Dynamical Criticality

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Overriding question:
How is it possible that the brain maintains the balance between excitation and inhibition?

A global strategy is architecturally divergent. We seek to find a simple, **local** model of excitation/inhibition homeostasis able to give us an interesting dynamical system with many degrees of freedom.

This is related, and confused, with the idea of criticality

- **Dynamical criticality**: the simultaneous presence of a large set of dynamically critical features such as Hopf bifurcations. Each would typically require independent fine-tuning; collectively they would require fine tuning of many parameters simultaneously, unless somehow "self-tuned". Example: extensive number of zero Lyapunov exponents in shell models of turbulence (self-tuned, but ill-understood)

- **Statistical criticality**: the presence of wide-range temporal and spatial scales, power-law distributions, etc. Can be obtained in phase transitions by tuning of a small number of parameters, and in some systems (self-organized critical) in the absence of tuning. Examples: critical Ising model (needs tuning) and standard sandpile (SOC). Standard examples are **not smooth** dynamical systems though.

- Dynamical systems theory holds that systems of interest should be **structurally stable**: their behavior should not drastically change with small changes in the formal definition of the dynamics.

- Thus high-order **dynamical criticality**, the simultaneous presence of many modes with critical features such being at a Hopf bifurcations, is **not expected to be ever observed** in a natural system.

- However natural systems lacking such structural stability are not infrequent: neuroscience provides many dynamically critical systems as examples.

Dynamical criticality in neuroscience

- line attractors in motor control
  Seung et al., Neural Networks 11, 1253-1258 (1998); Neuron 26, 259-271 (2000).

- ...and decision making
  Machens, Romo, Brody, Science 307, 1121-1124 (2005).

- self-tuned Hopf bifurcations in the auditory periphery
  Camalet et. al PNAS 97, 3183-3188 (2000), Eguíluz el al. PRL 84, 5232-5236 (2000), Moreau & Sontag PRE 68, 020901 (2003)

- ...and olfactory system
  Freeman & Holmes, Neural Networks 18, 497-504 (2005)

Statistical criticality

- phenomena displaying wide range of spatio-temporal scales, power law distributions.
- as with bifurcations, these states might require fine-tuning of parameters.
- or... self-organized critical states.
- needless to say: many instances in neuroscience.

Dynamical synapses causing self-organized criticality in neural networks

A. LEVINA, J. M. HERRMANN, AND T. GEISEL

Nature Physics 3, 857, 2007

$$\dot{h}_i = \delta_{i,\xi_\tau(t)} I^{\text{ext}} + \frac{1}{N} \sum_{j=1}^{N} u J_{ij} \delta\left(t - t_{\text{sp}}^j - \tau_{\text{d}}\right).$$

$$\dot{J}_{ij} = \frac{1}{\tau_J}\left(\frac{\alpha}{u} - J_{ij}\right) - u J_{ij} \delta\left(t - t_{\text{sp}}^j\right),$$

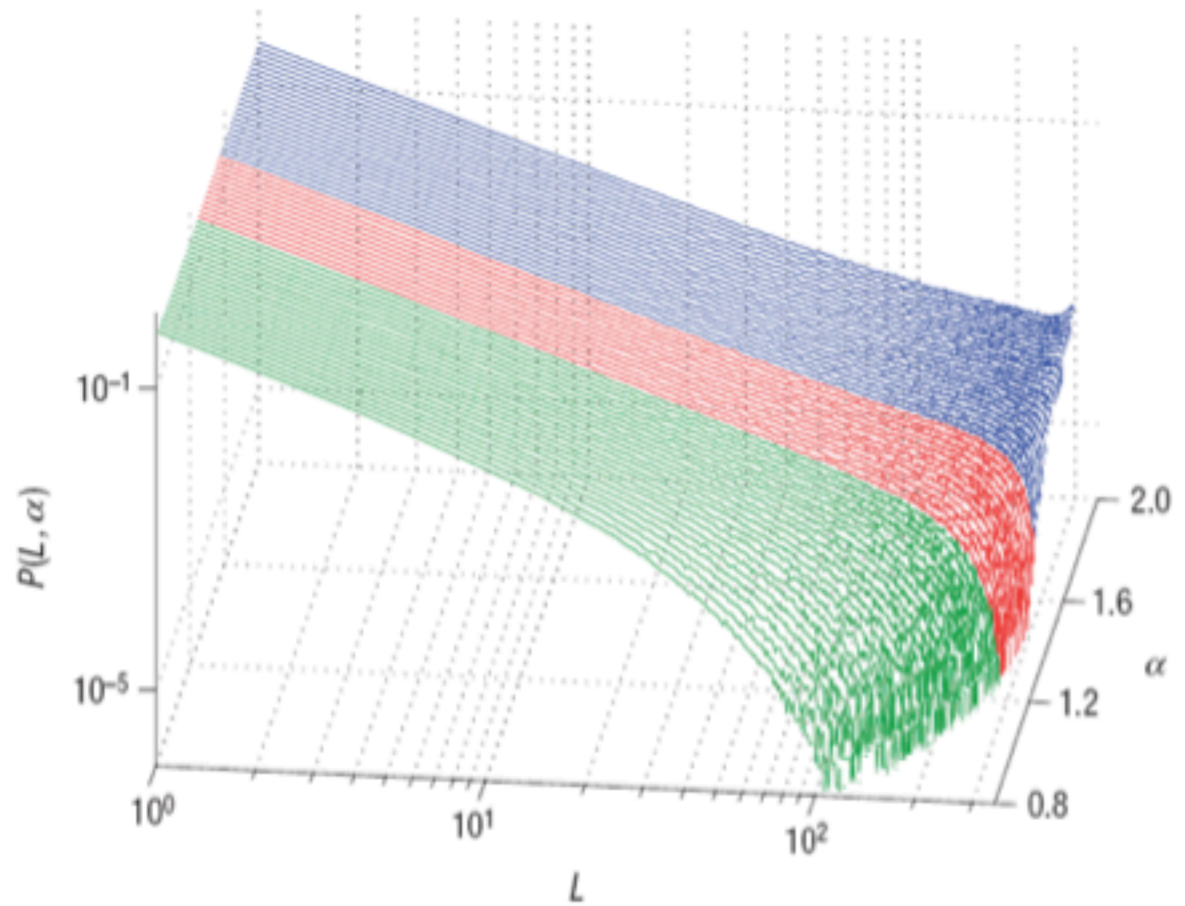


Figure 1 Distribution of avalanche sizes for different coupling strengths α. At $\alpha < 1.3$, small avalanches are preferred, yielding a subcritical distribution. The range of connectivity parameters near $\alpha = 1.4$ seems critical. For $\alpha > 1.6$, the distribution is supercritical, that is, a substantial fraction of firing events spreads through the whole system. These results are shown for $N = 300$, $\nu = 10$, $u = 0.2$, $I^{\text{ext}} = 0.025$.

See also Lin M. & Chen T.-L., Phys. Rev. E 71, 016133 (2005).

Avalanches in Cortical Slices

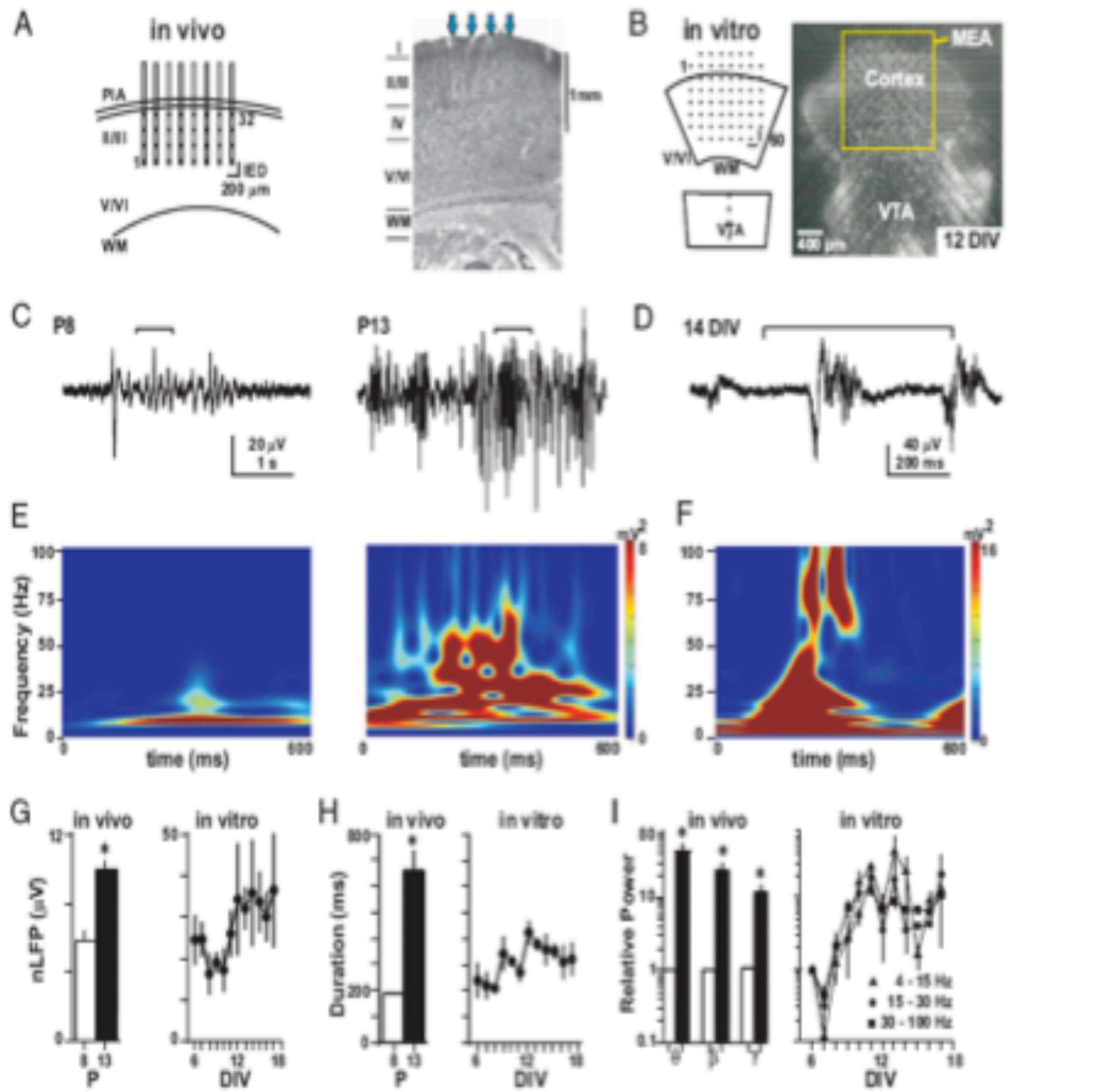
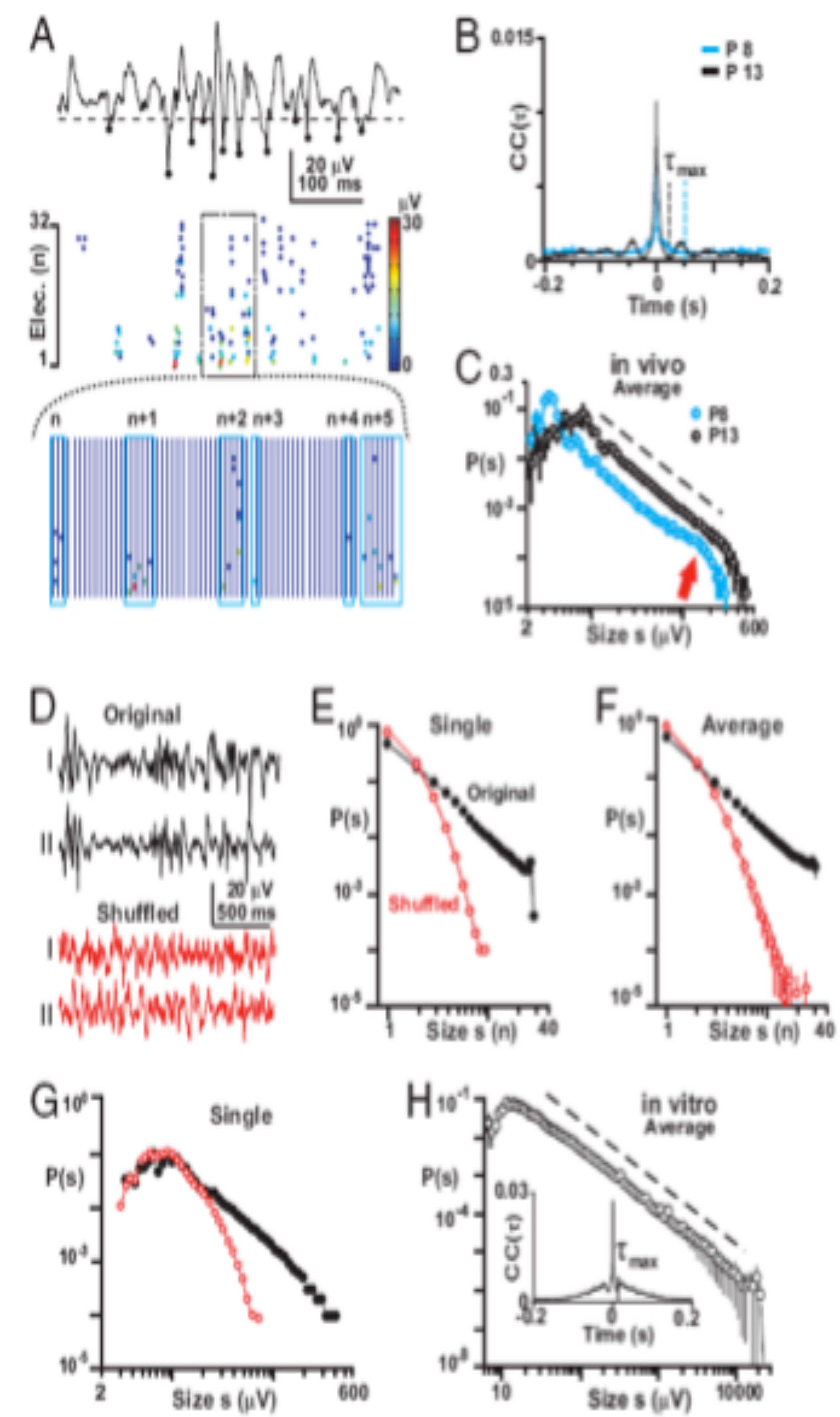


