Progress in Neurobiology xxx (2009) xxx–xxx

Contents lists available at ScienceDirect

Progress in Neurobiology

journal homepage: www.elsevier.com/locate/pneurobio

Stochastic dynamics as a principle of brain function

Gustavo Deco [a], Edmund T. Rolls [b,*], Ranulfo Romo [c]

[a] Institució Catalana de Recerca i Estudis Avançats (ICREA), Universitat Pompeu Fabra, Dept. of Technology, Computational Neuroscience, Passeig de Circumval.lació, 8, 08003 Barcelona, Spain
[b] Oxford Centre for Computational Neuroscience, Oxford, UK
[c] Instituto de Fisiología Celular-Neurociencias, Universidad Nacional Autónoma de México, 04510 México, D.F., Mexico

ARTICLE INFO

Article history:
Received 19 August 2008
Received in revised form 31 December 2008
Accepted 20 January 2009
Available online xxx

Keywords:
Decision-making
Stochastic neurodynamics
Noise
Signal detection
Probabilistic behavior

ABSTRACT

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.
© 2009 Elsevier Ltd. All rights reserved.

Contents

1. Introduction . . . 000
2. Stochastic dynamics in the brain . . . 000
3. Computational models of probabilistic decision-making . . . 000
4. Perceptual detection and stochastic dynamics . . . 000
   4.1. Psychophysics and neurophysiology of perceptual detection . . . 000
   4.2. Computational models of probabilistic signal detection . . . 000
5. Decision-making and stochastic dynamics . . . 000
   5.1. Probabilistic decision-making . . . 000
   5.2. The vibrotactile discrimination task . . . 000
   5.3. The computational bases of decision-making . . . 000
   5.4. Properties of this stochastic attractor model of decision-making . . . 000
6. Applications of this stochastic dynamical approach to brain function and decision-making . . . 000
7. Conclusions . . . 000
   References . . . 000

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

* Corresponding author.
E-mail address: Edmund.Rolls@oxcns.org (E.T. Rolls).
URL: http://www.oxcns.org
Abbreviations: AMPA, a-amino-3-hydroxy-5-methyl-4-isoxazole propionic acid; GABA, gamma-amino-butyric acid; NMDA, N-methyl-D-aspartate.

0301-0082/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.pneurobio.2009.01.006

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 inter-connected 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

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

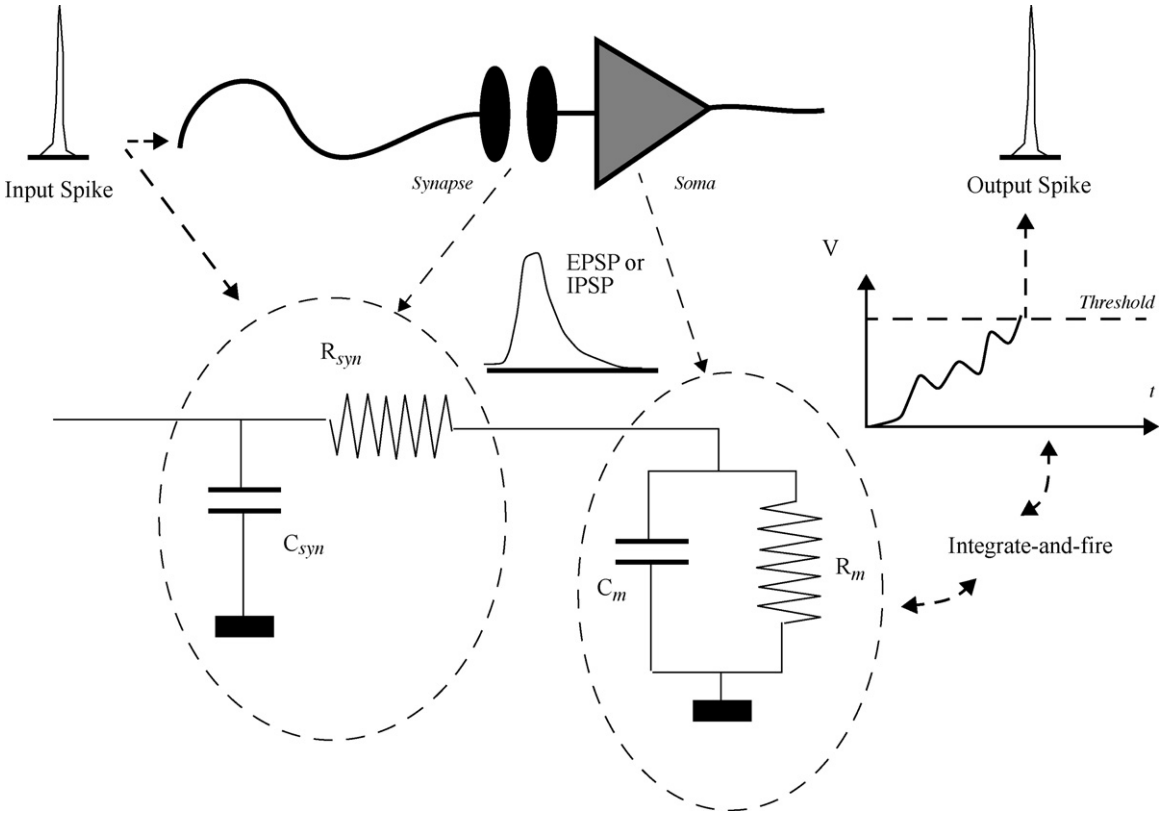

Fig. 1. Integrate-and-fire neuron. The basic circuit of an integrate-and-fire model consists of the neuron's membrane capacitance C_m in parallel with the membrane's resistance R_m (the reciprocal of the membrane conductance g_m) driven by a synaptic current with a conductance and time constant determined by the synaptic resistance R_{syn} (the reciprocal of the synaptic conductance g_j) and capacitance C_{syn} shown in the Figure. These effects produce excitatory or inhibitory post-synaptic potentials, EPSPs or IPSPs. These potentials are integrated by the cell, and if a threshold V_{thr} is reached a δ-pulse (spike) is fired and transmitted to other neurons, and the membrane potential is reset. (After Deco and Rolls, 2003).

reduced rate-equation describing the asymptotic steady states of the associated average population rate. Application of these mean-field techniques allows the values of, for example, the synaptic weights to be determined that will result in stable states. Once these parameters for the weights have been determined, they can be used in the integrate-and-fire simulations which then enable the probabilistic dynamics of the network to be investigated, and in particular the transient behavior of the network as it moves into a stable state. Usually, the simulations of the spiking dynamics of the network are integrated numerically, and the non-stationary evolution of spiking activity is averaged over many trials initialized with different random seeds. The mean-field approach has been successfully applied to model single neuronal responses, fMRI activation patterns, psychophysical measurements, and the effects of pharmacological agents and of local cortical lesions (Corchs and Deco, 2002; Deco and Rolls, 2005a; Deco et al., 2004; Rolls and Deco, 2002; Szabo et al., 2004). These and related models (Deco and Rolls, 2003; Loh et al., 2007a) utilize an elegant approach formalized by Brunel and Wang (2001) in which the same parameters are used in the mean-field and integrate-and-fire simulations, so that the parameter space can be analyzed with the mean-field approach, and then the probabilistic dynamics of the network are explored in the integrate-and-fire version with the same parameters. Further details of the mean-field approach, and how it can be extended to include some of the effects of noise as it could be generated by spiking neurons, are provided elsewhere (Deco and Marti, 2007a,b).

In Section 3, we review different approaches to modelling decision-making which apply also to signal detection, including a neuronally realistic approach based on networks of integrate-and-fire neurons. We then show how the integrate-and-fire approach has been used to help understand the brain mechanisms involved in signal detection in the brain (Section 4), and in decision-making (Section 5).

3. Computational models of probabilistic decision-making

Many excellent theoretical studies of behavioral data have enhanced our understanding of the computational mechanisms underlying decision-making. Diffusion models of performance and choice reaction time have been applied to a wide range of behavioral results (Smith and Ratcliff, 2004). Diffusion models postulate that the information driving the decision process is accumulated continuously over time until a decision boundary is reached. In more detail, a stimulus is represented in a diffusion equation by its influence on the mean drift rate of a random variable. This random variable accumulates the effects of the inputs over time until one of the boundaries is reached. Escaping through a specific boundary corresponds to making a specific decision. A key feature of diffusion models is randomness of the path taken under the influence of the noisy stimuli. These fluctuations provide an account of the generation of erroneous responses, and of the reaction times of both the correct and error responses. The well known speed–accuracy tradeoffs are usually reproduced by adjusting the boundaries. Moving the boundaries further apart results in better performance and slower response times, whereas moving the boundaries closer together produces more errors and faster responses. The astonishing capability of diffusion models to fit behavioral data seems to indicate that some decision-making processes in the nervous system are really computed by a similar mechanism that accumulates evidence. Similar phenomenological models have been proposed in which

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

the drift of the decision variable is proportional to the value of the variable itself (e.g., Usher and McClelland (2001), also called the ballistic model by Brown and Heathcote (2005)). The diffusion thus occurs not on a flat landscape but on a curved one, and the effective dynamics is equivalent to an Ornstein–Uhlenbeck process with fixed boundaries. Psychometric measures of performance as well as reaction times for 2-alternative forced choice paradigms can be analytically studied within such heuristic model frameworks, see for example Bogacz et al. (2006).

In spite of the success of these phenomenological models for accounting for behavioral performance, a crucial problem that they present is the lack of a link between the model variables and parameters and the biological substrate. Recently, a series of biologically plausible models, motivated and constrained by neurophysiological data, have been formulated to establish an explicit link between behavior and neuronal activity, see for example Wang (2002), Brody et al. (2003), Machens et al. (2005), Wong and Wang (2006), and Deco and Rolls (2006). The way in

