COMBINING INTER-AREAL, MESOSCOPIC, AND NEURODYNAMIC MODELS OF CORTICAL FUNCTION.

Response to Commentary on "The growth of cognition: Free energy minimization and the embryogenesis of cortical computation."

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Introduction

We thank all our commentators for their generous and wide-ranging contributions, testing our proposal [1] that maximization of zero-lag synchrony during embryogenesis generates mesoscopic cortical anatomy, and enables post-natal computation and learning. Two commentaries in particular led us to extend our account from mesoscopic to inter-areal scale, and we begin with these.

Heiko J Luhmann, and Anne Sinning

Members of this group provided crucial evidence [2] for the relationship between synchrony and apoptosis on which our theory depends, and have recently further demonstrated that physiologically realistic burst synchrony preferentially facilitates survival [3]. Luhmann and Sinning [4] say we have omitted the large-scale synaptic pruning that refines both local connections and cortico-cortical connections later in embryogenesis and post-natal life, and point out that cortex needs to be considered in depth as well as width. These concerns we address below – and initially remark that we consider synaptic pruning was implicitly included, arising as synaptic resource competition selects synapses that maximize synchrony.

They mention other unattended aspects: that early connections occur via gap junctions as well as synapses; the contrast of protomap and protocortex hypotheses; that short axon cells are generally inhibitory, although they are excitatory during embryogenesis. We consider the role of gap junctions later, in relation to Casper Hesp's commentary. Regarding protocortex versus protomap hypotheses, we now add a little further to that discussion, as will be seen. The change of GABA transmission from excitatory to inhibitory during neuro-development would affect the excitatory/inhibitory balance, rather than the qualitative class of neuro-dynamics, and our idealized short-axon "beta" excitatory cells should be taken at all stages to be mixed with short-axon inhibitory partners.

Pablo Varona and Mikhail I Rabinovich

These authors [5] stress the importance of heteroclinic sequential dynamics for information co-ordination and chunking, with balance of robustness and sensitivity, and temporal compression or expansion according to context. In their extensively developed analysis [6] they note that asymmetrical inhibition is essential for the cyclic recurrences leading to winnerless competition underlying heteroclinic dynamics, and that the same principles that apply in simple circuits apply also to larger scale networks and dynamics.

Asymmetrical inhibition was not specified as a necessity in the dynamic equations provided in our paper, but at mesoscopic level a degree of natural asymmetry is to be expected, and heteroclinic sequences would be selected as processes leading to maximum overall synchrony. Asymmetry at larger scales is accounted for in the following section.

### Extension from mesoscopic to inter-areal scales.

Our model generalizes from mesoscopic to inter-areal scale by taking into account the description by Shipp [7] of inter-areal connectivity in hierarchical order, and its relationship to predictive coding and self-evidencing [8]

Co-incidentally, current work reported by Imam and Finlay [9] shares similar basic assumptions to our mesoscopic model, and anticipates our generalization to the inter-areal scale. They assume that during embryonic growth, competition for neural growth factors occurs in association with a decline in pulse correlation with distance of cell body separation. In an ascending hierarchy of visual cortical areas, appropriately adjusted to realistic topography, they show these factors account for the mirror reversals, with increasing blurring, seen in the sequence of homotypic maps. Their assumptions, and their results, follow directly by generalization of our model to the larger scale. Mirror reversals of topography in sequential cortical areas arise since maximization of synchrony requires minimization of separation - thus maximum strength of connection - between homologous points within the two topographic images. The map blurring results from the terminal arborization of axons, increasing with sequential steps of relay from lower to higher in the cortical hierarchy – as shown in the Figure. The antenatal and ongoing postnatal production and pruning of synapses to which Luhmann and Sinning refer can therefore be seen as arising in part from synchrony maximization in the self-organization of long-range cortical connections.

Shipp and colleagues have shown that cortico-cortical connections are not reciprocal by cortical layer. Instead - shown in the lower part of the Figure in a form borrowed from Shipp's paper - there is hierarchical asymmetry of inputs, particularly to layer 6 of cortex, impling an asymmetrical impact biasing signal flow, and thus providing an analog of the inhibitory asymmetry needed to mediate inter-areal heteroclinic dynamics.

As Shipp has indicated, cortico-cortical connections exchange signals between areas with strong signal mixing in the middle cortical layers. Since these layers embody our putative Mobius-like "local maps", the signal mixing offers a means of prolific and various synchronous interactions among local synaptic representations with those in separate cortical areas – just as is required for the operation of Perlovsky's Dynamic Logic, and in accord with the free energy minimization we propose.