Fig. 1. Nested θ- and β/γ-oscillations emerge during maturation of cortical layer 2/3. (A) Sketch of the 8 × 4 MEA placement in somatosensory cortex *in vivo*. (*Left*) PIA, pia mater; WM, white matter; IED, interelectrode distance of 200 μm. (*Right*) The 60-μm-thick Nissl-stained section with tracks from four electrode shanks (arrows). (B) (*Left*) Sketch of the 8 × 8 MEA placement in the cortex-VTA coculture. (*Right*) Light microscopic image of the living coculture (12 DIV). IED, 200 μm. (C and D) Spontaneous bursts at P8 and P13 *in vivo* (C) and at DIV 14 *in vitro* (D). Brackets, Periods in E and F. (E) Nested θ- and β/γ-oscillations emerge during the second week postnatal *in vivo*. Time–frequency plot for burst periods in C at P8 (*Left*) and at P13 (*Right*) *in vivo*. (F) Nested θ- and β/γ-oscillations *in vitro*. Time–frequency plot for burst period in D. (G and H) Burst amplitude (G) and duration (H) increase significantly during the second week postnatal. (I) θ-, β-, and γ-frequency power increases significantly during second week postnatal (normalized to power at P8 *in vivo* and DIV 6 *in vitro*).



Elakkat D. Gireesh and Dietmar Plenz

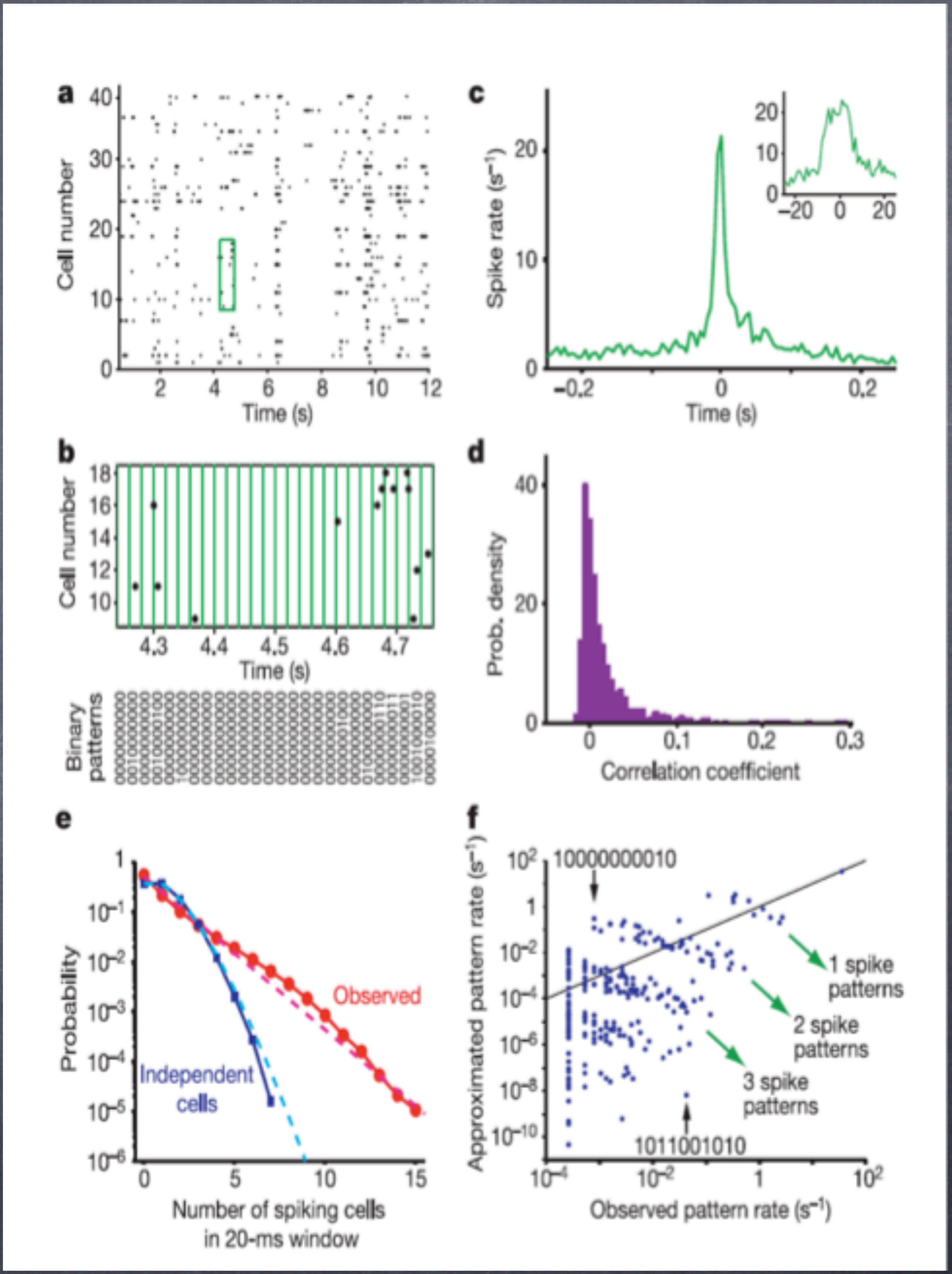
PNAS vol. 105, 7576-7581, 2008

Weak pairwise correlations imply strongly correlated network states in a neural population

Elad Schneidman, Michael J. Berry II, Ronen Segev & William Bialek

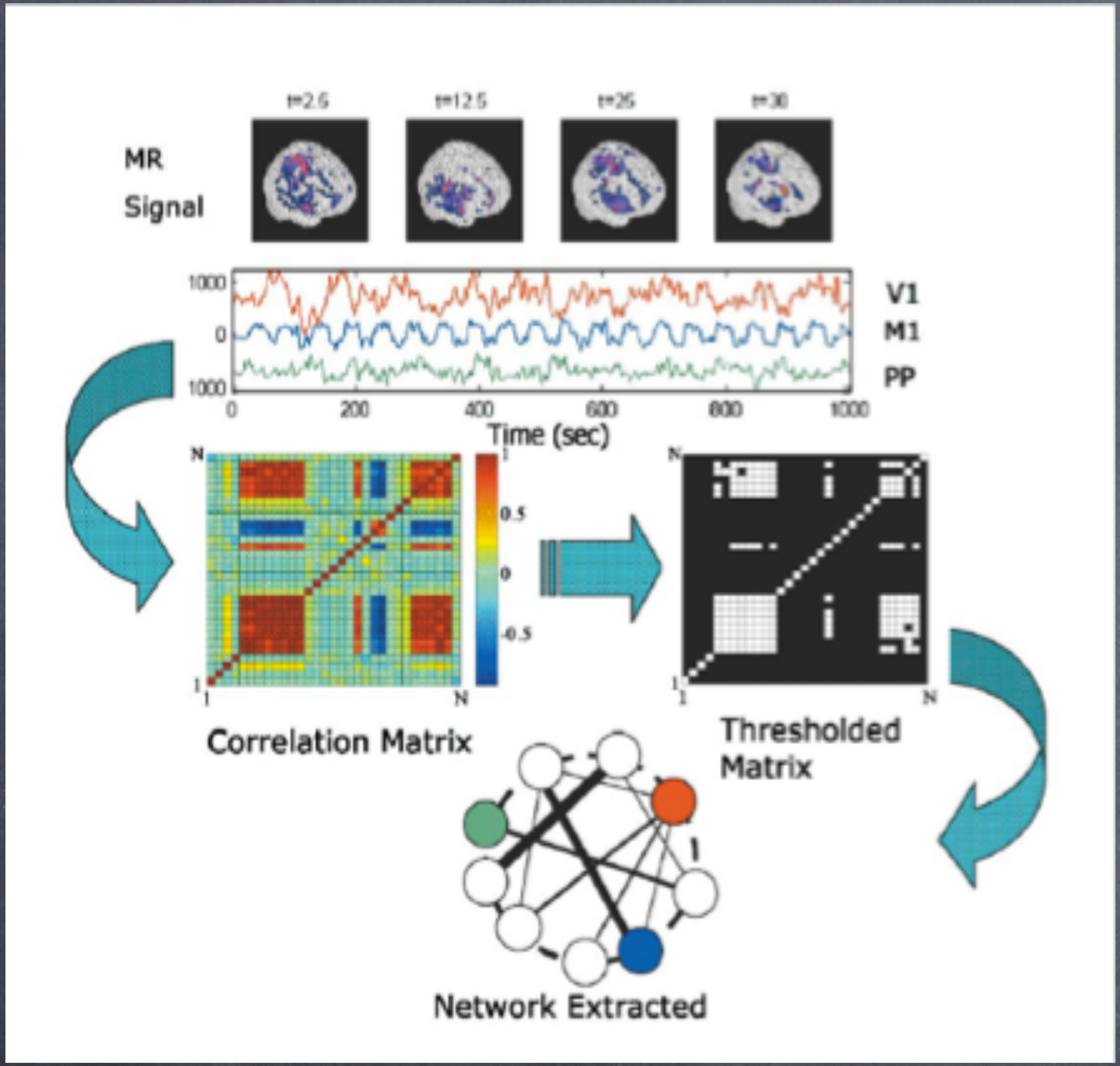
Nature 440, 1007, 2006

Analysis of experimental data from retinas of larval tiger salamander and guinea pigs.



Scale free correlations in the brain

(Functional MRI data)



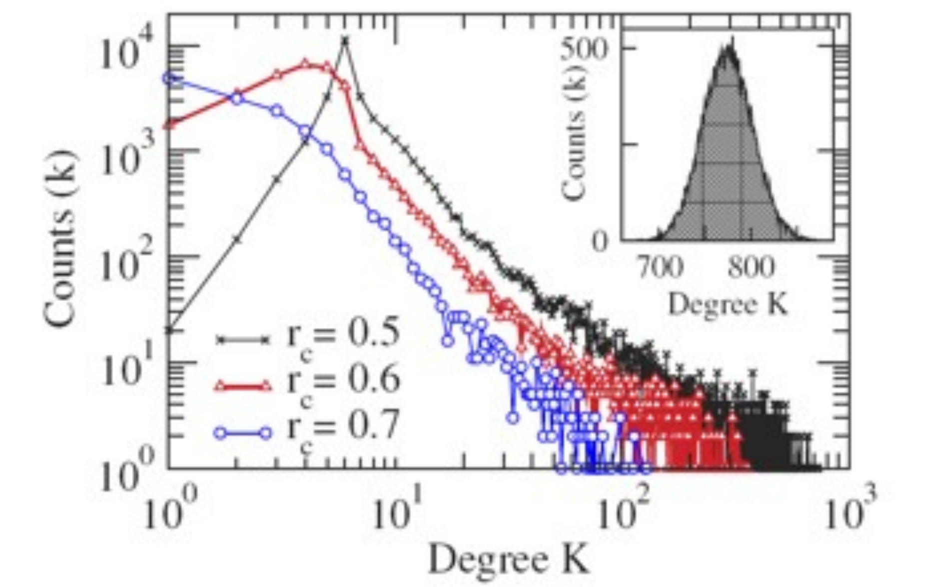
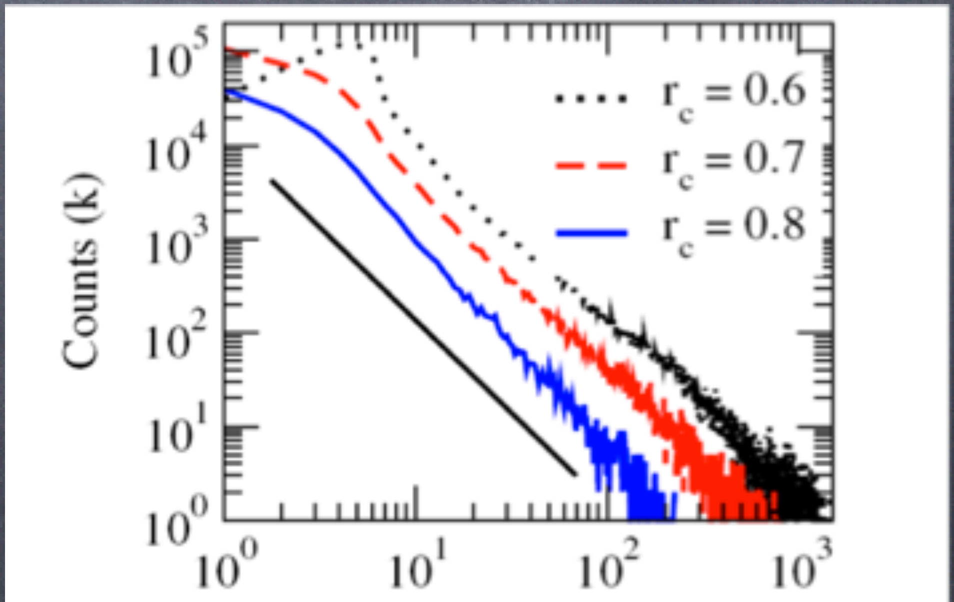


FIG. 2 (color online). Degree distribution for three values of the correlation threshold. The inset depicts the degree distribution for an equivalent randomly connected network.



