Recurrent neural network describing information integration

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Abstract: **In order to describe the process of information integration during perceptual decision-making, explaining the relationship between reaction time and neural activity in brain, many computational models have been proposed. Among them, Wong, &Wang, (2006) developed a simplified biophysically realistic recurrent neural network model of decision making. In this article, we reproduced this model and investigated it through several simulations and phase-plane analysis. Results show that the model well simulated the underlying neural activities during decision making, as well as its consequential behavioral revelations. The phase-plane analysis revealed that winner-take-all competition can be explained by the number of attractors in the "decision space" of the system. We again demonstrated this model offers a biophysically plausible framework for studying decision making in general.**

Keywords: **Recurrent neural network, Information integration, Decision-making**

Introduction

The mechanism of information integration in perceptual decision-making process has always been appealing to psychologists and neuroscientists. In a classic 2-alternative forced choice decision-making task like random dots motion (RDM) task, participants are required to decide whether the dots motion direction was toward one of two targets that appeared on either side of the stimulus (Shadlen, & Newsome, 2001). Participants need to gather visual information, weigh evidence for choice alternatives (information integration), and then form a perceptual decision and action selection.

Computational models have been used to describe the process of information integration. One classic model is diffusion model. The diffusion model is intuitively appealing and has been widely used to fit psychophysical data, but it is unclear whether several critical features of the model can be implemented in a biophysically realistic neural network in brain. Another model, i.e. recurrent neural network model, has been proved effective in describing the information integration process as well as the ongoing neural activities in the brain (Wang, 2003; Wong, & Wang, 2006). Here we reproduced the recurrent neural network model and implemented some analyses to see how the model works in detail.

Model description

We selected the simplified model (Wong, & Wang, 2006) for our analyses. This model is reduced from the original network of spiking neurons used for making binary decisions (Wang, 2002) through the following approximations.

1. "Mean-field" approach.

Briefly, the net input to a neuron in a large homogeneous population is treated as a Gaussian random process. Then, the mean activity of a (homogeneous) population can be represented by a single unit.

First, the driving force of the synaptic currents are assumed to be constant as in Brunel (2000). Second, the variance of the membrane potential of the cell is assumed to be mainly contributed by the external input to each neuron, while the contributions from the recurrent connections are averaged out because of the all-to-all connectivity (Renart et al., 2003) and by the averaging effect of the long time constant of NMDA receptors.

2. Constant activity of nonselective cells.

Under a wide range of conditions, the firing rate of the nonselective population changes only by a modest amount. Thus, the nonselective populations are assumed to fire at a constant mean rate. This reduces the system to three populations.

3. Linearization of the input-output relation of the interneuron.

In principle, the inhibitory population firing rate depends on itself (via inhibitory-inhibitory coupling) as well as the excitatory firing rates (via excitatory-inhibitory coupling) and hence is not given explicitly. This complication can be eliminated by a linear approximation of the input-output transfer function of the inhibitory cell. The mean firing rate of the inhibitory population typically falls between the range of 8-15 Hz. Within this range, the single-cell input-output relation is almost linear.

4. Slow dynamics of NMDA gating variable.

The model involves membrane time constants of neurons and those of synaptic gating variables. For the LIF neuron model driven by filtered noisy inputs, it has been shown that the firing response to a stimulus is instantaneous (Brunel et al., 2001; Fourcaud and Brunel, 2002). Hence, the membrane time constant of the single cell can be neglected. Furthermore, among the synaptic transmissions mediated by AMPA, NMDA, and GABAA receptors, the synaptic gating variable of NMDA receptors has the longest decay time constant. Therefore, it can be assumed that all other variables achieve their steady states much faster than the NMDA gating variable SNMDA, which dominates the time evolution of the system. The AMPA and GABAA gating variables reach their steady states much faster than that of NMDA receptors, which means that the average gating variables of AMPA and GABAA receptors become proportional to the average firing rates of presynaptic cells (Brunel and Wang, 2001).

