



Generation and annihilation of localized persistent-activity states in a two-population neural-field model

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ABSTRACT

We investigate the generation and annihilation of persistent localized activity states, so-called bumps, in response to transient spatiotemporal external input in a two-population neural-field model of the Wilson–Cowan type. Such persistent cortical states have been implicated as a biological substrate for short-term working memory, that is, the ability to store stimulus-related information for a few seconds and discard it once it is no longer relevant.

In previous studies of the same model it has been established that the stability of bump states hinges on the relative inhibitory constant τ , i.e., the ratio of the time constants governing the dynamics of the inhibitory and excitatory populations: persistent bump states are typically only stable for values of τ smaller than a critical value τ_{cr} . We find here that τ is also a key parameter determining whether a transient input can generate a persistent bump state (in the regime where $\tau < \tau_{cr}$) or not. For small values of τ generation of the persistent states is found to depend only on the overall strength of the transient input, i.e., as long as the magnitude and duration of the excitatory transient input are larger and/or long enough, the persistent state will be activated. For higher values of τ we find that only specific combinations of amplitude and duration leads to persistent activation. For the corresponding annihilation process, no such delicate selectivity on the transient input is observed.

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1. Introduction

A key ability of the brain is to transiently hold stimulus-related information in so-called working memory, i.e., that information is actively remembered in an online fashion even after the initial stimulus subsides (Goldman-Rakic, 1995; Wang, 2001). In a series of experiments, i.e., delayed-response task studies with awake behaving monkeys (Goldman-Rakic, 1995 and references therein), the persistent activation of groups of neurons in cortical areas such as the prefrontal cortex were identified as a neural correlate underlying this short-term memory. Various candidate models for how cortical networks may generate and sustain the selective activation of subpopulations of neurons have been put forward in the last few decades, amongst them persistent activation by thalamocortical and corticocortical loops, intrinsic cellular bistability, or attractor states of local recurrent networks (see Compte, 2006; Wang, 2001 and references therein). The idea of network attractor states

has in particular inspired many studies in the framework of spiking neuronal networks (e.g., Brunel, 2003; Compte, 2006; Compte, Brunel, Goldman-Rakic, & Wang, 2000; Compte et al., 2003; Renart, Brunel, & Wang, 2003) and neural-field models (e.g., Amari, 1977; Blomquist, Wyller, & Einevoll, 2005; Coombes, 2005; Laing, Troy, Gutkin, & Ermentrout, 2002; Machens & Brody, 2008; Oleynik, Wyller, Tetzlaff, & Einevoll, 2011; Wilson & Cowan, 1973).

One pivotal element behind stable persistent activation in network models is sufficient recurrent excitatory feedback to maintain the activation, while inhibition is needed in order to keep the system from entering a state of run-away excitation (see, however, Ermentrout & Drover, 2003; Rubin & Bose, 2004). In neural-field models the effective synaptic connectivity is therefore often assumed to be of ‘Mexican-hat’ type, i.e., nearby neurons predominantly excite each other, while cells further apart have a net inhibitory interaction, also called lateral inhibition. In combination with the assumption of translation-invariant symmetrical coupling such systems can stably sustain bump attractors, i.e., the persistent activation of a localized subpopulation of the network, e.g., Amari (1977), Blomquist et al. (2005), Laing et al. (2002), Oleynik et al. (2011) and Wilson and Cowan (1973). Neural-field models have provided a powerful tool to investigate the properties of such persistent bumps.

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A large number of modeling studies have focused on investigating generic properties of persistent bumps in the absence of external inputs, in particular their existence and stability (see, e.g., Cressman, Ullah, Ziburkus, Schiff, & Barreto, 2009; Ermentrout & McLeod, 1993; Gray & Robinson, 2009; Guo & Chow, 2005; Kilpatrick & Bressloff, 2010a, 2010b; Pinto & Ermentrout, 2001; Werner & Richter, 2001; Wyller, Blomquist, & Einevoll, 2007). However, a model for working memory must also account for how such persistent-activity states may arise in response to external stimulus presentation. Towards this, several one-population model studies have investigated the effect of external input on bump properties: The seminal paper by Amari (1977) investigated the existence and stability of bumps in a simplified neural-field model of the lateral-inhibition type with stationary and spatially uniform external input. Kishimoto and Amari (1979) subsequently addressed the same problem for a whole set of different firing-rate functions, while Laing et al. (2002) extended the approach to systems allowing for multiple-bump solutions.

Folias and Bressloff (2004) also investigated bumps in a one-population model with spatially localized external inputs and found that sufficiently large inputs can stabilize bump states, and that reduction of the input amplitude may induce a Hopf instability and the conversion of stable bumps into breather-like oscillatory waves. Rubin and Troy (2004) further showed that bumps can exist and be linearly stable in such systems, even if they have a symmetric off-center synaptic architecture instead of recurrent excitation.

To analyze the effect of spatially and temporally localized input on bump formation, Laing and Chow (2001) followed a combined approach of field modeling and spiking neuron simulations. They showed how bump attractors can be persistently activated by targeted transient localized external input, and that such a sustained activation can be switched off again by synchronizing excitatory input. In a very recent paper Marti and Rinzel (2013) moreover study the activation of multiple-bump states in lateral inhibition field models by repeated short subthreshold stimulation with various spatially structured inputs. They find that the resulting bump pattern then depends on which of the possible multistable states is closest to the average stimulus pattern.