A close resemblance is also apparent to the Structural Model of Tucker and Luu [10]. That model, which is further considered in relation to the commentary of Aggarwal and Wickens, includes the same interareal interaction described by Shipp et al., and draws additionally upon embryonic pre-arrangement of cortical areas, enabling sequential interaction of cortical areas in limbic and neocortex. Their model is therefore protocortex-like. Given this embryogenic pre-arrangement, the organization of the layer six asymmetric connections would promote cyclic organization and interaction of areas, as in heteroclinic winnerless competition. However, such a protocortex-like organization must emerge within the protomap genetic predisposition of cell types, and subcortical inputs, so it is not clear that the layer 6 connections could be formed by selection for maximum synchrony alone.
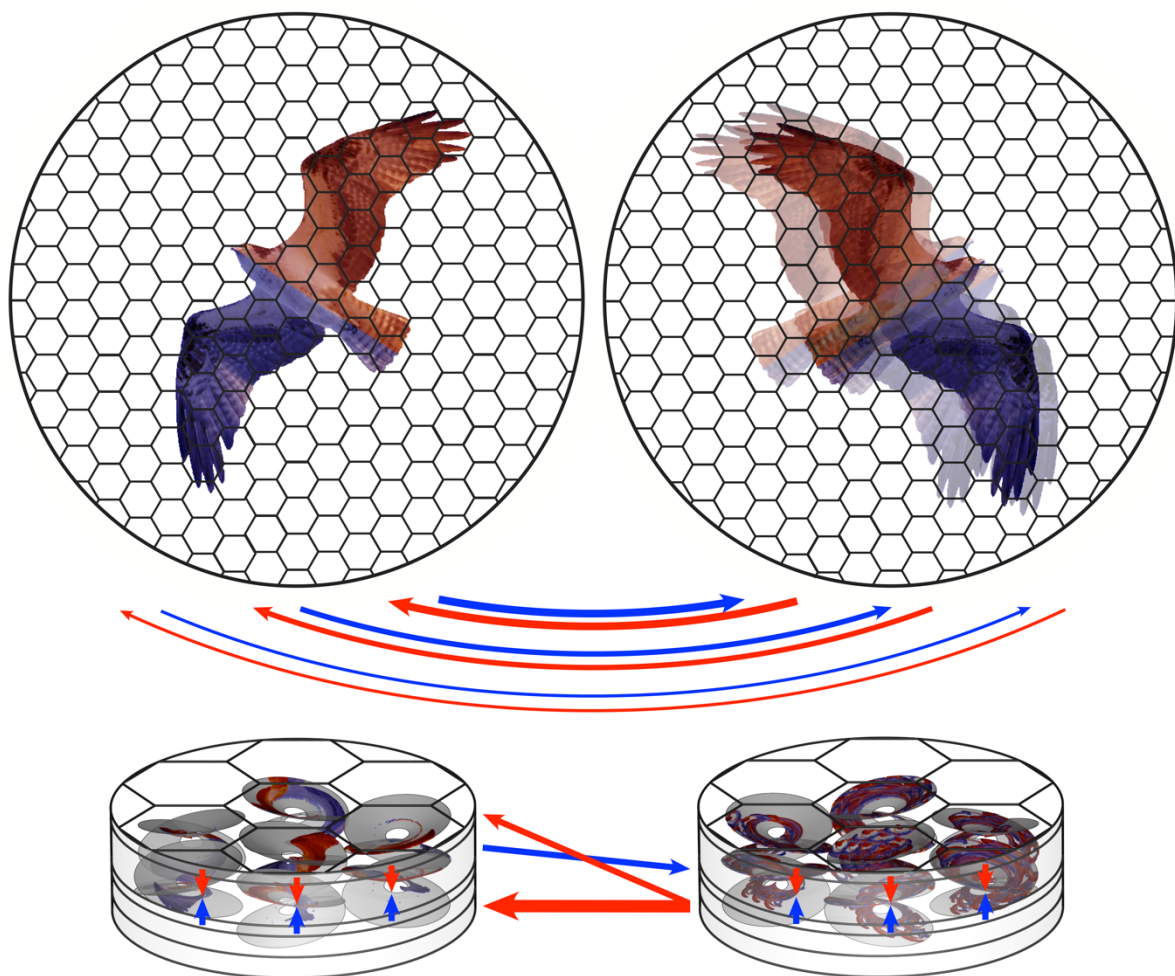
A schematic representation relating interareal and mesoscopic self-organization.
Top: two cortical areas in heirarchical order from lower (left) to higher (right). The scale of macrocolumns is shown as a hexagonal grid background. On the left neural representations of a domain of inputs is shown as an eagle, which is projected to

