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BOOK REVIEW

Ingredients for a brain

THE NOISY BRAIN
By *Edmund Rolls* and *Gustavo Deco* 2010.
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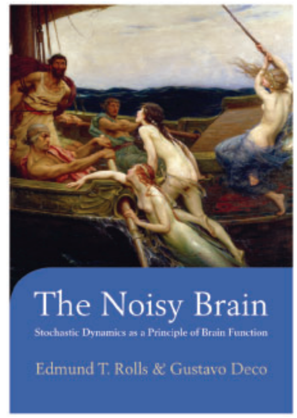

In thinking about components of the brain that are important for mental function, there are several obvious things to consider. The brain's wiring diagram, embodied by the structural connectivity, is one feature. Graph theory metrics applied to anatomical networks have shown patterns that are consistent with a small-world network with dense local connections and sparser distal connections (Bullmore and Sporns, 2009). This imparts an advantage in information processing capacity compared to wiring diagrams that are either random or more regular (e.g. lattice). Studies of the brain's wiring diagram also suggest the presence of regions that act as hubs, connecting local territories of specialized processing (Hagmann *et al*., 2008; Honey and Sporns, 2008). On top of the anatomical architecture, to capture function one would need to consider which nodes are active at a particular time and how the sequence of activations proceeds for a given operation (McIntosh, 2004). Associated with activation is co-activation (or functional connectivity), wherein anatomical connectivity enables activity changes in one node to affect, and be affected by, others (McIntosh and Korostil, 2008).

Another feature that seems less obvious in this consideration is the 'noise' that exists in these networks (Faisal *et al*., 2008). At one level, noise reflects the imprecision of cellular operations within an ensemble of neurons (e.g. ion channel opening and closing, membrane fluctuations). At a second level, involving connections between ensembles, variations in transmission timing affect synchrony between ensembles. Understanding the interplay of these features of noise with anatomical and functional connectivity may help to explain how the brain works. The importance of noise, or more generally spontaneous activity, in the brain was discussed as far back as the 1940s (Pinneo, 1966). While some researchers felt that spontaneous activity was an obstacle to be overcome for brain function (e.g. Triesman, Hebb), others considered that the internal dynamics of the brain serve an important role for consolidating memory traces and maintaining functional networks (e.g. Lashley).

More recently, the wide use of functional neuroimaging to study the human brain has spawned an entire industry around studies of resting-state activity (Bartlett *et al*., 1987; Biswal *et al*., 1995; Lowe *et al*., 1998; Greicius *et al*., 2003). What the brain does when it is doing nothing may seem a perverse question, but there are substantial consistencies in the observed patterns (Beckmann *et al*., 2005; Damoiseaux *et al*., 2006) that appear to have predictive power in the context of brain dysfunction (Wang *et al*., 2007; Greicius, 2008). While this focus on 'resting-state' to the exclusion of controlled experiments is not without its problems (Morcom and Fletcher, 2007), there are enough compelling data to suggest that we will learn some fundamental principles of brain organization if we better understand these resting-state dynamics (Fox *et al*., 2005; Fox and Raichle, 2007; Greicius *et al*., 2009).

The 'what' and 'why' of resting-state dynamics are not clear: what drives these intrinsic patterns and why would the brain evolve to have such a noisy background? Potential answers emerge from the book *The Noisy Brain* and recent computational work (Ghosh *et al*., 2008; Deco *et al*., 2009*a*, 2011). The predominant premise in *The Noisy Brain* is that the random activity in the brain acts to bias the probabilistic behaviour of the system, moving it towards or away from a particular configuration. Much of the exposition is phrased in the language of non-linear dynamical systems, but the translation to empirical examples helps to make the idea accessible for the general neuroscience community.

Combining the ingredients through computational neuroscience

The goal of computational neuroscience is to integrate empirical information into a formal mathematical model (Dayan and

Abbott, 2001). Simulations are created to mimic the important dynamics of a neural element (e.g. channel, neuron, ensemble, etc.) and then results of the simulation can be put forward as an explanation for the observed empirical phenomenon. For instance, directional selectivity of cellular receptive fields has been characterized both from the perspective of competition in local excitation and inhibition to an increase in local excitation balanced by a global level of inhibition (Somers *et al*., 1995). The computational models can serve as a vital accelerator to understanding since they provide a test ground on which to combine empirical observations into a single study to 'see if it makes a difference'. The exercise of building the model is a salient assessment of the knowledge in the field, where the failings in a model are usually an indication of empirical knowledge that is lacking. A powerful example of where computational neuroscience makes an impact is when a critical behaviour emerges from a combination of ingredients that, on their own, are not easily accessible to empirical investigation. Some recent studies of large-scale network models that combine accurate anatomical connectivity with non-linear dynamics have propelled us towards a better understanding of the relationship between structural and functional connectivity (Honey *et al*., 2007).

