Editorial

Computational models of the brain: From structure to function

Introduction

A graduate student entering physics would invariably be equipped with a strong grasp of quantum theory and the theory of relativity—the theories representing the two ends of the cosmological divide—as well as their historical development, principle premises and known limitations. Likewise, junior scientists studying phenomena in the intermediate scales enter their fields well-versed in theoretical frameworks such as the second law of thermodynamics (statistical mechanics), the Navier–Stokes equations (fluid mechanics) or the theory of molecular kinetics (chemistry), each being inexorably linked to advancing fields of mathematics. Science in these fields progresses by testing the extant theories, hence employing empirical research primarily to refine or refute these prevailing paradigms. At the heart of these endeavours is a principle objective to develop fundamental mechanistic models of the processes that govern observable phenomena and, in doing so, to unify apparently diverse phenomena.

The situation in neurosciences is fundamentally different. Overwhelmingly, the emphasis is on learning experimental methods, with a corresponding focus on undertaking and reporting empirical research. Neuroscience papers are judged, not by their reference to a theoretical framework, but primarily on their empirical merits, novelty, and robustness of analysis. This is particularly true of research into large-scale neural phenomena, such as functional neuroimaging data, and hence the subject material of a journal like *NeuroImage*. It is not only that computational models play a subordinate role, but more that traditionally their role has not been articulated *at all*. There do, of course, exist explanatory frameworks in the imaging and cognitive neurosciences, and these clearly play a critical role in the formulation of hypotheses and hence in the progress of science. However, for reasons we argue below, these frameworks may be more accurately thought of as heuristics rather than as computational models traversing spatial and temporal scales of organization. Fundamentally, the latter act to explain observed data without recourse to a deeper unifying theory that not only extends beyond a single neurocognitive domain, but perhaps also beyond neuroscience itself. Likewise, there exist powerful analytic models of the data, like the ubiquitous general linear model. However, these are perhaps better described as models that span the expected data space to facilitate valid statistical inferences, not models of the underlying generative process in the brain.

Given the complexity of the subject matter in neurosciences and the corresponding need to develop advanced experimental techniques—together with the traditional focus in the physical sciences on simple, isolated phenomena—such an empirical focus is very well justified and indeed a necessary historical stage. Is it possible, however, that advances in the mathematics of complex systems and the explosion of readily available computational resources are challenging this status quo? Will computational models of the brain—that address the generation of neuronal activity—play an increasingly central role in all branches of neurosciences, including neuroimaging? The rapidly increasing body of research in this field, and the increasing prominence of neurosciences in schools of mathematics and physics suggest this may be so.

The objective of this Special Issue of NeuroImage, *Computational Models of the Brain* is to highlight research into generative models of neuronal activity that link empirical data and cognitive operations. These endeavours are organised around four invited reviews, which we now overview.

Candidate theoretical frameworks

At their most fundamental level, theoretical frameworks in the physical sciences can all be written as mathematical forms in calculus: Their state variables (e.g. fluid velocity) and parameters (e.g. viscosity) have explicit quantifiable values whose temporal evolution and spatial interdependence obey deterministic laws derived from the physical properties of the system of interest. An illustrative example is the foundation of classical mechanics, namely Newton's second law $F = ma$, or more formally,

$$\frac{d\boldsymbol{v}}{dt} = \frac{F}{m}.$$

which expresses the acceleration of a particle. This simple equation introduces the distinction between a system's state variables (velocity $\boldsymbol{v}$ as a function of time t) fixed parameters (mass m) and external forces F. Given knowledge about parameters and external forces, this equation can be integrated over time to predict the evolution of $\boldsymbol{v}$ from any particular value $\boldsymbol{v}_0$. However, when modelling a system such as the cortex, which evolves in time *and* space, it is necessary to have corresponding spatial and temporal derivatives. The spatial derivative expresses a form of coupling between its microscopic elements (say the neurons), which may equivalently be expressed by other means such as an integral operation. A direct example of Newton's second law expressed in space and time is found in the viscous, incompressible fluid where particles of fluid move relatively freely, albeit constrained by the viscous forces between them. Their motion is governed by the Navier–Stokes equation, written as,

