically with higher level regions processing more abstract features and lower levels more concrete ones (Felleman and Van Essen, 1991).



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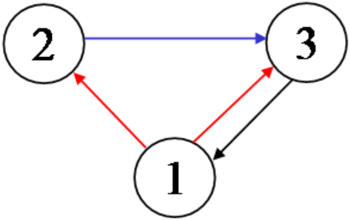

This figure shows regions 2 and 3 at a higher level and region 1 at a lower level. Regions at the same level are connected via lateral connections (blue).

Forward connections (red) and backward connections (black) connect between levels.

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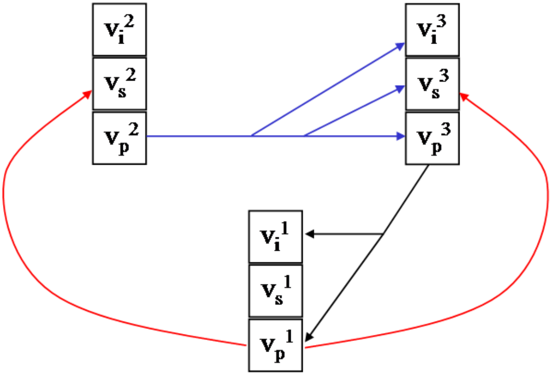
Macroscopic Model

This hierarchical organisation is also reflected in how different cortical laminae are connected (Felleman and Van Essen,



1991).

Here stellate cells are located in layer 4 or the granular layer. Pyramidal cells are located in agranular layers, either in superficial or deep layers. Inhibitory interneurons are also located in agranular layers.

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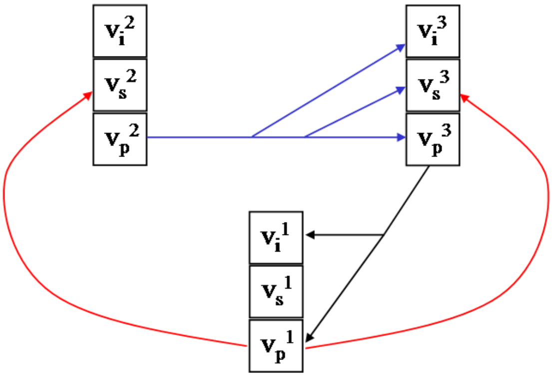
Macroscopic Model

All connections between regions originate from pyramidal cells. The colours depict forward connections (red), backward connections (black) and lateral connections (blue).



This knowledge is made use of in DCM-ERP (David et al. 2006). Connections between subpopulations within a region, γ, are referred to as 'intrinsic'. Connections between regions, C_{ij}, are 'extrinsic'.

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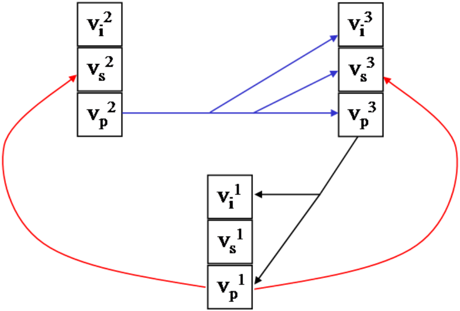
Extrinsic Connectivity

So, for example,

$$
\begin{aligned}
v_s^2 &= \left(C_{21} s(v_p^1 - \tau_{21}) + \gamma_1 s(v_p^2 - \tau_{22})\right) \otimes h_e \\
v_s^3 &= \left(C_{31} s(v_p^1 - \tau_{31}) + C_{32} s(v_p^2 - \tau_{32}) + \gamma_2 s(v_p^3 - \tau_{33})\right) \otimes h_e \\
v_i^1 &= \left(C_{13} s(v_p^3 - \tau_{31}) + \gamma_3 s(v_p^1 - \tau_{11})\right) \otimes h_e
\end{aligned}
$$

where C_{ij} is the connection strength from region j to region i, and τ_{ij} is the delay from region j to region i.