V.M. Eguíluz, et al.
Phy. Rev. Lett. 94, 018102 (2005).

The bare bones model

linear activity

not relevant yet

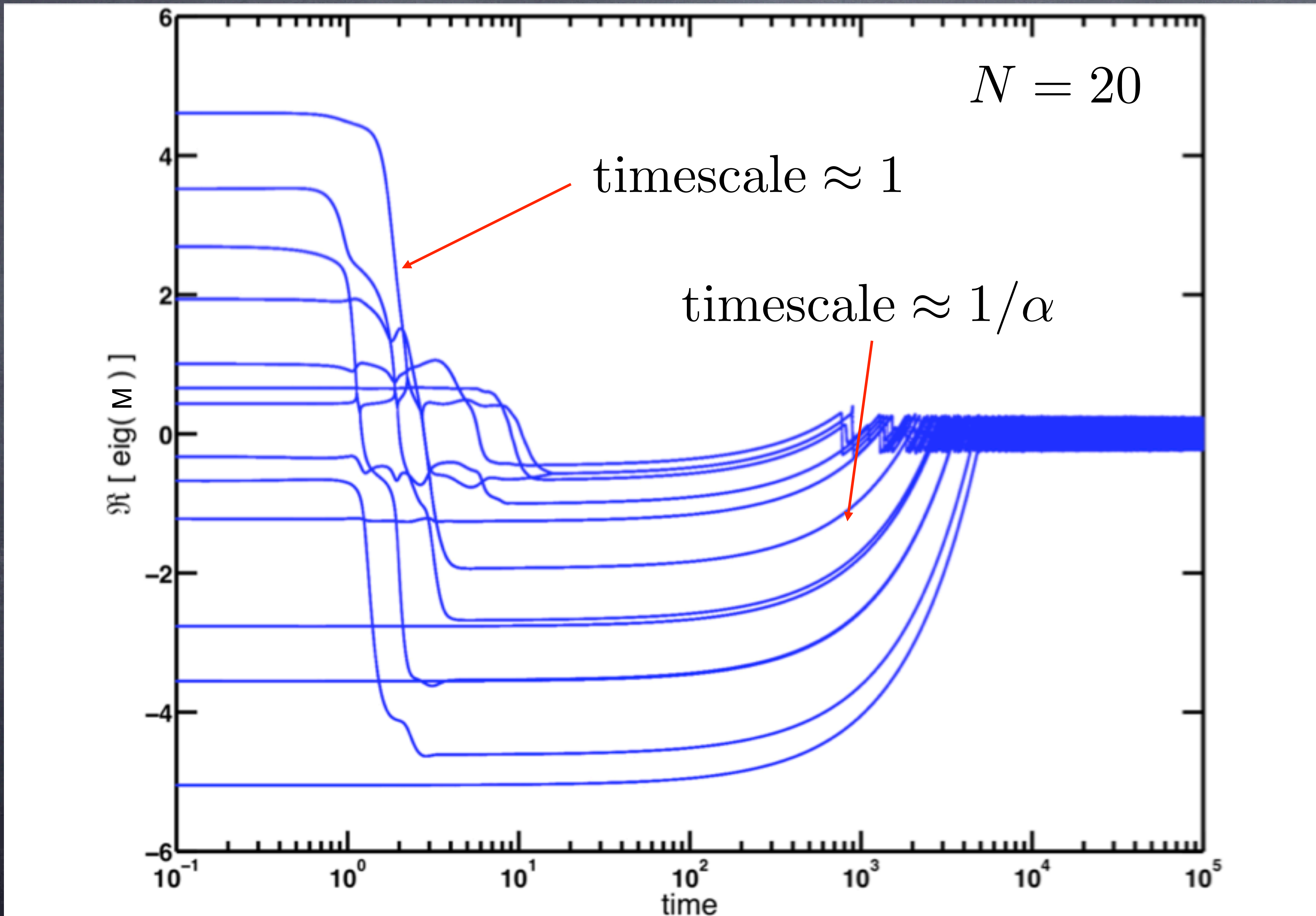
$$\dot{\mathbf{x}} = \mathbf{M}\mathbf{x} + \epsilon(t) + \mathcal{O}(x^2)$$

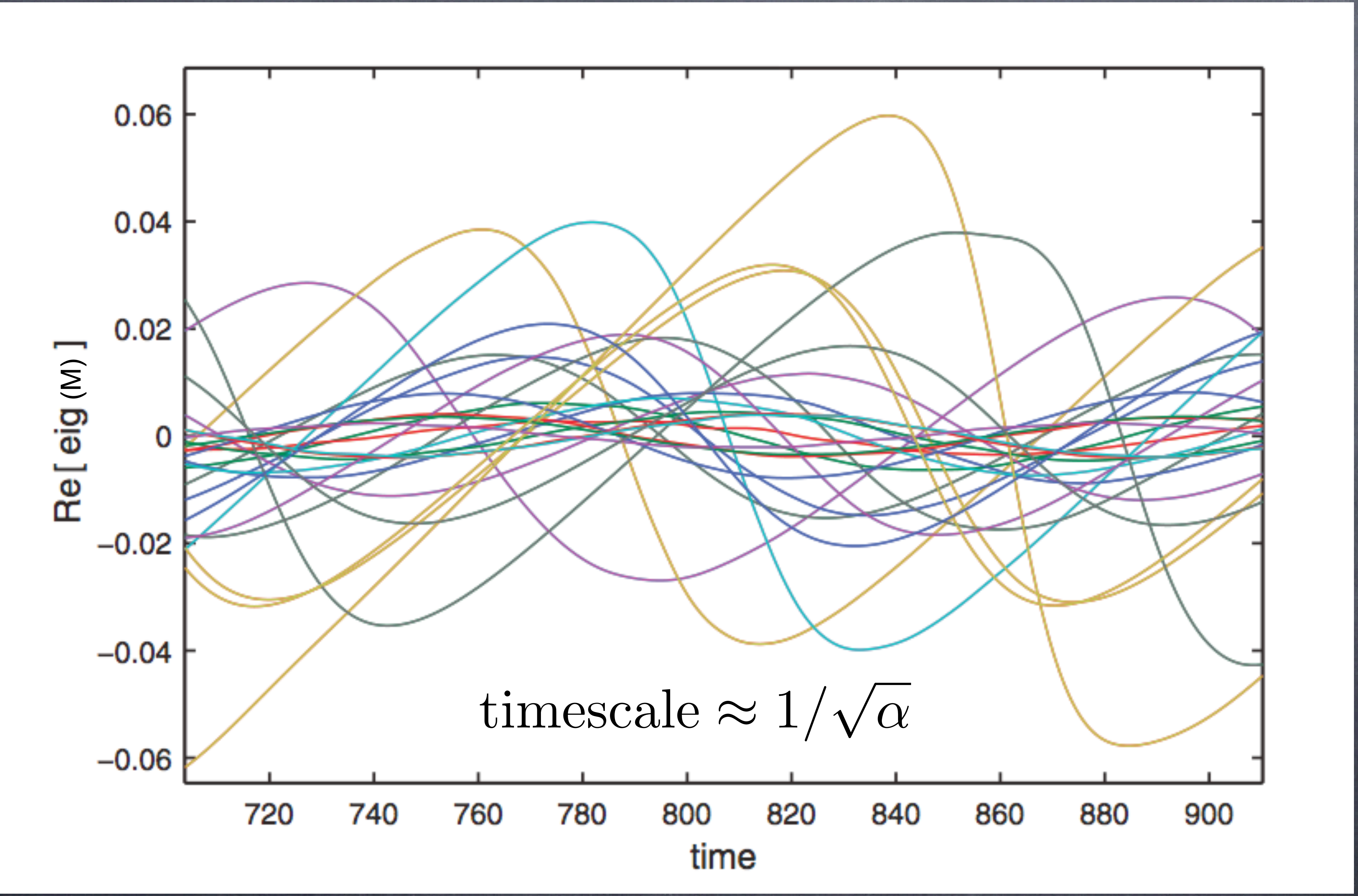
$$\dot{\mathbf{M}} = \alpha(\mathbf{I} - \mathbf{x}\mathbf{x}^T)$$

anti-Hebbian learning

Phys. Rev. Lett. (2009)

Evolution of the eigenvalues of a random initial matrix




0.06
0.04
0.02
0
−0.02
−0.04
−0.06
Re [eig (M)]
720
740
760
780
800
820
840
860
880
900
time
timescale ≈ 1/√α

Because the right-hand-side of the M equation is symmetric, the antisymmetric component is an invariant of the motion:

$$\dot{\mathbf{x}} = (\mathbf{A} + \mathbf{S})\mathbf{x}$$

$$\dot{\mathbf{A}} = 0$$

$$\dot{\mathbf{S}} = \alpha(\mathbf{I} - \mathbf{x}\mathbf{x}^T)$$

STDP

PNAS (2008), Front. Neural Circuits (2010)

$$\ddot{S} = \frac{d}{dt}\dot{S} = -\alpha\frac{d}{dt}\mathbf{x}\mathbf{x}^\top = -\alpha(\dot{\mathbf{x}}\mathbf{x}^\top + \mathbf{x}\dot{\mathbf{x}}^\top)$$

$$\mathbf{x}\mathbf{x}^\top = I - \dot{S}/\alpha$$

$$\ddot{S} = -\alpha\left((A+S)(I - \dot{S}/\alpha) + (I - \dot{S}/\alpha)(A+S)^\top\right)$$

$$\ddot{S} = -2\alpha S + [A, \dot{S}] + \{S, \dot{S}\}$$

$$\ddot{S} = -2\alpha S + [A, \dot{S}] + \{S, \dot{S}\}$$

$$\dot{S} = [A, S] = i[-iA, S]$$

time derivative of Heisenberg equation
with Hermitian Hamiltonian $-iA$

$$\ddot{S} + 2\alpha S = 0$$

harmonic oscillator

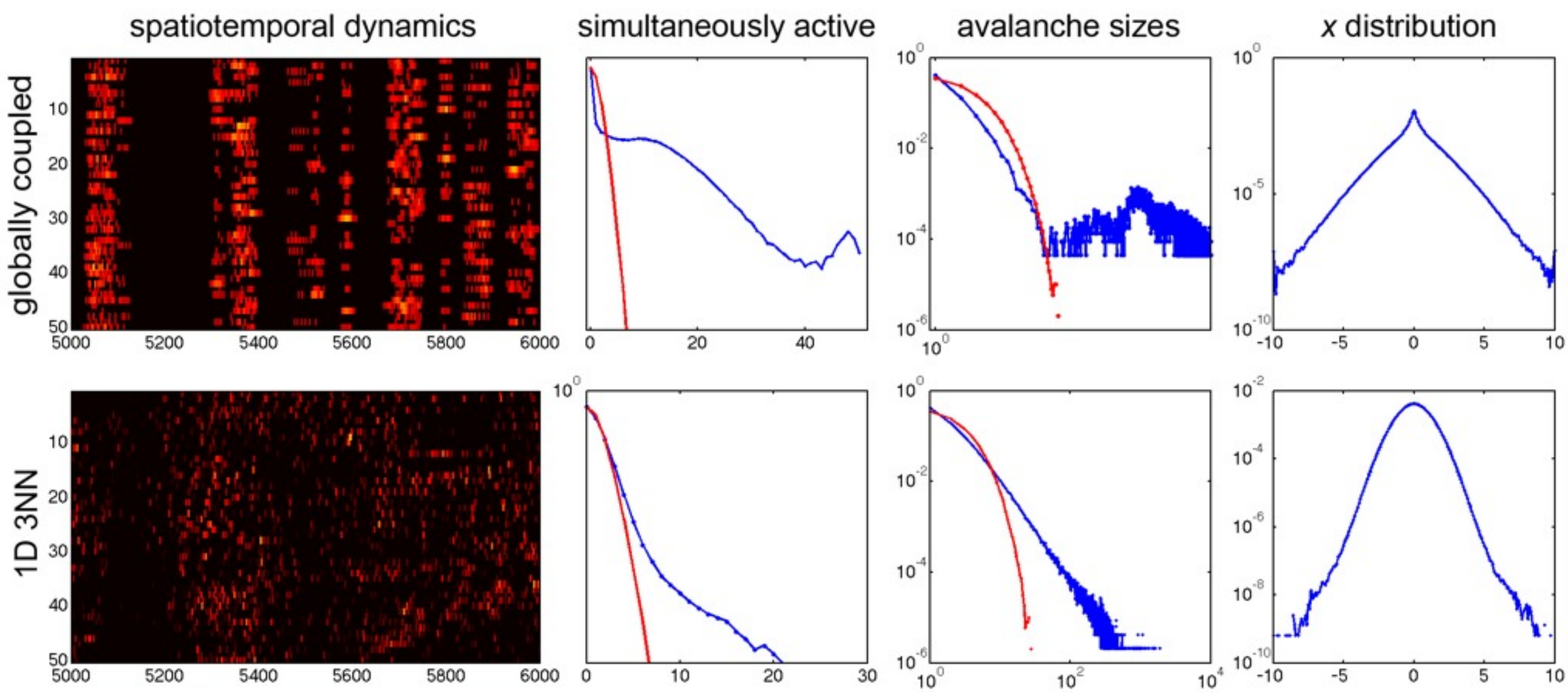
$$\mathcal{O}(\alpha)$$

i.e., synaptic plasticity timescale

$$\mathcal{O}(\sqrt{\alpha})$$

new timescale, between electrical, given by the non-evolving synaptic weights, and plastic, given by the learning rate