$$\rho\left(\frac{\partial \boldsymbol{v}}{\partial t} + \boldsymbol{v} \cdot \frac{\partial \boldsymbol{v}}{\partial \boldsymbol{x}}\right) = -\frac{\partial p}{\partial \boldsymbol{x}} + \mu\frac{\partial^2 \boldsymbol{v}}{\partial \boldsymbol{x}^2} + f$$

where $\boldsymbol{v} = \boldsymbol{v}(\mathbf{x}, t)$, the velocity of the fluid at position $\boldsymbol{x}$ and time t, is the principle state variable. The quantities, ρ (fluid density), p (pressure) and μ (viscosity) parameterize the flow in a particular setting. F denotes external forces (such as gravity). This equation hence details the expected influence of pressure, density and viscosity

on fluid flow and its spatial gradient and is strictly speaking an expression of the conservation of momentum.

One may ask, what is an equation for incompressible fluid doing in *NeuroImage*? Several features of this equation are of general interest and conceptually very instructive for models of large-scale neuronal systems. The central one is that although a fluid is composed of many millions of constituents parts (atoms/molecules) each reacting to purely local forces, the motion of the fluid is modelled at the macroscopic scale as a single, spatially continuous entity. That is, the individual motion of particles within the fluid are *not* of central importance. Rather their expected collective behaviour is modelled to obey the governing process, namely Newton's second law. The same is true of the very successful approach to modelling gas, diffusion, magnetization and a host of other macroscopic phenomena in physics. A related feature is that solutions to these equations typically exhibit a bewildering array of dynamic forms, including those with very high entropy, those with high order and those in between—such as turbulence—with dynamical structures at many spatial and temporal scales. That is, there is a one-to-many mapping between the algebraic form of the equation and the dynamical flows which ensue.

The principle of modelling the collective, aggregate "motion" of the many million individual components of a system has an obvious relevance in neuroscience, where computational and theoretical considerations argue against brute force attempts to model every individual neuron in even a small patch of neuronal tissue. This approach was pioneered in neuroscience by a variety of independent researchers including Wilson and Cowan (1972), Amari (1975), Freeman (1975), and Nunez (1975). It has received a wave of increasing attention again in the last decade, which has allowed the underlying theoretical and physiological grounding to be detailed with increasing accuracy (Jirsa and Haken 1996, 1997, Robinson et al., 1997, Liley et al., 2002, Coombes 2005, Deco et al., 2008, Daunizeau et al., 2009, Knock et al., 2009; Roberts and Robinson, 2008). The invited review by Coombes (2010) in the present issue provides a succinct overview of this field together with a tantalising presentation of some of the field's recent, striking accomplishments. These include the onset of oscillatory activity through temporal bifurcations and the emergence of large-scale spatial patterns through long-range synchronies—all of enormous current interest in neuroscience, and all couched within the framework of partial different equations for macroscopic neuronal fields. They take the general form,

$$D \cdot V(\boldsymbol{x}, t) = F_a(V(\boldsymbol{x}, t))$$

where D is a differential operator containing spatial and temporal derivatives acting on the local mean neuronal states V expressed in space $\boldsymbol{x}$ and time t, and $\boldsymbol{a}$ is vector of parameters.

The notion of a neural field embodies the concept that the activity of individual neurons is partly subordinate to the large-scale fluctuations in activity in which it is immersed, mediated by the appearance of coherent local synaptic inputs that the local field entails. Such "mass action" models—which have strong empirical founding (e.g. Hasenstaub et al., 2007)—form an important component of almost a third of the original research papers that appear in this special issue. These include the use of these models to understand the appearance of rhythmic behaviour in the cortex through detailed physiological considerations (e.g. Ziegler et al., 2010; Ursino, 2010; Molaee-Ardekani et al., 2010) or bifurcation analysis (Spiegler et al., 2010)—the study of sudden, discontinuous changes in activity following only incremental changes in the system's parameters.

