Neural Fields:
from vision to consciousness
A prospective mathematical perspective

Olivier Faugeras

MathNeuro project team - INRIA

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Outline

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Mathematical study of the NF equations

Visual orientation

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The goal of mathematical neuroscience is to develop predictive, falsifiable theories (Karl Popper).
Predictive mathematical models for Neuroscience

- The goal of mathematical neuroscience is to develop predictive, falsifiable theories (Karl Popper).
- One of the most famous ones is found in the work of H. Wilson and J. Cowan (1972-1973)
Work of H. Wilson and J. Cowan

Neural masses (Biophysical Journal 1972) Neural fields (Kybernetik 1973)
The neural mass equations

\[ E(t) \text{ (resp. } I(t)) \text{ average membrane potential of excitatory (resp. inhibitory) cells at } t, \]

\[
\tau \frac{dE}{dt} = -E + J_{ee}S_E(E(t)) - J_{ie}S_I(I(t)) + I^E_{ext}(t)
\]

\[
\tau' \frac{dl}{dt} = -l + J_{ei}S_E(E(t)) - J_{ii}S_I(I(t)) + I^I_{ext}(t)
\]

The celebrated Wilson and Cowan equations
This is the voltage-based neural mass model
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History

- Starts with the work of Wilson and Cowan, 1973, and Amari, 1977,
- Followed by many attempts by theoreticians and mathematicians to characterize the solutions, i.e. Bressloff, Coombes, Ermentrout and their followers Atay, Chow, Faugeras, beim Graben, Guo, Gutkin, Hutt, Laing, Pinto, Potthast, Troy, Veltz...
Functional analysis framework

- Functional spaces: Banach, Hilbert, Sobolev ...
- Fixed point theorems
- Spectral Theory
- Bifurcation Theory
Functional analytic setting

\[
\begin{align*}
\dot{V}(X, t) &= -V(X, t) + [J(t) \cdot S(\lambda V)](X) + I_{\text{ext}}(X, t) \\
V(\cdot, 0) &= V_0(\cdot)
\end{align*}
\]

- \(V\) and \(V_0\) are \(p\)-dimensional vector functions defined on a set \(\Omega\), an open bounded/unbounded piece of \(\mathbb{R}^{2,3}\), or a more complicated space. They represent the average membrane potential of the neural field.
- They both belong to some functional space \(\mathcal{F}\).
- \(J(t)\) is a linear operator \(\mathcal{F} \to \mathcal{F}\) (connectivity kernel). It describes the intensity of the projections from masses at \(X'\) to masses at \(X\).

\[
[J(t) \cdot U](X) = \int_{\Omega} J(X, X', t) U(X') \, dX'
\]
Functional analytic setting

\[
\dot{V}(X, t) = -V(X, t) + \left[J(t) \cdot S(\lambda V)\right](X) + I_{ext}(X, t)
\]

- \( S \) is a sigmoidal function (regular and bounded),
- \( \lambda \) determines its stiffness.
- \( X \), in \( \Omega \), represents space, features, \ldots
Choice of $\mathcal{F}$

Three criteria

1. The problem should be well-posed
2. Its biological relevance
3. Allow numerical computations

- Hilbert space: $\mathcal{F} = L^2(\Omega, \mathbb{R}^p)$
- More spatial regularity can be imposed
Choice of $J$

- If $J(\cdot, \cdot, t) \in L^2(\Omega \times \Omega, \mathbb{R}^{p \times p})$ for all $t > 0$ then $J(t)$ defines a continuous linear operator from $\mathcal{F}$ to $\mathcal{F}$
Neural Fields

NF Equations

Cauchy problem

- ODE defined on $\mathcal{F}$

\[
\begin{cases}
\frac{dV}{dt} = -V + R(t, V) \\
V(0) = V_0 \in \mathcal{F}
\end{cases}
\]

where

\[R(t, V) = J(t) \cdot S(\lambda V) + I_{\text{ext}}(t)\]


If

1. $J$ is in $C\left(\mathbb{R}^+; L^2(\Omega \times \Omega, \mathbb{R}^{p \times p})\right)$ and $\|J\|_{\mathcal{F}} \leq J$, $t \geq 0$
2. $I_{\text{ext}} \in C(\mathbb{R}^+; \mathcal{F})$

then for all $V_0 \in \mathcal{F}$ there is a unique solution $V$, defined on $\mathbb{R}^+$ and continuously differentiable of the Cauchy problem

Boundedness, absolute stability

- If $\|I_{\text{ext}}(t)\|_F \leq I_{\text{ext}}$ for all $t \geq 0$ the solution is bounded for all $V_0 \in F$.
- If $\lambda \rho(J_s) < 1$, $J_s = (J + J^*) / 2$, every solution is globally asymptotically stable, in particular unique.