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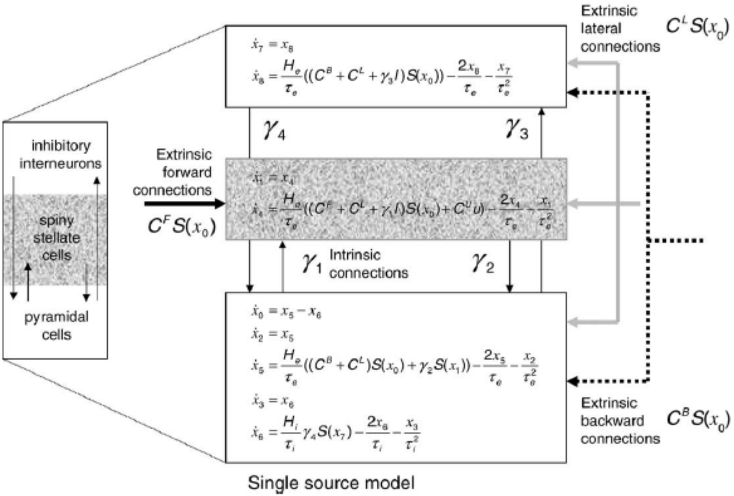
Differential Equations



Single Cortical Unit. Delays not shown.

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Delays

Delays within a region are typically 2ms. Between regions they are typically 8-32ms depending on distance and myelination.

Delay differential equations can be transformed to standard DEs using a first order Taylor series expansion about the delay

$$
\begin{aligned}
\dot{x}_i(t) &= f_i(x_1(t-\tau_{i1}), x_2(t-\tau_{i2}), .., x_n(t-\tau_{in})) \\
&= f_i(x(t)) - \sum_{j=1}^{n} \tau_{ij} \frac{df_i(x_j)}{d\tau_{ij}} \\
&= f_i(x(t)) - \sum_{j} \tau_{ij} \frac{df_i(x_j)}{dx_j} \frac{dx_j}{d\tau_{ij}} \\
&= f_i(x(t)) - \sum_{j} \tau_{ij} J_{ij} \dot{x}_j(t)
\end{aligned}
$$

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Delays

In vector form

$$\dot{x}(t) = f(x(t)) - (\tau \times J)\dot{x}(t)$$

where τ is a matrix with entries τ_{ij} , J is the Jacobian and $\times$ denotes the Hadamard (element by element) product.

Rearraging gives

$$\dot{x}(t) = D^{-1} f(x(t))$$

where

$$D = I + (\tau \times J)$$

is a delay matrix.

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Auditory Oddball

We illustrate DCM-ERP (David et al. 2006) using ERP data from an auditory processing experiment.

Subjects listened to auditory tones of two different frequencies, 1kHz and 2kHz, with the lower frequency occuring 80% of the time, and the higher (the ‘oddball’) 20% of the time.

Late ERP components, 250-350ms, which are characteristic of rare events were seen in most frontal electrodes. Early components (eg the N100) were almost identical for rare and frequent stimuli.

Data from 64 electrodes were projected onto three spatial modes found from Singular Value Decomposition (SVD) of sensor space data.

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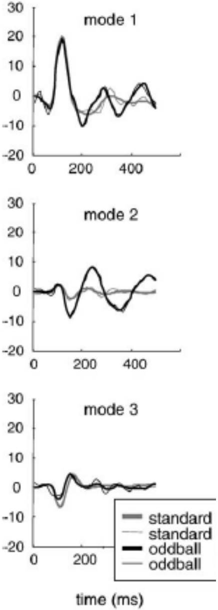
Modes

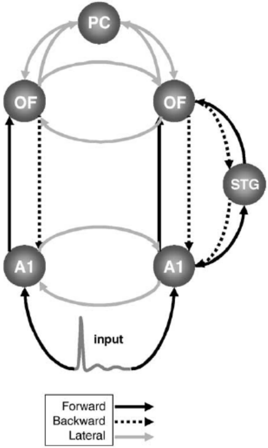


Early components project mainly onto mode 1 and late components onto mode 2.