multiple, overlapping, mirror symmetric topological maps at the higher cortical level, shown on the right.
Middle: the exchange of cortico-cortical connections in characteristic U-formation, leading the large-scale mirror representations.
Bottom: small areas of adjacent macrocolumns in the two cortical areas. Mesoscopic representations of the eagle stimulus in the local maps are shown as in Figure 3 of our Review. Inputs and outputs via cortico-cortical connections in hierarchical sequence, and signal flows in cortical depth, as described by Shipp et al, are indicated by colored arrows.

Erik De Schutter

De Schutter is unhappy about the completeness of our model, both dynamically and in a wider organic sense [11]. He points out that cortical pulse coding is not all accounted for as synchrony, and is multiplexed, with principal components describing relevant activity on low dimensional manifolds, citing elegant work of this type. Further, cortical computation depends on cortical/subcortical interactions, and finally, the evolution of the brain cannot be encompassed as merely free energy minimization, since biological evolution results in ever-increasing complexity.

These criticisms do not lead to contradictions with our proposal. Heteroclinic networks must exhibit exactly the pulse statistical properties mentioned, since their dynamics involve approach to synchronous states, and also less synchronous trajectories among them. There is no question but that cortical interactions with subcortex are critical to cortical operations, nor doubt that the number and variety of systems must increase with time, and total entropy increase – but the point is well made that our account leaves out the multitude of steps in cell differentiation during embryogenesis, to concentrate on the sculpturing of more definitive connectivity. In segregating different aspects of development, appropriate choices need to be made in defining Markov blankets - as is further discussed in relation to the commentary of Hipolito et al.

Felix Schoeller and Vsevolod Tverdislov

Schoeller and Tverdislov [12] argue almost in the opposite sense to De Schutter, that the brain's development, structure and function, must obey basic mathematical topological rules, despite immense biological complexity. They stress symmetry and symmetry breaking, with emphasis on chirality. This raises a point previously overlooked by us. Our model supposes that local cortical representations are each continuously ordered, overlapping groups of synaptic couplings, each group related to neighboring representations as (distorted) translations, magnifications, rotations and chiral reversals of their neighbors. Of these transformations in the plane, reversal of chirality would impose the most marked distinguishability of closely situated representations. Therefore, flips between activity in local representations of opposite chirality, as they converge towards co-synchrony between cortical areas, may act as a switching mechanism.

Ping Ao, and Hans Liljenstrom

These two commentators raise further important issues regarding the classes of neuronal dynamics underlying cortical synchrony.

Ping Ao [13] raises two concerns, from a strong philosophical background. First is our apparent restriction on application of the Free Energy Principle, as if bidirectional symmetry at synchronous equilibrium was essential for the minimization of free energy, whereas chaotic and limit-cycle attractor dynamics, which include asymmetric signal exchanges, also require free energy is minimised. Ao also asks, is it is not the case that the two ranges of axonal connection used in our account may lead to two wholly different dynamics?

Hans Liljenstrom [14] gently reminds us that it is timely to recognise debts to Freeman and Hopfield, Wilson and Cowan, Haken, and others. Liljenstrom's own work [15] on the laminar-structured olfactory system is a milestone, combining realistic Freeman dynamics with Hopfield storage, in attractors that are not simply point attractors, but limit and chaotic attractors.

There is, happily, no fundamental contradiction of dynamic principles involved in our work and that of Freeman, and of Liljenstrom. Most components in the dynamic equations are closely similar, and owe an ancestral debt to Freeman in particular. An important emphasis in our work, which we think has not been previously considered, is on bidirectional *polysynaptic* flux as an initial organizing principle, from which bidirectional monosynaptic couplings "condense" to provide much of the anatomical scaffold, while reducing the system dimensionality. In this process most synaptic connections remain asymmetric, not only permitting, but requiring the occurrence of complicated non-synchronous activities, as groups of neurons enter into transient active associations, during each of which a minimum of free energy is approached. Zero lag synchrony reflects bidirectional symmetry of synaptic flow – either monosynaptic or polysynaptic - and all degrees of symmetry and asymmetry of connection may be associated with the minima of free energy. Thus, assemblies of rapidly firing neurons can exhibit both synchrony and asynchrony – yet, on the global scale, the high degree of polysynaptic flux approximates overall symmetry of pre-synaptic flux, and thus wide-spread synchrony is seen in the EEG [16].