Dynamic and stochastic influences

Whilst these contributions concentrate on the deterministic forces shaping large-scale neuronal activity, there is of late, an increasing appreciation for the role of stochastic influences on neuronal activity (Faisal et al., 2008, Ghosh et al., 2008) and behaviour (McIntosh et al., 2008). These forces can be seamlessly introduced into neural field models through addition of appropriate stochastic terms,

$$D \cdot V(\boldsymbol{x}, t) = F_a(V(\boldsymbol{x}, t)) + \eta(t)$$

although the impact of these terms is by no means trivial. The invited review in the present issue by Braun and Mattia (2010) provides an intriguing account of this theoretical framework in which deterministic and stochastic influences can be undertaken in a unified framework. In particular, they consider a dynamical landscape that enables a system to exhibit multistability—different, co-occurring weakly stable modes of activity—and the role of noise in selecting which of these attractors should be expressed at a given time according to the system's spontaneous activity, or as selected according to biased inputs. Although they focus on activity in perceptual networks, and hence perceptual multistability, we believe that this approach has deep and fundamentally unifying potential across all cortical systems and is the key conceptual development that will facilitate a stronger mathematical foundation for neuroscience.

In a related vein, Lu et al. (2010) consider the role of stochastic processes in neuronal fields, extending the original contribution by Amari, noted above.

From dynamics to computation and function

The invited review by Friston and Dolan (2010) pick up on these developments, whilst also highlighting several other important emerging themes in computational models of the brain. The first concerns the crucial link between neuronal states and cognitive function. It is at this point, that an easy metaphor from the physical sciences threatens to break down because physics is concerned with a physical description of a system's activity, not its function. Friston and Dolan hence consider generative models of brain function that are cast in purely functionalist terms, focussing on optimal control and decision (game) theory. Two crucial aspects are noted—firstly that the models that are employed provide a mechanistic account of neuronal computations and the latent (mental) states that they represent, thus drawing a clear distinction between work in this field and the traditional domain of artificial intelligence. Secondly, they discuss recent trends in designing fMRI experiments to explicitly test these formal constructs, hence providing a link between conceptual and experimental work. Other contributions to the present issue that consider functional aspects of computational modelling include Roggeman et al. (2010), van Overwalle (2010) and Mavritsaki et al. (2010). For example Golfinopoulos et al. (2010) employ computational models to advance the employment of functional neuroimaging data for the purposes of understanding speech acquisition and production, whereas Schwabe et al. (2010) consider models of neuronal firing rates in the visual cortex to explain non-classic extra-receptive field effects of visual contrast. Peters et al. (2010) also address the issue of extra-receptive field visual effects and propose a neuroinformatics platform for a common representational "brain space" for the purpose of optimising the confluence of computational and experimental neuroscience. Rigotti et al. (2010) consider a mapping between the sequence of attractors expressed in the amygdala and orbito-frontal cortex and a routinized pattern of sensory inputs as the basis for contextual representation of spaces.

Using data to make inferences over model space

A frequent criticism of computational neuroscience models is that they are high dimensional and highly parameterized, rendering their direct use in experimental settings problematic. Friston and Dolan also review research which links computational models of the brain and empirical data, focussing here on Dynamic Causal Modelling

(DCM). They show with important further analysis, this challenge can be readily overcome. The first extra requirement is a forward model that links neuronal activity—mean local firing rates etc—to observables—such as local changes in the BOLD signal or extracranial currents. Several other contributions to the Special Issue deal with forward models, including those of Deshpande et al. (2010), Zheng et al. (2010) and Quiros et al. (2010).

In addition, one requires a means of selecting among competing models—penalising those complex models with many free parameters—and a means of performing an estimation of the likely values of those parameters. DCM employs a Bayesian framework that enables estimation and selection of potentially numerous underlying neural field models. Reflecting the growing awareness of the utility of this approach, several contributions to the Special Issue also tackle computational aspects of DCM, including its roproducibility and use in elucidating structure–function disturbances in Parkinson's disease (Rowe et al., 2010) and schizophrenia (Dima et al. 2010). Babajani-Feremi et al. (2010) present a complimentary approach to multi-area neural mass modelling and data inversion.