Data are shown as thick lines and model fit as thin lines.

Network Model

Auditory input is modelled as driving activity in bilateral primary auditory cortex (A1), which in turn connect to orbitofrontal cortex (OF) and posterior cingulate (PC) with a right hemisphere pathway via superior temporal gyrus (STG) (David et al 2006).



These regions were selected based on source reconstruction of ERPs, previous literature on auditory oddballs and known anatomical connectivity.

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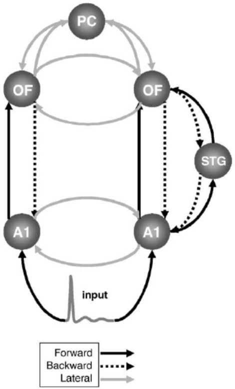
Context-dependent gain

Extrinsic parameters are allowed to vary as a function of experimental context k eg. standard or oddball ($k = 1$).

$$C_{ijk} = C_{ij} G_{ijk}$$

This allows one to test if connections depend on experimental context.



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Priors

Priors on positively valued parameters are expressed as exponential functions of associated Gaussian latent variables.

Table 1
Prior densities of parameters (for connections to the i-th source from the j-th, in the k-th ERP)

Extrinsic coupling parameters	$C^{F}_{ijk} = C^{F}_{ij} G_{ijk}$	$C^{F}_{ij} = \exp\left(\theta^{F}_{ij}\right)$	$\theta^{F}_{ij} \sim N\left(\ln 32, \frac{1}{2}\right)$
	$C^{B}_{ijk} = C^{B}_{ij} G_{ijk}$	$C^{B}_{ij} = \exp\left(\theta^{B}_{ij}\right)$	$\theta^{B}_{ij} \sim N\left(\ln 16, \frac{1}{2}\right)$
	$C^{L}_{ijk} = C^{L}_{ij} G_{ijk}$	$C^{L}_{ij} = \exp\left(\theta^{L}_{ij}\right)$	$\theta^{L}_{ij} \sim N\left(\ln 4, \frac{1}{2}\right)$
		$G_{ijk} = \exp\left(\theta^{G}_{ijk}\right)$	$\theta^{G}_{ij} \sim N\left(0, \frac{1}{2}\right)$
		$C^{U}_{i} = \exp\left(\theta^{U}_{i}\right)$	$\theta^{U}_{i} \sim N\left(0, \frac{1}{2}\right)$
Intrinsic coupling parameters	$\gamma_1 = 1 \quad \gamma_2 = \frac{4}{5} \quad \gamma_3 = \frac{1}{4} \quad \gamma_4 = \frac{1}{4}$		
Conduction delays (ms)	$\Delta_{ii} = 2 \quad \Delta_{ij} = \exp\left(\theta^{\Delta}_{ij}\right) \quad \theta^{\Delta}_{ij} \sim N\left(\ln 16, \frac{1}{16}\right)$		
Synaptic parameters (ms)	$T_i = 16$	$T^{(i)}_{e} = \exp\left(\theta^{T}_{i}\right)$	$\theta^{T}_{i} \sim N\left(\ln 8, \frac{1}{16}\right)$
	$H_i = 32$	$H^{(i)}_{e} = \exp\left(\theta^{H}_{i}\right)$	$\theta^{H}_{i} \sim N\left(\ln 4, \frac{1}{16}\right)$
Input parameters (s)	$u(t) = b(t, \eta_1, \eta_2) + \sum \theta^{c}_{i} \cos(2\pi(i-1)t)$		$\theta^{c}_{i} \sim N(0,1)$
	$\eta_1 = \exp\left(\theta^{\eta}_{1}\right)$		$\theta^{\eta}_{1} \sim N\left(\ln 96, \frac{1}{16}\right)$
	$\eta_2 = \exp\left(\theta^{\eta}_{2}\right)$		$\theta^{\eta}_{2} \sim N\left(\ln 1024, \frac{1}{16}\right)$

