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Stochastic dynamics as a principle of brain function

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The relatively random spiking times of individual neurons are a source of noise in the brain. We show that in a finite-sized cortical attractor network, this can be an advantage, for it leads to probabilistic behavior that is advantageous in decision-making, by preventing deadlock, and is important in signal detectability. We show how computations can be performed through stochastic dynamical effects, including the role of noise in enabling probabilistic jumping across barriers in the energy landscape describing the flow of the dynamics in attractor networks. The results obtained in neurophysiological studies of decision-making and signal detectability are modelled by the stochastical neurodynamics of integrate-and-fire networks of neurons with probabilistic neuronal spiking. We describe how these stochastic neurodynamical effects can be analyzed, and their importance in many aspects of brain function, including decision-making, memory recall, short-term memory, and attention.

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1. Introduction

Decisions may be difficult without noise. In the choice dilemma described in the medieval Duns Scotus paradox, a donkey who could not decide between two equidistant food rewards might suffer the consequences of the indecision. The problem raised is that with a deterministic system, there is nothing to break the symmetry, and the system can become deadlocked. In this situation, the addition of noise can produce probabilistic choice, which is advantageous, as will be described in this paper.

In this article, we consider how the noise contributed by the probabilistic spiking times of neurons plays an important and advantageous role in brain function. We go beyond the deterministic noiseless description of the dynamics of cortical networks, and show how the properties of the system are influenced by the

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Abbreviations: AMPA, a-amino-3-hydroxy-5-methyl-4-isoxazole propionic acid; GABA, gamma-amino-butyric acid; NMDA, N-methyl-D-aspartate.

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spiking noise. We show that the spiking noise is a significant contribution to the outcome that is reached, in that this noise is a factor in a network with a finite (i.e., limited) number of neurons. The spiking noise can be described as introducing statistical fluctuations into the finite-size system. It is important that the outcome that is reached, and not just its time course, is influenced on each trial by these statistical fluctuations.

We show that this stochastic dynamical approach can be used to help understand not only whether signals are perceptually detected on individual trials, but also how probabilistic decision-making appears to occur in the brain. In doing this, we use integrate-and-fire models with spiking neurons to model the actual neuronal data that are recorded during neurophysiological experiments. The integrate-and-fire simulations capture the stochastic nature of the computations. However, we show that to understand analytically (mathematically) the stable points of the network, for example what decisions may be reached, it is helpful to incorporate a mean field approach that is consistent with the integrate-and-fire model. The mean field approach enables one to determine for example the synaptic strengths of the interconnected neurons that will lead to stable states of the network, each of which might correspond to a different decision, or no decision at all. The spiking simulations then examine which fixed points (or decisions) are reached on individual trials, and how the probabilistic spiking of the neurons influences this.

We then go on to argue that similar stochastic settling of attractor networks in the brain may contribute to many aspects of brain function and behavior. They include the probabilistic settling of memory networks into recall states that may vary from trial to trial; the transition from one thought to another thought that in not being deterministic plays a major role in allowing thoughts to be creative; the probabilistic changing of perception as when the faces of a Necker cube reverse; and the taking of probabilistic decisions that on an individual trial may be non-optimal, but that may be adaptive by providing evidence about whether the probability of opportunities is changing in the world. We also argue that the stochastic nature of brain processing may contribute to instabilities in short-term memory and attentional systems that become especially apparent when the basins of attraction of attractor networks become shallow, and indeed relate such instabilities to some of the symptoms of schizophrenia. An important part of the approach is that it enables changes at the neuronal and synaptic level, such as reduced currents in NMDA receptor activated synaptic currents, to be related to the properties of a whole network, and thus of behavior, by a formal model. The approach thus enables predictions to be made about, for example, the effects of pharmacological agents on the global behavior of the whole system, and indeed thus on behavior.

