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Dynamical Synapses Enhance Mobility, Memory and Decoding

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Summary

Depending on their activities, synapses in neural systems are dynamical in relatively short time scales. This effect is known as short-term plasticity (STP), which appears as short-term facilitation (STF) or short-term depression (STD). In this paper, we describe the effects of STD and STF on the intrinsic phases and plateau states. Consequently, we find that STD enhances the tracking performance in continuous attractor neural networks, and provides a mechanism for an iconic memory to shut off naturally. On the other hand, STF improves the precision in population decoding.

1 Introduction

The short-term plasticity (STP) of dynamical synapses appears in two forms: short-term facilitation (STF) and short-term depression (STD). STF is due to the accumulation of calcium ions caused by the pre-synaptic spikes. This effect enhances the release probability of neurotransmitters, and hence the connection efficacy. STD is due to the fact that the recovery time of neurotransmitters is much slower than the synaptic time scale [1].

In this paper, we will briefly describe the effects of STD and STF on the intrinsic dynamics and plateau states of neural systems, and consequently their impact on the performance of neural computation. We will use continuous attractor neural networks (CANNs) as our working model, but the results are applicable to general cases. CANNs are recurrent networks that can hold a continuous family of localized states. These states are localized in position, with neuronal activities decreasing from a maximum at the center to a background level with increasing distance from the center, and is hence usually known as *bumps* [3]. When an external stimulus changes position, the bump shifts its position accordingly among the continuous attractors. This process is called tracking, and hence can model how the brain processes continuous stimuli, such as orientations, head directions and spatial locations. As we shall see, dynamical synapses can enhance the tracking performance of CANNs, provide a mechanism for an iconic memory to shut off naturally, and improve the precision in population

decoding.

2 Model

The state of a neuron is specified by the population-averaged neuronal current, $u(x, t)$, as well as the neuronal firing rate $r(x, t)$, where x is the *preferred stimulus* ranging from $(-\infty, \infty)$. $r(x, t)$ and $u(x, t)$ are related by $r(x, t) = u(x, t)^2 / [1 + k\rho \int dx'' u(x'', t)^2]$, in which k is the parameter controlling the global inhibition, and ρ is the density of neurons in the space of the preferred stimulus [2]. In simulations, there are N neurons with preferred stimulus ranging within $(-L/2, L/2)$. So, $\rho = N/L$ in simulations. The excitatory connection weight between different neurons are given by $J(x, x') \equiv (J_0/\sqrt{2\pi a^2}) \exp[-(x - x')^2/(2a^2)]$, where J_0 controls the strength of excitatory connection, and a represents the width of the tuning curves. For $a \ll L$, the results of simulations should be effectively the same as those with $L = \infty$.

The neuronal current is governed by [3, 4]

$$\tau_s \frac{\partial u}{\partial t} = I^{\text{ext}}(x, t) - u(x, t) + \rho \int dx' J(x, x') [1 + f(x', t)] p(x', t) r(x', t), \quad (1)$$

where I^{ext} is the external stimulus, and τ_s is the synaptic time constant of the order 1 ms. The effects of dynamical synapses are introduced by including $f(x, t)$ for STF and $p(x, t)$ for STD in the

Figure 1: Profiles of synaptic input current, $u(x, t)$, and synaptic depression, $p(x, t)$ for (a) static bumps and (b) moving bumps.

last term of Eq. (1). They are governed by

$$\begin{aligned} \frac{\partial f}{\partial t} &= -\frac{f(x, t)}{\tau_f} + \alpha (f_{\max} - f(x, t)) r(x, t), \quad (2) \\ \frac{\partial p}{\partial t} &= \frac{1 - p(x, t)}{\tau_d} - \beta [1 + f(x, t)] p(x, t) r(x, t), \end{aligned} \quad (3)$$

where α and β are the parameters controlling STF and STD respectively. τ_f and τ_d are time scales for STF and STD, respectively. They are of the order 100 ms. In this paper, we study STD and STF separately, focusing on their individual effects.

3 CANNs with STD

3.1 Intrinsic Dynamics

In this section, three key intrinsic phases are introduced in the (k, β) space when there are no external stimuli. They are the *static* phase, *metastatic* phase and *moving* phase.

For the case without STD and STF, if k is below a critical value k_c , the steady state solution for Eq. (1) is a bump with a Gaussian profile, whose width is $\sqrt{2}a$ and whose center of mass is $\hat{z}$ [2]. The value of $\hat{z}$ can take a continuous range, characteristic of continuous attractor neural networks. One may expect that, when β is small enough, the shape of the steady state of $u(x, t)$ is *effectively Gaussian*. Also, the steady state of $p(x, t)$ has a background level of 1 depressed by a bump-shaped profile. Their profiles are shown in Fig. 1(a). Based on this observation, we propose search for Gaussian-shaped solutions of Eqs. (1) and (3). We can then figure out the regions including *metastatic* and *static* phases (dashed line in Fig. 2) over the parameter space of (k, β) .

Figure 2: Phase diagram for STD. Symbols: simulations. Curves: theory. $\bar{\beta} \equiv \tau_d \beta / (\rho^2 J_0^2)$ and $\bar{k} \equiv k / k_c$ are rescaled β and k respectively.

In the static phase, the height of the bump is stable and the velocity of the bump is zero. In the metastatic phase, the height of the bump remains stable, but the position of the center of mass is metastable, and is hence described as metastatic. This means that when the static bump is given a small displacement, the bump will continue to move spontaneously. The condition for this happen can be studied by introducing a small asymmetric distortion to the solution of Eqs. (1) and (3). By considering whether the variations diverge or converge, we can obtain the boundary between metastatic and static phases respectively, separated by the phase boundary indicated by the dotted line in Fig. 2.

