



## Brain mechanisms for perceptual and reward-related decision-making

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### ARTICLE INFO

#### Article history:

Received 22 September 2011

Received in revised form 24 January 2012

Accepted 24 January 2012

Available online 2 February 2012

#### Keywords:

Decision making

Attractor network

Confidence

Dynamical neuropsychiatry

Noise in the brain

Vibrotactile decision-making

Reward value decision-making

### ABSTRACT

Phenomenological models of decision-making, including the drift–diffusion and race models, are compared with mechanistic, biologically plausible models, such as integrate-and-fire attractor neuronal network models. The attractor network models show how decision confidence is an emergent property; and make testable predictions about the neural processes (including neuronal activity and fMRI signals) involved in decision-making which indicate that the medial prefrontal cortex is involved in reward value-based decision-making. Synaptic facilitation in these models can help to account for sequential vibrotactile decision-making, and for how postponed decision-related responses are made. The randomness in the neuronal spiking-related noise that makes the decision-making probabilistic is shown to be increased by the graded firing rate representations found in the brain, to be decreased by the diluted connectivity, and still to be significant in biologically large networks with thousands of synapses onto each neuron. The stability of these systems is shown to be influenced in different ways by glutamatergic and GABAergic efficacy, leading to a new field of dynamical neuropsychiatry with applications to understanding schizophrenia and obsessive–compulsive disorder. The noise in these systems is shown to be advantageous, and to apply to similar attractor networks involved in short-term memory, long-term memory, attention, and associative thought processes.

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### Contents

1. Introduction . . . . .	195
2. Overview of different models of decision-making . . . . .	195
2.1. Sequential-sampling models . . . . .	195
2.1.1. Signal detection theory and the sequential probability ratio test (SPRT) . . . . .	195
2.1.2. The drift–diffusion model . . . . .	197
2.1.3. The race model . . . . .	198
2.2. Biologically motivated rate models . . . . .	198
2.2.1. Feedforward inhibition (FFI) . . . . .	199
2.2.2. Lateral inhibition and the leaky competing accumulator . . . . .	199
2.3. Attractor models . . . . .	199
2.3.1. Biophysically realistic attractor model with spiking neurons . . . . .	200
2.3.2. Model reductions . . . . .	202
2.4. Distinguishing model approaches . . . . .	203
3. Synaptic facilitation as part of the mechanism for sequential decision-making, and for decision-making with postponed responses . . . . .	204

**Abbreviations:** 2AFC, 2-alternative forced-choice; AMPA,  $\alpha$ -amino-3-hydroxy-5-methyl-4-isoazolepropionic acid; DDM, drift diffusion model; dlPFC, dorso-lateral prefrontal cortex; EPSC, excitatory post-synaptic current; ER, error rate; FEF, frontal eye-field; FF, feedforward; FFI, feedforward inhibition; GABA,  $\gamma$ -aminobutyric acid; IPSC, inhibitory post-synaptic current; LCA, leaky competing accumulator; LIF, leaky integrate-and-fire; LIP, lateral intraparietal cortex; LR, likelihood ratio; MT, middle temporal area; NMDA, N-methyl-D-aspartate acid; O-U, Ornstein–Uhlenbeck; PDF, probability density function; PFC, prefrontal cortex; PPC, posterior parietal cortex; PRR, parietal reach region; RDM, random-dot motion; RF, response field; R-target, response target; RT, reaction time; SAT, speed-accuracy tradeoff; SC, superior colliculus; SDT, signal detection theory; SPRT, sequential probability ratio test.

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3.1. Synaptic facilitation and sequential decision-making	204
3.2. Synaptic facilitation, graded firing rates, and postponed decisions	205
4. Confidence in decisions before the outcome is known	207
4.1. Decision confidence and discriminability	207
4.2. Decision confidence and correct vs incorrect decisions	208
4.3. Decisions about decisions: monitoring decisions	208
5. Predictions of decisions from noise in the brain even before the evidence for the decision has been provided	210
6. What influences noise in the brain, and does noise still apply in large biologically plausible networks?	210
6.1. Graded firing rate representations increase noise in decision-making networks	210
6.2. Diluted network connectivity decreases the noise in decision-making networks	211
7. Dynamical neuropsychiatry	211
8. Decision-making, oscillations, and communication through coherence	211
9. Conclusions	211
Acknowledgements	212
References	212