No work has yet been done on neuronal wave dynamics within the complex Mobius-like and patch connectivity of cortex, other than to deduce the connectivity required for maximum magnitude of synchrony, as described in our paper. As pointed out above, these may involve symmetry breaking events much more complicated than the simple waves seen in simulations of electrocortical dynamics in isotropic systems.

Ines Hipoloto, Maxwell Ramstead, Axel Constant and Karl J Friston

Our Review paper owes a heavy debt to discussions between the first author and Karl Friston. Hipoloto et al. [17] underline our fusion of the free energy principle and dynamic logic by emphasizing the importance of the Markov blanket – ie, conditional independence between external and internal states given blanket states. There is reciprocal definition of a system minimizing free energy, and a system enclosed in a Markov blanket. The way the boundaries of the Markov blanket are defined, so that the internal system is one seeking a minimum free energy equilibrium, is central to controversies around Friston's formulation of the free energy principle. Issues of this sort arise in the subsequent commentaries of Henderson, and Guevara, and, in a different way, in the commentary of Aggarwal and Wickens.

James A Henderson, and Ramon Guevara

These two authors raise further questions related to our definition of free energy as the difference between total pre-synaptic flux and synchronous pre-synaptic flux. James Henderson [18] wonders if our definition properly aligns with Markov blankets in the brain. Our definition of free energy fits the mathematical requirement of analogy to thermodynamic free energy, since (a) synchronous equilibria are stable states of the system (b) the system dimension falls as bidirectional monosynaptic connections increase in number, and (c) progressive learning, by restricting the range of possible responses to a given stimulus that *might* occur, meets the requirement of minimizing surprise. So, mathematical analogy to a thermodynamic system is established, and existence of a Markov blanket boundary follows from definition.

Ramon Guevara [19] raises further considerations concerning definition, measurement, and interpretation of entropy in relation to synchrony and equilibrium. These are indeed slippery terms, requiring caution as to exactly which variables are being considered. Especial care is necessary when contrasting pulse and wave activity, versus synaptic connectivity. Pulse synchrony (we argue) is a near-equilibrium multi-stable state, and high levels of synchrony indicate low entropy of temporal pulse rates. So, as bidirectional monosynaptic connections increase with learning, temporal pulse entropy of individual cells continues to decrease. But from the point of view of spatial organization of synaptic connectivity, the ante-natal state is one of high joint entropy of synaptic connections, forming only simple patterns, and with modification by later learning, as the patterns increase in complexity, the conditional entropy of synaptic patterns increases, although their total entropy remains bounded.

Aggarwal and Wickens

Aggarwal and Wickens [20] raise an issue that is not yet resolved in the minds of many – the contrast between free-energy minimization generative models, and model-free reward-based learning – learning that they regard as non-Bayesian, since it is related to the reward value of the stimulus, rather than the sensory content *per se*. In so doing they place stress of the importance of subcortical mechanisms, as does de Schutter. Wickens has shown that the reward circuit architecture forming re-entrant loops via the subcortical routes to and from cortex, exert, via dopaminergic effects upon STDP, modulation of learning by rewarded experience.

How is this apparent violation of the global "self-evidencing" of the free energy principle to be resolved, and is violation of a Bayesian framework necessary? Do the reward pathways constitute a hole in the cortical Markov blanket, since they exert an effect directly upon the internal systems of the cortex?

There is no paradox if the subcortical/dopaminergic circuits are regarded as equivalent to a sensory class, whose action contributes to the blanket states. With this modification, the maximization of reward becomes a part of the weighting of Bayesian priors and posteriors. The brain then acts to achieve optimization in that part of the experiential world for which the organism is better suited, rather than to the world in the large. The reward pathways thus restrict the domain within which Bayesian principles apply, without otherwise changing the nature of learning. This impact of the reward pathways, independent of the details of the associated primary sensory experiences, yet still enabling selective responses to different stimuli, was illustrated in an early experiment by the first author, in which it was shown that depth electrode stimulation of intracranial self-stimulation (ICSS) sites could reinforce opposite responses in each hemisphere of split-brain cats [21]. Therefore it appears reward induces a cortex-wide diffuse effect, stabilising learning of those events taking place within a brief temporal window. This implies that natural learning involves attaining a consistency between activity in lower, evolutionary-old systems, and the individual, neocortically mediated, experiences of the subject. Conflicts necessarily abound – as is well known in psychiatric practice.