Structural attributes underlying the brain's computations

The structural attributes of the brain, and the role of these architectures in constraining neuronal activity, is a subject of considerable ongoing research activity (e.g. Honey et al., 2007, 2009, Stephan et al., 2009, Knock et al., 2009, Rubinov et al., 2009) and a special issue on computational models that failed to highlight this area would be amiss of the mark. In their invited review Honey et al. (2010) directly address the central issues in this area by posing the question, "Can structure predict function in the human brain?" They review both empirical findings from the microscopic to macroscopic scale that evidence direct correspondences between structural linkage and dynamical correlation and clear perturbations of these in several candidate clinical disorders. They also note that large-scale computational models can now combine neuroanatomical and physiological connectivity data with unprecedented comprehensiveness and detail. The scientific significance of these models grows in tandem with the accumulation of highly-resolved neural connectivity data, including the recently NIH-sponsored Human Connectome Project (U54) and the rapid emergence of network-based measures of structural and functional cortical connectivity (Rubinov and Sporns, 2010).

The relationship between brain structure, neuronal activity and cognitive activity is a theme that occupies a significant number of other contributions in this Special Issue. Giacomantonio et al. (2010) employ a computational model of the formation of activity-dependent maps of the visual world in the visual cortex to predict the effect of restricted orientation rearing on the topology of the visual cortex. They hence propose a variety of empirically testable perturbations of the normal map layout. Gollo et al. (2010) consider the unique structural configuration of corticothalamic connections and bring insights from time delayed systems in the physical sciences to show how this configuration might generate zero-lag synchrony between distant cortical areas. They further show how changing the balance of intra-thalamic inputs can in turn control the spatial expression of corticothalamic synchrony and hence the computational attributes of the cortex. Ponten et al. (2010) employ a neural mass model to understand the relationship between the topology of structural and functional networks in the healthy brain. Pons et al. (2010) extend this approach to understand changes in this relationship in the ageing brain.

Other contributions employ a computational approach in order to understand the expression of neuronal activity at different spatial scales and their relationship to underlying anatomical connectivity. This includes the differences between multi-unit recordings and local field potentials (Mattia et al., 2010), spike rates and oscillatory activity in LFPs and the EEG (Mazzoni et al., 2010), and multimodal EEG and fMRI data (Lei et al., 2010). Stratton and Wiles (2010) study networks of spiking neurons to show that sustained and complex activity critically depends upon both synaptic plasticity and a mixture of short and long-range axonal connections. Smith et al. (2010) study the relationship between structure and function in the motor system and employ a data inversion approach in order to optimise the anatomical specification of the appropriate model.

Discussion: what is a computational model of the brain?

Shortly following the call-to-papers for this special issue, it became apparent from the range of submissions we received that our understanding of a computational model of the brain was not defined sufficiently clearly. We did receive numerous papers detailing a range of computational techniques for the analysis of functional and anatomical neuroimaging data. We hence adopted a working definition for the Special Issue that required contributions to be of clear relevance for generative models of neuronal activity, either through directly studying such models, understanding their role in the integration of empirical data, or investigating the relationship between anatomical and functional topologies. Given their direct importance to generative models, we did also include biophysical forward models that allow a principled mapping between model space and empirical data. Contributions that were concerned primarily with novel techniques for the analysis of empirical data were referred back to the regular portal of NeuroImage and we do apologize for any confusion in these regards. Of course, there also exists an enormous field of computational research that primarily addresses activity at smaller scales. Due to the scope of *NeuroImage* we naturally restricted the domain of the Special Issue to papers that addressed neural systems and networks, or the relationship between micro-, meso- and macroscopic scales of organization, function and measurement.