2. Stochastic dynamics in the brain

The challenge to unravel the primary mechanisms underlying brain functions requires explicit description of the computation performed by the neuronal and synaptic substrate (Rolls, 2008b; Rolls and Deco, 2002). Computational neuroscience aims to understand that computation by the construction and simulation of microscopic models based on local networks with large numbers of neurons and synapses that lead to the desired global behavior of the whole system. However, simulation, without elucidation of a computational mechanism, will tell us little more than we already know from observing highly complex biological systems in action. A simulation only of phenomena of a complex system, such as the brain, is in general not useful, because there are usually no explicit underlying first principles. The main aim of computational neuroscience is, rather, to provide a theoretical framework for formulating explicitly our theoretical assumptions in the light of observed experimental constraints (at both physiological and psychological levels of analysis) in order to infer the nature of the underlying neural system from the model. In this sense, we are faced with an inverse problem: we have to extract the free parameters of a system that cannot be measured directly (e.g., the connectivity between the thousands of neurons making up any plausible sub-network) but which can be inferred by (i) studying the dynamical capabilities of the system and (ii) looking for regions within a parameter space that generate an emergent behavior consistent with the experimentally measured observations.

So, what might be an appropriate level of analysis to enable an explicit bridge to be built from physiology to behavior? There has been interest for some time in the application of complex systems theory to understanding brain function and behavior (Blackerby, 1993; Heinrichs, 2005; Lewis, 2005; Peled, 2004; Riley and Turvey, 2001). A suitable level of description of the complex system is captured for many purposes by the spiking and synaptic dynamics of one-compartment, point-like models of neurons, such as *Integrate-and-Fire-Models* (Amit and Brunel, 1997; Brunel and Wang, 2001; Rolls, 2008b; Tuckwell, 1988), which form networks of neurons. Fig. 1 shows an integrate-and-fire neuron, and typical models implement both the dynamics of the neuron and the dynamics of the different types of synapse on a neuron using differential equations and using parameters that have been measured biophysically (Brunel and Wang, 2001; Deco and Rolls, 2003, 2006; Rolls, 2008b; Rolls and Deco, 2002; Wang, 1999). These dynamics allow the use of realistic biophysical constants (like conductances, delays, etc.) in a thorough study of the actual time scales and firing rates involved in the evolution of the neural activity underlying cognitive processes for comparison with experimental data. Very importantly, networks of these neurons display the noisy property very commonly found of neurons recorded in the brain, that the spike times of each neuron have approximately Poisson statistics, that is, the spike times from a neuron firing at a given rate are approximately random and independent (Jackson, 2004; Tuckwell, 1988). The stochastic (random) firing times of neurons introduces noise into neuronal networks, and it is the consequences of this randomness expressed in a finite (limited) sized network of such neurons with which we are concerned in this review. We show that the noise in such systems not only helps us to understand many aspects of decision-making as implemented in the brain, but also is in fact beneficial to the operation of decision-making processes.

Networks of integrate-and-fire neurons are able to capture the probabilistic spiking of neurons found in many parts of the brain, and thus to provide models not only with realistic probabilistic dynamics, but in which the spiking behavior of the neurons can be compared to those found in the brain. However, in-depth analytical (formal mathematical) study of these detailed integrate-and-fire models is not feasible. Apart from the time required to explore the parameters that would make a given model approximate a network in the brain, the results of these simulations are probabilistic (i.e., there will be a certain probability that the neurons in a population are in a given state). This makes it particularly difficult to explore the parameter space (including the appropriate values for the synaptic weights in a systematic fashion, because any parameters must describe a probability distribution and not a single point in the parameter space. Therefore, a reduction of the integrate-and-fire models is necessary in order to establish a systematic relation between structure (parameters), dynamics, and functional behavior (i.e., to solve the "inverse" problem). Fortunately, statistical physics methods have been introduced to mathematically analyze a reduced version of the system. *Mean-field* techniques (Amit and Brunel, 1997; Brunel and Wang, 2001; Renart et al., 2003; Ricciardi and Sacerdote, 1979) allow us to express the steady state of a population of neurons by a