In summary, the simplified network model is a two-variable system described by the dynamical equations as follows:

$$\frac{dS_1}{dt} = -\frac{S_1}{\tau_S} + (1 - S_1)\gamma r_1 \tag{1}$$

$$\frac{dS_2}{dt} = -\frac{S_2}{\tau_S} + (1 - S_2)\gamma r_2 \tag{2}$$

where the two excitatory neural populations (selective for rightward and leftward motion directions) are labeled by 1 and 2, and, for the sake of convenience, we denote S for S_{NMDA} and τ_S for τ_{NMDA}. The firing rates r_1 and r_2 are given by Equation 3 and 4:

$$r_1 = \phi(I_{syn,1}) \tag{3}$$

$$r_2 = \phi(I_{syn,2}) \tag{4}$$

$$I_{syn,1} = J_{N,11}S_1 - J_{N,12}S_2 + J_{A,11}r_1 - J_{A,12}r_2 + I_0 + I_1 + I_{noise,1} \tag{5}$$

$$I_{syn,2} = J_{N,22}S_2 - J_{N,21}S_1 + J_{A,22}r_2 - J_{A,21}r_1 + I_0 + I_1 + I_{noise,2} \tag{6}$$

where I_i represents the visual motion stimulus to the population i and depends on the motion strength. $I_{noise,i}$ is a noise term, and I_0 is the mean effective external input common to both populations. Because of the background input into nonselective excitatory cells and interneurons, I_0 includes not only direct background input to a selective population but also indirect background inputs from these nonselective cells. $I_{syn,i}$ is the total synaptic current from both recurrent connections and inputs fed from outside the local network. The coefficients $J_{N,ij}$ and $J_{A,ij}$ are effective coupling constants from neuron j to i mediated by NMDAR and AMPAR, respectively. The negative sign indicates that the overall effective connectivity between the two selective populations is inhibitory.

The noise term I_{noise} is described by an Ornstein–Uhlenbeck process (Uhlenbeck and Ornstein, 1930):

$$\tau_{AMPA}\frac{dI_{noise}(t)}{dt} = -I_{noise}(t) + \eta(t)\sqrt{\tau_{AMPA}\sigma_{noise}^2} \tag{7}$$

The synaptic currents attributable to the stimulus alone are as follows:

$$I_1 = J_{A,ext}\mu_0\left(1 + \frac{c\prime}{100\%}\right) \tag{8}$$

$$I_2 = J_{A,ext}\mu_0\left(1 - \frac{c\prime}{100\%}\right) \tag{9}$$

where $J_{A,ext} = 0.2243 \times 10^{-3}\, nA \cdot Hz^{-1}$ is the average synaptic coupling with AMPARs, and c' is the coherence level of the biased stimulus, favoring population 1.
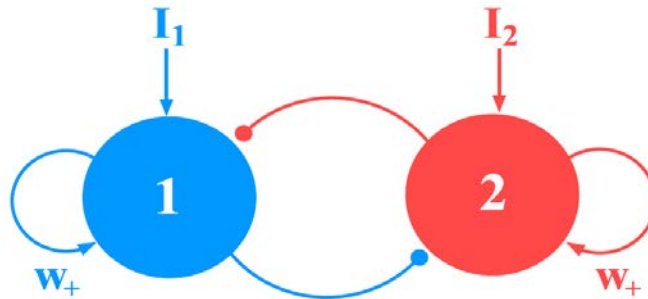
Figure 1. Illustration of two-variable neural network model.