Conclusion

The complexity of the neurosciences and the traditional onus in mathematics towards descriptions of simple phenomena provides ample explanation for the traditional bias in neuroscience towards empirical research. Ironically, the expanding volume of empirical data from high throughput technologies means that the feasibility of a purely empirical approach is quickly diminishing. Moreover, the rapid maturation of mathematical techniques that frame nonlinear, stochastic and high-dimensional systems in unifying form mean that empirical and computational neuroscientists can realistically work together to address important questions and frame problems at a deeper and more biologically informed level than by working independently. Given the lack of a broadly accepted theoretical framework, it seems unlikely that in the short term mathematical models will play the same obligatory role in neuroscience as they do in the physical sciences. Their longer-term role will no doubt depend on the impact of computational modelling on informing and interpreting empirical studies. This will in turn require that computational models are able to unify the neurosciences whilst also generating new empirical findings.

The study of spatio-temporal systems in the physical sciences has lead to tractable, quantitative insights into a range of complex phenomena including self-organization, multistability, long-range coherence, and critical transitions. Computational models of the neuronal systems have tremendous potential in bringing this knowledge to bear on the relationship between cortical structure, cognitive function and neuronal activity.

References

Amari, S., 1975. Homogeneous nets of neuron-like elements. Biol. Cybern. 17, 211–220.

Coombes, S., 2005. Waves, bumps, and patterns in neural field theories. Biol. Cybern. 93, 91–108.

Daunizeau, J., Kiebel, S.J., Friston, K.J., 2009. Dynamic causal modelling of distributed electromagnetic responses. Neuroimage 47, 590–601.

Deco, G., Jirsa, V.K., Robinson, P.A., Breakspear, M., Friston, K., 2008. The dynamic brain: from spiking neurons to neural masses and cortical fields. PLoS Comput. Biol. 4, e1000092.

Faisal, A.A., Selen, L.P.J., Wolpert, D.M., 2008. Noise in the nervous system. Nat. Rev., Neurosci. 9, 292–303.

Freeman, W.J., 1975. Mass Action in the Nervous System. Academic Press, New York.

Ghosh, A., Rho, Y., McIntosh, A.R., Kötter, R., Jirsa, V.K., 2008. Noise during rest enables the exploration of the brain's dynamic repertoire. PLoS Comput. Biol. 4, e1000196.

Honey, C., Kotter, R., Breakspear, M., Sporns, O., 2007. Network structure of cerebral cortex shapes functional connectivity on multiple time scales. PNAS 104, 10240–10245.

Honey, C.J., Sporns, O., Cammoun, L., Gigandet, X., Thiran, J.-P., Meuli, R., Hagmann, P., 2009. Predicting human resting-state functional connectivity from structural connectivity. PNAS 106, 2035–2040.

Hasenstaub, A., Sachdev, R.N.S., McCormick, D.A., 2007. State changes rapidly modulate cortical neuronal responsiveness. J. Neurosci. 27, 9607–9622.

Jirsa, V.K., Haken, H., 1996. Field theory of electromagnetic brain activity. Phys. Rev. Lett. 77, 960–963.

Jirsa, V.K., Haken, H., 1997. A derivation of a macroscopic field theory of the brain from the quasi-microscopic neural dynamics. Physica, D 99, 503–526.

Knock, S.A., McIntosh, A.R., Sporns, O., Kötter, O., Hagmann, P., Jirsa, V.K., 2009. The effects of physiologically plausible connectivity structure on local and global dynamics in large scale brain models. J. Neurosci. Meth. 183, 86–89.

Liley, D.T.J., Cadusch, P.J., Dafilis, M.P., 2002. A spatially continuous mean field theory of electrocortical activity. Network 13, 67–113.

McIntosh, A.R., Kovacevic, N., Itier, R.J., 2008. Increased brain signal variability accompanies lower behavioral variability in development. PLoS Comput. Biol. 4, e1000106.

Nunez, P.J., 1975. The brain wave equation: a model for the EEG. Math. Biosci. 21, 279–297.

Roberts, J.A., Robinson, P.A., 2008. Modeling distributed axonal delays in mean-field brain dynamics. Phys. Rev. E 78, 051901.

Robinson, P.A., Rennie, C.J., Wright, J.J., 1997. Propagation and stability of waves of electrical activity in the cerebral cortex. Phys. Rev. E 56, 826–840.