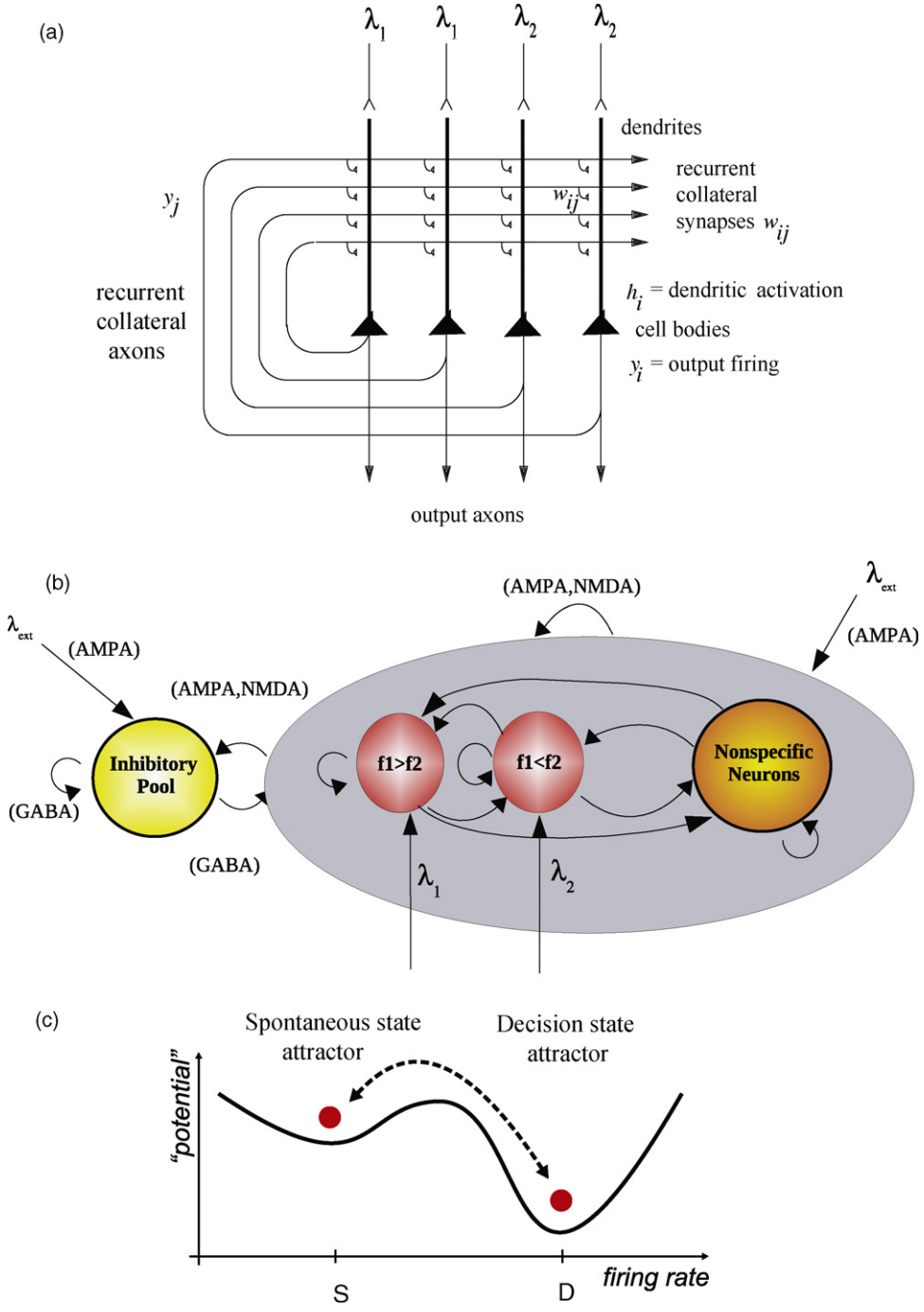

Fig. 2. (a) Attractor or autoassociation network architecture for decision-making. The evidence for decision 1 is applied via the λ_1 inputs, and for decision 2 via the λ_2 inputs. The synaptic weights w_{ij} have been associatively modified during training in the presence of λ_1 and at a different time of λ_2. When λ_1 and λ_2 are applied, each attractor competes through the inhibitory interneurons (not shown), until one wins the competition, and the network falls into one of the high firing rate attractors that represents the decision. The noise in the network caused by the random spiking of the neurons means that on some trials, for given inputs, the neurons in the decision 1 attractor are more likely to win, and on other trials the neurons in the decision 2 attractor are more likely to win. This makes the decision-making probabilistic, for, as shown in (c), the noise influences when the system will jump out of the spontaneous firing stable (low energy) state S, and whether it jumps into the high firing state for decision 1 or decision 2 (D). (b) The architecture of the integrate-and-fire network used to model vibrotactile decision-making (see text).

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

which these neuronal network models operate is as follows. The particular model we describe is that of Wang (2002), and then we describe different but related models.

An attractor network of the type illustrated in Fig. 2a is set up to have two possible high firing rate attractor states, one for each of the two decisions. The evidence for each decision (1 vs 2) biases each of the two attractors via the external inputs λ_1 and λ_2. The attractors are supported by strengthened synaptic connections in the recurrent collateral synapses between the (e.g., cortical pyramidal) neurons activated when λ_1 is applied, or when λ_2 is applied. (This is an associative or Hebbian process set up during a learning stage by a process like long-term potentiation.) Inhibitory interneurons (not shown in Fig. 2a) receive inputs from the pyramidal neurons and make negative feedback connections onto the pyramidal cells to control their activity. When inputs λ_1 and λ_2 are applied, there is positive feedback via the recurrent collateral connections, and competition implemented through the inhibitory interneurons so that there can be only one winner. The network starts in a low spontaneous state of firing. When λ_1 and λ_2 are applied, there is competition between the two attractors, each of which is pushed towards a high firing rate state, and eventually, depending on the relative strength of the two inputs, and the noise in the network caused by the random firing times of the neurons, one of the attractors will win the competition, and it will reach a high firing rate state, with the firing of the neurons in the other attractor inhibited to a low firing rate. The process is illustrated in Fig. 3. The result is a binary decision, with one group of neurons due to the positive feedback firing at a high firing rate, and the neurons corresponding to the other decision firing with very low rates. Because it is a non-linear positive feedback system, the final firing rates are in what is effectively a binary decision state, of high firing rate or low firing rate, and do not reflect the exact relative values of the two inputs λ_1 and λ_2 once the decision is reached. The noise in the network due to the random spiking of the neurons is important to the operation of the network, because it enables the network to jump out of a stable spontaneous rate of firing to a high firing rate, and to do so probabilistically, depending on whether on a particular trial there is relatively more random firing in the neurons of one attractor than the other attractor. This can be understood in terms of energy landscapes, where each attractor (the spontaneous state, and the two high firing rate attractors) is a low energy basin, and the spiking noise helps the system to jump over an energy barrier into another energy minimum, as illustrated in Fig. 2c. If λ_1 and λ_2 are equal, then the decision that is taken is random and probabilistic, with the noise in each attractor determining which decision is taken on a particular trial. If one of the inputs is larger than the other, then the decision is biased towards it, but is still probabilistic, as illustrated in Fig. 6a. Because this is an attractor network, it has short-term memory properties implemented by the recurrent collaterals, which tend to promote a state once it is started, and these help it to accumulate evidence over time, an important part of a decision-making mechanism, and also to maintain the firing once it has reached the decision state, enabling a suitable action to be implemented even if this takes some time.

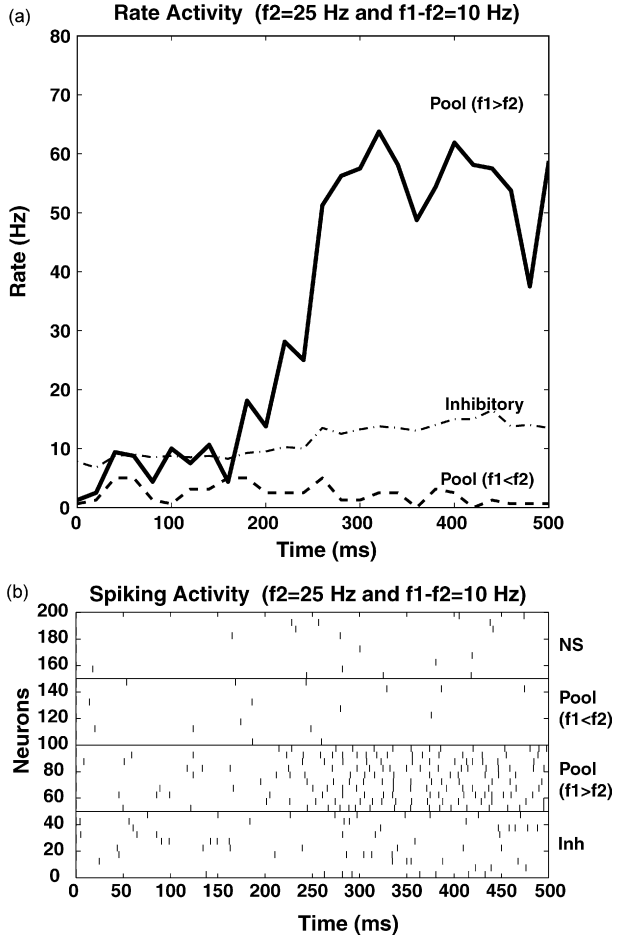

Fig. 3. Decision-making in a model of vibrotactile decision-making. Dynamical evolution of the network activity of Ventral Premotor Cortex neurons during the comparison period between vibrotactile frequency f1 = 30 Hz and frequency f2 = 20 Hz. (a) The evolution as a function of time of the spiking rate of the populations (f1 > f2) (corresponding to a decision that f1 is greater than f2), (f1 < f2), and the inhibitory population. (b) The corresponding rastergrams of 10 randomly selected neurons for each pool (population of neurons) in the network. Each vertical line corresponds to the generation of a spike. The spatio-temporal spiking activity shows the transition to the correct final single-state attractor, i.e., a transition to the correct final attractor encoding the result of the discrimination (f1 > f2). (After Deco and Rolls, 2006.).

The model developed by Wang (2002) provided a remarkable qualitative match with behavioral measures of performance and reaction times as well as certain aspects of neuronal activity. In general, the dynamics relevant for decision-making in these non-linear networks depends on the stability of the spontaneous activity state, i.e., the state in which no decision has yet been made. If, once the stimulus is presented, the spontaneous state destabilizes, then the dynamics rapidly evolves towards one of the two decision states (Wong and Wang, 2006). This is not dissimilar to the repelling Ornstein–Uhlenbeck connectionist model, although the decision boundary is no longer a free variable but rather related to the time needed to reach the stable decision fixed point.

Deco and Rolls (2006) studied an alternative scenario to that in the Wang-like models (Brody et al., 2003; Wang, 2002; Wong and Wang, 2006). In the Deco and Rolls model, the spontaneous state does not lose stability when the inputs λ are presented, but coexists with stable decision states, hence leading to multi-stability between three possible fixed points of the average firing rate. At the local level, the dynamics is similar to the leaky or attracting Ornstein–Uhlenbeck process. The multi-stability is present only if the recurrent excitation (cohesion) within each neuronal population is strong enough. In this scenario, a decision is driven by spiking noise-driven fluctuations which provoke an escape from the stable spontaneous state to one of the two decision states, as illustrated in Fig. 2c. This differs from the Wang-like models in which the system will evolve towards one of the two choices after the inputs λ are presented even in the absence of fluctuations. Thus in the multi-stable regime investigated by Deco and Rolls (2006) noise-related fluctuations are essential for decision-making. In contrast, in Wang (2002) the same network is used, but in the regime where the spontaneous state is unstable after the inputs λ are applied and only the two attractors corresponding to the choices are possible stable states.

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

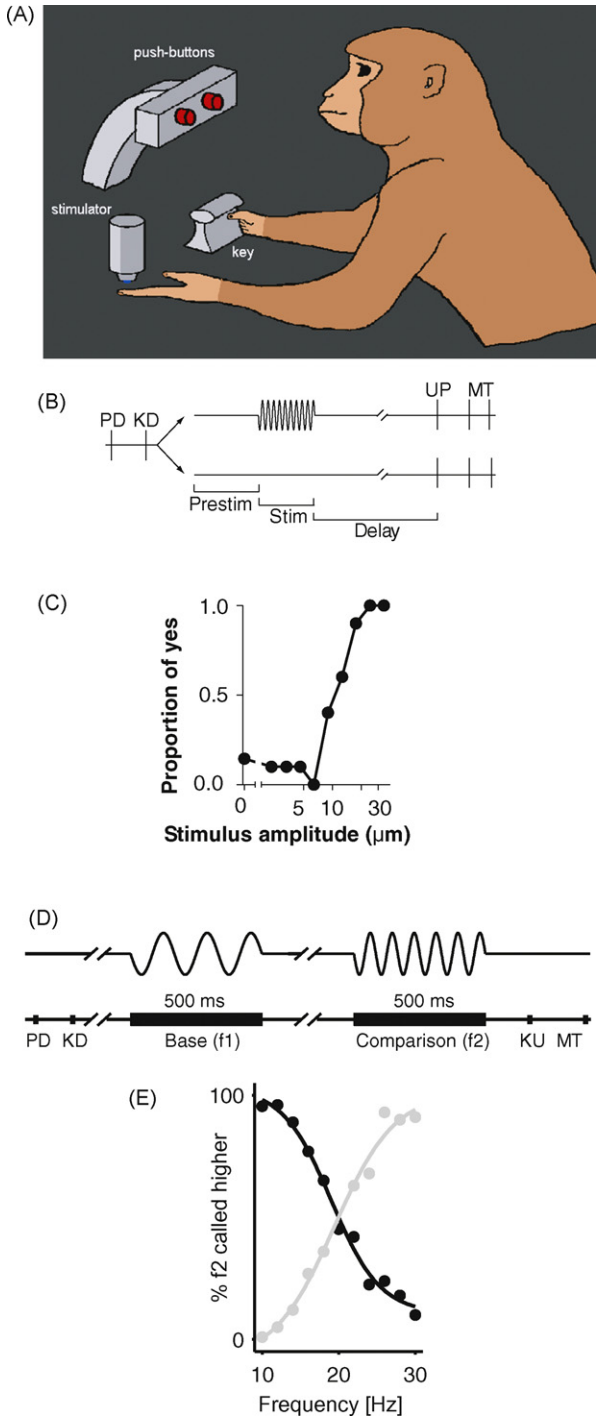

Fig. 4. (a) Drawing of a monkey working in the detection or discrimination tasks. (b) The sequence of events during the detection trials. Trials began when the stimulation probe indented the skin of one fingertip of the left, restrained hand (probe down, PD). The monkey then placed its right, free hand on an immovable key (key down, KD). On half of the randomly selected trials, after a variable pre-stimulus period (Prestim, 1.5–3.5 s), a vibratory stimulus (Stim, 20 Hz, 0.5 s) was presented. Then, after a fixed delay period (Delay, 3 s), the stimulator probe moved up (probe up, UP), indicating to the monkey that it could make the response movement (MT) to one of the two buttons. The button pressed indicated whether or not the monkey felt the stimulus (henceforth referred to as 'yes' and 'no' responses, respectively). Depending on whether the stimulus was present or absent and on the behavioral response, the trial outcome was classified as a hit, miss, false alarm or correct reject. Trials were pseudo-randomly chosen: 90 trials were with the stimulus absent (amplitude 0), and 90 trials were with the stimulus present with varying amplitudes (9 amplitudes with 10 repetitions each). (c) Classical psychometric detection curve obtained by plotting the proportion of 'yes' responses as a function of the stimulus amplitude. (d) Sequence of events during the discrimination trials. Trials began exactly as in the detection task but the probe oscillates at the base frequency (f1), and after a delay (3 s), a second mechanical vibration is delivered at the comparison frequency (f2). The monkey then releases the key (KU) and presses either the medial or lateral push-button to indicate whether the comparison frequency was lower (black line) or higher (grey line) than the base frequency. (e) Discrimination performance curve, plotted as the animal's capacity to judge whether f2 is higher or lower than f1. (Adapted from de Lafuente and Romo, 2005 and Hernandez et al., 1997.).