Several studies also analyzed bump formation in response to external inputs in network simulations of spiking neurons with realistic biophysical parameters. Camperi and Wang (1998), e.g., studied how bumps can be initiated in a ring network with lateral inhibition when the network is stimulated by spatially modulated external input, and can in turn be deactivated by a global inhibitory input. They showed, moreover, how neuron properties, such as cellular bistability, can enhance the stability of such stationary bumps.

A similar effect of activation and deactivation of bumps by excitatory stimulation as described by Laing and Chow (2001) was investigated by Gutkin, Laing, Colby, Chow, and Ermentrout (2001) in a spiking neuron network model with lateral inhibition, that used more biologically realistic Hodgkin–Huxley neurons equipped with neurophysiologically motivated synaptic time courses and parameters. In both studies the importance of asynchronous spiking – which corresponds to time-independent rate dynamics in field models – for bump maintenance was stressed, while excess synchrony was shown to work as a deactivation signal.

In the line of bump formation studies in spiking neuron networks the study by Rubin and Bose (2004) should not go unmentioned. They demonstrated that by taking into account the intricate interplay between cellular excitability and input structure localized stimulation can lead to bump formation also in networks with purely excitatory distance-dependent coupling.

Even if one-population lateral-inhibition type models can reflect some aspects of cortical network behavior, they inherently

cannot capture the individual dynamics of the two basic neuron populations in cortex, i.e., excitatory and inhibitory cells. These populations are present in different fractions (about four to five times more excitatory than inhibitory neurons), and will in general have different dynamical time scales, synaptic footprints, firing-rate functions, etc.. Two-population neural-field models are the minimal model for incorporating this aspect of cortical dynamics, and have also been used in the study of existence and stability of persistent bump states in the absence of external inputs (Blomquist et al., 2005; Oleynik et al., 2011). In a recent study we investigated how stationary localized external input modifies the bump structure in such a two-population model (Yousaf, Wyller, Tetzlaff, & Einevoll, 2013). In terms of being a model for working memory, however, the more interesting case is when *transient* external inputs both generate and annihilate persistent bump activity, and this is the topic of the present study.

We generalize a two-population model considered in Blomquist et al. (2005), Oleynik et al. (2011) and Yousaf et al. (2013) by adding terms corresponding to transient external inputs and consider the following Wilson–Cowan-like neural-field model:

$$\begin{aligned} \frac{\partial}{\partial t} u_e(x, t) &= -u_e(x, t) + \int_{-\infty}^{\infty} \omega_{ee}(x' - x) \\ &\quad \times P_e(u_e(x', t) - \theta_e) dx' - \int_{-\infty}^{\infty} \omega_{ie}(x' - x) \\ &\quad \times P_i(u_i(x', t) - \theta_i) dx' + H_e(x, t) \\ \tau \frac{\partial}{\partial t} u_i(x, t) &= -u_i(x, t) + \int_{-\infty}^{\infty} \omega_{ei}(x' - x) \\ &\quad \times P_e(u_e(x', t) - \theta_e) dx' - \int_{-\infty}^{\infty} \omega_{ii}(x' - x) \\ &\quad \times P_i(u_i(x', t) - \theta_i) dx' + H_i(x, t). \end{aligned} \quad (1)$$

Here u_e and u_i stand for excitatory and inhibitory activity levels, P_m , with $m = e, i$, are firing-rate functions, ω_{mn} denotes the distance-dependent connectivity strengths, θ_m and θ_i are the respective firing-threshold values of the excitatory and inhibitory populations, and τ is the relative inhibition time, i.e., the ratio between the inhibitory and excitatory time constants (Blomquist et al., 2005). Finally, H_e and H_i represent the spatiotemporal, transient external inputs to the excitatory and inhibitory populations, respectively.

Wyller et al. (2007) investigated the Turing instability and pattern formation in this model (1) in the case of no external input, i.e., $H_m \equiv 0$. They explored the generation and formation of stationary periodic spatial patterns from a spatially homogeneous rest state by Turing-type instabilities, while Blomquist et al. (2005) derived the conditions for existence, uniqueness and stability of stationary symmetric solutions of (1) for $H_m \equiv 0$. The generic picture consists of two bump-pairs (BPs) in this case, one narrow BP and one broad BP. The narrow BP is generically unstable while the broad BP is stable for small and moderate value of the relative inhibition time τ . The generalization of this work to a wider class of temporal kernels was performed by Oleynik et al. (2011). In Yousaf et al. (2013) the model (1) was investigated for spatially dependent, but temporally constant external input, i.e., $H_m(x, t) = H_m(x)$. In particular, the existence and stability of bump solutions of (1) were investigated as a function of the amplitude of the external input. At most four BPs were detected, with a maximum of three of them being stable.

As a direct extension of Yousaf et al. (2013), we here study the full dynamics of (1) when both spatially and temporally varying external input H_m ($m = e, i$) are present. In particular, we study the phenomenon of emergence and annihilation of persistent activity bumps in such networks in response to transient external inputs. Such a selective persistent activation and deactivation of

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