Rubinov, M., Sporns, O., van Leeuwen, C., Breakspear, M., 2009. Symbiotic relationship between brain structure and dynamics. BMC Neurosci. 10, 55.

Stephan, K.E., Tittgemeyer, M., Knösche, T.R., Moran, R.J., Friston, K.J., 2009. Tractography-based priors for dynamic causal models. Neuroimage 47, 1628–1638.

Wilson, H.R., Cowan, J.D., 1972. Excitatory and inhibitory interactions in localized populations of model neurons. Biophys. J. 12, 1–23.

Current issue references

Babajani-Feremi, A., Soltanian-Zadeh, H., 2010. Multi-area neural mass modeling of EEG and MEG signals. NeuroImage 52, 793–811.

Braun, J., Mattia, M., 2010. Attractors and noise: Twin drivers of decisions and multistability. NeuroImage 52, 740–751.

Coombes, S., 2010. Large-scale neural dynamics: Simple and complex. NeuroImage 52, 731–739.

Deshpande, G., Sathian, K., Hu, X., 2010. Effect of hemodynamic variability on Granger causality analysis of fMRI. NeuroImage 52, 884–896.

Dima, D., Dietrich, D.E., Dillo, W., Emrich, H.M., 2010. Impaired top-down processes in schizophrenia: A DCM study of ERPs. NeuroImage 52, 824–832.

Friston, K.J., Dolan, R.J., 2010. Computational and dynamic models in neuroimaging. NeuroImage 52, 752–765.

Giacomantonio, C.E., Ibbotson, M.R., Goodhill, G.J., 2010. The influence of restricted orientation rearing on map structure in primary visual cortex. NeuroImage 52, 875–883.

Golfinopoulos, E., Tourville, J.A., Guenther, F.H., 2010. The integration of large-scale neural network modeling and functional brain imaging in speech motor control. NeuroImage 52, 862–874.

Gollo, L.L., Mirasso, C., Villa, A.E.P., 2010. Dynamic control for synchronization of separated cortical areas through thalamic relay. NeuroImage 52, 947–955.

Honey, C.J., Thivierge, J.-P., Sporns, O., 2010. Can structure predict function in the human brain? NeuroImage 52, 766–776.

Lei, X., Qiu, C., Xu, P., Yao, D., 2010. A parallel framework for simultaneous EEG/fMRI analysis: Methodology and simulation. NeuroImage 52, 1123–1134.

Lu, W., Rossoni, E., Feng, J., 2010. On a Gaussian neuronal field model. NeuroImage 52, 913–933.

Mattia, M., Ferraina, S., Del Giudice, P., 2010. Dissociated multi-unit activity and local field potentials: A theory inspired analysis of a motor decision task. NeuroImage 52, 812–823.

Mavritsaki, E., Allen, H.A., Humphreys, G.W., 2010. Decomposing the neural mechanisms of visual search through model-based analysis of fMRI: Top-down excitation, active ignoring and the use of saliency by the right TPJ. NeuroImage 52, 934–946.

Mazzoni, A., Whittingstall, K., Brunel, N., Logothetis, N.K., Panzeri, S., 2010. Understanding the relationships between spike rate and delta/gamma frequency bands of LFPs and EEGs using a local cortical network model. NeuroImage 52, 956–972.

Molaee-Ardekani, B., Benquet, P., Bartolomei, F., Wendling, F., 2010. Computational modeling of high-frequency oscillations at the onset of neocortical partial seizures: From 'altered structure' to 'dysfunction'. NeuroImage 52, 1109–1122.

Peters, J.C., Jans, B., van de Ven, V., De Weerd, P., Goebel, R., 2010. Dynamic brightness induction in V1: Analyzing simulated and empirically acquired fMRI data in a "common brain space" framework. NeuroImage 52, 973–984.

Pons, A.J., Cantero, J.L., Atienza, M., Garcia-Ojalvo, J., 2010. Relating structural and functional anomalous connectivity in the aging brain via neural mass modeling. NeuroImage 52, 848–861.