A link between the phenomenological diffusion models and the biologically inspired models can now be rigorously established. The dynamics of detailed biophysical firing rate and spike-based models can be reduced to a one dimensional *Diffusion Equation* typically used with phenomenological models (Smith and Ratcliff, 2004). Roxin and Ledberg (2008) have shown that the dynamics of multi-stable neuronal models can be expressed by a noise-driven amplitude equation given by the normal form for a saddle-node bifurcation. This reduced amplitude normal form can be derived analytically from the original neuronal dynamics (Roxin and Ledberg, 2008). The main idea is that the dynamics close to the bifurcation point are slow and confined to a center manifold. The reduced amplitude equation corresponds to a non-linear diffusion equation which describes properly the original neuronal dynamics. In this way, the phenomenological diffusion description is extended (from linear to non-linear), and at the same time explicitly linked with a realistic biological implementation. More specifically, the reduced one-dimensional diffusion equation describes the motion of a noise-driven over-damped particle in a potential.

4. Perceptual detection and stochastic dynamics

Pioneering investigations in several sensory systems have shown how neural activity represents the physical parameters of sensory stimuli in the peripheral nervous system and in the brain (Hubel and Wiesel, 1968; Mountcastle et al., 1967; Talbot et al., 1968). These investigations have paved the way for new questions that are more closely related to cognitive processing. For example, where and how in the brain do the neuronal responses that encode the sensory stimuli translate into responses that encode a perceptual decision (Romo and Salinas, 2001; Schall, 2001)? What components of the neuronal activity evoked by a sensory stimulus are directly related to perception (Newsome et al., 1989; Romo et al., 1998)? Where and how in the brain is sensory information stored in memory (Romo et al., 1999)? In Section 4.1, neurophysiological approaches to these issues are described, and in Section 4.2 computational approaches to understanding the processing are described that build on the foundation in Section 3.

4.1. Psychophysics and neurophysiology of perceptual detection

The detection of sensory stimuli is among the simplest perceptual experiences and is a prerequisite for any further sensory processing. A fundamental problem posed by sensory detection tasks is that repeated presentation of a near-threshold stimulus might unpredictably fail or succeed in producing a sensory percept. Where in the brain are the neuronal correlates of these varying perceptual judgments? This problem has been recently addressed by de Lafuente and Romo (2005, 2006). These authors trained monkeys to perform a detection task (Fig. 4a). On each trial, the animal had to report whether the tip of a mechanical stimulator vibrated or not on the skin of a finger tip (Fig. 4b). Crucially, the stimuli varied in amplitude across trials. Stimulus-present trials were interleaved with an equal number of stimulus-absent trials in which no mechanical vibrations were delivered (Fig. 4b). Depending on the monkey's responses, trials could be

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

classified into four response types: hits and misses in the stimulus-present condition, and correct rejections and false alarms in the stimulus-absent condition. Stimulus detection thresholds were calculated from the behavioral responses (Fig. 4c). Previous studies seeking the neuronal correlates of sensory detection showed that, in the case of the vibrotactile stimuli, the responses of neurons of the primary somatosensory cortex (S1) account for the measured psychophysical accuracy (Mountcastle et al., 1969). However, imaging and physiological studies show that, in addition to the sensory cortices, areas of the frontal lobes are also active during sensory detection and discrimination (Hernandez et al., 2002; Romo et al., 2004; Romo et al., 2003; Shulman et al., 2001). This evidence raises an important question: what are the specific functional roles of primary sensory cortices and association areas of the frontal lobes in perceptual detection?

To further test the contributions of these cortical areas in perceptual detection, de Lafuente and Romo (2005, 2006) recorded the activity of S1 and medial premotor cortex (MPC, a frontal lobe area involved in decision-making and motor planning (Hernandez et al., 2002; Tanji, 2001)) neurons, while monkeys performed the task (Fig. 4). They basically found that the responses of S1 neurons varied as a function of the stimulus strength but did not predict the behavioral responses. Conversely, the responses of MPC neurons did not vary as a function of the stimulus strength, but predicted the behavioral responses on a trial-by-trial basis. These results further support a detection model in which, to judge the stimulus presence or absence, a central area (or areas) with internal fluctuations must track the activity of S1. These results suggest that perceptual judgments emerge from the activity of frontal lobe neurons but not in sensory cortices. Importantly, the internal fluctuations of frontal lobe neurons are closely related to the animal's behavior, as shown by the data of de Lafuente and Romo (2005, 2006).

4.2. Computational models of probabilistic signal detection

An aim of this paper is to show how stochastic dynamics helps to understand the computational mechanisms involved in perceptual detection. The computational analysis of detection focuses on the paradigm and experimental results of de Lafuente and Romo (2005) described above. To summarize, they used a behavioral task where trained awake monkeys reported the presence or absence of a mechanical vibration applied to their fingertips by pressing one of two pushbuttons. The firing rates of S1 neurons did not covary with the animals' perceptual reports, but their firing rate did show a monotonically increasing graded dependence on the stimulus amplitude (Fig. 3c and f in de Lafuente and Romo (2005)). On the other hand, the activity of MPC neurons was only weakly modulated by the stimulus amplitude, but was related to the monkeys' trial-by-trial reports of whether they detected a stimulus. The fact that the firing rates of MPC neurons correlate with whether the stimulus is detected, with a high firing rate for a 'yes' report and a low firing rate for a 'no' report, suggests not only that this area is involved in the decision-making, but also that the decision-making is implemented by an attractor network with bistable dynamics.

Deco et al. (2007a) investigated two integrate-and-fire attractor network models of this stimulus detection. One (Fig. 5 top left) has one population or pool of neurons that when the stimulus λ is presented can either remain in the spontaneous state which represents that no stimulus has been detected (a 'No' response), or can transition to a high firing rate state indicating that the stimulus has been detected (a 'Yes' response). This was called a NCYN model (non-competing yes neurons). The arrows indicate the recurrent synaptic connections between the different neurons in a pool. The strengths of these synaptic connections $\omega+$ were obtained by a mean field analysis to produce two stable states, one where the activity of the Yes neurons was low (spontaneous firing rate, representing a 'No' decision), and the other where the Yes neurons fire fast, representing a 'Yes' decision. The performance of this model is shown in Fig. 5 (Modeling Results, left), where it can be seen that the network probabilistically enters a 'Yes' state with a probability influenced by the stimulus strength λ. Once the network is in the 'Yes' state the firing rate is high, independently of the stimulus strength (see Deco et al. (2007a)). It is the spiking noise in the network that makes the detection probabilistic. The model captures the probabilistic detection of the monkeys (Fig. 5, middle left), and also the neurophysiological data that the MPC neurons after the decision has been made have either a low firing rate (usually when the stimulus is weak, see Fig. 5, middle right), or have a high firing rate (usually when the stimulus is strong, see Fig. 5, middle right).

The second integrate-and-fire model (Fig. 5 top right) has two populations of neurons that compete with each other, one which starts with a relatively high firing rate at the beginning of a trial and remains in this attractor for a 'No' decision, and a second population that receives the stimulus λ and can remain in its spontaneous state, or can transition to a high firing rate state indicating that the stimulus has been detected (a 'Yes' response). This was called a CYNN model (competing yes-no neurons). The arrows indicate the recurrent synaptic connections between the different neurons in a pool. The strengths of these synaptic connections were set to be stronger $\omega+$ or weaker $\omega-$ than the other connections in the network following a mean field analysis to produce two stable states, one where the activity of the Yes neurons was low (spontaneous firing rate, representing a 'No' decision), and the other where the Yes neurons fire fast, representing a 'Yes' decision. The firing of the 'No' population is approximately the reciprocal of the 'Yes' population. The performance of this model is shown in Fig. 5 (Modeling Results, right), where it can be seen that the network probabilistically enters a 'Yes' state with a probability influenced by the stimulus strength λ. Once the network is in the 'Yes' state the firing rate is high, independently of the stimulus strength (see Deco et al., 2007a). It is again the spiking noise in the network that makes the detection probabilistic.

By analysing the temporal evolution of the firing rate activity of neurons on trials associated with the two different behavioral responses of 'Yes' or 'No', Deco et al. (2007a) produced evidence in favor of the CYNN (2 population competing) model compared to the non-competing one population model (NCYN). Specifically, the CYNN model predicts the existence of some neurons that encode the 'no' response, and other neurons that encode the 'yes' response. The first set of neurons slightly decrease their activity at the end of the trial, whereas the second group of neurons increase their firing activity when a stimulus is presented, which is what is found neurophysiologically. Thus in this case, the simulations indicate that the CYNN model fits the experimental data better than the NCYN model.

The important aspects of both models are as follows. First, the spiking noise in the network is part of the mechanism by which the detection outcome for a given stimulus strength is probabilistic. Second, once the decision has been taken, the firing rates of the population(s) reach a binary state, of being high or low, and do not reflect the exact value of the stimulus strength. This property, and the fact that a binary decision state is reached, is a property of attractor networks. The competition implemented by the inhibitory neurons helps a binary decision to be reached, and this is facilitated by the non-linear positive feedback implemented by the recurrent collateral excitatory connections within a population of neurons. Third, the mean-field analysis is important because it enables the synaptic connection strengths that can produce the required stable states to be determined; and the integrate-and-fire simulations with those weights are important in allowing the probabilistic dynamical transition into a decision state to be investigated, and to be compared with the responses of neurons recorded in the brain. Fourth, these integrate-and-fire models