The reduced two-variable model is in its simplest form if we assume that there is no AMPA at the recurrent synapses. In this case, the system can be completely described by the following equations:

$$\frac{dS_i}{dt} = -\frac{S_i}{\tau_S} + (1 - S_i)\gamma H_i \tag{10}$$

$$H_i = \frac{ax_i - b}{1 - \exp\left[-d(ax_i - b)\right]} \tag{11}$$

$$x_1 = J_{N,11}S_1 - J_{N,12}S_2 + I_0 + I_1 + I_{noise,1}1 \tag{12}$$

$$x_2 = J_{N,22}S_2 - J_{N,21}S_1 + I_0 + I_2 + I_{noise,2} \tag{13}$$

$$I_i = J_{A,ext}\mu_0\left(1 \pm \frac{c\prime}{100\%}\right) \tag{14}$$

$$\tau_{AMPA}\frac{dI_{noise,i}(t)}{dt} = -I_{noise,i}(t) + \eta_i(t)\sqrt{\tau_{AMPA}\sigma_{noise}^2} \tag{15}$$

where $i = 1, 2$ labels the selective population. Parameter values for the input-output function are $a = 270(VnC)^{-1}$, $b = 108Hz$, and $d = 0.154s$. The kinetic parameters are $\gamma = 0.641$, $\tau_S = 100ms$, and $\tau_{AMPA} = 2ms$. The synaptic couplings are $J_{N,11} = J_{N,22} = 0.2609nA$, $J_{N,12} = J_{N,21} = 0.0497nA$, and $J_{A,ext} = 5.2 \times 10^{-4}nA \cdot Hz^{-1}$. The overall effective external input is $I_0 = 0.3255nA$, noise amplitude is $\sigma_{noise} = 0.02nA$, and the stimulus is $\mu_0 = 30Hz$. The value of σ_{noise} is chosen such that the psychometric and chronometric functions are close to that of Roitman and Shadlen (2002). For convenience, the following analyses are based on this simplified model.
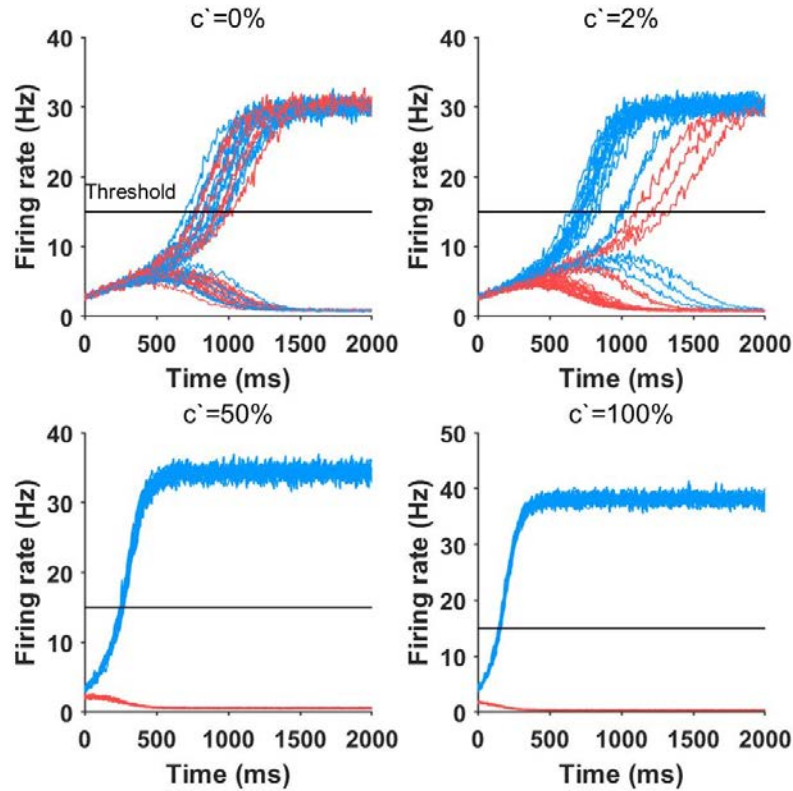
Figure 2. Simulated firing rates over time for different c'. The blue lines show the firing rate of neurons responding to the biased stimulus, and the red lines show the firing rate of neurons responding to the other one.

Results

Firing rates

In figure 2, we showed simulated firing rates of LIP neurons for four different coherence levels c'. We can see that as c' increases, the ramping activity of the neural population, whose response field is the biased stimulus, becomes earlier and steeper, while the activity of the neural population responding to the other one goes slower and remains inhibited at the end.