Statistical criticality in our model



Top row, globally coupled (unrestricted A). Bottom row, nodes arranged in one dimension with periodic boundary conditions; only entries of A up to third nearest neighbor are allowed to be nonzero. First column, a display of the spatio-temporal dynamics. Second column: the distribution of the number of simultaneously active units in the dynamics (blue) and in surrogate data (red); compare to [9]. Third column, sizes of avalanches (blue), vs. surrogate data (red); note in the 1D case the power-law distribution of avalanche sizes, while the globally coupled (1-D) case shows a piece of a power-law followed by a large lump of rather large avalanches (as clearly visible in the spatiotemporal plot). Fourth column, marginal distribution of the values of x (invariant under surrogation).

Model summary

- Simple model of “neural tissue”, with anti-Hebbian dynamics that permits the system to use the symmetric components of its synaptic connectivity to poise itself at a dynamically critical state and becomes infinitely susceptible to input which, once applied, can reverberate for long times.

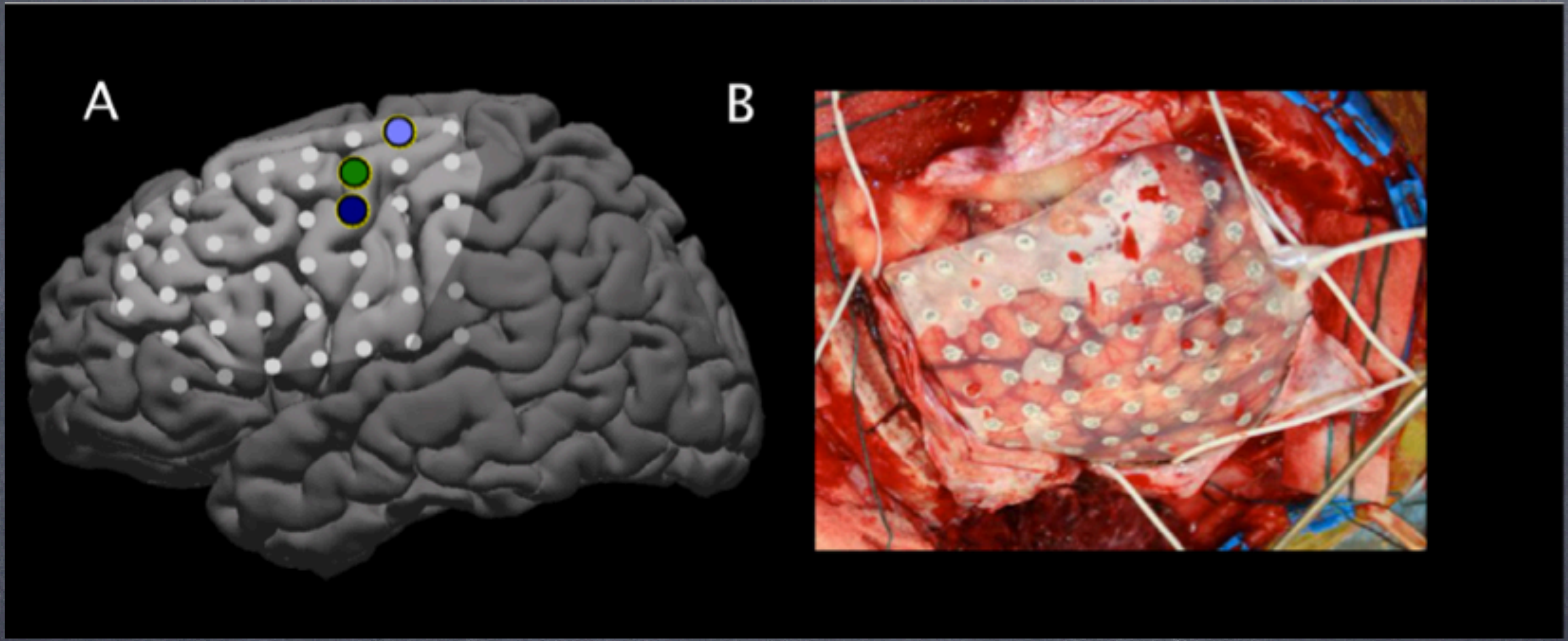
- In the absence of inputs, the system evolves around the line of instability with three time-scales; two of these, electrical neural activity and the synaptic timescale, are physical timescales and the third one bridges other two.

- Learning can be encoded in the antisymmetric part of the connectivity. Possibly, only inputs that are Granger causal can be learned.

- The system generates power law statistics with sometimes anomalous heavy tails as well.

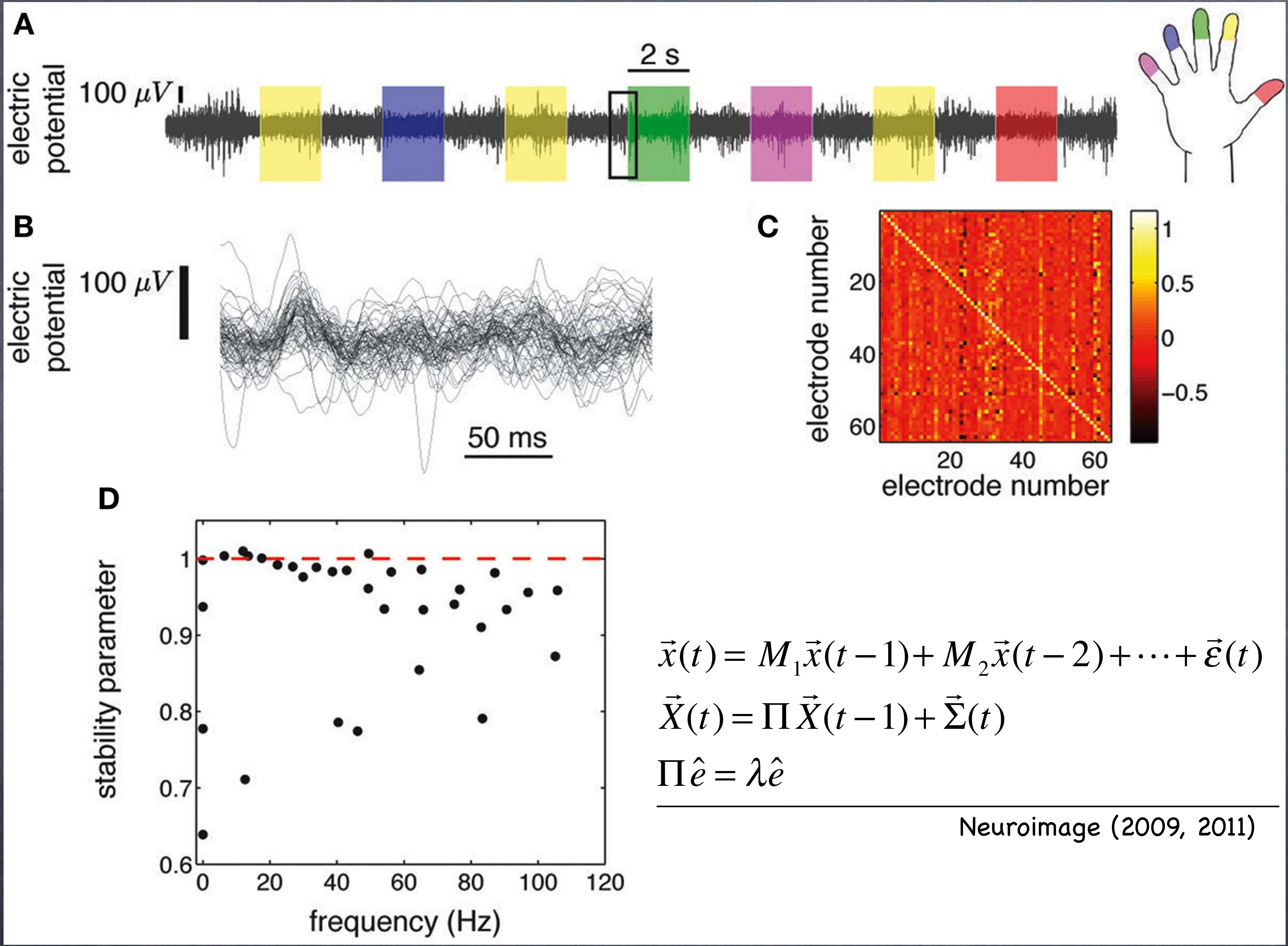
Testing the model

ElectroCorticoGraphy (ECoG)



Subjects performing finger tapping

Miller et al, J. Neurosci. (2009)



$$\vec{x}(t) = M_1\vec{x}(t-1) + M_2\vec{x}(t-2) + \cdots + \vec{\varepsilon}(t)$$

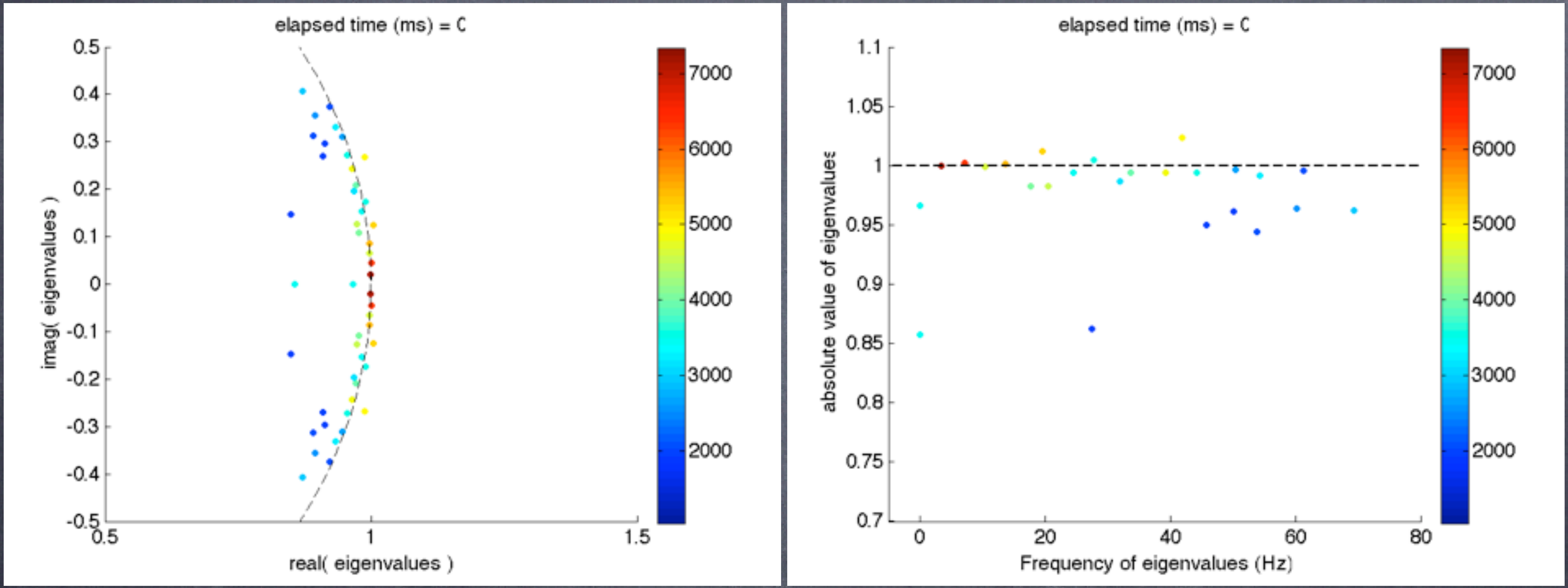
$$\vec{X}(t) = \Pi\,\vec{X}(t-1) + \vec{\Sigma}(t)$$