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

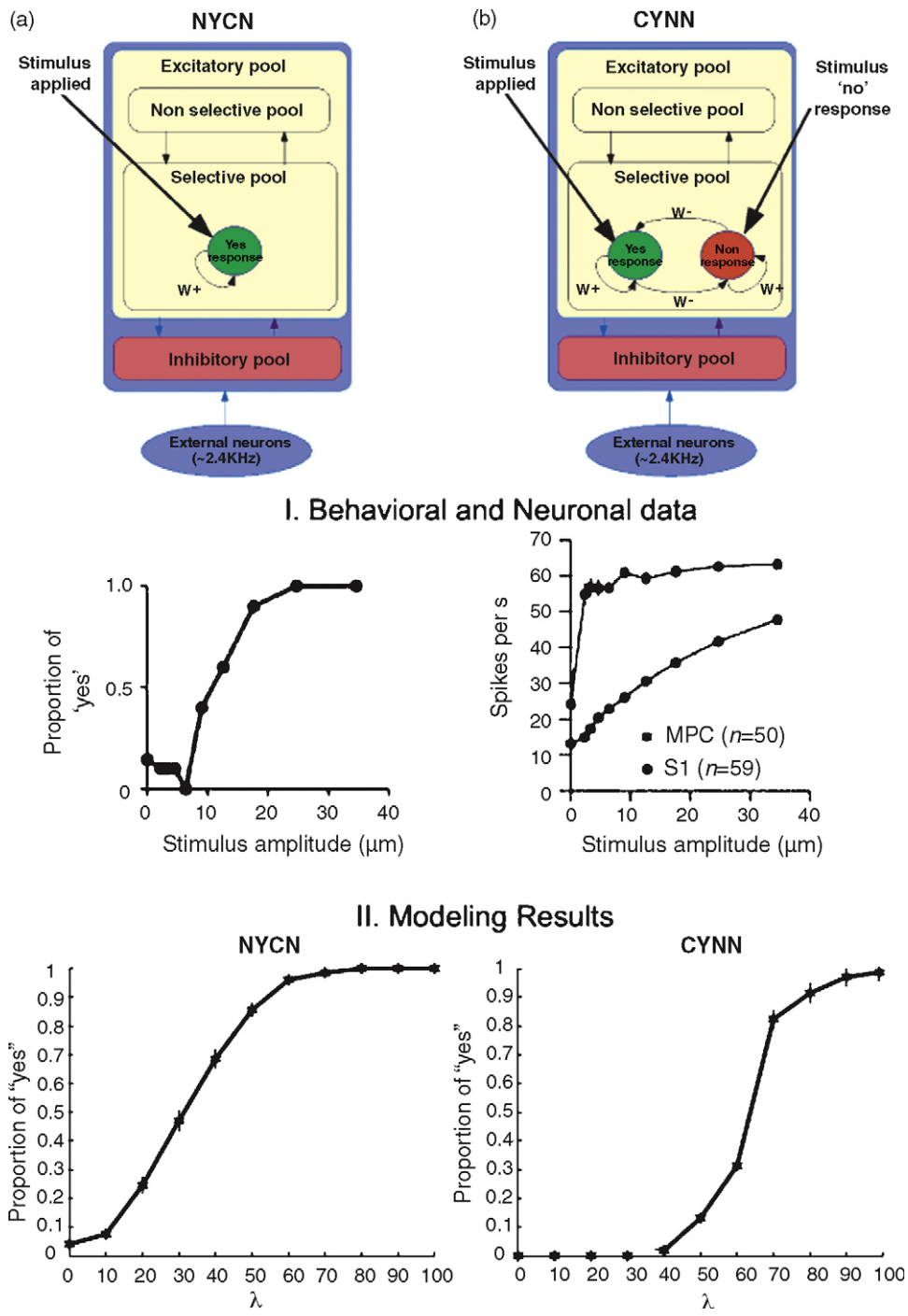

Fig. 5. Stimulus detection. Top. (a) Left: a stimulus detection model with one population or pool of neurons that when the stimulus λ is presented can either remain in the spontaneous state which represents that no stimulus has been detected (a 'No' response), or can transition to a high firing rate state indicating that the stimulus has been detected (a 'Yes' response). This was called a NCYN model (non-competing yes neurons). (b) Right: a stimulus detection model with two populations of competing neurons. The 'No' population starts at a high rate, and remains in this attractor state if the stimulus is not detected. The 'Yes' population receives inputs λ from the sensory stimulus, and if this populations wins the competition, this corresponds to detection and a 'Yes' response. This was called a CYNN model (competing yes-no neurons). The arrows indicate the recurrent synaptic connections between the different neurons in a pool, and the synaptic weights ω as determined from a mean field analysis are indicated as being stronger ω+ or weaker ω− that the other connection strengths in the network. Neurons in the networks are connected via three types of receptors that mediate the synaptic currents flowing into them: AMPA and NMDA glutamate receptors, and GABA receptors. Below. I. Behavioral and neuronal data. (Left) Behavioral detection curve of the macaques. Proportion of 'yes' responses as a function of the amplitude of a 20-Hz vibratory stimulus applied to a fingertip. (Right) Mean response of Medial Premotor Cortex neurons as a function of stimulus amplitude. In contrast to what has been observed in primary somatosensory areas, stimulus amplitude has little effect on the firing rate of MPC neurons once the decision has been taken: they either fire very little, or at a high rate. II. Integrate-and-fire modeling results. The probability of a high firing rate 'yes'-response (hit) as a function of the stimulus strength λ for (left) the NCYN model and (right) the CYNN model. (After Deco et al., 2007a,b.).

incorporate synaptically activated ion channels and neurons with realistic dynamics, and so pave the way for relating detailed experimental neuroscience measurements and manipulations to the overall decision-making at the global level of behavior.

In conclusion, computational stochastic neurodynamical models provide a deeper understanding of the fundamental mechanisms underlying perceptual detection and how these are related to experimental neuroscience data. We argue that this type of

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

analysis is a prerequisite for grounding empirical neuroscience in a cogent theoretical framework.

5. Decision-making and stochastic dynamics

5.1. Probabilistic decision-making

During the last decade, numerous neurophysiological experiments started to reveal the neuronal correlates of decision-making (Glimcher, 2003, 2005; Gold and Shadlen, 2002; Platt and Glimcher, 1999; Romo and Salinas, 2001, 2003; Schall, 2001; Shadlen and Newsome, 1996; Smith and Ratcliff, 2004; Thompson et al., 1996). By recording the activity of single neurons, signals that are correlated with the subjects' decisions have been found in several areas of the cerebral cortex, most notably in area LIP, in the parietal lobe, and premotor areas of the frontal lobe. An important finding is that cortical areas involved in generating motor responses also show trial-averaged activity exhibiting a gradual accumulation of evidence for choosing one or another decision (Gold and Shadlen, 2000). In fact, it has been suggested that, at the neurophysiological level, the process of making a decision and action generation cannot be differentiated (see for example Romo et al., 2004).

Decision-making is often probabilistic, with different decisions being taken on different trials even when the evidence is the same. This is found for example not only with binary decision-making, but also with decision-making (for the direction of motion) when there are four alternatives (Churchland et al., 2008). Probabilistic decision-making is also found when making choices for rewards that are delivered probabilistically. In such tasks, the proportion of choices reflects, and indeed may be proportional to, the expected value of the different choices. This pattern of choices is known as the Matching Law (Sugrue et al., 2005). Indeed, decision-making is probabilistic in many situations, and some of these are considered further when applications of computational models of decision-making are considered in Section 6.

To relate decision-making to its underlying computational mechanisms, we will concentrate here on the probabilistic behavior in a decision-making task well characterized at both the cellular and behavioral level, namely the perceptual discrimination of vibrotactile stimuli within the flutter range (5–40 Hz) and for which a biologically plausible computational model has been developed, as described next.

5.2. The vibrotactile discrimination task

The behavioral and neurophysiological work of Romo and colleagues has investigated the neural substrate of the complex processes underlying the ability to discriminate two sequential vibrotactile stimuli (Hernandez et al., 1997, 2002; Romo et al., 2002, 2003, 2004; Romo and Salinas, 2001, 2003). In this two-alternative forced-choice task, subjects (highly trained macaque monkeys) must decide which of two mechanical vibrations applied sequentially to their fingertips has the higher frequency of vibration (see Fig. 4d). This decision-making paradigm requires the perception of the first stimulus (a 500-ms long vibration at frequency f1), the storing of a trace of that f1 stimulus in short-term memory during a delay of typically 3 s, the perception of the second stimulus (a 500-ms long vibration at frequency f2), and the comparison of the second stimulus f2 to the trace of f1, and choosing a motor act based on this comparison, f2–f1. The vibrotactile stimulation f1 and f2 utilized was in the range of frequencies called *flutter*, i.e., within ca. 5–40 Hz. The neurophysiological and behavioral work of Romo and colleagues using this task has been reviewed by Romo and Salinas (2003).

Neurons recorded from the primary somatosensory cortex (S1) responded only during the presence of the vibrations, and their spiking rate was strongly tied to stimulus frequency. The responses of neurons recorded from the primary motor cortex (M1) were completely predictive of the monkey's arm movement involved in the response action. Neurons in the areas intervening between the primary sensory and motor cortices (S2: secondary somatosensory cortex, VPC: ventral prefrontal cortex, and MPC: medial premotor cortex) implemented the perceptual comparison process and, to a considerable extent, seemed to underlie the cognitive process of decision-making. One of the most important features of some of these neurons is that their spiking rate was an almost binary function of the difference between the frequencies of the two vibrotactile stimuli to be compared (Romo et al., 2004). In particular, their firing rates were high for one decision, and low for the other decision. These neurons, which are shown in Fig. 2(G-H-I) of Romo et al. (2004) and which are captured by the attractor models described in this paper and elsewhere (Deco and Rolls, 2006), reflect the decision-making step of the comparison illustrated in Fig. 3.

The probabilistic aspects of vibrotactile discrimination have also been investigated in humans (Deco et al., 2007b). They assessed the proportion of base-higher responses ($f2 > f1$) as a function of the comparison frequency for each participant and base frequency, and then fitted a Weibull-function to the observed data. From there they calculated the average of individual Just Noticeable Difference (JND) thresholds (difference-limen) (calculated consistently as 1/2 the difference between the frequency identified as higher than the standard on 85% of the trials and the frequency identified as smaller on 15% of the trials). They found that the JND was linearly related to the stimulus magnitude (in this case the base vibrotactile frequency), thereby illustrating that Weber's Law ($\Delta I/I$ is a constant) applies to vibrotactile flutter frequency discrimination in humans.

The human behavioral data complement the neurophysiological evidence, helping to constrain the underlying neurodynamics and computational principles involved in perceptual discrimination.

5.3. The computational bases of decision-making

A theoretical analysis of the underlying neurodynamical mechanisms was performed by Deco and Rolls (2006). They designed a neurodynamical model to account for the experimental neurophysiological data of Romo et al. (2004) that can account for the most relevant characteristics of the decision-related neuronal activity. The behavior of the model also provides an account for Weber's Law, if the model is tuned to work in a multi-stable regime.

The model has the attractor network architecture illustrated in Fig. 2b, with populations of neurons formed into separate attractors for the decision $f1 > f2$ or the decision $f1 < f2$. The spiking and synaptic dynamics of the *Integrate-and-Fire* network were as introduced in Section 2, with AMPA (fast) and NMDA-glutamate (slow) excitatory receptors, and GABA inhibitory receptors (see Deco and Rolls (2006)). A mean field analysis was used to find the values for the synaptic strengths between the different populations of neurons that supported stable states for the spontaneous activity, or for either of the two decision-related populations of neurons having high activity, ($f1 > f2$) or ($f1 < f2$).

Fig. 3 shows a typical trial of the network of Ventral Premotor Cortex (VPC) neurons during the comparison period for f1 = 30 Hz and f2 = 20 Hz for a single correct trial in which the $f1 > f2$ population wins the competition. As introduced in Section 3, after 200 ms the populations ($f1 > f2$) and ($f1 < f2$) start to separate in such a way that the population ($f1 > f2$) wins the competition and the network performs a transition to a single-state final attractor corresponding to a correct discrimination (i.e., high activity in the population ($f1 > f2$) and low activity in the population ($f1 < f2$)). The bottom part of Fig. 3 plots the corresponding rastergrams of 10 randomly selected neurons for each pool in the network. Fig. 3 thus