Ponten, S.C., Daffertshofer, A., Hillebrand, A., Stam, C.J., 2010. The relationship between structural and functional connectivity: Graph theoretical analysis of an EEG neural mass model. NeuroImage 52, 985–994.

Quirós, A., Diez, R.M., Wilson, S.P., 2010. Bayesian spatiotemporal model of fMRI data using transfer functions. NeuroImage 52, 995–1004.

Rigotti, M., Ben Dayan Rubin, D., Morrison, S.E., Salzman, C.D., Fusi, S., 2010. Attractor concretion as a mechanism for the formation of context representations. NeuroImage 52, 833–847.

Roggeman, C., Fias, W., Verguts, T., 2010. Salience maps in parietal cortex: Imaging and computational modeling. NeuroImage 52, 1005–1014.

Rowe, J.B., Hughes, L.E., Barker, R.A., Owen, A.M., 2010. Dynamic causal modelling of effective connectivity from fMRI: Are results reproducible and sensitive to Parkinson's disease and its treatment? NeuroImage 52, 1015–1026.

Rubinov, M., Sporns, O., 2010. Complex network measures of brain connectivity: Uses and interpretations. NeuroImage 52, 1059–1069.

Schwabe, L., Ichida, J.M., Shushruth, S., Mangapathy, P., Angelucci, A., 2010. Contrast-dependence of surround suppression in Macaque V1: Experimental testing of a recurrent network model. NeuroImage 52, 777–792.

Smith, J.F., Pillai, A., Chen, K., Horwitz, B., 2010. Identification and validation of effective connectivity networks in functional magnetic resonance imaging using switching linear dynamic systems. NeuroImage 52, 1027–1040.

Spiegler, A., Kiebel, S.J., Atay, F.M., Knösche, T.R., 2010. Bifurcation analysis of neural mass models: Impact of extrinsic inputs and dendritic time constants. NeuroImage 52, 1041–1058.

Stratton, P., Wiles, J., 2010. Self-sustained non-periodic activity in networks of spiking neurons: The contribution of local and long-range connections and dynamic synapses. NeuroImage 52, 1070–1079.

Ursino, M., Cona, F., Zavaglia, M., 2010. The generation of rhythms within a cortical region: Analysis of a neural mass model. NeuroImage 52, 1080–1094.

van Overwalle, F., 2010. Infants' teleological and belief inference: A recurrent connectionist approach to their minimal representational and computational requirements. NeuroImage 52, 1095–1108.

Ziegler, D.A., Pritchett, D.L., Hosseini-Varnamkhasti, P., Corkin, S., Hämäläinen, M., Moore, C.I., Jones, S.R., 2010. Transformations in oscillatory activity and evoked responses in primary somatosensory cortex in middle age: A combined computational neural modeling and MEG study. NeuroImage 52, 897–912.

Zheng, Y., Pan, Y., Harris, S., Billings, S., Coca, D., Berwick, J., Jones, M., Kennerley, A., Johnston, D., Martin, C., Devonshire, I.M., Mayhew, J., 2010. A dynamic model of neurovascular coupling: Implications for blood vessel dilation and constriction. NeuroImage 52, 1135–1147.

Michael Breakspear
Queensland Institute of Medical Research and the Royal Brisbane and Woman's Hospital, Brisbane, Queensland 4006, Australia
School of Psychiatry, University of New South Wales and The Black Dog Institute, Sydney, New South Wales 2031, Australia
E-mail address: michael.breakspear@qimr.edu.au.
Corresponding author. School of Psychiatry, University of New South Wales and The Black Dog Institute, Sydney, New South Wales 2031, Australia.

Viktor Jirsa
Theoretical Neuroscience Group, Institut Sciences de Mouvement, Centre National de la Recherche Scientifique (CNRS), Universite de la Mediterranee, Marseilles, France
Center for Complex Systems and Brain Sciences, Department of Physics, Florida Atlantic University, Boca, Florida, USA

Gustavo Deco
Institucio' Catalana de Recerca i Estudis Avançats (ICREA), Universitat Pompeu Fabra, Department of Technology, Computational Neuroscience, Barcelona, Spain