O.F., R. Veltz, F. Grimbert, Neural Computation, 2009
Geometry of persistent states

- Assume $I_{\text{ext}}$ and $J$ do not depend upon time
- Study the equilibrium states: bumps, persistent states, stationary solutions

Solve:

$$V = J \cdot S(\lambda V) + I_{\text{ext}} := F(V, \lambda)$$

Questions:
- How many?
- Manifold of solutions when varying the parameters
Geometry of persistent states

Define $B_\lambda = \{ \mathbf{V} \mid F(\mathbf{V}, \lambda) = 0 \}$, note $\mathbf{V}_\lambda^f$ the solutions.


1. $\| \mathbf{V}_\lambda^f - \mathbf{V}_0^f \|_F \leq B(\lambda)$
Geometry of persistent states

Define $\mathcal{B}_\lambda = \{ \mathbf{V} \mid F(\mathbf{V}, \lambda) = 0 \}$, note $\mathbf{V}_\lambda^f$ the solutions.


2. If $|\mathcal{B}_\lambda|$ is finite then it must be odd (Leray–Schauder degree theory)
Geometry of persistent states

Define $\mathcal{B}_\lambda = \{ \mathbf{V} \mid F(\mathbf{V}, \lambda) = 0 \}$, note $\mathbf{V}^f_\lambda$ the solutions.


3. Let $0 \leq a < b$.
   $\mathcal{B} = \bigcup_{\lambda \in [a,b]} \mathcal{B}_\lambda \times \{ \lambda \}$ contains a connected component which intersects $\mathcal{B}_a \times \{ a \}$ and $\mathcal{B}_b \times \{ b \}$ (Leray–Schauder Theorem)
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Visual Orientation sensitivity or how symmetries make things more complicated

- V1 is organized as a set of orientation sensitive columns and hypercolumns (D. Hubel and T. Wiesel, 1974)
- Periodic preferred orientation (PO) map

Neural field model

\[
\frac{d}{dt} V(x, t) = -V(x, t) + \int_{\Omega} J(x, y) S(\sigma V(y, t)) \, dy
\]

with

\[ J(x, y) = J_{\text{loc}}(\|x-y\|) + \varepsilon J_{\text{LR}}(x, y) \quad \varepsilon \ll 1 \]

weaker strength of LR connections

\( J_{\text{loc}} \) is "Mexican-hat"-like (local excitation, remote inhibition)
Bifurcation analysis of the homogeneous model ($\varepsilon = 0$)

- Solve in a square $\Omega$ with periodic boundary conditions ($\Omega$ is a torus)
- Emergence of Turing patterns
  - Stripes always unstable
  - Spots stable on a very short interval
  - Two subcritical secondary branches recover stability
Symmetries

- Because of the translation invariance, solutions "live" on a torus
- Assume that the spatial period matches that of the PO map T. Kenet et al., Nature, 2003
- Black lines: hypercolumns
- White lines: fundamental domain $\Omega_0$
- Pinwheels are clockwise or counterclockwise
Long range connections

\[ J_{LR}(x, y) = G_{\sigma_\theta}(\theta(x) - \theta(y)) J_0 \left( \chi, R^\circ_{-2\theta(x)}(x - y) \right) \]

\( \theta \) is the PO map. \( \chi \) controls the anisotropy.