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

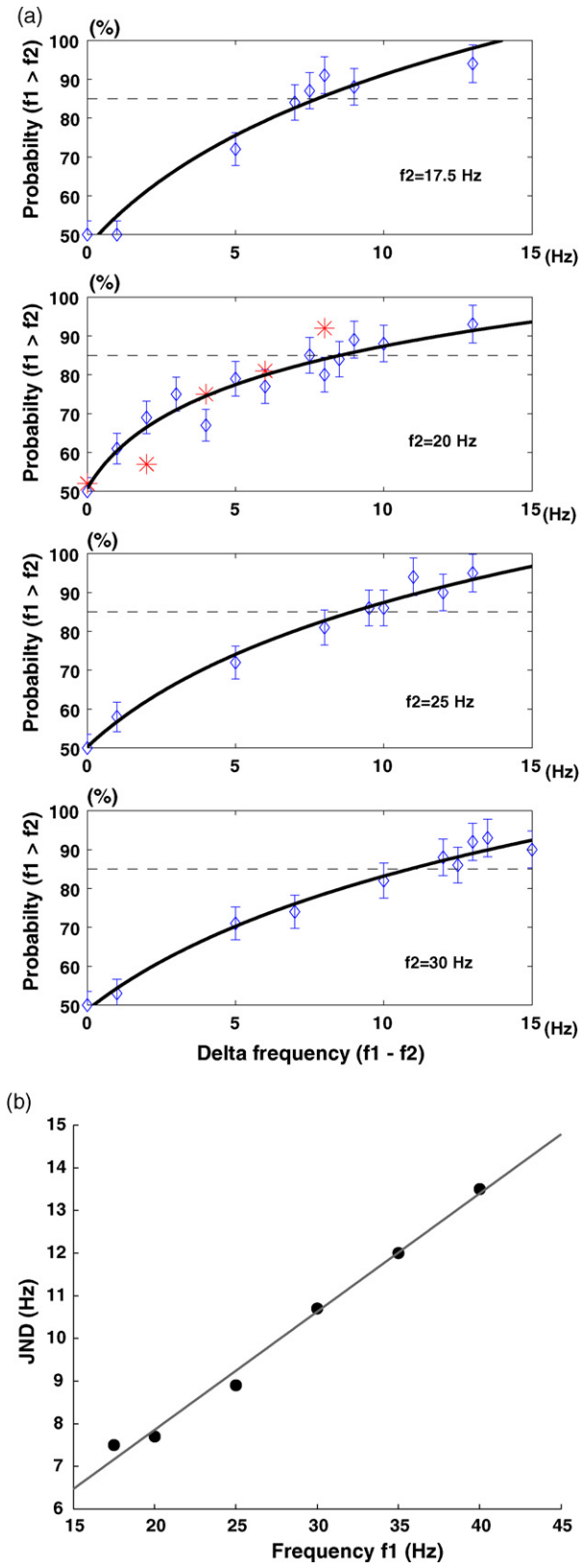

Fig. 6. (a) Probability of correct discrimination (±S.D.) as a function of the difference between the two presented vibrotactile frequencies to be compared. In the simulations, we assume that f1 > f2 by a Δ-value (labelled 'Delta frequency (f1–f2)'), i.e., f1 = f2 + Δ. The horizontal dashed line represents the threshold of correct classification for a performance of 85% correct discrimination. The different panels are for different base frequencies f2. The second panel down includes actual neuronal data described by Romo and Salinas (2003) for the f2 = 20 Hz condition (indicated by *). (After Deco and Rolls, 2006.). (b) Weber's Law for the vibrotactile discrimination task in the integrate-and-fire simulations. The critical discrimination Δ-value ('difference-threshold') is shown corresponding to an 85% correct performance level as a function of the base frequency f2. The 'difference-threshold' (labelled JND) increases linearly as a function of the base frequency. (After Deco and Rolls, 2006.).

shows how the network, because it is a short-term memory attractor network, can accumulate evidence over time but stochastically, is influenced by the probabilistic spiking of the neurons so that the firing rates of the two populations of neurons gradually and noisily diverge over the first 200 ms, and eventually increase rapidly as the network falls into one of its attractors representing a binary decision (see below and Marti et al. (2008) for more detail). It is important that because of the attractor properties a binary decision is reached, with one population by the end of each trial having a high firing rate, and the other population a low firing rate, which no longer reflect the exact values of the stimuli, but just the binary decision reached, in correspondence with what is found neurophysiologically (see Fig. 2 of Romo et al., 2004). It is also an important property of this class of decision-making network that it takes longer to settle into an attractor state if the decision is difficult, that is if the inputs are very similar. This class of network thus provides a model of reaction time data (Deco and Rolls, 2006; Wang, 2002).

Fig. 6a shows the probabilistic behavior of the network averaged across trials. The probability of correct discrimination as a function of the difference between the two presented vibrotactile frequencies (the 'Delta frequency (f1–f2)') is shown. One can observe from the different panels corresponding to different base vibrotactile frequencies f2 that for the network to reach a criterion of correct classification of for example 85% (horizontal dashed line in Fig. 6a), the difference between f1 and f2 must become larger as f2 increases. The second panel of Fig. 6a shows a good fit between the actual neuronal data (Romo and Salinas, 2003) for the f2 = 20 Hz condition (indicated by *), and the results obtained with the model.

Fig. 6b plots the critical discrimination Δ-frequency corresponding to an 85% correct performance level (the 'difference-threshold' labelled JND) as a function of the base-frequency f2. The 'difference-threshold' increases linearly as a function of the base-frequency. This corresponds to Weber's Law for the vibrotactile discrimination task. The analysis shown in Fig. 6 suggests that Weber's Law, and consequently the ability to discriminate two stimuli, is encoded in the probability of performing a transition to the correct final attractor, and indeed once in the attractor the neurons have a high firing rate that reflects the binary decision, and not the Δ-value (Deco and Rolls, 2006). It is a remarkable finding that Weber's Law can be accounted for by the performance of this network. The underlying mechanism may be related to the linear increase in the firing of the inhibitory neurons in the network as a function of the baseline stimulus 'strength' f2, for the GABA inhibition on the pyramidal cells is shunting (i.e., acts like a short circuit) due to the equilibrium potential of the Cl^- channels activated by the GABA receptors, and this corresponds mathematically to division by the base frequency, as explored by Deco and Rolls (2006).

In their exploration of Weber's Law applying to vibrotactile flutter frequency discrimination in humans, Deco et al. (2007b) concluded that the neurodynamical mechanisms and computational principles underlying the decision-making processes in this perceptual discrimination task are consistent with a fluctuation-driven scenario in a multi-stable regime as incorporated in the model of Deco and Rolls (2006). Further evidence for this was obtained by Deco et al. (2007b), who used a mean-field analysis with a system of non-linear coupled differential equations of the Wilson–Cowan type (La Camera et al., 2004; Renart et al., 2003) which describe the evolution of the average firing rate of each population, and added a noise fluctuation term to drive the transitions. Fig. 7

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

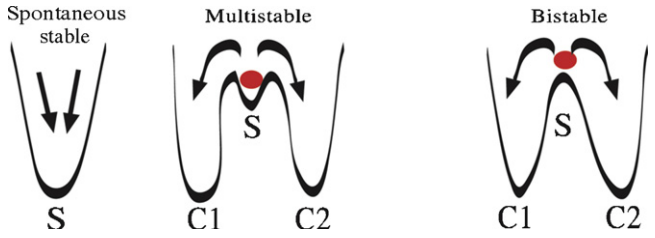

Fig. 7. Computational principles underlying the different dynamical regimes of the decision-making attractor network (see text). The *x*-axis represents the neuronal activity of one of the populations (ν_i) and the landscape represents an energy landscape regulating the evolution of the system. S is a stable state of spontaneous activity, C2 is a high firing rate state of this neuronal population corresponding to the choice implemented by this population, and C1 is a low firing rate state present when the other population wins the competition.

represents schematically the different ways in which the network can operate, depending on the value of λ, the input. The *x*-axis represents the neuronal activity of one of the populations (ν_i) and the landscape represents an energy landscape regulating the evolution of the system. The energy landscape reflects the synaptic values and the effects of the incoming sensory information (the λ_1 and λ_2 values in Fig. 2). For values of $\lambda < \lambda_{c1} = 20$ Hz (Fig. 7, left panel), only the spontaneous state is stable, and no decision states appear (for the unbiased case). For increasing $\Delta\lambda$ (biased case), one decision state (corresponding to the choice where the increased value of $\lambda + \Delta\lambda$ is applied) emerges, attracting the dynamics towards this decision state. For values of λ between $\lambda_{c1} = 20$ Hz, $\lambda_{c2} = 40$ Hz (Fig. 7, middle panel) there is a region of multi-stability between the spontaneous state and the decision states. In this λ interval, the fluctuations are responsible for driving the system from the initial stable spontaneous state to one of the two decision states corresponding to the two possible response choices. (C2 is a high firing rate of the population shown in Fig. 7 middle that corresponds to the decision implemented by that population of neurons.) Thus, in this scenario, fluctuations play a crucial role in the computation of decision-making. It is only in this region that Weber's Law is found to apply to the network. For values of $\lambda > \lambda_{c2} = 40$ Hz (Fig. 7, right panel) a region of bistability is found where the initial spontaneous state is unstable, and only the two decision states are stable. In this regime, the spontaneous state destabilizes, so that the dynamics rapidly evolves towards one of the two decision states, resembling therefore a pure diffusion integrating the relative evidence for one choice over another. The fact that the network can implement Weber's Law, and does so only in a range of values for λ in which the network operates as a fluctuation-driven multi-stable system, provides further evidence to support the hypothesis that decision-making is implemented by a multi-stable fluctuation-driven attractor system, where there are in the unbiased case stable states for the spontaneous firing state, and for each of the decisions.

With respect to the multi-stable scenario (in the middle of Fig. 7), the attractor network acts as a short-term memory that can accumulate evidence over time, and usually gradually though stochastically the firing rates of the two groups of neurons corresponding to the two choices diverge, one set of neurons stochastically increasing their firing rate, and the other set being inhibited by the first set of neurons. A situation like this is probably occurring in Fig. 3, and is analyzed in more detail by Marti et al. (2008). We can illustrate this point by the middle landscape in Fig. 7, and note that the accumulation of evidence corresponds to the position in the space indicated by the ball moving noisily in a direction towards, for example, C2, but not yet jumping over the energy barrier into the C2 attractor.

It is important to stress that the effect of the noise is particularly relevant in the multi-stable regime (middle of Fig. 7), because the fluctuations are the driving force that allow the system to escape the decision barriers around the stable spontaneous state. In the multi-stable scenario, the choices are associated with stable attractors, and the starting condition is also given by a stable spontaneous state. To make a decision, the system has to escape the stable spontaneous state towards one of the choice-attractors. This is related to the so-called 'Kramers' escape problem' (Kramers, 1940). On the other hand, in the bistable regime (right of Fig. 7, the so-called 'ballistic' regime), the noise is of course relevant as the basis of the diffusion process, but it is not the main driving force. This is because in the bistable scenario the spontaneous state is not a stable state, and therefore with or without noise, the system will necessarily evolve to one or the other decision-attractor just because of the neurodynamical flow (Deco and Marti, 2007a,b).

The importance of the noise in the system related to the probabilistic spiking of the neurons was confirmed in these simulations by altering the size of the network. When the network was increased in size to 4000 neurons, the variability of the decision-making from trial to trial decreased due to the smoothing effect on the noise of a large number of neurons, showing that the statistical fluctuations due to the spiking of the neurons do play an important role in finite-sized networks (Deco and Rolls, 2006).

5.4. Properties of this stochastic attractor model of decision-making

We conclude this section on decision-making with some key properties of this stochastic biased attractor model of decision-making.

The decisions are taken probabilistically because of the finite size noise due to spiking activity in the integrate-and-fire dynamical network, with the probability that a particular decision is made depending on the biasing inputs provided by the sensory stimuli via λ_1 and λ_2 (Deco and Rolls, 2006). The statistical fluctuations in the network are due to the finite size noise, which approximates to the square root of the (firing rate/number of neurons in the population) (Mattia and Del Giudice, 2002), as shown by Deco and Rolls (2006).

The results show that Weber's Law does not depend on the final firing rates of neurons in the attractor, but instead reflects the nature of the probabilistic settling into a binary decision-related attractor, which depends on the statistical fluctuations in the network, the synaptic connectivity, and the difference between the bias input frequencies f1 and f2 scaled by the baseline input f2. This is the first time we know when the implementation of a psychophysical law is not the firing rate of the neurons, nor the spike timing, nor is single-neuron based, but instead is based on the synaptic connectivity of the network and on statistical fluctuations due to the spiking activity in the network.

Another interesting aspect of the model is that the recurrent connectivity, and the relatively long time constant of the NMDA receptors (Wang, 2002), together enable the attractor network to accumulate evidence over a long time period of several hundred milliseconds. This is an important aspect of the functionality of attractor networks. Nevertheless, long reaction times can also be obtained without NMDA receptors, using the alternative scenario of multi-stability (Marti et al., 2008). In this case, the level of noise is the main variable that drives the escape from the stable spontaneous firing rate state, and low levels of noise can produce long reaction times.

Although the attractor model described here is effectively a single network, the network need not be localized to one brain region. Long-range connections between cortical areas enable networks in different brain areas to interact in the way needed to implement an attractor single network. The requirement is that the synapses between the neurons in any one pool be set up by Hebb-like associative synaptic modification, and this is likely to be a property of connectivity between areas as well as within areas

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

(Rolls, 2008b; Rolls and Deco, 2002; Rolls and Treves, 1998). In this sense, the decision could be thought of as distributed across different brain areas. Consistent with this, Romo and colleagues have found neurons related to vibrotactile decisions not only in VPC, but also in a number of connected brain areas including the medial prefrontal cortex (Romo and Salinas, 2003). In order to achieve the desired probabilistic settling behavior, the network we describe must not have very high inhibition, and, related to this, may sometimes not settle into one of its attractor states. In a forced choice task in which a decision must be reached on every trial, a possible solution is to have a second decision-making network, with parameters adjusted so that it will settle into one of its states (chosen at chance) even if a preceding network in the decision-making chain has not settled. This could be an additional reason for having a series of networks in different brain regions involved in the decision-making process.