In contrast to this broad-acting interaction of cortex with subcortical systems, a more refined interaction unifying affective information with other activity in all neocortical areas and the limbic system, appears in the paper by Tucker and Luu previously cited.

Casper Hesp, and Naoum P Issa

Each of these authors ask, directly or indirectly, what might be the minimum necessary set of assumptions needed to account for cortical development.

Casper Hesp [22] begins by reminding us of earlier and more fundamental work on the free energy principle and morphogenesis that provides an even wider embracing framework than we have drawn

upon. He then suggests a further principle that may act in early neurogenesis – the interaction of ephaptic and synaptic interactions, creating circular fields of more intensive cellular interaction, and thus patch connectivity, by a mechanism different to that we have proposed. We welcome this suggestion, which might be investigated further in simulations utilizing both the dual conduction velocities, and variable axonal lengths, to determine which factor (or both) is most appropriate. Hopefully he may address this in his upcoming work.

Naoum Issa,[23] who's work on the associations of orientation preference with temporal and spatial preferences helped trigger our own work, reviews literature on antenatal development of cortical columns, and asks whether or not morphogens are essential. We remain non-committal on the latter. Our initial proposal required genetic specification only of available cell types and axonal lengths, but the selection of inter-areal connections to layer 6 may be one indication of many other organizing factors. As Issa says, an adequate minimal model is essential for both the further development of artificial intelligence, and for our understanding of recovery following disruption of circuits in trauma/epilepsy.

Paul E Rapp; KL Rossi, BRR Boaretto, and RC Budzinski; Michael Breakspear

Paul Rapp [24] stresses the importance of developmental models for problems of clinical significance. Computational analysis of information flow in EEG [25] offers a means of linking clinical data to cortical models, and by analyzing inter-areal signal flows, might enable test of the operation of winnerless competition heteroclinic dynamics in the models of Shipp et al., and Tucker and Luu.

Rossi et al [26] offer further evidence that synchrony and neuronal survival are linked, since synchrony promotes the release of neurotropic growth factors. They further suggest that moving simulations from coarse-grained neural field equations, to simulations with spiking neurons might further understanding of this linkage. Such an approach may have significance for neuronal transplantation.

Michael Breakspear reminds us that the transition from intrauterine to extrauterine life is one of momentous change of organization and metabolic shock to the subject [27]. This sudden discontinuity is marked by changes in pulse activity and information exchange. We may add that there are also distinct changes from early foetal EEG, which is highly disorganized, to near-mature patterns in later foetal life [28,29]. Thus, investigation of changes in information exchange and interareal mutual information, using methods such as those of Rapp, may help understanding of the developmental transitions, from early random patterns and small world organization, to later maximal synchrony, and then to adult learning.

Moshe Bar

Moshe Bar [30] returns us to psychological phenomenology, by asking how a fixed architecture can mediate many different, polar opposite, mental states. He advances a view shared with Perlovsky [31] and others, for which he has contributed experimental verification. This view is the strongest assertion that predictive coding and dynamic logic, mediating the balance between feed-forward and feedback processes among cortical areas, is the very essence of all our mental world. We hope he will find this point of view now a little more advanced.

Conclusion

Our mesoscopic account has survived critique so far, we believe. It provides a link between the overarching concepts of the free energy principle, predictive coding, and the inter-areal organization of limbic and neocortex on the one hand, and synaptic connectivity and neural near-equilibrium heteroclinic dynamics on the other – concepts all also interlinked in other ways. Thus, a coherent overall account of brain function appears to be emerging. Deficits include a full account of the fusion of subcortical inputs mediating activation and reward with intracortical processes, and simulated demonstration of the applicability of dynamic logic in the expanded anatomical context.

We have neglected all the unfolding in sequence of genetically controlled species of neural cell types, but have explained their subsequent competitive selection into functional array. Since the selection principle can be extended from mesoscopic to whole-cortex scale, its wider application to neurodevelopment outside cortex may be possible – anywhere there is apoptosis and synchrony.

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