Accuracy and response time

In figure 3, we show the simulated participants' accuracy and reaction time for different coherence levels c'. We can see that as c' increases, accuracy gets higher and finally reaches 100%. Moreover, for correct trials, the reaction time decreases while accuracy increases.

This is an expected result because the higher the overall external inputs strength is, the steeper will be the ramping activities, and the faster will be the accumulation of sensory evidence before a decision is made.
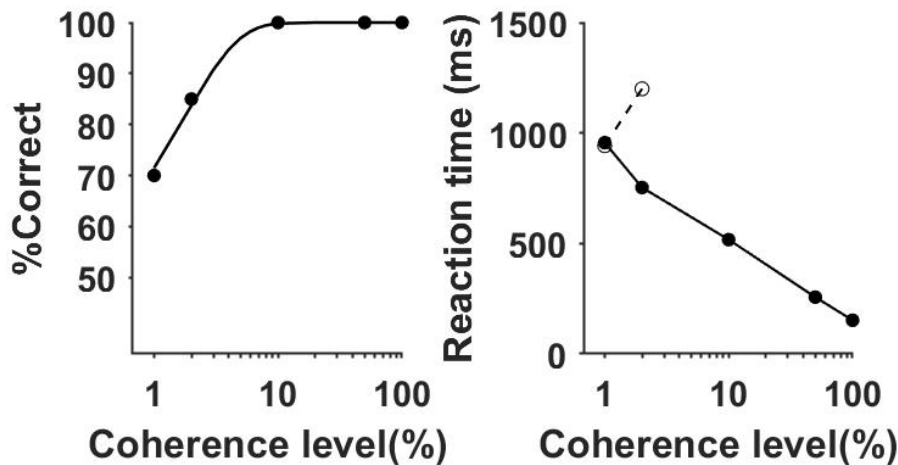

Figure 3. Accuracy (left panel) and reaction time (right panel) for different c'. In the right panel, black dots show the reaction time for correct trials, and the white dots show the reaction time for incorrect ones.

Phase-plane analysis

To investigate how the recurrent neural network model responds to a stimulus and integrates information over time, we performed a phase-plane analysis of the model dynamic system. We first set the dynamical equations $dS_1/dt = 0$ and $dS_2/dt = 0$, and then plotted these two lines (i.e. nullclines) in the (S1, S2) phase space. The intersections of the two lines are steady states of the system. Noting that S_1 and S_2 are variables related to the accumulated evidence for decision, the steady state points (attractors) can be where S1 and S2 stay after the decision is made. Here in Figure. 4 we plotted the phase plots against 4 different levels of coherence (c') in the task.