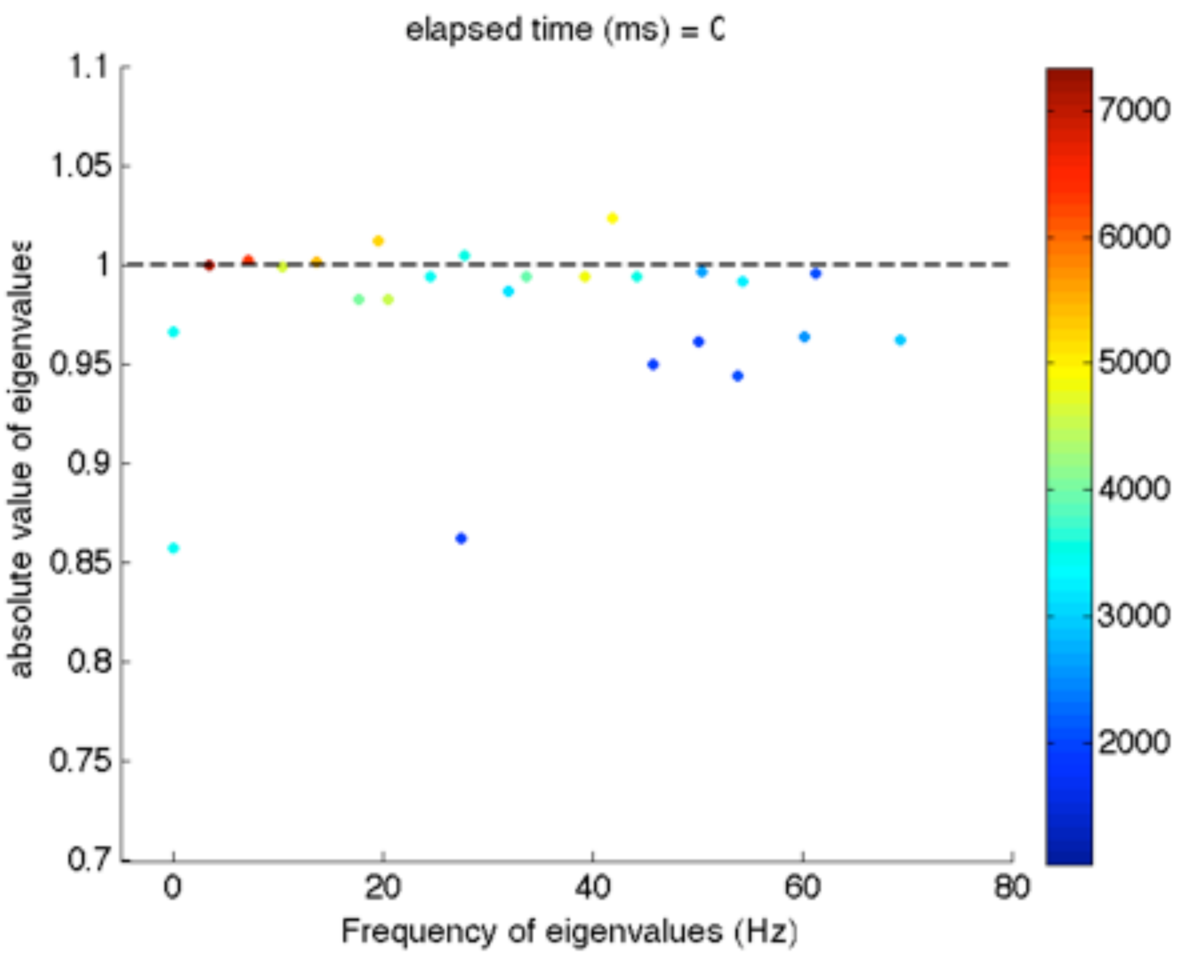
$$\Pi\hat{e} = \lambda\hat{e}$$

Neuroimage (2009, 2011)

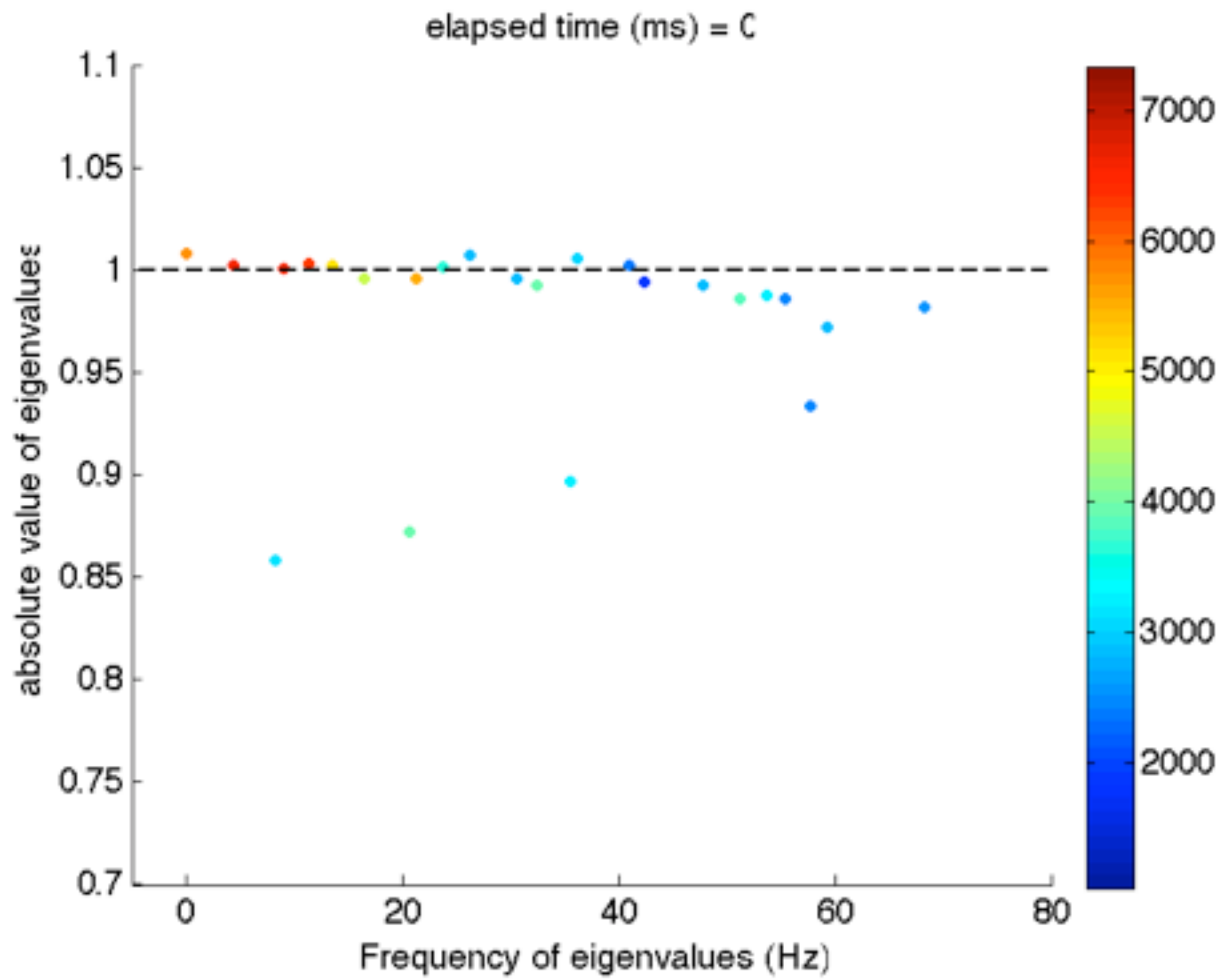
Frontiers Integ. Neurosci. (2012)

time evolution of eigenvalues during 200 ms. color indicates the magnitude of the projection of the signal in each mode.