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Priors

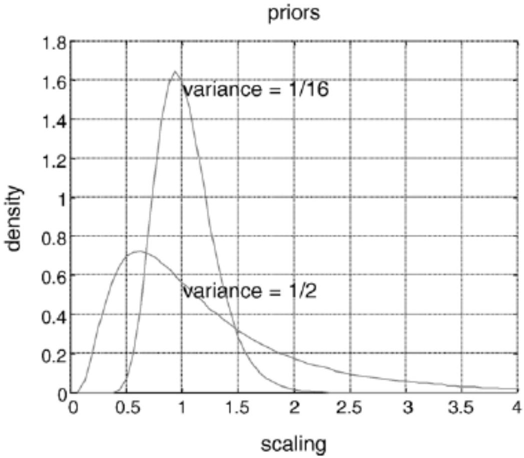

Fig. 4. Log-normal densities on $\exp(\theta)$ entailed by Gaussian priors on θ with a prior expectation of zero and variances of 1/2 and 1/16. These correspond to fairly uninformative (allowing for changes up to an order of magnitude) and informative (allowing for changes up to a factor of two) priors, respectively.

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Likelihood

The differential equations of the macroscopic model

$$\dot{x}(t) = D^{-1} f(x(t), u(t), k)$$

are integrated to produce time series of activity for each cell population in each region. Pyramidal cell PSPs, $v_p(t)$ then produce EEG modes

$$y(t) = L v_p(t) + e$$

where L is a lead field operator, and e is additive Gaussian noise.

The model is fitted using the Variational Laplace algorithm (lecture 4).

In a later version of this approach (Kiebel et al. 2006) the lead field is parameterised, allowing one to also estimated the locations of the sources.

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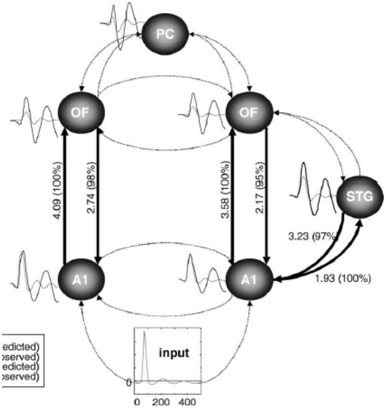
Estimated Model

The mismatch response is expressed in nearly every source (black: oddballs, gray: standards). In all extrinsic connections, coupling was stronger for oddballs relative to standards. These effects are significant for the connections in bold.



For eg. left OF to A1 the oddball induced gain is $G_{A1,OF,1} = 2.74$.

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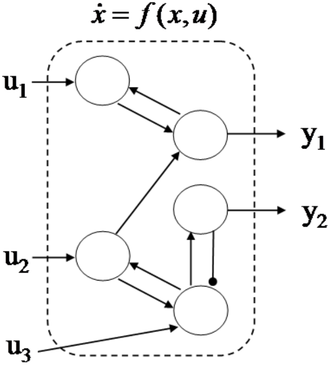
Linear Systems Analysis

The effect of input $u_k(t)$ on output $y_i(t)$, in a linear system, is described completely by the kernel response function

$$y_i(t) = \int_0^t h_{ik}(\tau) u_k(t-\tau) d\tau$$

Equivalently

$$h_{ik}(\tau) = \frac{dy_i(t)}{du_k(t-\tau)}$$



Observation function

$$y = g(x)$$

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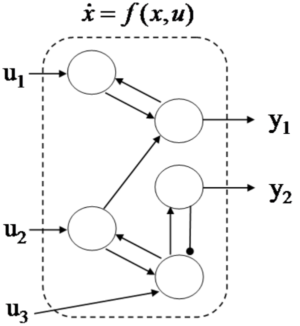
Linear Systems Analysis

The kernel response can be found via the chain rule

$$
\begin{aligned}
h_{ik}(\tau) &= \frac{dy_i(t)}{du_k(t-\tau)} \\
&= \frac{dy_i(t)}{dx(t)} \frac{dx(t)}{dx(t-\tau)} \frac{dx(t-\tau)}{du_k(t-\tau)}
\end{aligned}
$$

Past inputs, $u_k(t-\tau)$, affect previous hidden states, $x(t-\tau)$ which affect current hidden states, $x(t)$ which affect current outputs, $y(t)$.