Symmetries of the PO map

Action of the rotations on the PO map:

\[ \theta(R^p_{\Phi_0} \mathbf{x}) = \theta(x) + \frac{\epsilon \Phi_0}{2} \mod \frac{\pi}{2} \quad \Phi_0 = \frac{\pi}{2} \]

\[ \epsilon = 1 \text{ if } p \text{ is counterclockwise, } -1 \text{ otherwise} \]
Symmetries

- Form $\Omega$ with $(2N + 1)^2$ copies of $\Omega_0$
- Symmetries are $D_4 \rtimes (\mathbb{Z}/2N\mathbb{Z})^2$
- The PO map reduces it to one of the 17 wallpaper groups Evgraf Fedorov, 1891. D. Schattschneider, Am Math Mon, 1978
- Further constraints from the PO map reduces it to pmm (or cmm)
Remaining symmetries when $\varepsilon \neq 0$

- As shown in R. Veltz, P. Chossat, O.F., 2015 the symmetry group $\Gamma$ of the NF equations is p4m or p4 meaning:

- Write

$$F(V, \lambda) \overset{\text{def}}{=} -\frac{d}{dt}V(x, t) - V(x, t) + [J \cdot S(\lambda V)](x, t)$$

- The neural field equation $F$ is equivariant w.r.t $\Gamma$

$$\gamma \cdot F(V, \lambda) = F(\gamma \cdot V, \lambda)$$

- When the long range connections are turned on the system undergoes spontaneous symmetry breaking
Dynamics with the long-range connections active

- Unperturbed torus $\mathcal{T}_0 \overset{\text{def}}{=} \{ V_0(\cdot + x) \}, \ x \in \Omega$

- A torus, flow-invariant manifold $\mathcal{T}_{LR}$, persists as long as the perturbations are small ($\varepsilon << 1$) enough (P. Chossat and R. Lauterbach, Methods in equivariant bifurcations and dynamical systems, 2000)

- Questions:
  - How many steady-states do actually persist?
  - What are the observed phase portraits?

- Topology of the torus is an important constraint

- Analysis of the perturbed torus is done by identifying $V_0(\cdot + x)$ and $x$
Proposition (R. Veltz, P. Chossat, O.F., 2015)

Let us assume that there is a finite number of equilibria on the perturbed torus which are all non-degenerate when $\varepsilon \neq 0, \chi \geq 0$. There are at least 8 equilibria on the perturbed torus, four of which are saddles and the other four are nodes/foci.

Proof:
Application of the Poincaré–Hopf theorem: $n - 2s = \chi$, $n = f + s$, $\chi = 0$, hence $f = s$. Looking at rotations: $f = 4$
Example of dynamics
Examples of cortical activations
Final Remarks

- Group theory is underutilized in neuroscience
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Taking noise into account

- Neurons are intrinsically noisy:
  - Ion channels and thermal noise
  - Synaptic noise
Noisy neural field equation

\[
dV(t, x) = \left[ -V(t, x) + \int_{\mathbb{R}^n} J(x, y)S(V(t, y)) \, dy \right] dt + \sigma(V(t, x)) \, dW(t, x)
\]

- \( S, \sigma \) are globally Lipschitz, \( S \) is bounded
- \((W(t, x))_{x \in \mathbb{R}^n, t \geq 0}\) is a stochastic process
- What do we mean by "a solution"?
- Must involve an object of the form

\[
\int \sigma(V(t, x)) \, dW(t, x)
\]

This approach has been used "empirically" by Bressloff and Webber (2012), Bressloff and Wilkerson (2012), Kilpatrick and Ermentrout (2013)
Walsh stochastic integral (1986)

- Cleanly defines a white noise $\dot{W}$ on $\mathbb{R}^+ \times \mathbb{R}^n$,
- a *white noise process* $W := (W_t(A))_{t \geq 0, A \in \mathcal{B}(\mathbb{R}^n)}$,
- and a set of functions, $\mathcal{P}_W$, that can be integrated against the white noise process $W$. 
Spatial smoothing

- Informally we may think of the object $\dot{W}(t, x)$ as a random distribution, hence
- any solution of the stochastic neural field equation is distribution valued in the $x$-direction
- For $\varphi \in L^2(\mathbb{R}^n)$ define the (Gaussian) random field
  $$W^\varphi(t, x) := \int_0^t \int_{\mathbb{R}^n} \varphi(x - y) W(ds \, dy)$$
- Easy to verify that $\varphi(x - \cdot) \in \mathcal{P}_W$
Time and space regularity of $W^\varphi$

- The time regularity is the same as that of a Brownian path.
- H"older continuity in space can be enforced by imposing a (very) weak regularity on $\varphi$:

