

Decision-making mechanisms in the brain

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Abstract. Behavioral, neurophysiological, and theoretical studies are converging to a common theory of decision-making that assumes an underlying diffusion process which integrates both the accumulation of perceptual and cognitive evidence for making the decision and motor choice in one unifying neural network. In particular, neuronal activity in the ventral premotor cortex (VPC) is related to decision-making while trained monkeys compare two mechanical vibrations applied sequentially to the tip of a finger to report which of the two stimuli have the higher frequency (Romo et al. 2004, *Neuron* 41: 165). In particular, neurons were found whose response depended only on the difference between the two applied frequencies, the sign of that difference being the determining factor for correct task performance. We describe an integrate-and-fire attractor model with realistic synaptic dynamics including AMPA, NMDA and GABA synapses which can reproduce the decision-making related response selectivity of VPC neurons during the comparison period of the task. Populations of neurons for each decision in the biased competition attractor receive a bias input that depends on the firing rates of neurons in the VPC that code for the two vibrotactile frequencies. It was found that if the connectivity parameters of the network are tuned, using mean-field techniques, so that the network has two possible stable stationary final attractors respectively related to the two possible decisions, then the firing rate of the neurons in whichever attractor wins reflects the sign of the difference in the frequencies being compared but not the absolute frequencies. Thus Weber's law for frequency comparison is not encoded by the firing rate of the neurons in these attractors. An analysis of the nonstationary evolution of the dynamics of the network model shows that Weber's law is implemented in the probability of transition from the initial spontaneous firing state to one of the two possible attractor states. In this way, statistical fluctuations due to finite size noise produced by the spiking dynamics play a crucial role in the decision-making process.

Keywords: Spiking Neurodynamics, Decision-Making

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INTRODUCTION

Recently, the problem of decision-making has become the center of interest of many neuroscientists aiming to understand the neural basis of intelligent behavior by linking perception and action. Behavioral, neurophysiological, and theoretical studies are converging to a common theory that assumes an underlying diffusion process which integrates both the accumulation of perceptual and cognitive evidence for making the decision and motor choice in one unifying neural network. A number of neurophysiological experiments on decision-making are providing information on the neural mech-

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anisms underlying perceptual comparison, by analyzing the responses of neurons that correlate with the animal's behavior [1, 2, 3]. An important finding is that cortical areas involved in generating motor responses also show activity reflecting a gradual accumulation of evidence for choosing one or another decision, such that the process of making a decision and action generation are closely related.

In this work, we review the neurodynamical mechanisms engaged in the process of comparison in a decision-making paradigm from the perspective of Weber's law, that is, we investigate the probabilistic behavior of the neural responses responsible for detecting a just noticeable stimulus difference. An ideal paradigm for studying this is the vibrotactile sequential discrimination task [3]. In this two-alternative, forced-choice task, subjects must decide which of two mechanical vibrations applied sequentially to their fingertips has the higher frequency of vibration. The neurophysiological and behavioral work of Romo and colleagues using this task has been recently reviewed by Romo and Salinas [4]. In particular, single neuron recordings in the ventral premotor cortex (VPC) reveal neurons whose firing rate was dependent only on the difference between the two applied frequencies, the sign of that difference being the determining factor for correct task performance [3]. These neurons, which are shown in Fig. 2(G-H-I) of Romo et al. [3], reflect the decision-making step of the comparison, and therefore we model here their probabilistic dynamical behavior as reported by the experimental work; and through the theoretical analyses we will relate these neurons' behavior to Weber's law. We analyze and model the activity of these VPC neurons by means of a theoretical framework first proposed by Wang [5], but investigating now the role of finite-size fluctuations in the probabilistic behaviour of the decision-making neurodynamics, and especially the neural encoding of Weber's law.

The most interesting result is that, if the connectivity parameters of the network are tuned, using mean-field techniques, so that the network has two possible stable stationary final attractors respectively related to the two possible decisions, then the firing rate of the neurons in whichever attractor wins reflects the difference in the frequencies (Δf) being compared but not on the absolute frequencies. Thus Weber's law for frequency comparison is not encoded by the firing rate of these attractors. An analysis of the nonstationary evolution of the dynamics of the network model, performed by explicit full spiking simulations, shows that Weber's law is implemented in the probability of transition from the initial spontaneous firing state to one of the two possible attractor states. In this way, statistical fluctuations due to finite size noise play a crucial role in the decision-making process. This results also change our view of neural coding. In this decision-making paradigm, the rate of neurons in VPC encode the results of the comparison and therefore the motor-response, but not if the difference will be noticeable or not, i.e. what Weber called "sensation". The probability of obtaining a specific decision, i.e. of noticing a change, is encoded in the stochastic dynamics of the network; and more specifically, in the connectivity between the different populations and in the size of the populations, which are the origin of the fluctuations that drive the transitions. In other words, the neural code is not only reflected by the rate of activity of the neurons, but also by the probability of getting that rate. This means that an essential part of the encoding of information is contained in the *synapses* and in the *finite size* of the network. This is the basis of a probabilistic rate code.