The model described here and by Wang, 2002, is different in a number of ways from accumulator or counter models which may include a noise term and which undergo a random walk in real time, which is a diffusion process (Carpenter and Williams, 1995; Ratcliff et al., 1999; Usher and McClelland, 2001; Wang, 2002). In accumulator models, a mechanism for computing the difference between the stimuli is not described, whereas in the current model this is achieved, and scaled by f, by the feedback inhibition included in the attractor network. Second, in the current model the decision corresponds to high firing rates in one of the attractors, and there is no arbitrary threshold that must be reached. Third, the noise in the current model is not arbitrary, but is accounted for by finite size noise effects of the spiking dynamics of the individual neurons with their Poisson-like spike trains in a system of limited size. Fourth, because the attractor network has recurrent connections, the way in which it settles into a final attractor state (and thus the decision process) can naturally take place over quite a long time, as information gradually and stochastically builds up due to the positive feedback in the recurrent network, the weights in the network, and the biasing inputs, as shown in Fig. 3.

The model of decision-making described here is also different to a model in which it is suggested that the probabilistic relative value of each action directly dictates the instantaneous probability of choosing each action on the current trial (Sugrue et al., 2005). The present model shows how probabilistic decisions could be taken depending on the two biasing inputs (λ_1 and λ_2 in Fig. 2, which could be equal) to a biased competition attractor network subject to statistical fluctuations related to finite size noise in the dynamics of the integrate-and-fire network.

We may raise the conceptually important issue of why the operation of what is effectively memory retrieval is probabilistic. Part of the answer is shown in Fig. 10 of Deco and Rolls (2006), in which it is seen that even when a fully connected recurrent attractor network has 4000 neurons, the operation of the network is still probabilistic. Under these conditions, the probabilistic spiking of the excitatory (pyramidal) cells in the recurrent collateral firing, rather than variability in the external inputs to the network, is what makes the major contribution to the noise in the network (Deco and Rolls, 2006). Thus, once the firing in the recurrent collaterals is spike implemented by integrate-and-fire neurons, the probabilistic behavior seems inevitable, even up to quite large attractor network sizes.

We may then ask why the spiking activity of any neuron is probabilistic, and what the advantages are that this may confer. The answer suggested (Rolls, 2008b) is that the spiking activity is approximately Poisson-like (as if generated by a random process with a given mean rate), because the neurons are held close to their firing threshold, so that any incoming input can rapidly cause sufficient further depolarization to produce a spike. It is this ability to respond rapidly to an input, rather than having to charge up the cell membrane from the resting potential to the threshold, a slow process determined by the time constant of the neuron and influenced by that of the synapses, that enables neuronal networks in the brain, including attractor networks, to operate and retrieve information so rapidly (Battaglia and Treves, 1998; Panzeri et al., 2001; Rolls, 2008b; Rolls and Treves, 1998; Treves, 1993). The spike trains are essentially Poisson-like because the cell potential hovers noisily close to the threshold for firing, the noise being generated in part by the Poisson-like firing of the other neurons in the network (Jackson, 2004). The noise and spontaneous firing help to ensure that when a stimulus arrives, there are always some neurons very close to threshold that respond rapidly, and then communicate their firing to other neurons through the modified synaptic weights, so that an attractor process can take place very rapidly (Rolls, 2008b).

The implication of these concepts is that the operation of networks in the brain is inherently noisy because of the Poisson-like timing of the spikes of the neurons, which itself is related to the mechanisms that enable neurons to respond rapidly to their inputs (Rolls, 2008b). However, the consequence of the Poisson-like firing is that, even with quite large attractor networks of thousands of neurons with hundreds of neurons representing each pattern or memory, the network inevitably settles probabilistically to a given attractor state. This results, *inter alia*, in decision-making being probabilistic. Factors that influence the probabilistic behavior of the network include the strength of the inputs (with the difference in the inputs/the magnitude of the inputs as shown here being relevant to decision-making and Weber's Law); the depth and position of the basins of attraction, which if shallow or correlated with other basins will tend to slow the network; and, perhaps, the mean firing rates of the neurons during the decision-making itself, and the firing rate distribution (see below). In this context, the probabilistic behavior of the network gives poorer and poorer and slower and slower performance as the difference between the inputs divided by the base frequency is decreased, as shown by Deco and Rolls (2006).

6. Applications of this stochastic dynamical approach to brain function and decision-making

This approach to how networks take decisions has implications throughout the brain, as follows (see Rolls, 2008b; Rolls and Deco, in preparation).

In one example, the model is effectively a model of the dynamics of the recall of a memory in response to a recall cue. The way in which the attractor is reached depends on the strength of the recall cue, and inherent noise in the attractor network performing the recall because of the spiking activity in a finite size system. The recall will take longer if the recall cue is weak. Spontaneous stochastic effects may suddenly lead to the memory being recalled, and this may be related to the sudden recovery of a memory which one tried to remember some time previously.

This framework can also be extended very naturally to account for the probabilistic decision taken about, for example, which of several objects has been presented in a perceptual task. The model can also be extended to the case where one of a large number of possible decisions must be made (cf. Churchland et al., 2008). An example is a decision about which of a set of objects, perhaps with different similarity to each other, has been shown on each trial, and where the decisions are only probabilistically correct. When a decision is made between different numbers of alternatives, a classical result is Hick's Law, that the reaction time increases linearly with $\log_2$ of the number of alternatives from which a choice is being made. This has been interpreted as supporting a

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

series of binary decisions each one taking a unit amount of time (Welford, 1980). As the integrate-and-fire model we describe works completely in parallel, it will be very interesting to investigate whether Hick's Law is a property of the network. If so, this could be related to the fact that the activity of the inhibitory interneurons is likely to increase linearly with the number of alternatives between which a decision is being made (as each one adds additional bias to the system through a λ input) and that the GABA inhibitory interneurons implement a shunting, that is divisive, operation (Rolls, 2008b).

Another application is to changes in perception. Perceptions can change 'spontaneously' from one to another interpretation of the world, even when the visual input is constant, and a good example is the Necker cube, in which visual perception flips occasionally to make a different edge of the cube appear nearer to the observer. We hypothesize that the switching between these multi-stable states is due in part to the statistical fluctuations in the network due to the Poisson-like spike firing that is a form of noise in the system. It will be possible to test this hypothesis in integrate-and-fire simulations. (This may or may not be supplemented by adaptation effects (of the synapses or neurons) in integrate-and-fire networks.) The same approach should provide a model of pattern and binocular rivalry, where one image is seen at a time even though two images are presented simultaneously. When these are images of objects or faces, the system that is especially important in the selection is the inferior temporal visual cortex (Blake and Logothetis, 2002; Maier et al., 2005), for it is here that representations of whole objects are present (Rolls, 2008b; Rolls et al., 2008d), and the global interpretation of one object can compete with the global interpretation of another object. These simulation models are highly feasible, in that the effects of synaptic adaptation and neuronal adaptation in integrate-and-fire simulations have already been investigated (Deco and Rolls, 2005b,c).

Another potential application of this model of decision-making is to probabilistic decision tasks. In such tasks, the proportion of choices reflects, and indeed may be proportional to, the expected value of the different choices. This pattern of choices is known as the Matching Law (Sugrue et al., 2005). An example of a probabilistic decision task in which the choices of the human participants in the probabilistic decision task clearly reflected the expected value of the choices is described elsewhere (Rolls et al., 2008c). A network of the type described here in which the biasing inputs λ_1 and λ_2 to the model are the expected values of the different choices will alter the proportion of the decisions it makes as a function of the relative expected values in a way similar to that shown in Fig. 6, and provides a model of this type of probabilistic reward-based decision-making (Marti et al., 2006).

Another application of this approach is to the detectability of signals. In a perceptual signal detection task, noise, of which one type is the noise contributed by statistical fluctuations related to spiking dynamics, can help as follows. If we had a deterministic neuron without noise and a fixed threshold above which spikes were emitted, then if the signal was below the threshold there would be no output, and if the signal was above threshold the neuron would emit a spike, and indeed continuous spike trains if the signal remained above threshold. In particular, if the signal was just below the threshold of the neuron, there would be no evidence that a signal close to threshold was present. However, if noise is present in the system (due for example to the afferent neurons having probabilistic spiking activity similar to that of a Poisson process), then occasionally with a signal close to threshold a spike would occur due to the summation of the signal and the noise. If the signal was a bit weaker, then the neuron might still occasionally spike, but at a lower average rate. If the signal was a bit closer to threshold, then the neuron would emit spikes at a higher average rate. Thus in this way some evidence about the presence of a sub-threshold signal can be made evident in the spike trains emitted by a neuron if there is noise in the inputs to the neuron. The noise in this case is useful, may have an adaptive function, and the process is termed stochastic resonance (Faisal et al., 2008; Stocks, 2000). The source of the noise in the detection mechanism in the brain, and in fact the noise in signal detection theory (Green and Swets, 1966), may be at least in part due to the statistical fluctuations caused by the probabilistic spiking of neurons in networks. We may note that decisions about whether a signal has been detected are not typically taken at the periphery, in that the distribution of false positive decisions, etc. does not necessarily accurately reflect on a trial by trial basis variations at the periphery, but instead fluctuations in more central brain areas (de Lafuente and Romo, 2005). A good example of this is that the explicit, conscious recognition of which face was seen is set with a threshold which is higher than that at which information is present in the inferior temporal visual cortex, and at which guessing can be much better than chance (Rolls, 2007).

Another application of this type of model is to taking decisions between the implicit and explicit systems in emotional decision-making (Rolls, 2005; Rolls, 2008a; Rolls, 2008b), where again the two different systems could provide the biasing inputs λ_1 and λ_2 to the model.

It is of interest that the noise that contributes to the stochastic dynamics of the brain through the spiking fluctuations may be behaviorally adaptive, and that the noise should not be considered only as a problem in terms of how the brain works. This is the issue raised for example by the donkey in the Duns Scotus paradox, in which a donkey situated between two equidistant food rewards might never make a decision and might starve. 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. We have shown here that stochastic neurodynamics caused, for example, by the relatively random spiking times of neurons in a finite sized cortical attractor network can lead to probabilistic decision-making, so that in this case the stochastic noise is a positive advantage.

Probabilistic decision-making can be evolutionarily advantageous in another sense, in which sometimes taking a decision that is not optimal based on previous history may provide information that is useful, and which may contribute to learning. Consider for example a probabilistic decision task in which choice 1 provides rewards on 80% of the occasions, and choice 2 on 20% of the occasions. A deterministic system with knowledge of the previous reinforcement history would always make choice 1. But this is not how animals including humans behave. Instead (especially when the overall probabilities are low and the situation involves random probabilistic baiting, and there is a penalty for changing the choice), the proportion of choices made approximately matches the outcomes that are available, in what is called the Matching Law (Corrado et al., 2005; Rolls et al., 2008c; Sugrue et al., 2005). By making the less favored choice sometimes, the organism can keep obtaining evidence on whether the environment is changing (for example on whether the probability of a reward for choice 2 has increased), and by doing this approximately according to the Matching Law minimizes the cost of the disadvantageous choices in obtaining information about the environment. This probabilistic exploration of the environment is very important in trial-and-error learning, and indeed has been incorporated into a simple reinforcement algorithm in which noise is added to the system, and if this improves outcomes above the expected value, then changes are made to the synaptic weights in the correct direction (Barto, 1985; Rolls, 2008b; Sutton and Barto, 1981). In perceptual

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

learning, probabilistic exploratory behavior may be part of the mechanism by which perceptual representations can be shaped to have appropriate selectivities for the behavioral categorization being performed (Sigala and Logothetis, 2002; Szabo et al., 2006). Another example is in food foraging, which probabilistically may reflect the outcomes (Kacelnik and Brito e Abreu, 1998; Krebs and Davies, 1991), and is a way optimally in terms of costs and benefits to keep sampling and exploring the space of possible choices.

Another sense in which probabilistic decision-making may be evolutionarily advantageous is with respect to detecting signals that are close to threshold, as described above.