**Condition (C1):**
\[ \exists C_\varphi \text{ such that } \| \varphi - \tau_z(\varphi) \|_{L^2(\mathbb{R}^n)} \leq C_\varphi |z|^\alpha, \forall z \in \mathbb{R}^n \]

for some $\alpha \in (0, 1]$ where $\tau_z(\varphi)(x) = \varphi(x + z)$

- Then for all $t \geq 0 \ x \rightarrow W^\varphi(t, x)$ has an $\eta$-H"older continuous modification for all $\eta \in (0, \alpha)$.
The SNF equation driven by spatially smoothed space-time white noise

\[ \partial_t V(t, x) = -V(t, x) + \int_{\mathbb{R}^n} J(x, y) S(V(t, y)) \, dy + \sigma(V(t, x)) \frac{\partial}{\partial t} W^\varphi(t, x) \]

By a solution we mean a real-valued random field

\[ (V(t, x))_{t \geq 0, x \in \mathbb{R}^n} \]

\[ V(t, x) = e^{-t} V_0(x) + \int_0^t e^{-(t-s)} \int_{\mathbb{R}^n} J(x, y) S(V(s, y)) \, dy \, ds + \int_0^t \int_{\mathbb{R}^n} e^{-(t-s)} \sigma(V(s, x)) \varphi(x - y) \, W(ds \, dy) \]
Sufficient conditions on $J$ for the existence of a solution

Condition (C2):
\[ \forall x \in \mathbb{R}^n \ (y \to J(x, y)) \in L^1(\mathbb{R}^n), \quad \text{and} \quad \sup_{x \in \mathbb{R}^n} \| J(x, \cdot) \|_{L^1(\mathbb{R}^n)} \leq C_J \]


If $x \to V_0(x)$ is Borel measurable almost surely and
\[ \sup_{x \in \mathbb{R}^n} \mathbb{E} \left[ |V_0(x)|^2 \right] < \infty \]

If the NF kernel $J$ satisfies the condition (C2), then there exists an almost surely unique predictable random field $(V(t, x))_{t \geq 0, x \in \mathbb{R}^n}$ which is a solution of the SNF equation in the sense of the above definition and such that
\[ \sup_{t \in [0, T], x \in \mathbb{R}^n} \mathbb{E} \left[ |V(t, x)|^2 \right] < \infty \quad \text{for any } T > 0 \]
Spatio-temporal regularity of the solution

Condition (C3):

\[ \exists K_J \text{ s.t. } \| J(x_1, \cdot) - J(x_2, \cdot) \|_{L^1(\mathbb{R}^n)} \leq K_J |x_1 - x_2|^\alpha, \forall x_1, x_2 \in \mathbb{R}^n \]

\[ \alpha \in (0, 1]. \]


If \( x \to V_0(x) \) is Borel measurable almost surely and

\[ \sup_{x \in \mathbb{R}^n} \mathbb{E} \left[ |V_0(x)|^2 \right] < \infty. \]

Suppose moreover that \( \exists \alpha \in (0, 1] \) s.t.

- \( J \) satisfies (C2) and (C3)
- \( \varphi \) satisfies (C1)
- \( x \to V_0(x) \) is \( \alpha \)-Hölder continuous

Then \( (V(t, x))_{t \geq 0, x \in \mathbb{R}^n} \) has a modification such that

\( (t, x) \to V(t, x) \) is \( (\eta_1, \eta_2) \)-Hölder continuous, for any \( \eta_1 \in (0, 1/2) \) and \( \eta_2 \in (0, \alpha). \)
Final remarks

- Probability Theory
- Stochastic calculus
- Large deviations

are important tools in mathematical neuroscience
Consciousness

- In the late 80s, consciousness was a tolerated hobby for the aging scientist
- "consciousness" is loaded with fuzzy meanings
- Distinguish between at least three meanings, vigilance (wakefulness), attention (focusing of mental resources), conscious access (reportable)
Three ingredients for making consciousness accessible to experiments

- focusing on conscious access
- manipulating conscious perception
- carefully recording introspection

Thanks to the ”new” brain ”imaging” modalities, fMRI, EEG, MEG, Optical Imaging

From S. Dehaene, Consciousness and the brain, 2014.
Unconscious versus conscious

Virtually all the brain’s regions can participate in both conscious and unconscious thought

- Unconscious meaning: unseen color word primes the corresponding color Anthony Marcel, 1970
- Unconscious number comparisons: deciding whether a seen digit is larger or less than 5 depends on whether you have been primed with an invisible congruent/non-congruent digit
- Unconscious Attention: an invisible spot of light makes you more accurate to responding to stimuli presented in the same area
What is the unconscious?