There are several steady states in this dynamic system, from which the attractors are marked as dark dots and saddle points are marked as grey dots. There are at most two attractors, each represents a state where the decision is made. At the beginning of a new trial, the system starts from a resting state and moves towards either one of the two attractors. The moving trajectory (black line) is also shown on the plot. When it reaches one attractor, the favored choice will be selected.
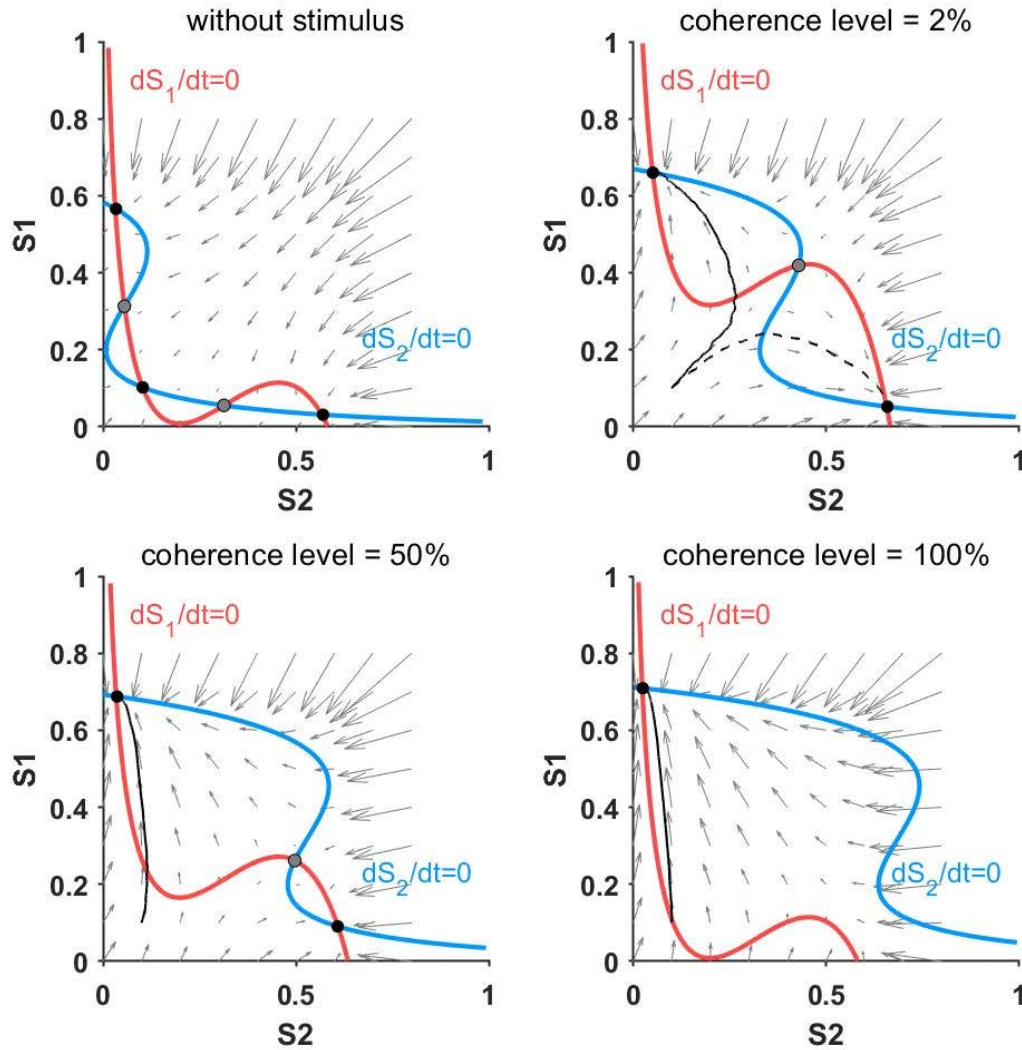
Figure 4. Phase planes for different c'. Black dots show attractors, and the grey dots show saddle points.

Apparently, the difference in the coherence level of stimulus will change the dynamic properties of the system, thus causing different moving trajectories and final decisions. When the coherence level equals to zero, which means the stimulus do not favor either of the two choices. The system starts in a resting state will at first be attracted to the saddle point, then move towards one attractor due to the existence of noise. And the chances of falling to each of the two attractors are equal. As the coherence level increases, the phase space is no longer symmetrical. A lager part of the phase plane will be basin of the favored attractor, leading to a

bigger chance for trajectory starting from resting state to fall to the favored attractor. When the coherence level is set to be 100%, there's no longer two attractors. According to Wang, & K.-F. (2006), when coherence is above 70% the less favored attractor annihilates with the saddle point, so that only the favored attractor exists and the system always make the correct choice regardless of the noise level. This can be explained that when the task is very easy and no one will make any mistake.

Discussion

We have successfully reproduced the simplified recurrent neural network and implemented several simulations. As can be seen above, this model is capable of describing the decision-making dynamics using a biologically based network model. Here we want to share our understanding about what specialties of the model are, the comparison between this model and diffusion models, and reflection on the recurrent neural network model and our analyses.