Another way in which probabilistic decision-making may be evolutionarily advantageous is in creative thought, which is influenced in part by associations between one memory, representation, or thought, and another. If the system were deterministic, i.e., for the present purposes without noise, then the trajectory through a set of thoughts would be deterministic and would tend to follow the same furrow each time. However, if the recall of one memory or thought from another were influenced by the statistical noise due to the random spiking of neurons, then the trajectory through the state space would be different on different occasions, and we might be led in different directions on different occasions, facilitating creative thought (Rolls, 2008b). Of course, if the basins of attraction of each thought were too shallow, then the statistical noise might lead one to have very unstable thoughts that were too loosely and even bizarrely associated to each other, and to have a short-term memory and attentional system that is unstable and distractible, and indeed this is an account that we have proposed for some of the symptoms of schizophrenia (Loh et al., 2007a,b; Rolls, 2005, 2008b; Rolls et al., 2008b). The stochastic noise caused by the probabilistic neuronal spiking plays an important role in these hypotheses, because it is the noise that destabilizes the attractors when the depth of the basins of attraction is reduced. If the basins of attraction were too deep, then the noise might be insufficient to destabilize attractors, and this leads to an approach to understanding obsessive-compulsive disorders (Rolls et al., 2008a).

Similar noise-driven processes may lead to dreams, where the content of the dream is not closely tied to the external world as the role of sensory inputs is reduced in paradoxical (desynchronized) sleep, and the cortical networks, which are active in fast-wave sleep, may move under the influence of noise somewhat freely on from states that may have been present during the day (Horne, 2006; Kandel et al., 2000). In slow-wave sleep, and more generally in resting states, the activity of neurons in many cortical areas is on average low, and stochastic spiking-related noise may contribute strongly to the states that are found.

An area where the spiking-related noise in the decision-making process may be evolutionarily advantageous is in the generation of unpredictable behavior, which can be advantageous in a number of situations, for example, when a prey is trying to escape from a predator, and perhaps in some social and economic situations in which organisms may not wish to reveal their intentions (Dawkins, 1995; Maynard Smith, 1982, 1984). We note that such probabilistic decisions may have long-term consequences. For example, a probabilistic decision in a 'war of attrition' such as staring down a competitor, e.g., in dominance hierarchy formation, may fix the relative status of the two individual animals involved, who then tend to maintain that relationship stably for a considerable period of weeks or more (Dawkins, 1995; Maynard Smith, 1982, 1984).

More generally, each cortical area can be conceived as performing a local type of decision-making using attractor dynamics of the type described (Rolls, 2005). Even memory recall is in effect the same local 'decision-making' process. The orbitofrontal cortex, for example, is involved in decisions about which visual stimulus is currently associated with reward, in, for example, a visual discrimination reversal task. Its computations are about stimuli, primary reinforcers, and secondary reinforcers (Rolls, 2005). The dorsolateral prefrontal cortex takes an executive role in decision-making in a working memory task, in which information must be held available across intervening stimuli (Rolls, 2008b). The dorsal and posterior part of the dorsolateral prefrontal cortex may be involved in short-term memory-related decisions about where to move the eyes (Rolls, 2008b). The parietal cortex is involved in decision-making when the stimuli are, for example, optic flow patterns (Glimcher, 2003). The hippocampus is involved in decision-making when the allocentric places of stimuli must be associated with rewards or objects (Rolls, 2008b; Rolls and Kesner, 2006). The somatosensory cortex and ventral premotor cortex are involved in decision-making when different vibrotactile frequencies must be compared (see above). The cingulate cortex may be involved when action–outcome decisions must be taken (Rolls, 2008b). In each of these cases, local cortical processing that is related to the type of decision being made takes place, and all cortical areas are not involved in any one decision. The style of the decision-making-related computation in each cortical area appears to be of the form described here, in which the local recurrent collateral connections enable the decision-making process to accumulate evidence in time, falling gradually into an attractor that represents the decision made in the network. Because there is an attractor state into which the network falls, this can be described statistically as a non-linear diffusion process, the noise for the diffusion being the stochastic spiking of the neurons, and the driving force being the biasing inputs.

7. Conclusions

The principles of stochastic dynamics that have been described are important for understanding how computations can occur in the noisy environment of the brain, and how the noise can be beneficial and biologically adaptive. The concepts are important for understanding how decisions can be made probabilistically, and for how choice deadlock is broken. The approaches are important for computational neuroscience, because they provide a theoretical framework that goes beyond the traditional noiseless neurodynamical analyses. The concepts are important for neurophysiology, because they show that transitions between states and not just averages across states are important to analyze.

However, the principles described here go far beyond this, and have widespread implications for understanding brain function, and allow testable hypotheses and predictions to be generated.

The principles show, for example, that brain function should not be regarded as purely deterministic, in the sense that it is subject to trial-by-trial variation that is generated by the essentially almost random spike firing times of the neurons (for a given mean rate), which themselves are influenced by noise in the synapses.

The principles show that this element of probabilistic outcome of decision, memory, and perceptual processes can be advantageous in ways described in this paper, including sampling choices even though they are usually unfavorable; probabilistic memory recall and thought processes that, in the right amount, produce useful variation in thinking and thus help creativity; the ability not to become stuck in some short-term memory or attentional task, but to have a natural way to escape from it; and the ability for behavior to be to some extent unpredictable, which can have utility to the individual in some social, agonistic, and economic situations.

The principles show that this probabilistic aspect of brain function is natural, and arises in part out of the noisy (random) spiking properties of neurons, and from noise in synaptic transmission. This provides a fundamental way of understanding probabilistic behavior that goes beyond only postulating some diffusion or random walk process, to understanding how the noise is generated, and thereby being able to make predictions about

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

how treatments that work in different ways on the machinery of the brain will influence behavior.

The principles can be tested, by comparing predictions from the stochastic neurodynamical approach and models with, for example, neuronal firing in the brain during decision processes, as exemplified in the work of Deco and Rolls (2006). One of the hypotheses that are generated and testable is that factors that influence the variability of the firing of neurons, such as synaptic or neuronal adaptation, will influence decision-making, memory recall, and the stability of short-term memory and attention independently of any change in the firing rate of the neurons. It is predicted that, for example, the variability of the choice will be altered by this, even though the proportion of the choices made for one vs another option is not altered (Deco and Rolls, 2006). Further, it is predicted that two types of manipulation of the system can influence the stability of cognitive operations. One set of factors that alter how fast the neurons fire when active is predicted to affect the stability of short-term memory and attention once started. These include NMDA activated receptor activated synaptic conductances. Another set of factors, such as alterations of GABA receptor activated synaptic ion channel conductances, is predicted to influence how stable the spontaneous state is, and thus how likely the system is to jump incorrectly into a pathological state of high activity. Evolution needs to set parameters for the operation of the system that makes it work with a suitable level of stability of both the spontaneous and the high firing rate attractor state, and as is always the case, natural selection operates on variation in the parameters found in the population of genotypes.

The principles and hypotheses are already finding applications in understanding pathological brain stability states, such as schizophrenia and obsessive-compulsive disorder. Indeed, these concepts lead to the interesting idea that there will be a range of stability scenarios present in different individuals in a population, with too little stability at one end of the distribution contributing to the symptoms of schizophrenia (Rolls et al., 2008b), and too much stability at the other end of the distribution contributing to the symptoms of obsessive-compulsive disorder (Rolls et al., 2008a). Of potentially great importance is that by having a model that is based on the ion channel conductances affected by different neurotransmitters, it is becoming possible to make predictions about what could be favorable combinations of treatments for particular disorders.

The approach and principles effectively enable one to link from the ion channel and synaptic level to the level of global effects on the operation of a large collection of neurons involved in a cognitive function such as memory recall, and to do this in the context of the stability of the whole system, which is influenced by the stochastic firing of the neurons.

References

Amit, D.J., Brunel, N., 1997. Model of global spontaneous activity and local structured activity during delay periods in the cerebral cortex. Cereb. Cortex 7, 237–252.
Barto, A.G., 1985. Learning by statistical cooperation of self-interested neuron-like computing elements. In: Computer and Information Science, vol. 85. Massachusetts, Amherst.
Battaglia, F.P., Treves, A., 1998. Stable and rapid recurrent processing in realistic auto-associative memories. Neural Comput. 10, 431–450.
Blackerby, R.F., 1993. Application of Chaos Theory to Psychological Models. Performance Strategies Publications, Austin, TX.
Blake, R., Logothetis, N.K., 2002. Visual competition. Nat. Rev. Neurosci. 3, 13–21.
Bogacz, R., Brown, E., Moehlis, J., Holmes, P., Cohen, J.D., 2006. The physics of optimal decision making: a formal analysis of models of performance in two-alternative forced-choice tasks. Psychol. Rev. 113, 700–765.
Brody, C.D., Romo, R., Kepecs, A., 2003. Basic mechanisms for graded persistent activity: discrete attractors, continuous attractors, and dynamic representations. Curr. Opin. Neurobiol. 13, 204–211.
Brown, S., Heathcote, A., 2005. A ballistic model of choice response time. Psychol. Rev. 112, 117–128.
Brunel, N., Wang, X.J., 2001. Effects of neuromodulation in a cortical network model of object working memory dominated by recurrent inhibition. J. Comput. Neurosci. 11, 63–85.
Carpenter, R.H.S., Williams, M.L., 1995. Neural computation of log likelihood in control of saccadic eye movements. Nature 377, 59–62.
Churchland, A.K., Kiani, R., Shadlen, M.N., 2008. Decision-making with multiple alternatives. Nat. Neurosci. 11, 693–702.
Corchs, S., Deco, G., 2002. Large-scale neural model for visual attention: integration of experimental single-cell and fmri data. Cereb. Cortex 12, 339–348.
Corrado, G.S., Sugrue, L.P., Seung, H.S., Newsome, W.T., 2005. Linear–nonlinear–Poisson models of primate choice dynamics. J. Exp. Anal. Behav. 84, 581–617.
Dawkins, M.S., 1995. Unravelling Animal Behaviour. Longman, Harlow.
de Lafuente, V., Romo, R., 2005. Neuronal correlates of subjective sensory experience. Nat. Neurosci. 12, 1698–1703.
de Lafuente, V., Romo, R., 2006. Neural correlate of subjective sensory experience gradually builds up across cortical areas. Proc. Natl. Acad. Sci. U.S.A. 103, 14266–14271.
Deco, G., Marti, D., 2007a. Deterministic analysis of stochastic bifurcations in multistable neurodynamical systems. Biol. Cybern. 96, 487–496.
Deco, G., Marti, D., 2007b. Extended method of moments for deterministic analysis of stochastic multistable neurodynamical systems. Phys. Rev. E: Stat. Nonlin. Soft Matter Phys. 75, 031913.
Deco, G., Perez-Sanagustin, M., de Lafuente, V., Romo, R., 2007a. Perceptual detection as a dynamical bistability phenomenon: a neurocomputational correlate of sensation. Proc. Natl. Acad. Sci. U.S.A. 104, 20073–20077.
Deco, G., Rolls, E.T., 2003. Attention and working memory: a dynamical model of neuronal activity in the prefrontal cortex. Eur. J. Neurosci. 18, 2374–2390.
Deco, G., Rolls, E.T., 2005a. Neurodynamics of biased competition and co-operation for attention: a model with spiking neurons. J. Neurophysiol. 94, 295–313.
Deco, G., Rolls, E.T., 2005b. Sequential memory: a putative neural and synaptic dynamical mechanism. J. Cogn. Neurosci. 17, 294–307.
Deco, G., Rolls, E.T., 2005c. Synaptic and spiking dynamics underlying reward reversal in orbitofrontal cortex. Cereb. Cortex 15, 15–30.
Deco, G., Rolls, E.T., 2006. Decision-making and Weber's law: a neurophysiological model. Eur. J. Neurosci. 24, 901–916.
Deco, G., Rolls, E.T., Horwitz, B., 2004. "What" and "Where" in visual working memory: a computational neurodynamical perspective for integrating fmri and single-neuron data. J. Cogn. Neurosci. 16, 683–701.
Deco, G., Scarano, L., Soto-Faraco, S., 2007b. Weber's law in decision making: integrating behavioral data in humans with a neurophysiological model. J. Neurosci. 27, 11192–11200.
Faisal, A.A., Selen, L.P., Wolpert, D.M., 2008. Noise in the nervous system. Nat. Rev. Neurosci. 9, 292–303.
Glimcher, P.W., 2003. The neurobiology of visual-saccadic decision making. Annu. Rev. Neurosci. 26, 133–179.
Glimcher, P.W., 2005. Indeterminacy in brain and behavior. Annu. Rev. Psychol. 56, 25–56.
Gold, J.I., Shadlen, M.N., 2000. Representation of a perceptual decision in developing oculomotor commands. Nature 404, 390–394.
Gold, J.I., Shadlen, M.N., 2002. Banburismus and the brain: decoding the relationship between sensory stimuli decisions reward. Neuron 36, 299–308.
Green, D., Swets, J., 1966. Signal Detection Theory and Psychophysics. Wiley, New York.
Heinrichs, D.W., 2005. Antidepressants and the chaotic brain: implications for the respectful treatment of selves. Phil. Psychiatr. Psychol. 12, 215–227.
Hernandez, A., Salinas, E., Garcia, R., Romo, R., 1997. Discrimination in the sense of flutter: new psychophysical measurements in monkeys. J. Neurosci. 17, 6391–6400.
Hernandez, A., Zainos, A., Romo, R., 2002. Temporal evolution of a decision-making process in medial premotor cortex. Neuron 33, 959–972.
Horne, J., 2006. Sleepfaring: A Journey Through the Science of Sleep. Oxford University Press, Oxford.
Hubel, D.H., Wiesel, T.N., 1968. Receptive fields and functional architecture of macaque monkey striate cortex. J. Physiol. 195, 215–243.
Jackson, B.S., 2004. Including long-range dependence in integrate-and-fire models of the high interspike-interval variability of cortical neurons. Neural Comput. 16, 2125–2195.
Kacelnik, A., Brito e Abreu, F., 1998. Risky choice and Weber's law. J. Theor. Biol. 194, 289–298.
Kandel, E.R., Schwartz, J.H., Jessel, T.H. (Eds.), 2000. Principles of Neural Science. McGraw-Hill, New York.
Kramers, H., 1940. Brownian motion in a field of force and the diffusion model of chemical reactions. Physicas 7, 284–304.
Krebs, J.R., Davies, N.B. (Eds.), 1991. Behavioural Ecology. Blackwell, Oxford.
La Camera, G., Rauch, A., Luscher, H.R., Senn, W., Fusi, S., 2004. Minimal models of adapted neuronal response to in vivo-like input currents. Neural Comput. 16, 2101–2124.
Lewis, M.D., 2005. Bridging emotion theory and neurobiology through dynamic systems modeling. Behav. Brain Sci. 28, 169–194 (discussion 194–245).
Loh, M., Rolls, E.T., Deco, G., 2007a. A dynamical systems hypothesis of schizophrenia. PLoS Comput. Biol. 3, e228 doi:210.1371/journal. pcbi.0030228.
Loh, M., Rolls, E.T., Deco, G., 2007b. Statistical fluctuations in attractor networks related to schizophrenia. Pharmacopsychiatry 40, S78–S84.
Machens, C.K., Romo, R., Brody, C.D., 2005. Flexible control of mutual inhibition: a neural model of two-interval discrimination. Science 307, 1121–1124.
Maier, A., Logothetis, N.K., Leopold, D.A., 2005. Global competition dictates local suppression in pattern rivalry. J. Vis. 5, 668–677.