Henri Poincaré Science and Hypothesis, 1902

*The subliminal self is in no way inferior to the conscious self; it is not purely automatic; it is capable of discernment; it has tact, delicacy; . . .*
What is consciousness good for?

- Unconscious statistics versus conscious sampling: the brain performs Bayesian inference
- Lasting thoughts: once a piece of information is conscious, it stays fresh in our mind for as long as we care to attend to it and remember it
- The human Turing machine: consciousness gives us the power of a sophisticated serial computer
- A social sharing device
The four signatures of consciousness

I: Sudden ignition of parietal and prefrontal circuits

▶ Perception of masked words (images)

▶ Making additional sounds conscious

From S. Dehaene, Consciousness and the brain, 2014.
The four signatures of consciousness

II: Late slow wave: the P3 wave

- Masked digits
- Increase of delay between digit and mask
- Sudden ignition of activity if delay $> 50$ ms, digit visible:
- Bifurcation in the dynamics of the neural networks

From S. Dehaene, Consciousness and the brain, 2014.
The four signatures of consciousness

III: Late and sudden burst of high-frequency oscillations (deep electrodes)

- Masked image
- Increase of delay between mask and face image
- Lasting burst of high-frequency activity

From S. Dehaene, Consciousness and the brain, 2014.
The four signatures of consciousness

IV: Synchronization of information exchanges across distant brain regions

- Invisible faces/words
- Synchronization of many distinct brain areas

From S. Dehaene, Consciousness and the brain, 2014.
Theorizing consciousness

- Awareness of a piece of information $\overset{\text{def}}{=} \text{it has entered a specific storage area which makes it available to the rest of the brain}$
Theorizing consciousness

- Awareness of a piece of information $\overset{\text{def}}{=} \text{it has entered a specific storage area which makes it available to the rest of the brain}$

- Hippolite Taine’s ”theater of consciousness” (1870): “The conscious mind is like a narrow stage that lets us hear only a single actor”. But there are lots of invisible actors.

- Raj Reddy et al.’s ”blackboard” (1973) of the HEARSAY system
Theorizing consciousness

- Bernard Baars’ "global workspace" (1989),
- Changeux and Dehaene’s "global neuronal workspace" (1998)

From S. Dehaene, Consciousness and the brain, 2014.
Mathematics and consciousness

- Graph $G := (V, E)$
- Each vertex $v \in V$ represents some brain areas (visual, auditory, somatosensory, etc.)
- Its mathematical description is a set of (S)NF equations
- Each edge $e \in E$ represents the connections between the various brain areas.
- These can be anatomical (connectome) or functional
- They introduce delays (delayed (S)NF equations)
Mathematical challenges

▶ Provide mathematical models of the four signatures of consciousness
▶ e.g. bifurcations, metastable states, etc....
▶ Study rigorously how and when they can appear in the solutions of the (delayed) (S)NF equations
▶ Provide mathematical models of the global neuronal workspace
Other challenges

- Computational, e.g. HBP, TVB (*Jirsa et al*) . . .
- Clinical (*Naccache, Dehaene*)
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▶ The “unreasonable effectiveness of mathematics” in Physics E. Wigner, 1960) is not (yet) verified in neuroscience or in biology in general.

▶ Conversely, there are few of the mathematical problems raised by these disciplines that are studied by “professional” mathematicians.
Announcing a new Journal: Mathematical Neuroscience and Applications

- It bifurcates from the Journal of Mathematical Neuroscience (ends end of this year)
- Focuses on using mathematics as the primary tool for elucidating the fundamental mechanisms responsible for experimentally observed behaviours in neuroscience.
- Publishes work that uses advanced mathematical techniques to illuminate these questions.
- Papers that introduce and help develop those new pieces of mathematical theory which are likely to be relevant to future studies of the nervous system are welcome.
- **Diamond Open Access model**: free Open Access, thanks to the support of episciences.org
Announcing a new Journal: Mathematical Neuroscience and Applications

Mathematical Neuroscience and Applications is an international journal that publishes research articles on the mathematical modeling and analysis of all areas of neuroscience, i.e., the study of the nervous system and its dysfunctions. The focus is on using mathematics as the primary tool for elucidating the fundamental mechanisms responsible for experimentally observed behaviors in neuroscience at all relevant scales, from the molecular world to that of cognition. The aim is to publish work that uses advanced mathematical techniques to illuminate these questions. Papers that introduce and help develop those new pieces of mathematical theory which are likely to be relevant to future studies of the nervous system in general and the human brain in particular are also welcome.