THEORETICAL FRAMEWORK

The model of decision-making consists of a network of integrate-and-fire neurons with realistic synaptic dynamics including AMPA, NMDA and GABA synapses which can reproduce the decision-making related response selectivity of VPC neurons during the comparison period of the task. In the model, competition and cooperation mechanisms, implemented in an attractor network with two recurrently connected populations of excitatory neurons, mutually connected with a common inhibitory population, can account for the most relevant characteristics of the experimentally measured decision-related neuronal activity. This neurodynamical formulation is based on the principle of biased competition/cooperation that has been able to simulate and explain, in a unifying framework, attention, working memory, and reward processing in a variety of tasks and at different cognitive neuroscience experimental measurement levels [6, 7, 8].

In this framework, probabilistic decision-making is implemented by a network of interacting neurons organized into a discrete set of populations, as depicted in Fig. 1. Populations are defined as groups of excitatory or inhibitory neurons sharing the same inputs and connectivities. The network contains N_E (excitatory) pyramidal cells and N_I inhibitory interneurons. In our simulations, we use $N_E = 800$ and $N_I = 200$, consistent with the neurophysiologically observed proportion of 80% pyramidal cells versus 20% interneurons [9, 6]. The neurons are fully connected (with synaptic strengths as specified below). The specific populations have specific functions in the task. In our minimal model, we assume that the specific populations encode the categorical result of the comparison between the two sequentially applied vibrotactile stimulation, f_1 and f_2 , i.e. if $f_1 > f_2$ or $f_1 < f_2$. Each specific population of excitatory cells contains rN_E neurons (in our simulations $r = 0.1$). In addition there is one non-specific population, named "Non-specific", which groups all other excitatory neurons in the modeled brain area not involved in the present task and one inhibitory population, named "Inhibitory", grouping the local inhibitory neurons in the modeled brain area. The latter population regulates the overall activity and implements competition in the network by spreading a global inhibition signal.

Because we are mainly interested in the nonstationary probabilistic behavior of the network, the proper level of description at the microscopic level is captured by the spiking and synaptic dynamics of one-compartment *Integrate-and-Fire* (IF) neuron models. An IF neuron integrates the afferent current generated by the incoming spikes, and fires when the depolarization of the cell membrane crosses a threshold. At this level of detail the model allows the use of realistic biophysical time constants, latencies and conductances to model the synaptic current, which in turn allows a thorough study of the realistic time scales and firing rates involved in the evolution of the neural activity. Consequently, the simulated neuronal dynamics, that putatively underly cognitive processes, can be quantitatively contrasted with experimental data. For this reason, it is convenient to include a thorough description of the different time courses of the synaptic activity. The IF neuronal cells will be modeled as having three types of receptor mediating the synaptic currents flowing into them: AMPA, NMDA glutamate and GABA receptors: the excitatory recurrent post-synaptic currents (EPSCs) are considered to be mediated by AMPA (fast) and NMDA (slow) receptors; external EPSCs imposed onto the network from outside are assumed to be driven only by AMPA receptors. Inhibitory post-synaptic

