Synaptic rewiring for topographic mapping and receptive field development

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ABSTRACT

A model of topographic map refinement is presented which combines both weight plasticity and the formation and elimination of synapses, as well as both activity-dependent and activity-independent processes. The question of whether an activity-dependent process can refine a mapping created by an activity-independent process is addressed statistically. A new method of evaluating the quality of topographic projections is presented which allows independent consideration of the development of the centres and spatial variances of receptive fields for a projection. Synapse formation and elimination embed in the network topology changes in the weight distributions of synapses due to the activity-dependent learning rule used (spike-timing-dependent plasticity). In this model, the spatial variance of receptive fields can be reduced by an activity-dependent mechanism with or without spatially correlated inputs, but the accuracy of receptive field centres will not necessarily improve when synapses are formed based on distributions with on-average perfect topography.

1. Introduction

The development of topographic mappings in the connections between brain areas is a subject that continues to occupy neuroscientists. There have been a number of theoretical investigations on the development of maps through networks with fixed connectivity and changes to synaptic weights (Goodhill, 1993; Miller, Keller, & Stryker, 1989; Song & Abbott, 2001; Willshaw, 2006; Willshaw & von der Malsburg, 1976). Other models have considered the formation and elimination of synapses with fixed weight (Elliott & Shadbolt, 1999). There have been few attempts to include both of these forms of plasticity in a model, i.e. both synaptic weight change and synaptic formation and elimination. Theories of topographic map formation can be divided by the extent to which activity-dependent processes, based on Hebbian reinforcement of the correlated activity of neighbouring cells, are deemed responsi-

ble for the formation of topography. Some assume that activity-independent processes, based on chemoaffinity (Sperry, 1963) provide an approximate mapping, which is then refined (Ruthazer & Cline, 2004). Others (Willshaw, 2006) show how activity-independent processes may fully determine the basic topography. This paper presents a model of topographic map development, which combines both weight plasticity and the formation and elimination of synapses, as well as both activity-dependent and activity-independent processes. In Section 2, synaptic plasticity and models of topographic map development are briefly reviewed, in order to place the model in context. Section 3 then presents the model, developing it from a general to a more specific form. Section 4 describes the parameterisation of the model for the purpose of simulation, as well as describing a novel approach to analysing map quality. Simulation results are then presented in Section 5, and some interesting consequences of the model are explored. This work is part of a project to implement synaptic rewiring in neuromorphic VLSI (Bamford, Murray, & Willshaw, in press), however the results presented here are purely computational.

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2. Review

2.1. Synaptic plasticity

The term "synaptic plasticity" encompasses the formation and elimination of synapses and changes in their physiological strength. The growth of axons to form synapses between neurons of different brain areas is a prerequisite for the development of topographic maps. Synaptic connections can also be eliminated; a process which has been well studied, for example at the neuromuscular junction. In neonatal mammals, each muscle fibre is innervated by axons from several different motor neurons and then during development most of these synapses are eliminated so that in the adult, each muscle fibre is innervated by only one motor neuron. The process is known to be competitive and various mechanisms have been proposed to account for this (Buffelli, Busetto, Bidoia, Favero, & Cangiano, 2004), including Hebbian mechanisms. The formation and elimination of synapses (as well as the remodelling of axons and dendrites that underlies it) is collectively referred as synaptic rewiring (Chklovskii, Mel, & Svoboda, 2004).

Hebbian mechanisms are those in which changes in the strengths of synapses between neurons are related to the correlation of the neurons' activity. In models of synaptic plasticity in which coincidence of pre- and post-synaptic activity causes potentiation, additional constraints are typically applied to prevent the run-away potentiation of synapses, such as global normalisation or decay of synaptic strength (Miller et al., 1989). However, Hebb's (1949) original postulate implies causality; for a pre-synaptic spike to cause a post-synaptic neuron to fire it is necessary that the pre-synaptic spike precede the post-synaptic spike. Bi and Poo (1998) observed that in cultured hippocampal neurons, the potentiation or depression of a synapse was dependent on the temporal order of induced pre- and post-synaptic activity. In this study, pre-synaptic activity preceding post-synaptic activity caused potentiation (and *vice versa*) in accordance with the causality condition, though in other studies the opposite temporal dependence has been observed (Bell, Han, Sugawara, & Grant, 1997). Such Spike-Timing-Dependent Plasticity (STDP), as it has become known, has been investigated extensively in computational neuroscience. Song, Miller, and Abbott (2000) modelled STDP to show that in a neuron whose dendritic synapses implemented STDP, the synaptic weights would diverge into a strong group and weak group, with the effect that groups of synapses whose input spikes were more correlated, i.e. more likely to arrive within a narrow time window of each other, would be preferentially strengthened over synapses whose input spikes were less correlated. Thus, competition between inputs is implemented without the need for additional weight normalisation mechanisms.