It publishes full length original papers, rapid communications and review articles. Papers that combine theoretical results supported by convincing numerical experiments are especially encouraged but any paper that will encourage exchange of ideas between mathematics and neuroscience applications will be considered.

The journal Mathematical Neurosciences and Applications uses a Diamond Open Access model. We provide free Open Access, thanks to the support of episciences.org. This means there is immediate access to the final, published, version of accepted articles, and no charge to readers. Unlike Gold Open Access we also do not charge authors to publish in the journal; there is no Author Processing Charges (APC). In this way we can address the needs and interests of scientists working on mathematical neuroscience and its application, regardless of funding or location.

The journal is in part a continuation of the Journal of Mathematical Neuroscience that started publishing articles in 2011 and will cease publication in December 2021. These articles can be freely accessed at the following address.

https://mna.episciences.org/
Supplementary slides
Mathematical state of the art: stochastic partial differential equations (SPDEs)

- Solutions are random processes that take their values in a Hilbert space of functions

- Integration theory w.r.t. a class of random measures: Walsh (1986)
- Solutions are random fields in both $t$ and $x$

The two approaches are equivalent
Walsh’s stochastic integral (1986)

- Centered Gaussian random field
  \[ \mathring{\mathcal{W}} := (\mathring{\mathcal{W}}(A))_{A \in \mathcal{B}(\mathbb{R}^+ \times \mathbb{R}^n)}, \]

- with covariance function
  \[ \mathbb{E} \left[ \mathring{\mathcal{W}}(A)\mathring{\mathcal{W}}(B) \right] = |A \cap B| \]

- \( \mathring{\mathcal{W}} \) is a white noise on \( \mathbb{R}^+ \times \mathbb{R}^n \)

- White noise process \( \mathcal{W} := (\mathcal{W}_t(A))_{t \geq 0, A \in \mathcal{B}(\mathbb{R}^n)} \)
  \[ \mathcal{W}_t(A) := \mathring{\mathcal{W}}([0, t] \times A), \quad t \geq 0 \]
Define the norm

\[ \| f \|_{W}^{2} = \mathbb{E} \left[ \int_{0}^{T} \int_{\mathbb{R}^{n}} |f(t, x)|^2 \, dt \, dx \right], \]

for any (random) function that is knowable at time \( t \) given \( (W_s(A))_{s \leq t}, A \in \mathcal{B}(\mathbb{R}^{n}) \).

\( \mathcal{P}_{W} \) is the set of all such functions \( f \) for which \( \| f \|_{W} < \infty \).

It is the set of functions that can be integrated against the white noise process \( W \).
Theorem (Walsh 1986)

For all $f \in \mathcal{P}_W$, $t \in [0, T]$ and $A \in \mathcal{B}(\mathbb{R}^n)$,

$$\int_0^t \int_A f(s, x) \, W(ds \, dx)$$

can be well-defined. Moreover for all $t \in (0, T]$ and $A, B, \in \mathcal{B}(\mathbb{R}^n)$, $\mathbb{E} \left[ \int_0^t \int_A f(s, x) \, W(ds \, dx) \right] = 0$ and

$$\mathbb{E} \left[ \int_0^t \int_A f(s, x) \, W(ds \, dx) \int_0^t \int_B f(s, x) \, W(ds \, dx) \right] =$$

$$\mathbb{E} \left[ \int_0^t \int_{A \cap B} f(s, x) \, W(ds \, dx) \right]$$
Computational challenges

- Already partially addressed
- Bluebrain (Europe), Human Brain Project (Europe), The Virtual Brain Project (Europe), Brain (USA) etc...
Testing in the clinic

- Epileptic seizures, e.g. TVB: V. Jirsa et al.
- Vegetative states, S. Dehaene et al.