The Macroscopic Brain
Will Penny

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Linear Systems Analysis

Past inputs, $u_k(t-\tau)$, affect previous hidden states, $x(t-\tau)$ which affect current hidden states, $x(t)$ which affect current outputs, $y(t)$.

$$h_{ik}(\tau) = \frac{dy_i(t)}{dx(t)} \frac{dx(t)}{dx(t-\tau)} \frac{dx(t-\tau)}{du_k(t-\tau)}$$

For the first term we have

$$\frac{dy_i(t)}{dx(t)} = g_i'(x)$$

For the second term we note that

$$x(t) = \exp(J\tau)x(t-\tau)$$

where the Jacobian has elements

$$J_{ij} = \frac{df_i}{dx_j}$$

Hence

$$\frac{dx(t)}{dx(t-\tau)} = \exp(J\tau)$$

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Linear Systems Analysis

To evaluate the third term as a function of f we can write

$$\begin{aligned}\frac{dx(t-\tau)}{du_k(t-\tau)} &= \frac{dx(t-\tau)}{d\dot{x}(t-\tau)}\frac{d\dot{x}(t-\tau)}{du_k(t-\tau)} \\ &= J^{-1}\frac{df}{du_k}\end{aligned}$$

Putting this all together gives

$$h_{ik} = g_i'(x)\exp(J\tau)J^{-1}\frac{df}{du_k}$$

This will provide an accurate description of input-output relationships close to the fixed point around which the derivatives are evaluated.

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Frequency Response

The frequency response of the transfer function from input k to output i is given by the Fourier transform

$$H_{ik}(w) = F(h_{ik}(t))$$

The covariance between outputs i and j at frequency w induced by input k is

$$\Gamma_{ijk}(w) = |H_{ik}(w) H_{jk}(-w)|$$

The cross-spectral density is then

$$G_{ij}(w) = \sum_k \Gamma_{ijk}(w) U_k(w)$$

where $U_k(w)$ is the frequency content of the kth input. The spectrum or auto-spectrum is $G_{ii}(w)$.

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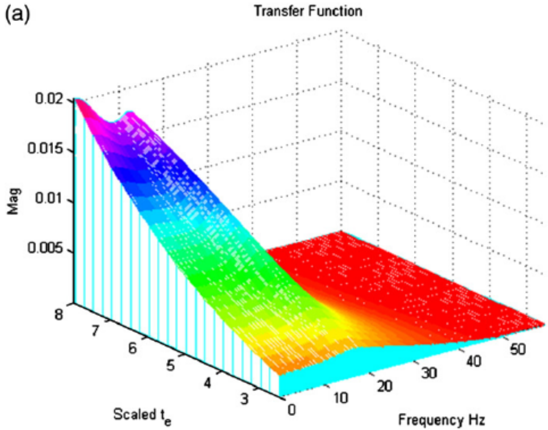
Single cortical unit

Moran et al (2007) investigated how the steady state spectrum of a single cortical unit, $\Gamma_{111}(w)$, depended on various model parameters.



Increasing τ_e caused a slowing of the dynamics with an excess of power at lower frequencies.

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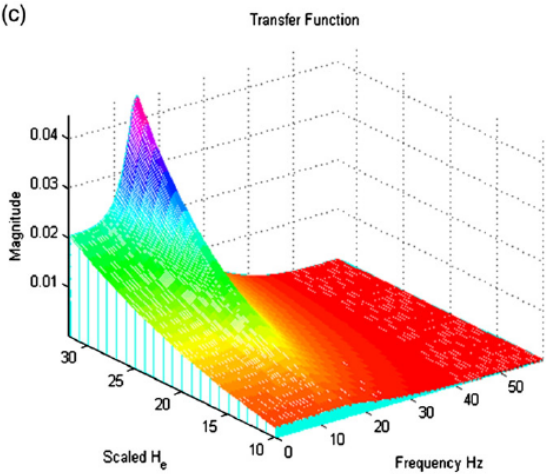
Single cortical unit



Increasing H_e caused a marked increase and sharpening of the spectral mass of the lower frequency mode.