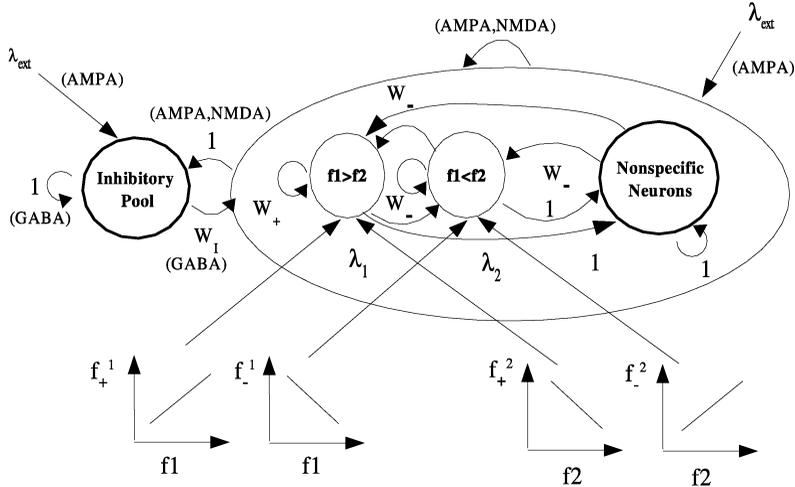


FIGURE 1. Minimal neurodynamical model for a probabilistic decision-making network that performs the comparison of two mechanical vibrations applied sequentially (f_1 and f_2). The model implements a dynamical competition between different neurons. The network contains excitatory pyramidal cells and inhibitory interneurons. The neurons are fully connected (with synaptic strengths as specified in the text). Neurons are clustered into populations or populations. There are two different types of population: excitatory and inhibitory. There are two subtypes of excitatory population, namely: specific and nonselective. Specific populations encode the result of the comparison process in the two-interval vibrotactile discrimination task, i.e. if $f_1 > f_2$ or $f_1 < f_2$. The recurrent arrows indicate recurrent connections between the different neurons in a population.

currents (IPSCs) to both excitatory and inhibitory neurons are mediated by GABA receptors. The details of the mathematical formulation are summarized in previous works [10, 11].

We modulate the conductance values for the synapses between pairs of neurons by connection weights, which can deviate from their default value 1. The structure and function of the network is achieved by differentially modulating these weights within and between populations of neurons. The labeling of the weights is defined in Fig. 1. We assume that the connections are already formed, e.g. by earlier self organization mechanisms, as if they were established by Hebbian learning, i.e. the coupling will be strong if the pair of neurons have correlated activity, and weak if they are activated in an uncorrelated way. We assume that the two decisions ‘ $f_1 > f_2$ ’ and ‘ $f_1 < f_2$ ’, corresponding to the two categories, are already encoded, in the sense that the monkey is already trained that pushing one or the other button, but not both, might bring him some reward. As a consequence of this, neurons within a specific excitatory population are mutually coupled with a strong weight w_+ . Further more, the populations encoding these two decisions are likely to have anti-correlated activity in this behavioral context, resulting in weaker than average connections between them. Consequently, we choose a weaker value $w_- = 1 - r(w_+ - 1)/(1 - r)$, so that the overall recurrent excitatory synaptic drive in the spontaneous state remains constant as w_+ is varied [10]. Neurons in the inhibitory

population are mutually connected with an intermediate weight $w = 1$. They are also connected with all excitatory neurons in the same layer with the same intermediate weight, which for excitatory-to-inhibitory connections is $w = 1$, and for inhibitory-to-excitatory connections is denoted by a weight w_I . Neurons in a specific excitatory population are connected to neurons in the nonselective population in the same layer with a feedforward synaptic weight $w = 1$ and a feedback synaptic connection of weight w_- . Each individual population is driven by two different kinds of input. First, all neurons in the model network receive spontaneous background activity from outside the module through $N_{ext} = 800$ external excitatory connections. Each connection carries a Poisson spike train at a spontaneous rate of 3 Hz, which is a typical value observed in the cerebral cortex. This results in a background external input with a rate of 2.4 kHz for each neuron. Second, the neurons in the two specific populations additionally receive external inputs encoding stimulus specific information. They are assumed to originate from the somatosensory area S2 and from the PFC, encoding the frequency of both stimuli f_1 (stored) and f_2 (present) to be compared during the comparison period, i.e. when the second stimulus is applied. As we mention above, there are two types of S2 and PFC neurons, namely: neurons with a positive and others with a negative monotonic relationship between the stimulus and the firing rate. Based on the experimental results [3], we model the firing rate of positive monotonic neurons by $f_+^x = 5 + 2.3f_x$ Hz, and the firing rate of negative monotonic neurons by $f_-^x = 25 - 0.6f_x$ Hz, where f_x is the frequency of the vibrotactile stimulation in Hz (i.e., f_x is equal to f_1 or f_2). When stimulating, the rate of the Poisson train to the neurons of both specific populations $f_1 > f_2$ and $f_1 < f_2$ is increased by an extra value of $\lambda_1 = f_+^1 + f_-^2$ and $\lambda_2 = f_-^1 + f_+^2$, respectively, coding the two vibrotactile stimuli to be compared.