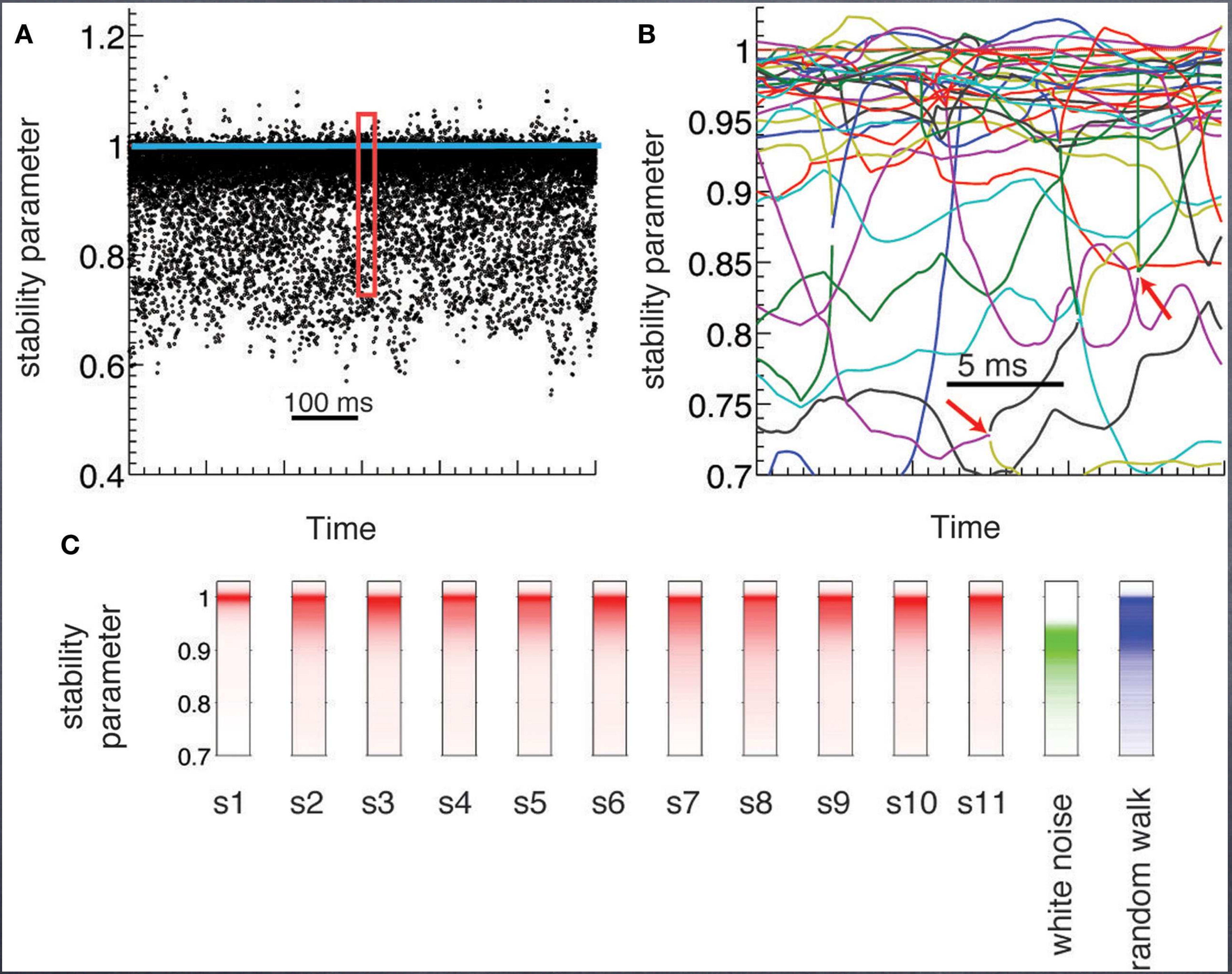




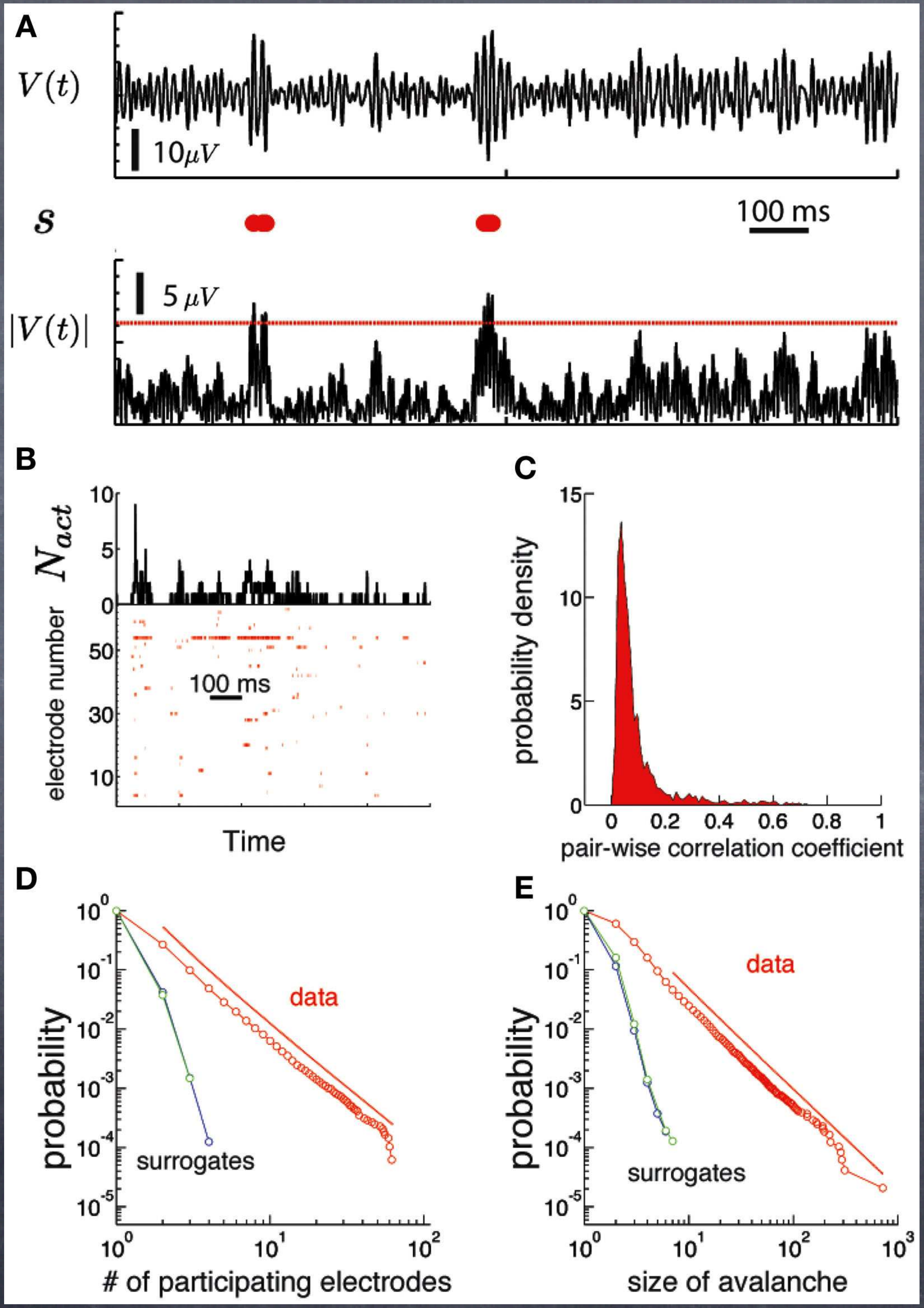
elapsed time (ms) = C
absolute value of eigenvalues
Frequency of eigenvalues (Hz)

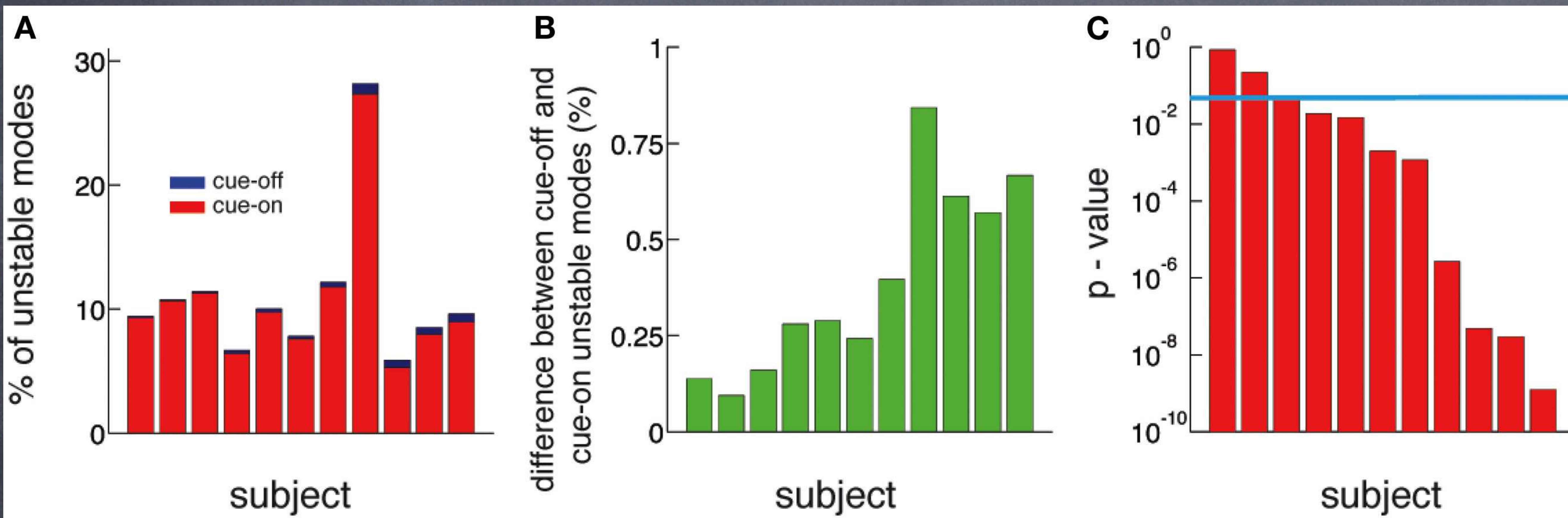


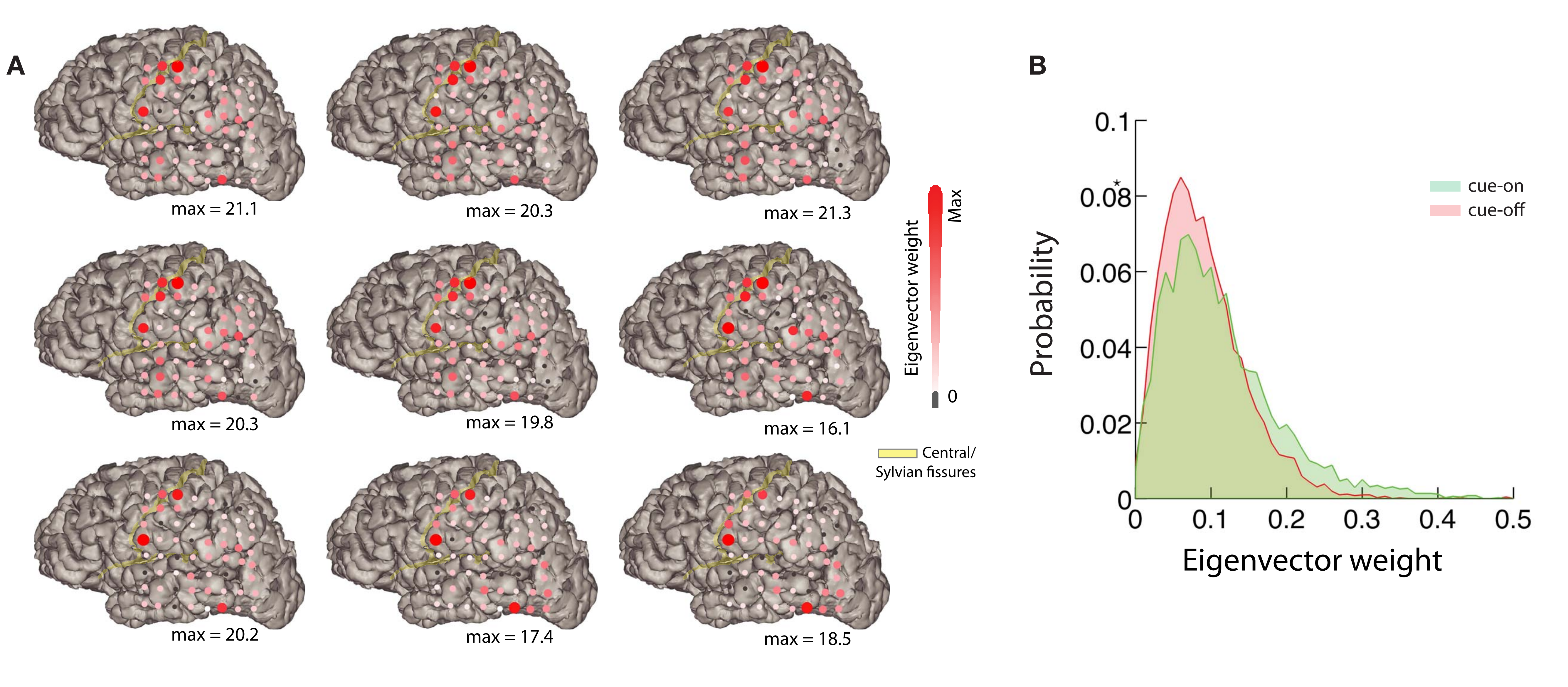
elapsed time (ms) = C
absolute value of eigenvalues
Frequency of eigenvalues (Hz)



A
B
C
stability parameter
1.2
1
0.8
0.6
0.4
100 ms
Time
1
0.95
0.9
0.85
0.8
0.75
0.7
5 ms
0.9
0.8
0.7
s1
s2
s3
s4
s5
s6
s7
s8
s9
s10
s11
white noise
random walk


A
$V(t)$
$10\mu V$
s
100 ms
$5\ \mu V$
$|V(t)|$
B
N_{act}
electrode number
100 ms
Time
C
probability density
pair-wise correlation coefficient
D
probability
data
surrogates
# of participating electrodes
E
probability
data
surrogates
size of avalanche


A
% of unstable modes
30
20
10
0
cue-off
cue-on
subject
B
difference between cue-off and cue-on unstable modes (%)
1
0.75
0.5
0.25
0
subject
C
p - value
10^{0}
10^{-2}
10^{-4}
10^{-6}
10^{-8}
10^{-10}
subject


A
max = 21.1
max = 20.3
max = 21.3
max = 20.3
max = 19.8
max = 16.1
max = 20.2
max = 17.4
max = 18.5
Eigenvector weight
Max
0
Central/
Sylvian fissures
B
Probability
0.1
0.08
0.06
0.04
0.02
0
0
0.1
0.2
0.3
0.4
0.5
Eigenvector weight
cue-on
cue-off

Anesthesia

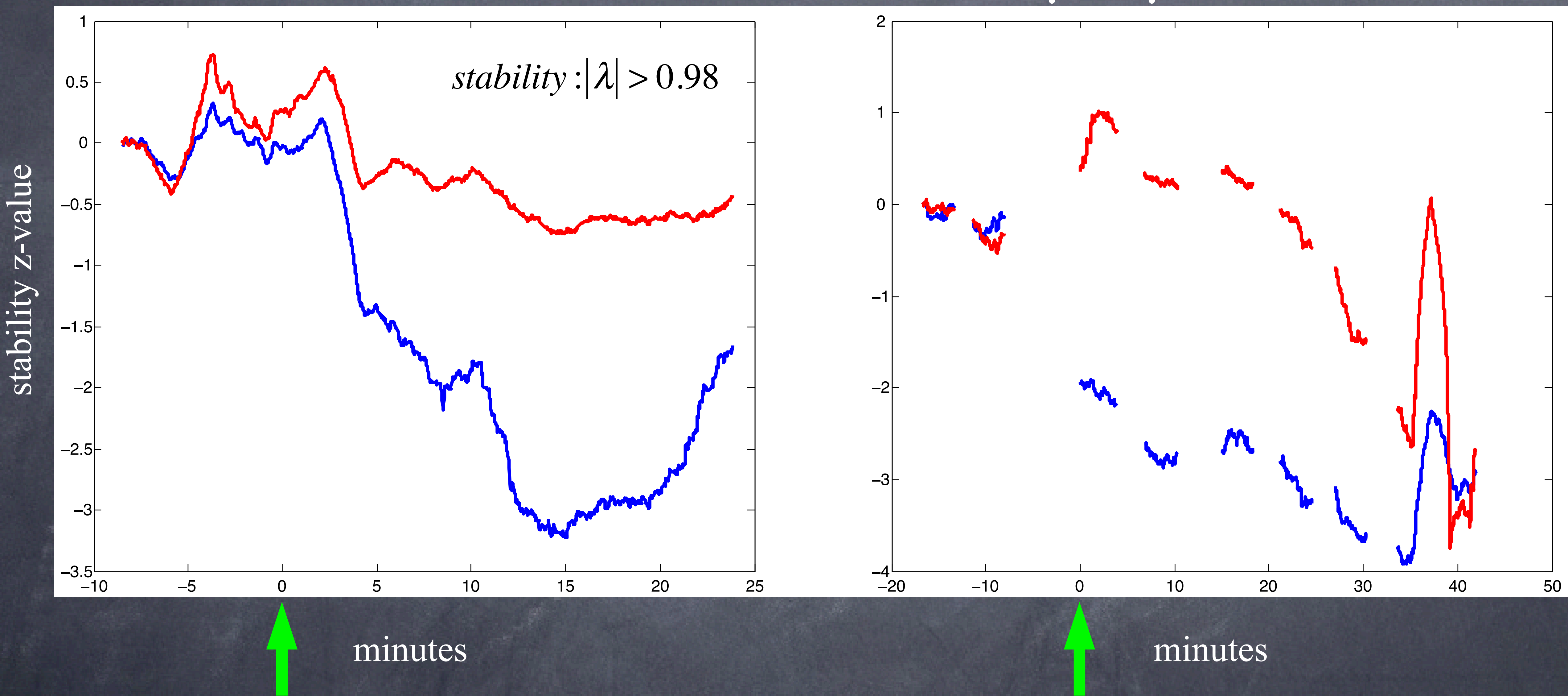
- **Plurality of targets**
  - Molecular: neurotransmitters, ion channels
  - Anatomical: cortex, thalamus, brain stem
- **Traditional measure of "depth of anesthesia"**
  - Spectral changes in specific bands (e.g. delta, gamma) inconsistent: some up, some down
  - Changes inconsistent across subjects
  - Changes inconsistent across drugs

Franks (2008), Nat. Rev. Neurosci.