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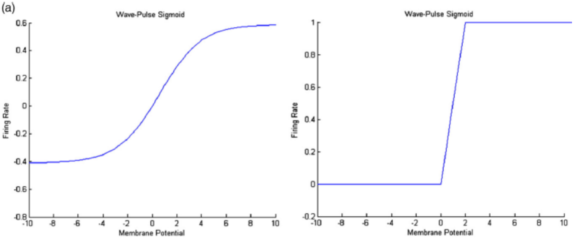
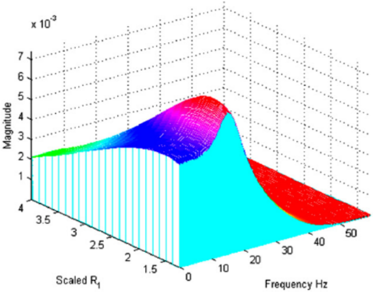
Single cortical unit

Increasing the gain



increased the frequency up to a point, after which bandpass characteristics are lost.



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Synaptic Physiology

In a rat model of schizophrenia weaning rats are deprived of social contact. This results in reduced levels of extracellular glutamate in prefrontal cortex.

Table 2
Microdialysis measures of extracellular glutamate neurotransmitter levels from two groups (Social and Isolated) of Wistar rats

	Glutamate
Social	4.2±1.4 μM (100%)
Isolated	1.5±0.8 μM (36%)

Measurements were taken from the medial prefrontal cortex.

This should be compensated for by upregulation of AMPA synapses reflected in eg. increases in H_e and increases in excitatory coupling (γ_1,γ_2,γ_3) Larger PSPs are also associated with greater SFA so we expect an increase in ρ_2 (Moran et al. 2008).

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Spectra

These parameters can be estimated from LFP spectra using DCM-SSR (Moran et al. 2007).

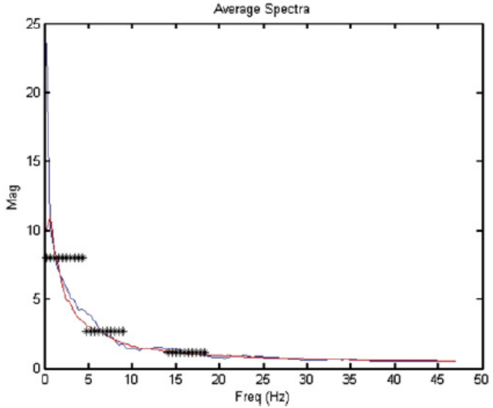
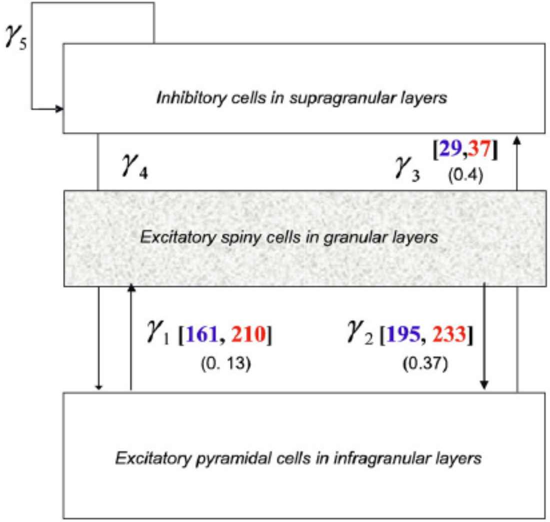


Fig. 9. Average Spectra of isolated (red) and control (blue) animals. Significant between-group differences ($p<0.05$ corrected for multiple comparisons and binned to mean freq across 5 Hz) are indicated by an asterisk. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Intrinsic Connections

The intrinsic coupling parameters were not significantly different between control (blue) and isolated (red) groups.