A first requirement is that at least for the stationary conditions, i.e. for periods after the dynamical transients, different possible attractors are stable. The attractors of interest for our task correspond to the activation (high spiking rates) or not activation (low spiking rates) of the neurons in the specific populations $f_1 > f_2$ and $f_1 < f_2$. The activation of the specific population $f_1 > f_2$ ($f_1 < f_2$) and the simultaneous non activation of the specific population $f_1 < f_2$ ($f_1 > f_2$), corresponds to an encoding "*single state*" associated with a motor response of the monkey reporting the categorical decision $f_1 > f_2$ ($f_1 < f_2$). The non activation of both specific populations ("*spontaneous state*") corresponds to an encoding state that can not take a behavioral decision, i.e. the monkey does not answer, or generates a random motor response by chance. The same happens if both specific populations are activated ("*pair state*"). Because the monkey responds in a probabilistic way conditioned by the different stimuli, the operating working point of the network should be such that both possible categorical decisions, i.e. both possible single states, and eventually (depending on the stimuli) the other pair and spontaneous state, are possible stable states. We use mean-field techniques for analyzing the nonstationary asymptotic states via a reduced model.

A full characterization of the dynamics, and specially of its probabilistic behavior, including the non-stationary regime of the system, can only be obtained through computer simulations of the spiking network model. Moreover, these simulations enable comparisons between the model and neurophysiological data. The simulations of the spiking dynamics of the network were integrated numerically (1000 integrate-and-fire equations for each neuron in the network and simultaneously 2,600,000 AMPA, NMDA

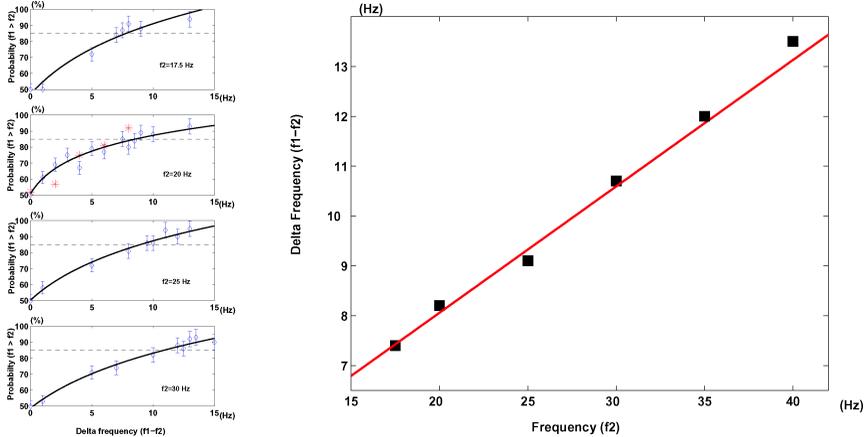


FIGURE 2. (Color online) (Left) Probability of correct discrimination as a function of the difference between the two presented vibrotactile frequencies to be compared, and (Right) Weber’s law for the vibrotactile discrimination task.

and GABA-synaptic equations) using the second order Runge-Kutta method with step size 0.05 ms. Each simulation was started by a period of 500 ms where no stimulus was presented, to allow the network to stabilize. The nonstationary evolution of spiking activity is averaged over 200 trials initialized with different random seed. In the next section, we present and interpret the probabilistic behavioral response and the underlying neural correlates, obtained by the analysis and simulations of the nonstationary stochastic spiking dynamics.

The left panel of Fig. 2 shows the probability of correct discrimination as a function of the difference between the two presented vibrotactile frequencies to be compared. We assume that $f_1 > f_2$ by a Δ -value, i.e. $f_1 = f_2 + \Delta$. (In the figure this value is called “Delta frequency ($f_1 - f_2$)”). Each diamond-point in the figure corresponds to the result calculated by averaging 200 trials of the full spiking simulations. The lines were calculated by fitting the points with a quadratic interpolating polynomial. A correct classification occurs when during the 500 ms comparison period, the network evolves to a “single-state” attractor that shows a high level of spiking activity (larger than 10 Hz) for the population ($f_1 > f_2$), and simultaneously a low level of spiking activity for the population ($f_1 < f_2$) (at the level of the spontaneous activity). One can observe from the different panels corresponding to different base-frequencies f_2 , that for reaching a threshold of correct classification of for example 85% (horizontal dashed line), the difference between f_1 and f_2 must become larger as f_2 increases. The right panel of the figure plots this critical discrimination Δ -value corresponding to an 85% correct performance level (the “difference-threshold”) as a function of the base-frequency f_2 . The “difference-threshold” increases linearly as a function of the base-frequency. This corresponds to Weber’s law for the vibrotactile discrimination task.