Avidan et al. (2011), New Eng. J. Med.

Monkey subjects

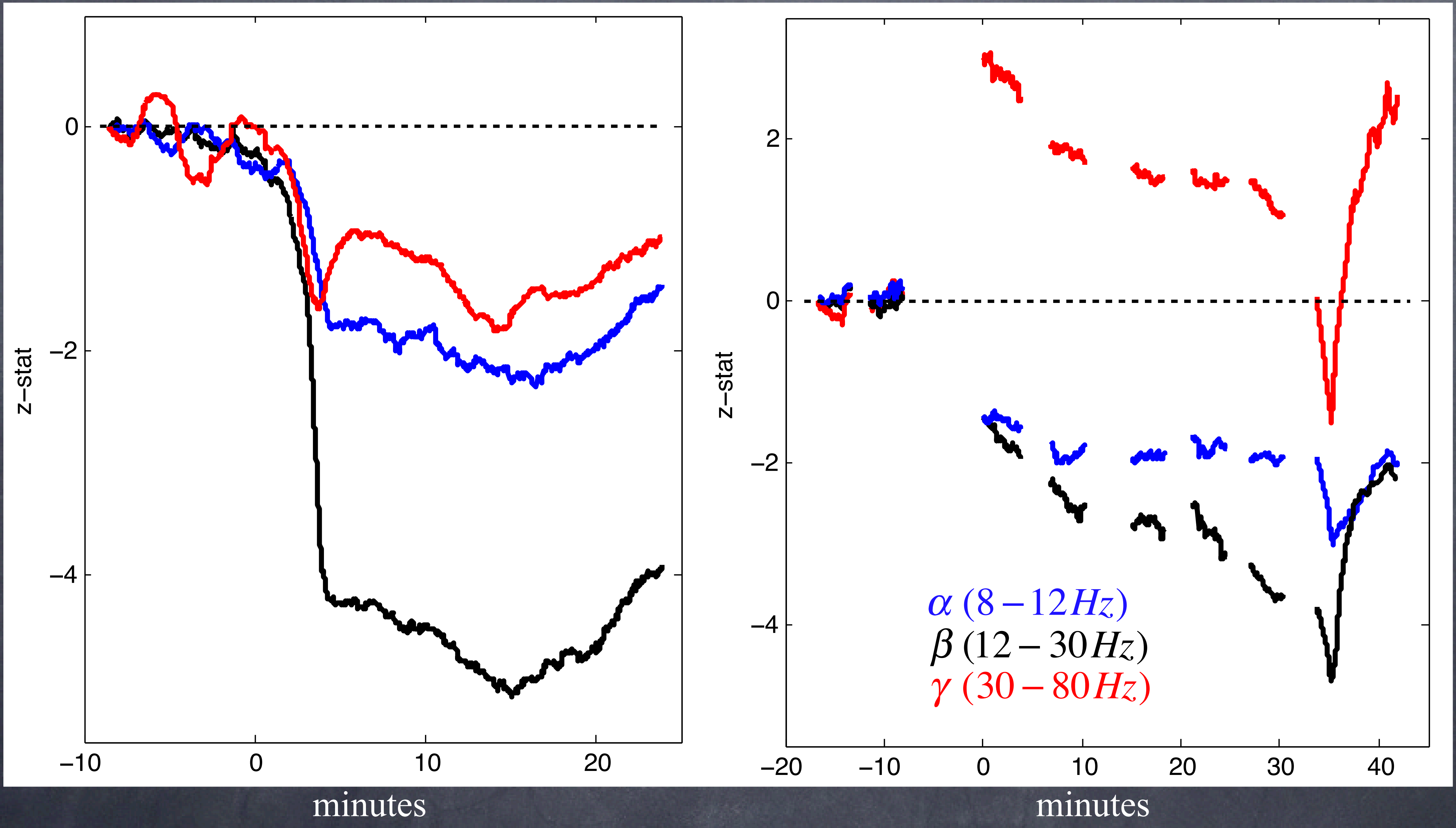
ketamine   propofol



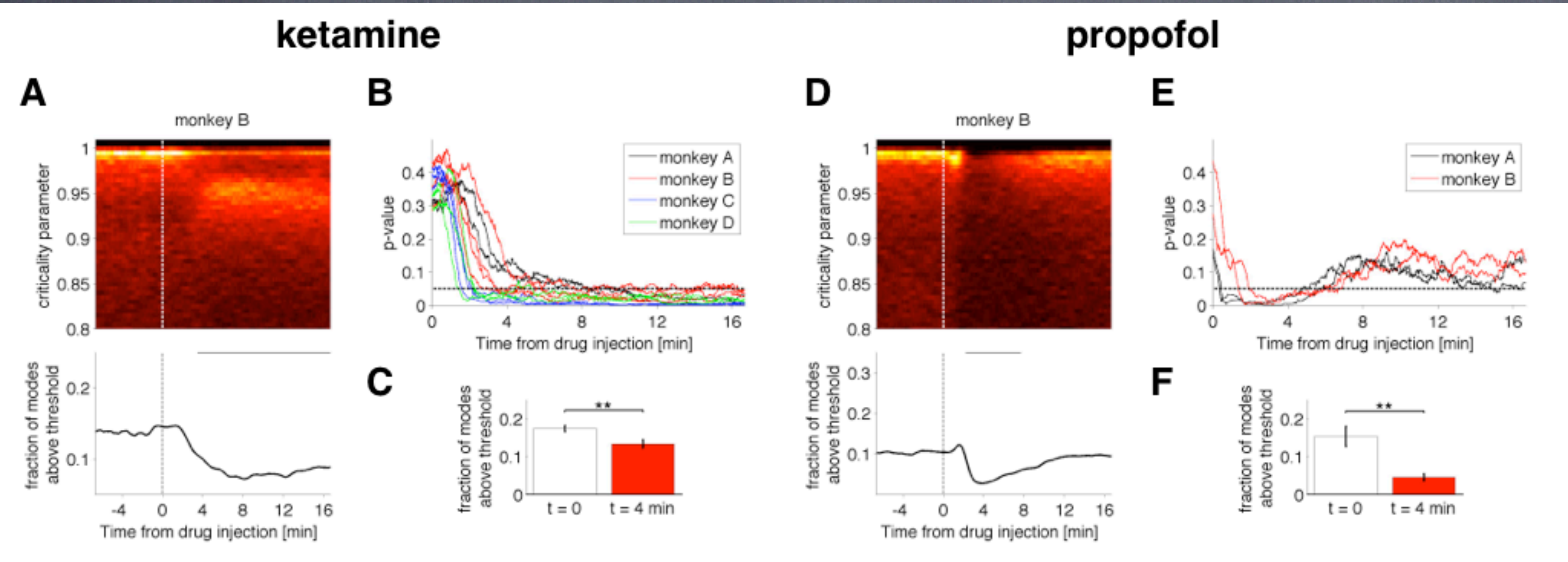
data

surrogate data (50 msec width gaussian time shift)