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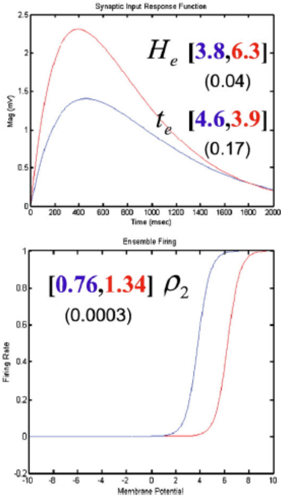
Synaptic Response

Isolated rats had increased PSPs and greater spike frequency adaptation as evidenced by the $f - I$ curve shifting to the right (Benda and Herz, 2003).



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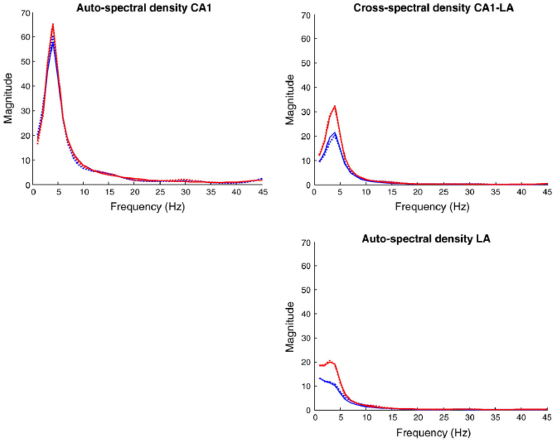
Cross-Spectra

LFPs were recorded from the lateral nucleus of the amygdala (LA) and CA1 region of dorsal hippocampus in adult mice as they responded to acoustic tones, one of which they had been conditioned to fear (CS+, red) through foot schock, and of which had no such association (CS-, blue).



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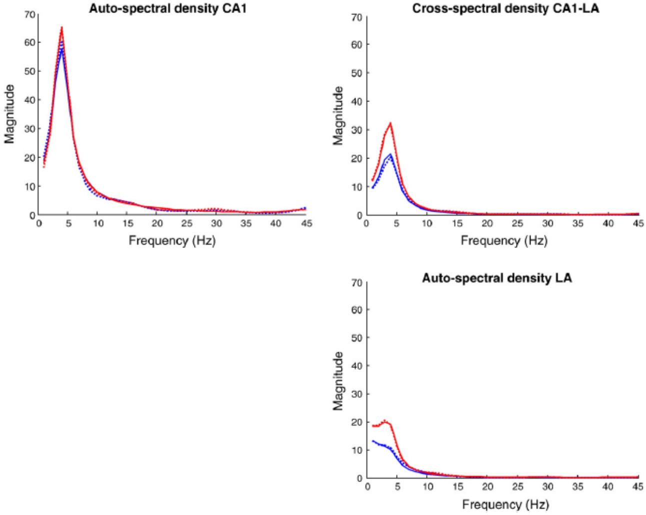
Cross-Spectra

Moran et al. (2009) fitted a two-region neural mass model to the cross-spectra using DCM-SSR, with data shown as solid lines and model fit with dotted lines.



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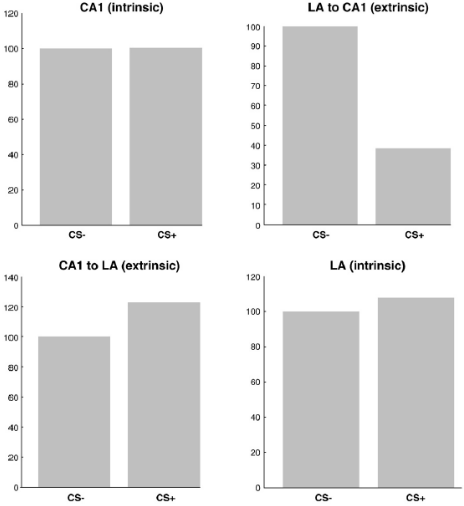
CS+ is associated with increasing extrinsic connections from CA1 to LA and decreasing extrinsic connections from LA to CA1.



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