The existence of spontaneously moving bumps in the network can be attributed to the presence of STD. This is because neurons tend to be less active in the locations of low values of $p(x, t)$, causing the bump to move away from locations of strong synaptic depression. For the moving bumps, the profile of $p(x, t)$ is no longer symmetric about the center of mass of $u(x, t)$, as shown in Fig. 1(b). Therefore, the assumption of a Gaussian-shaped depression is not appropriate for the case of moving bumps. To solve this problem, higher order distortions are included in the term $1 - p(x, t)$. We note that a Gaussian distortion is the lowest order member of a family of distortions, commonly used to describe wave functions of the quantum harmonic oscillator. Successively higher order functions of this family can describe distortions in the position,

Figure 3: The bump position when the stimulus abruptly changes from $z_0/a = 0$ to $z_0/a = 3.0$ at $t = 0$. Symbols: numerical solutions. Lines: theory.

width, and skewness etc. of the bump. Mathematically, this family of functions is complete, meaning that any arbitrary distortion can be expressed as a combination of these functions. This enables us to predict the boundary of the moving phase (solid line in Fig. 2). Beyond the boundary, only the silent phase with $u(x, t) = 0$ exists.

In the moving phase, the static bump cannot exist, and there are only moving bumps.

The metastatic nature of the bumps enhances the tracking performance of CANNs. When the network is tracking an external stimulus that changes position rapidly, metastability speeds up the movement of the bump, as shown in Fig. 3. Interestingly, when the synaptic depression is very strong, the network state can even overtake the moving stimulus, reminiscent of the phase precessing behavior of place cells in the hippocampus [5].

3.2 Plateau State

The plateau state provides a possible mechanism for the iconic memory. The presence of STD provides an extra parameter region in which the bump states are marginally unstable in amplitude, such as point P in Fig. 2.

Fig. 4 shows two examples of plateau states, A and B , corresponding to different kinds of initial conditions. A corresponds to the initial condition that the network is under the influence of a stimulus for a long enough time, while B is for the case

Figure 4: Examples of plateau states. Symbols: simulations. Lines: theory. Parameters: $(\bar{k}, \bar{\beta}) = (0.95, 0.0085)$, i.e. point P in Fig. 2. $\bar{u} = \rho J_0 u(x, t)$ is the rescaled variable of $u(x, t)$.

the the presence of stimulus is just long enough to excite function $u(x, t)$.

Consider the initial state B . In the marginally unstable regime, the static bump solution just loses its stability. The bump is stable if the synaptic depression is fixed at a low level, but unstable at high level. Since the synaptic time scale is much shorter than that of STD, a bump can build up before the synaptic depression becomes effective. This maintains the bump in the plateau state with a slowly decaying amplitude as shown in Fig. 4(a). After a time duration of the order τ_d , the STD reaches a threshold, as shown in Fig. 4(b), and the bump state eventually decays to the silent state.

The plateau state for initial condition A does not last as long as that of B . However, since the system is marginally unstable, there are states at which the dynamics is very slow. When the system dynamics passes through these states, the relaxation of the bump is slowed down.

4 CANNs with STF

Compared with STD, STF has a qualitatively opposite effect on CANNs with dynamical synapses. STF provides an extra translational stability to a bump. To check this, we consider a noisy stimulus, $I^{\text{ext}}(x, t)$, which is a Gaussian function of width $\sqrt{2}a$, height A and centered at position $\eta(t)$, $\eta(t)$ being a white noise satisfying $\langle \eta(t)\eta(t') \rangle = 2Ta^2\tau_s\delta(t-t')$. In the inset of Fig. 5, the decoding results of CANNs with and without STF are shown. With STF, the CANNs can filter out the fluctuational effects due to the noises considerably. We calculate the influence of the noise on the de-

Figure 5: Comparison of influences by the noisy stimuli of systems with and without STF. Parameters: $N = 80$, $a = 0.5$, $x \in [-\pi, \pi)$, $k/k_c = 0.25$, $\rho J_0 A = 1.596$ and $T = 0.02$.

coding result is shown in Fig. 5. This figure shows that the presence of STF can improve the decoding efficiency when noises are present.

5 Discussion

In the absence of the stimulus, the CANN with STD favors different phases with different system parameters, (k, β) . For $k < k_c$ and small β , the static bump is stable. If one increases the strength of STD, β , the system will become translationally unstable. York *et al* found similar behaviors in a system with uniform input current [6], while we found that this instability can improve the network reaction to changes of stimuli.

The plateau state is due to the marginal instability of the bump state. It can make the bump state last for a longer period such that the signal may have more time to propagate to neurons of subsequent layers. Hence we predict that STD should be important in early information pathways of the brain. For systems without dynamical synapses, this behavior is not easily seen. However, the presence of STD provides an extra parameter region so that the plateau state can be seen more easily. Indeed, how to shut off the activity of a CANN has been a challenging issue that received wide attention in theoretical neuroscience. Here, we show that STD may provide an important mechanism that supports the signal for a relatively long time and allows the neuronal activity to turn off natu-

rally.

STF has an effect qualitatively opposite to STD. Unlike STD, STF provides translational stability such that it can improve the decoding performance. With this property, CANNs with STF can be used as a noise filter processing noisy stimuli. Based on the different advantages of STD and STF, we predict that each of them should be dominant in different areas of the brain. STD should be dominant in areas where time-varying stimuli are processed, whereas STF should prevail in areas where accurate decoding of stimuli is required.

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