A dynamical system approach to decision making

This model is a nonlinear dynamical system that can be conceptualized as a circuit of neural populations coupled effectively by mutual inhibition and within-group recurrent excitation. If an excitatory perturbation is applied to one neural pool during sensory stimulation, not only will it accelerate the perceived evidence accumulation process for the favored choice, but also slow that down for another choice because of the mutual inhibition. If the sensory stimulation is not strong enough, then the within-group recurrent excitation can magnify the effect of some small perturbations caused by noise, thus guarantees there will always be a decision formed regardless of the evidence strength. Under the underlying winner-take-all competition like 2 alternative forced choice tasks, there will always be one and only one choice wins out. The mutual inhibition and within-group recurrent excitation are capable of capturing this feature.

This model also offers flexibilities in the parameters. The coherence level (c') changes the dynamics in the (S1, S2) phase plane, thus lead to different evidence accumulation trajectories. The starting point (resting state) can be used to describe the participant's response tendency before stimulus onset. And also, the coefficients of mutual inhibition and self-excitation can be set to modify the dynamic strength. These flexibilities allow this model to capture more neural or behavior features based on different tasks.

The comparison between the recurrent neural network model and diffusion model

Diffusion models are wildly used to describe decision-making process in 2 alternative forced choice tasks. Usually a diffusion model will contain an evidence accumulation variable and two decision bounds. When the variable reaches one bound, the corresponding choice will be made. Previous work has shown that network models with mutually inhibitory neural pools

can be reduced to a one-dimensional diffusion model, under two conditions. First, the system can be approximately described by a single dynamical variable, the firing rate difference between the two neural populations. Second, the time constant for this dynamical variable is arbitrarily long, which typically requires fine-tuning of parameters (Brown, et al., 2001). The inhibition process in the recurrent network model is similar to that in diffusion model: when the evidence favors one choice, the evidence accumulation variable will move towards the corresponding bound and meanwhile away from another bound. But the within-group excitation process usually is missing in diffusion models. Certainly, this can be modified by adding a drift term to the evidence accumulation variable in common diffusion models. But the reason to do that and the form of drift term are still to be discussed. However, the recurrent neural network model offers a biological plausible explanation to the mechanism of evidence accumulation process.

Reflection

This recurrent neural network model can be used to describe the neural activities of neurons in LIP, thus sheds light on the deeper mechanism of how the brain works in decision-making. However, there are still some detailed questions to be discussed in this model.

Firstly, the starting point (resting state) of the decision trajectory is not easily determined. As the neural activities are continual over time, the starting point of a new decision formation is still to be specified. Moreover, the reaction tendency and sequential effect will also influence the location of starting point. Secondly, inputs from visual cortex may not depend linearly on the stimulus coherence. The neural circuits between LIP and visual cortex are also neglected in the model and our analysis. Thus, the dynamics and predictions can be a little different when the model is applied to real decision-making tasks. Last but not least, it is not easy to directly compute the expectation of accuracy using this model. However, when it comes to diffusion models, it's easier to compute the expectation of accuracy via drift rate. Thus, variables in this model are more related to biological neural activities in a decision-making process while variables in diffusion models are more related to the decision-making process itself.

We have reproduced the recurrent neural network model for LIP neurons and have done several analyses to better understand how this model works. As can be seen, this model is capable of combining neural activities with decision-making process. This model can be a good tool to unravel the mechanism of decision-making on the neuron level. Later works have shown this possibility by applying this model to several different tasks or different types of data such as MEG (Gold,& Shadlen, 2007; Hunt, et al, 2012). Exploring the dynamics in this model also helps to better understand other neural network models.

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Appendix

We use MATLAB file *Simulation.m* to simulate the model and *PhasePlot.m* to do phase-plane analysis. All code can be found in the zip file.

Contribution

Li Shucheng: papers reading and writing, model reproducing, simulation and analysis
Pan Deng: papers reading and writing, model reproducing, simulation and analysis
Lin Yiqing: papers reading and writing, model reproducing, simulation and analysis