The way in which the system settles (i.e. the probability of reaching one attractor state vs the other from the initial spontaneous state, and the time it takes) depends on factors

that include the distortion of the attractor landscapes produced by the biasing inputs λ_1 and λ_2 which will influence both the shapes and the depth of the attractor basins, and the finite size noise effects. Of particular importance in relation to Weber's law is likely to be that when λ_1 and λ_2 increase, the increased firing of the neurons in the two attractors results in more activity of the inhibitory feedback neurons, which then produce effectively divisive inhibition on the principal cells of the attractor network. This is reflected in the conductance change produced by the GABA inputs to the pyramidal cells. The inhibitory feedback is mainly divisive because the GABA activated channels operate primarily as a current shunt, and do not produce much hyperpolarization, given that V_I is relatively close to the membrane potential. After the division implemented by the feedback inhibition, the differential bias required to push the network reliably into one of the attractors must then be larger, and effectively the driving force ($\lambda_1 - \lambda_2$ or $\Delta\lambda$) must get larger in proportion to the inhibition. As the inhibition is proportional to λ , this produces the result that $\Delta\lambda/\lambda$ is approximately a constant. We thus propose that Weber's Law, $\Delta I/I$ is a constant, is implemented by shunting effects acting on pyramidal cells that are produced by inhibitory neuron inputs which increase linearly as the baseline input I increases, so that the difference of intensities ΔI required to push the network reliably into one of its attractors must increase in proportion to the base input I .

Although the model described here is effectively a single attractor network, we note that 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 a single attractor 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 [12, 6]. 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 in a number of connected brain areas [3].

This approach to how networks takes decisions probably has implications throughout the brain. For 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. 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.

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 this is due to adaptation effects in integrate-and-fire networks, and that

the time of flipping depends on the average adaptation rate interacting with 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. The same approach should provide a model of binocular rivalry. 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 [13, 14].

Key properties of the model are that the decisions are taken probabilistically in the dynamical network, with the probability that a particular decision is made depending on the biasing inputs provided by the sensory stimuli f_1 and f_2 . The relevant parameters for the decision to be made by the network are found not to be the absolute value of f_1 or f_2 , but the difference between them scaled by their absolute value. If the difference between the two stimuli $\Delta f = f_1 - f_2$, then it is found that Δf increases linearly as a function of the base frequency f_2 , which is Weber's Law. Decision-making is thus understood as probabilistic settling into one or another attractor state using competition biased by the stimulus values in an integrate-and-fire neuronal network with finite size noise effects.

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REFERENCES

1. R. Romo, A. Hernandez, A. Zainos, L. Lemus, and C. Brody, *Nature Neurosci.* **5**, 1217–1225 (2002).
2. R. Romo, A. Hernandez, A. Zainos, and E. Salinas, *Neuron* **38**, 649–657 (2003).
3. R. Romo, A. Hernandez, and A. Zainos, *Neuron* **41**, 165–173 (2004).
4. R. Romo, and E. Salinas, *Nature Rev. Neurosci.* **4**, 203–218 (2003).
5. X. J. Wang, *Neuron* **36**, 955–968 (2002).
6. E. T. Rolls, and G. Deco, *Computational Neuroscience of Vision*, Oxford University Press, Oxford, 2002.
7. G. Deco, and E. T. Rolls, *Prog. Neurobiol.* **76**, 236–256 (2005).
8. G. Deco, and E. T. Rolls, *J. Neurophysiol.* **94**, 295–313 (2005).
9. A. Abeles, *Corticonics*, Cambridge University Press, New York, 1991.
10. N. Brunel, and X. Wang, *J. Comp. Neurosci.* **11**, 63–85 (2001).
11. G. Deco, and E. T. Rolls, *J. Neurophysiol.* **94**, 295–313 (2005).
12. E. T. Rolls, and A. Treves, *Neural Networks and Brain Function*, Oxford University Press, Oxford, 1998.
13. G. Deco, and E. T. Rolls, *Cereb. Cortex* **15**, 15–30 (2005).
14. G. Deco, and E. T. Rolls, *J. Cogn. Neurosci.* **17**, 294–307 (2005).