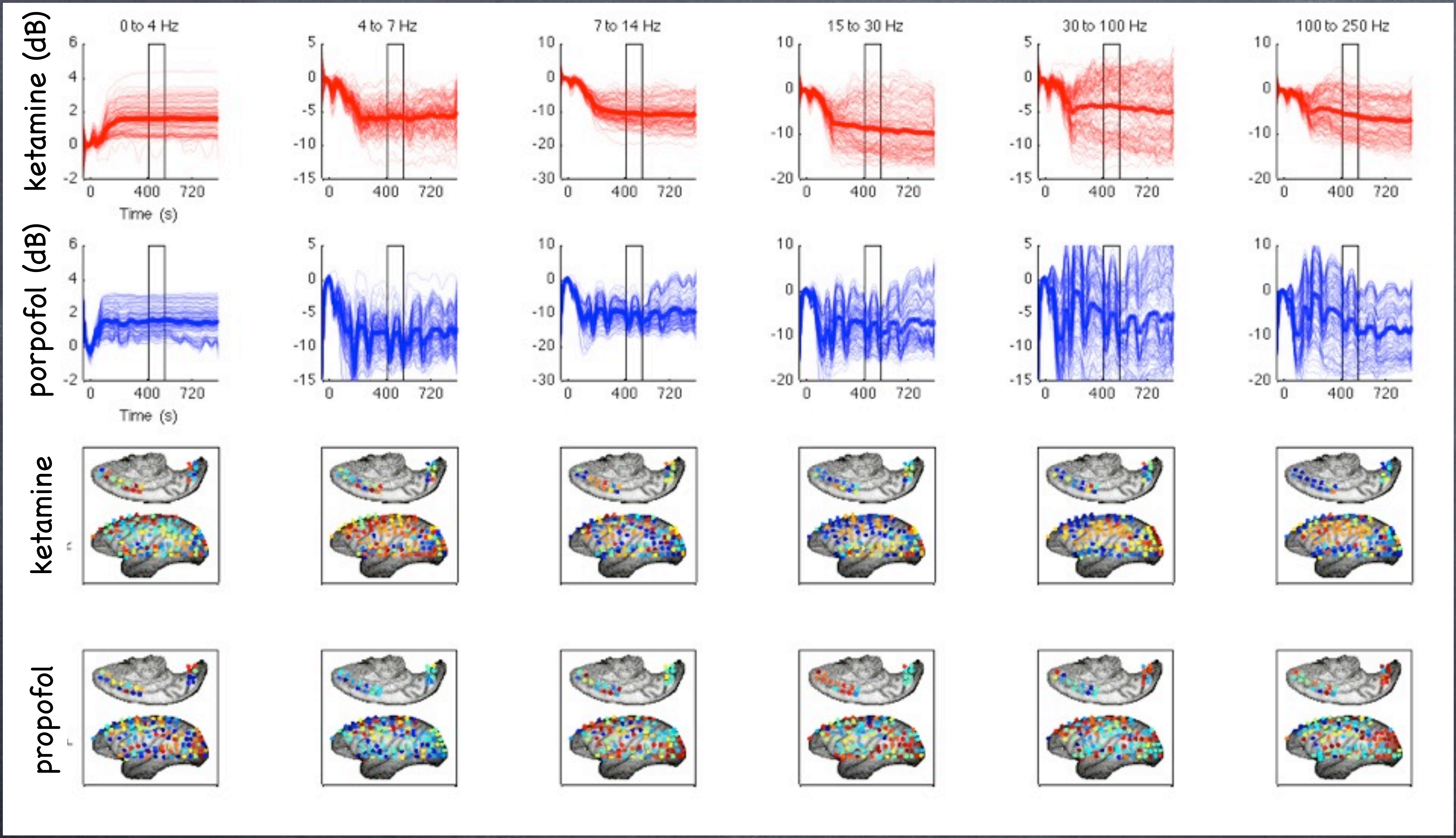
spectral analysis



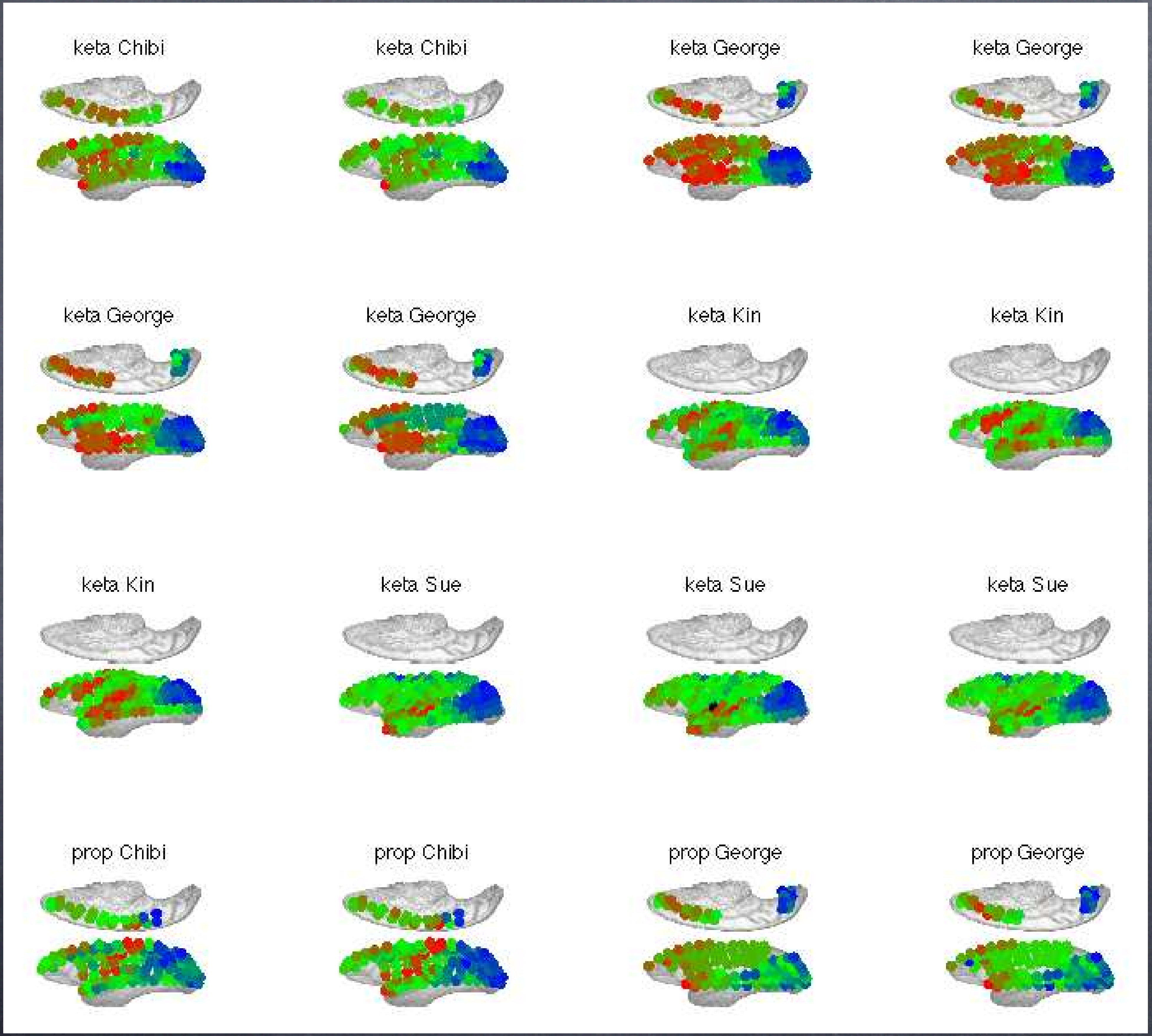
Monkey Subjects



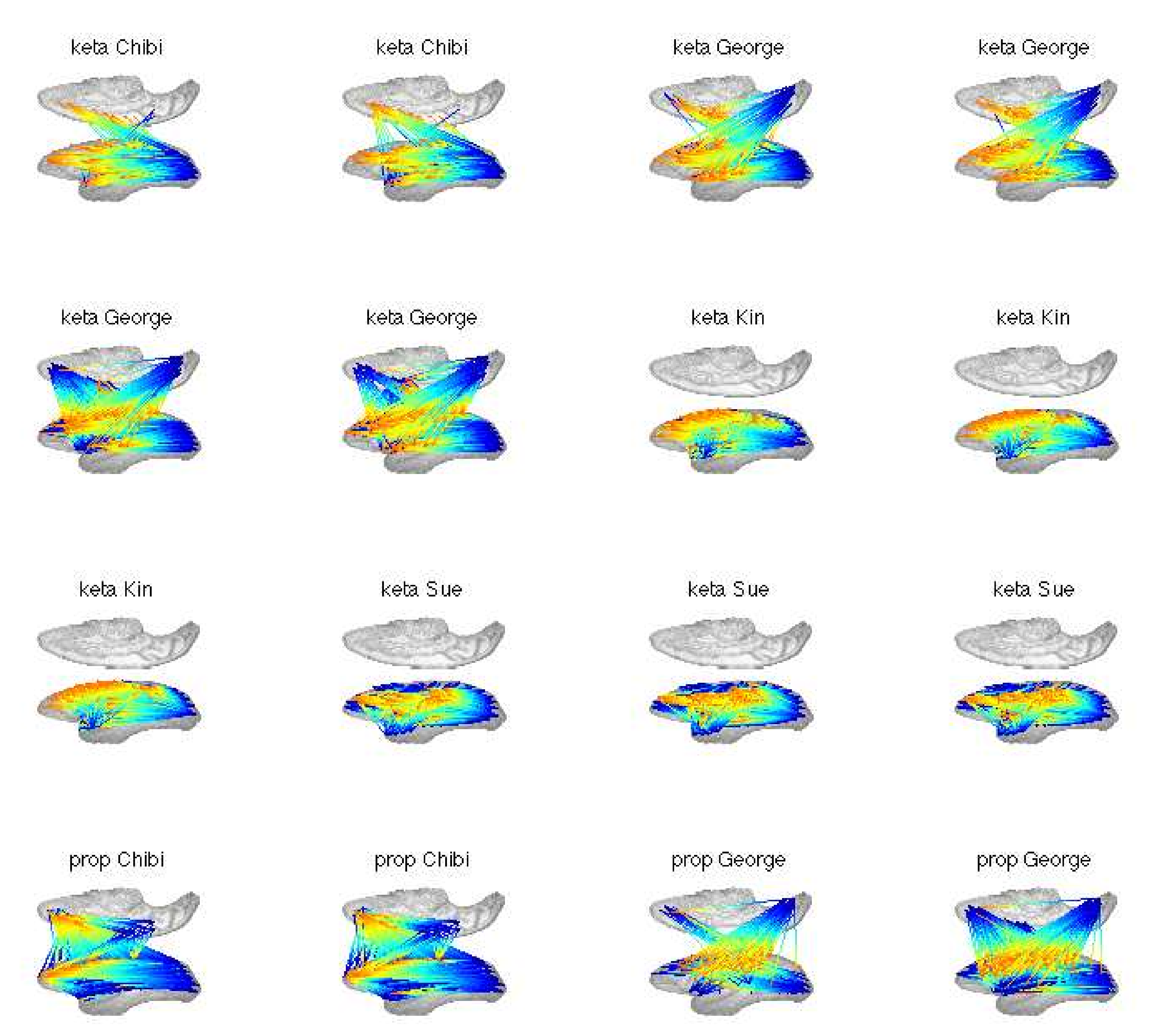
spectral analysis



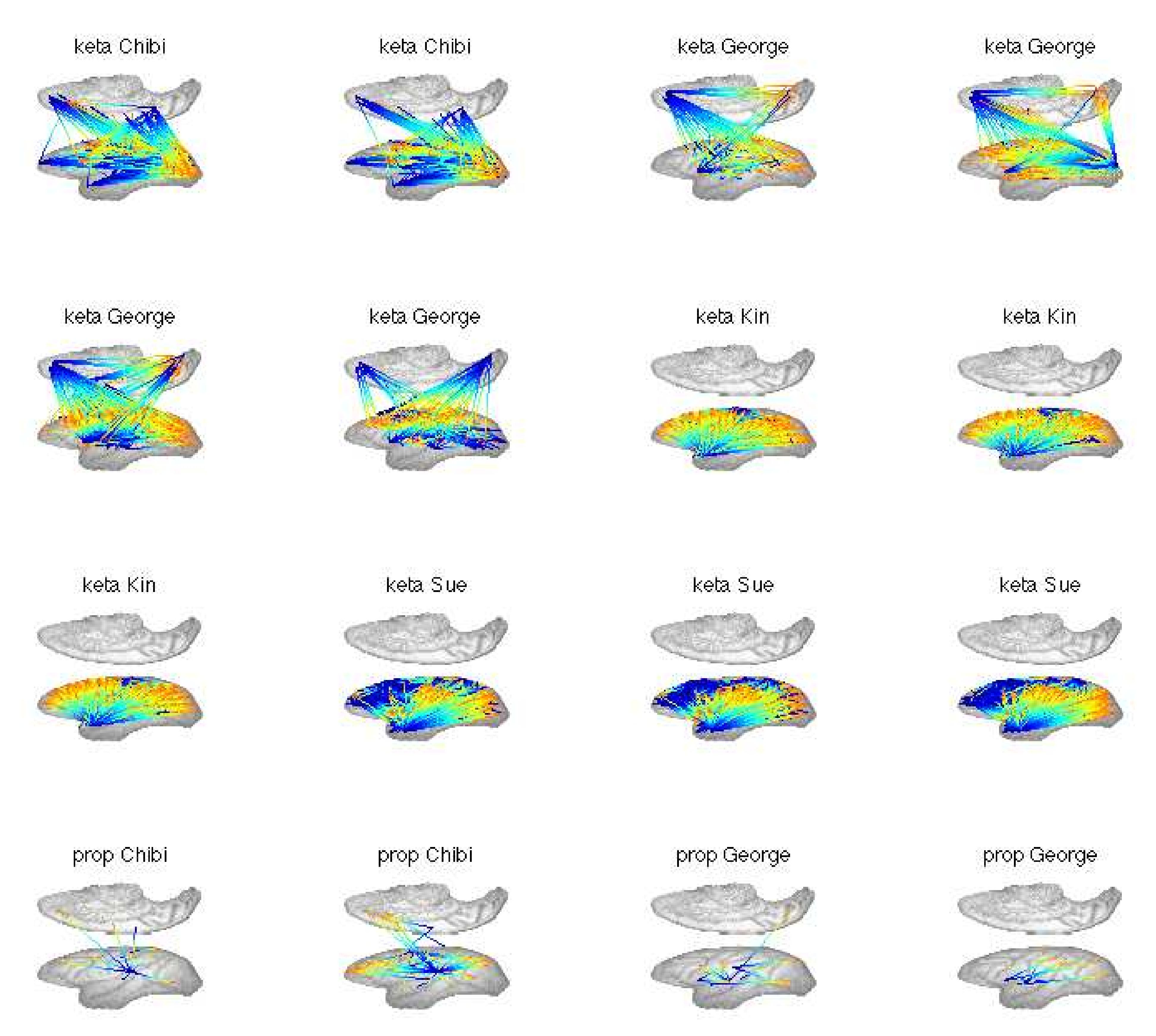
Changes in diagonal weight [before-after]



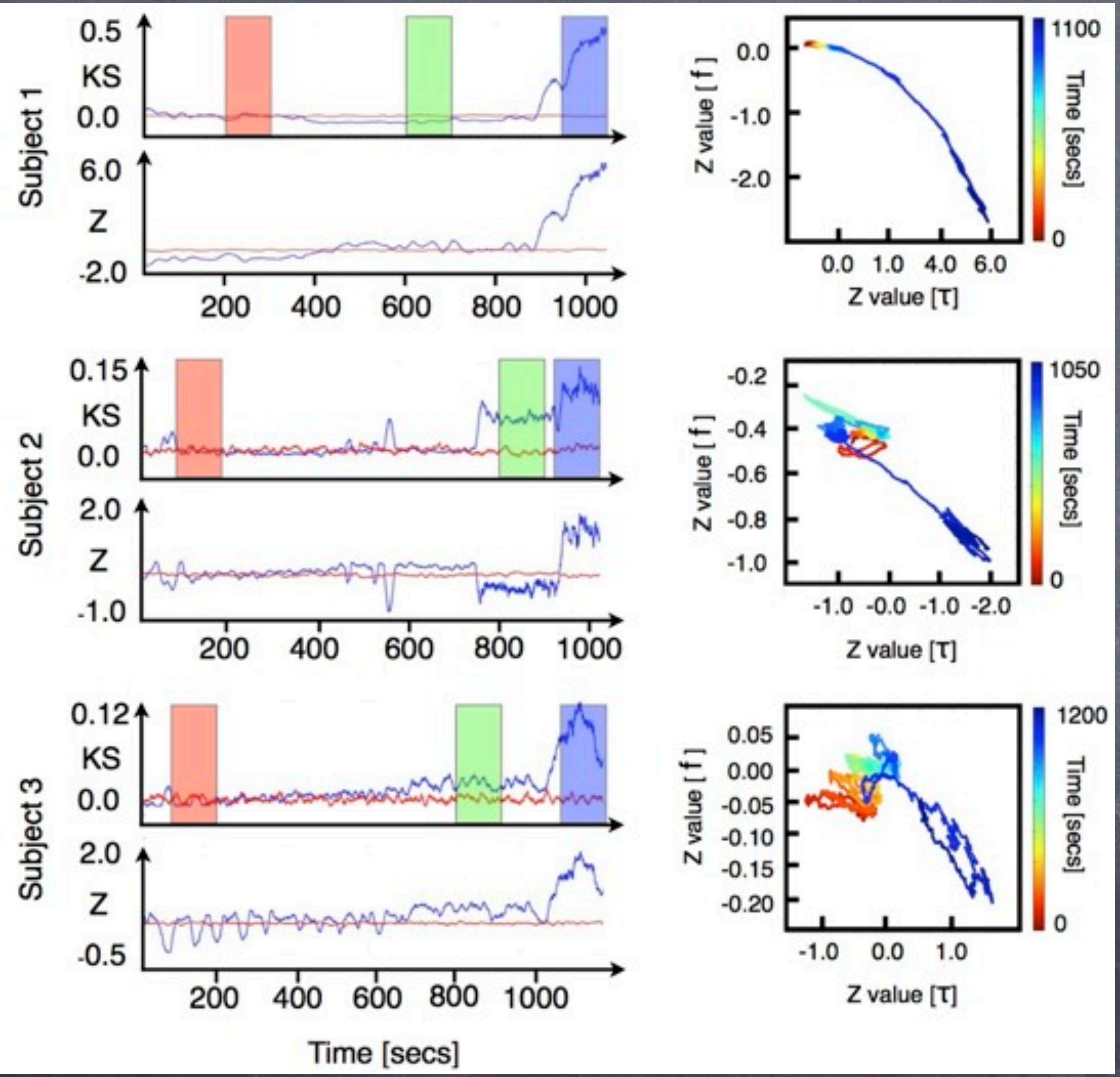
Off-diagonal elements (degree>1) before [source-target]



Off-diagonal elements (degree>1) after [source-target]



Human Subjects



Frontiers Neural Circuits (in press)