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006

Marti, D., Deco, G., Del Giudice, P., Mattia, M., 2006. Reward-based probabilistic decision-making: mean-field predictions and spiking simulations. Neurocomputing 69, 1175–1178.
Marti, D., Deco, G., Mattia, M., Gigante, G., Del Giudice, P., 2008. A fluctuation-driven mechanism for slow decision processes in reverberant networks. PLoS ONE 3, e2534.
Mattia, M., Del Giudice, P., 2002. Attention and working memory: a dynamical model of neuronal activity in the prefrontal cortex. Phys. Rev. E 66, 51917–51919.
Maynard Smith, J., 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge.
Maynard Smith, J., 1984. Game theory and the evolution of behaviour. Behav. Brain Sci. 7, 95–125.
Mountcastle, V.B., Talbot, W.H., Darian-Smith, I., Kornhuber, H.H., 1967. Neural basis of the sense of flutter-vibration. Science 155, 597–600.
Mountcastle, V.B., Talbot, W.H., Sakata, H., Hyvarinen, J., 1969. Cortical neuronal mechanisms in flutter-vibration studied in unanesthetized monkeys. Neuronal periodicity and frequency discrimination. J. Neurophysiol. 32, 452–484.
Newsome, W.T., Britten, K.H., Movshon, J.A., 1989. Neuronal correlates of a perceptual decision. Nature 341, 52–54.
Panzeri, S., Rolls, E.T., Battaglia, F., Lavis, R., 2001. Speed of information retrieval in multilayer networks of integrate-and-fire neurons. Netw. Comput. Neural Syst. 12, 423–440.
Peled, A., 2004. From plasticity to complexity: a new diagnostic method for psychiatry. Med. Hypotheses 63, 110–114.
Platt, M.L., Glimcher, P.W., 1999. Neural correlates of decision variables in parietal cortex. Nature 400, 233–238.
Ratcliff, R., Van Zandt, T., McKoon, G., 1999. Connectionist and diffusion models of reaction time. Psychol. Rev. 106, 261–300.
Renart, A., Brunel, N., Wang, X.-J., 2003. Mean field theory of irregularly spiking neuronal populations and working memory in recurrent cortical networks. In: Feng, J. (Ed.), Computational Neuroscience: A Comprehensive Approach. Chapman and Hall, Boca-Raton, pp. 431–490.
Ricciardi, L.M., Sacerdote, L., 1979. The Ornstein-Uhlenbeck process as a model for neuronal activity. I. Mean and variance of the firing time. Biol. Cybern. 35, 1–9.
Riley, M.A., Turvey, M.T., 2001. The self-organizing dynamics of intentions and actions. Am. J. Psychol. 114, 160–169.
Rolls, E.T., 2005. Emotion Explained. Oxford University Press, Oxford.
Rolls, E.T., 2007. A computational neuroscience approach to consciousness. Neural Netw. 20, 962–982.
Rolls, E.T., 2008a. Emotion, higher order syntactic thoughts, and consciousness. In: Weiskrantz, L., Davies, M.K. (Eds.), Frontiers of Consciousness. Oxford University Press, Oxford, pp. 131–167.
Rolls, E.T., 2008b. Memory, Attention, and Decision-making: A Unifying Computational Neuroscience Approach. Oxford University Press, Oxford.
Rolls, E.T., Deco, G., 2002. Computational Neuroscience of Vision. Oxford University Press, Oxford.
Rolls, E.T., Deco, G., in preparation. Stochastic Dynamics as a Principle of Brain Function.
Rolls, E.T., Kesner, R.P., 2006. A computational theory of hippocampal function, and empirical tests of the theory. Prog. Neurobiol. 79, 1–48.
Rolls, E.T., Loh, M., Deco, G., 2008a. An attractor hypothesis of obsessive-compulsive disorder. Eur. J. Neurosci. 28, 782–793.
Rolls, E.T., Loh, M., Deco, G., Winterer, G., 2008b. Computational models of schizophrenia and dopamine modulation in the prefrontal cortex. Nat. Rev. Neurosci. 9, 696–709.
Rolls, E.T., McCabe, C., Redoute, J., 2008c. Expected value, reward outcome, and temporal difference error representations in a probabilistic decision task. Cereb. Cortex 18, 652–663.
Rolls, E.T., Treves, A., 1998. Neural Networks and Brain Function. Oxford University Press, Oxford.
Rolls, E.T., Tromans, J., Stringer, S.M., 2008d. Spatial scene representations formed by self-organizing learning in a hippocampal extension of the ventral visual system. Eur. J. Neurosci. 28, 2116–2127.
Romo, R., Brody, C.D., Hernandez, A., Lemus, L., 1999. Neuronal correlates of parametric working memory in the prefrontal cortex. Nature 399, 470–473.
Romo, R., Hernandez, A., Zainos, A., 2004. Neuronal correlates of a perceptual decision in ventral premotor cortex. Neuron 41, 165–173.
Romo, R., Hernandez, A., Zainos, A., Lemus, L., Brody, C.D., 2002. Neuronal correlates of decision-making in secondary somatosensory cortex. Nat. Neurosci. 5, 1217–1225.
Romo, R., Hernandez, A., Zainos, A., Salinas, E., 1998. Somatosensory discrimination based on cortical microstimulation. Nature 392, 387–390.
Romo, R., Hernandez, A., Zainos, A., Salinas, E., 2003. Correlated neuronal discharges that increase coding efficiency during perceptual discrimination. Neuron 38, 649–657.
Romo, R., Salinas, E., 2001. Touch and go: decision-making mechanisms in somatosensation. Annu. Rev. Neurosci. 24, 107–137.
Romo, R., Salinas, E., 2003. Flutter discrimination: neural codes, perception, memory and decision making. Nat. Rev. Neurosci. 4, 203–218.
Roxin, A., Ledberg, A., 2008. Neurobiological models of two-choice decision making can be reduced to a one-dimensional nonlinear diffusion equation. PLoS Comput. Biol. 4, e1000046.
Schall, J.D., 2001. Neural basis of deciding, choosing and acting. Nat. Rev. Neurosci. 2, 33–42.
Shadlen, M.N., Newsome, W.T., 1996. Motion perception: seeing and deciding. Proc. Natl. Acad. Sci. U.S.A. 93, 628–633.
Shulman, G.L., Ollinger, J.M., Linenweber, M., Petersen, S.E., Corbetta, M., 2001. Multiple neural correlates of detection in the human brain. Proc. Natl. Acad. Sci. U.S.A. 98, 313–318.
Sigala, N., Logothetis, N.K., 2002. Visual categorization shapes feature selectivity in the primate temporal cortex. Nature 415, 318–320.
Smith, P.L., Ratcliff, R., 2004. Psychology and neurobiology of simple decisions. Trends Neurosci. 27, 161–168.
Stocks, N.G., 2000. Suprathreshold stochastic resonance in multilevel threshold systems. Phys. Rev. Lett. 84, 2310–2313.
Sugrue, L.P., Corrado, G.S., Newsome, W.T., 2005. Choosing the greater of two goods: neural currencies for valuation and decision making. Nat. Rev. Neurosci. 6, 363–375.
Sutton, R.S., Barto, A.G., 1981. Towards a modern theory of adaptive networks: expectation and prediction. Psychol. Rev. 88, 135–170.
Szabo, M., Almeida, R., Deco, G., Stetter, M., 2004. Cooperation and biased competition model can explain attentional filtering in the prefrontal cortex. Eur. J. Neurosci. 19, 1969–1977.
Szabo, M., Deco, G., Fusi, S., Del Giudice, P., Mattia, M., Stetter, M., 2006. Learning to attend: modeling the shaping of selectivity in infero-temporal cortex in a categorization task. Biol. Cybern. 94, 351–365.
Talbot, W.H., Darian-Smith, I., Kornhuber, H.H., Mountcastle, V.B., 1968. The sense of flutter-vibration: comparison of the human capacity with response patterns of mechanoreceptive afferents from the monkey hand. J. Neurophysiol. 31, 301–334.
Tanji, J., 2001. Sequential organization of multiple movements: involvement of cortical motor areas. Annu. Rev. Neurosci. 24, 631–651.
Thompson, K.G., Hanes, D.P., Bichot, N.P., Schall, J.D., 1996. Perceptual and motor processing stages identified in the activity of macaque frontal eye field neurons during visual search. J. Neurophysiol. 76, 4040–4055.
Treves, A., 1993. Mean-field analysis of neuronal spike dynamics. Network 4, 259–284.
Tuckwell, H., 1988. Introduction to Theoretical Neurobiology. Cambridge University Press, Cambridge.
Usher, M., McClelland, J.L., 2001. The time course of perceptual choice: the leaky, competing accumulator model. Psychol. Rev. 108, 550–592.
Wang, X.-J., 1999. Synaptic basis of cortical persistent activity: the importance of NMDA receptors to working memory. J. Neurosci. 19, 9587–9603.
Wang, X.J., 2002. Probabilistic decision making by slow reverberation in cortical circuits. Neuron 36, 955–968.
Welford, A.T. (Ed.), 1980. Reaction Times. Academic Press, London.
Wong, K.F., Wang, X.J., 2006. A recurrent network mechanism of time integration in perceptual decisions. J. Neurosci. 26, 1314–1328.

Please cite this article in press as: Deco, G., et al., Stochastic dynamics as a principle of brain function. Prog. Neurobiol. (2009), doi:10.1016/j.pneurobio.2009.01.006