Rolls and Deco (2010) have epitomized this aspiration for computational neuroscience, producing a substantial body of work that merges critical features of brain structure and function into neural models that provide testable explanations of behavioural phenomena. *The Noisy Brain* builds on work of the two authors that covers a broad range of cognitive functions from short-term memory to decision making. While many of these models were not developed explicitly to demonstrate the effects of noise, they are recast in the framework of stochastic dynamics to underscore the importance of noise in enabling realistic behaviours for the simulations. A condensed version of the book can be found in a review paper from these authors (Deco *et al*., 2009*b*).

The opening provides a great deal of background information on neurophysiology and neural modelling that, while helpful, is not critical to the remainder of the book. The essential background information is captured in the second chapter on Stochastic Neurodynamics. This chapter explains the integrate-and-fire modelling approach and the effect of stochastic events on model dynamics. A critical point is that the inherent noise from the firing of neural populations acts first to allow a state of rapid responsiveness to inputs. To use an analogy from Deco *et al.* (2009*a*), noise in the brain acts in a manner similar to a tennis player waiting for the service of his opponent. The player is not static, but continues to move with small jumps left and right to be able to react more effectively to the serve. The book develops the general notion that the dynamics inherent in the brain set up a landscape of potential network configurations (attractors) and the capacity to move from one configuration to another is enabled by the intrinsic noise.

In linear systems, noise obscures the ability to extract meaningful signals. In non-linear dynamical systems, specifically the brain, noise contributes directly to the spatiotemporal pattern of network configurations. In general terms, the brain usually functions at the 'edge of criticality' (Kelso, 1995; Haken, 1996) between any number of possible states or functional network configurations (Ghosh *et al*., 2008). In the absence of noise, there is little capacity for the system to explore these states, and potential for the system to settle into a single state. With noise, the system approaches one state and then, with noise fluctuations, moves towards another. Such an exploration can occur spontaneously, in the absence of external stimulation.

This basic mechanism is then expanded in the book to explain cognitive operations such as memory recall and decision making. Changes in the intrinsic dynamics are also offered as an explanation for dysfunction, including cognitive changes in ageing, schizophrenia and obsessive-compulsive disorder. In each case, the dynamics change the capacity of the brain to adopt one functional configuration versus another. For example, in schizophrenia, noise is thought to be too high (Winterer *et al*., 1999, 2000), and thus the networks will not stay in a particular configuration long enough for its normal evolution. In obsessive–compulsive disorder, the regional changes in noise make it more difficult to alter the configuration (i.e. move away from an attractor), thus the behaviour from that network configuration is repeated.

One item is missing from this book. Aside from a brief paragraph on perception, there is virtually no mention of the phenomenon of stochastic resonance, which is probably the most salient example of the functional impact of noise (McNamara and Wiesenfeld, 1989; Wiesenfeld and Moss, 1995; Kosko and Mitaim, 2003). Simplistically, stochastic resonance is the observation that for non-linear systems, an optimal level of noise in the presence of weak stimuli actually improves stimulus detection. Stochastic resonance in the brain has been observed from the operations of single neurons to intercellular communication and perceptual and cognitive phenomena. It remains an open question as to whether the noise effects observed in stochastic resonance and the probabilistic bias in the Rolls and Deco (2010) models represent different manifestations of the same stochastic process.

How does this model taste?

It is often the case that models such as the one described by Rolls and Deco (2010), while serving as persuasive explanations of brain function, may also be criticized for mere relabelling of phenomena in a different language, but not really advancing our understanding. A cynical reader could question whether describing the core of schizophrenia as shallower basins of attractors on a manifold caused by lower firing rates, which results in working memory deficits and poor attention, really brings a better understanding about the disorder. Such a view, however, misses the singular power of computational neuroscience to merge data from several sources into a single entity in an attempt not only to explain, but also to predict. In the computational framework, the researcher has the capacity to test the effects of changing structural connections, conduction, pharmacology etc. and combinations thereof. By pulling various ingredients together, the computational modeller essentially develops a recipe for the brain. The elements of the recipe are then ripe for testing in the empirical arena.

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