## 1. Introduction

One approach to understanding decision-making is incorporated in a class of phenomenological “sequential sampling” models, which analyze the decision process in terms of a decision variable that evolves in time until it reaches a decision threshold (e.g. Laming, 1968; Ratcliff and Smith, 2004; Stone, 1960; Vickers, 1970). Recordings of single neuron activity during decision-making in primates (reviewed by Gold and Shadlen, 2007; Hernandez et al., 2010; Opris and Bruce, 2005; Romo and Salinas, 2003) provided constraints for these models, and also stimulated the development of biologically plausible models of decision-making (Deco and Rolls, 2006; Rolls and Deco, 2010; Wang, 2002). In Section 2 of this paper we provide an overview of different approaches to decision-making, describing the evolution from phenomenological models to neurophysiologically plausible integrate-and-fire attractor models of decision-making. We particularly highlight differences between the models and approaches.

In Section 3 we describe the development of these biologically plausible models to incorporate synaptic facilitation. We show how synaptic facilitation can be an important component in sequential decision-making tasks, and in tasks in which the report of the decision must be postponed for a delay period.

In Section 4 we show how confidence in a decision before the outcome is known is an emergent property of the decision-making mechanism in the brain. We also show how a second decision based on the confidence in the first decision can be made using a second attractor network. This provides a mechanism for monitoring previous decisions.

In Section 5 we show how noise in the brain can be used to predict a decision even before the evidence for the decision has been provided.

In Section 6 we consider factors that influence the level of noise in a decision-making network. This treatment provides a crucial foundation for understanding how the proposed mechanisms operate in large decision-making cortical networks with graded firing rate representations and diluted connectivity in the human brain.

In Section 7 we describe the applications of this stochastic neurodynamics approach to neuropsychiatry, including schizophrenia and obsessive-compulsive disorder.

In Section 8, we consider some effects of oscillations in the brain on decision-making processes.

## 2. Overview of different models of decision-making

In the following, we will review the most common models of two-alternative forced choice (2AFC) decision-making and their theoretical origins. We will start with basic, linear, conceptual models, which successfully capture decision behavior, followed by

attempts to implement these models in a physiologically plausible way. Then we will turn to nonlinear attractor models and describe a biophysically inspired implementation of an attractor model with spiking neurons (Deco and Rolls, 2006; Rolls and Deco, 2010; Wang, 2002, 2008). Our objective is to provide an intuitive overview. Consequently, we restrict our formal presentation to basic equations and characteristic model features and refer to the original publications for detailed theoretical analysis.

### 2.1. Sequential-sampling models

Present conceptual models of decision behavior considering noisy evidence build on signal detection theory (SDT), developed to describe categorical choices under uncertainty (Green and Swets, 1966; Tanner and Swets, 1954). SDT typically assumes fixed, short stimulus times that are out of the subject's control. The class of models summarized as ‘sequential sampling models’ forms the logical extension of SDT to temporally stretched streams of (noisy) data (Stone, 1960; Wald, 1947). In addition to the probability of correct responses, these models give predictions of subjects' reaction times in ‘free response’ 2AFC paradigms. To form a decision, evidence for each of the two alternatives is integrated over time. Whether an independent integration for each alternative (e.g. a race model), or an integration of the difference in evidence (e.g. a drift-diffusion model) gives a better account of experimental 2AFC data, is, however, still open to debate, although the latter seems to fit a wider set of experimental observations (Bogacz et al., 2006; Ratcliff et al., 2003; Ratcliff and Smith, 2004).

#### 2.1.1. Signal detection theory and the sequential probability ratio test (SPRT)

In simple perceptual 2AFC tasks, subjects are often faced with problems such as: ‘Has a dim light been flashed or not?’ or: ‘Which of two similar images has been presented?’ Signal detection theory provides a prescription for these kinds of decisions, where one of two hypotheses has to be chosen on the basis of a single observation in the presence of uncertainty, or noise (Gold and Shadlen, 2007). If the sensory observation is informative about the hypotheses, it provides ‘evidence’ favoring one alternative. We will generally refer to information that is indicative of a choice as evidence  $e$ . The two hypotheses  $H_1$  and  $H_2$  stand for the two choice-alternatives. The conditional probability  $p(e|H_1)$  denotes the probability of observing evidence  $e$  if  $H_1$  is true.

Depending on the signal-to-noise ratio ( $\mu/\sigma$ ) and the similarity of the hypotheses ( $\mu_1-\mu_2$ ), the probability density functions (PDFs) of the two alternatives overlap to some degree (Fig. 1).

The smaller the signal-to-noise ratio is, the higher is the overlap of the PDF. Likewise, the more distinguishable the stimuli are, the smaller is the overlap. In the case of sensory stimuli the PDFs are

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