There is ongoing debate about the nature of STDP, the molecular mechanisms that give rise to it and its relevance as a candidate mechanism for memory and learning. To give some example of the range of questions that exist: STDP-like behaviour can arise from a synaptic update rule dependent on post-synaptic membrane voltage rather than post-synaptic spikes (Brader, Senn, & Fusi, 2007); there are experiments which indicate that individual synapses may have binary strengths and experience all-or-nothing plasticity events (Petersen, Malenka, Nicoll, & Hopfield, 1998), which are apparently at odds with studies showing that synapses have unimodal distributions; and there are questions over how the contributions of different spike pairs should be combined (Butts, Kanold, & Shatz, 2007; Sjostrom, Turrigiano, & Nelson, 2001). Experiments demonstrating the nature of STDP have typically used *in vitro* preparations (Bi & Poo, 1998) or unrealistic levels of stimulation (Zhang, Tao, Holt, Harris, & Poo, 1998) leading to questions about their relevance to normal cellular processes. STDP models include weight update rules which are dependent on

the weight of a synapse (Gutig, Aharonov, Rotter, & Sompolinsky, 2003); arguably these better model experimental data (Morrison, Aertsen, & Diesmann, 2007).

Notwithstanding the above, weight-independent STDP rules similar to the formalism of Song et al. (2000) have been used to investigate: topographic map formation (Song & Abbott, 2001); the response to latency in inputs (Guyonneau, Van Rullen, & Thorpe, 2005); visual feature map learning (Masquelier & Thorpe, 2007); receptive field reorganisation (Young et al., 2007); learning cross-modal spatial transformations (Davison & Fregnac, 2006) etc. The study of Jun and Jin (2007) is notable as a study of the formation of synfire chains using a combination of STDP and a form of rewiring plasticity. In the present work, STDP is adopted as a form of competitive Hebbian plasticity, in line with the above body of work.

2.2. Topographic maps

A topographic map is an area of the brain where the response to input parameters varies continuously across the area. Where a sheet of neurons in one area (the "source" area) innervates a sheet of neurons in another ("target") area, the mapping between the areas can be said to be topographic if neighbouring neurons in the target area are (maximally) responsive to the activity of neighbouring neurons in the source area (Udin & Fawcett, 1988). The receptive field of a neuron in a target area is a region of the source area in which stimulation causes activity in the neuron. The topographic maps present in the cortex receive input from both eyes. Although these projections are intermixed, tracing the connections from the eyes to V1 (via LGN) reveals that in many mammals there are alternating stripes in V1 in which cells predominantly receive input from one eye or the other (Hubel, Wiesel, & LeVay, 1977), known as patterns of ocular dominance.

The development of topographic maps between two brain areas requires that axons grow from the source area to the correct target area and then form synapses with neurons in the correct location. This paper excludes consideration of axon guidance to the correct brain area and additionally does not consider the questions of how to target the correct layer (in projections to layered tissue) or how to terminate on the correct part of a dendritic tree. Furthermore, it does not model the growth of neural areas and overall changes in topology during development. Rather it is primarily concerned with the development of receptive fields. The model assumes a mechanism for axons to find the correct topographic position.

The purpose of topographic maps in the brain is a matter of debate. There are suggestions that they may serve to perform dimension reduction, that they may have arisen through reasons of wiring efficiency (Chklovskii & Koulakov, 2004), and that in some cases they serve as a basis for multimodal integration (Holmes & Spence, 2005). A distinction can be drawn between maps which perform some transformation between one layer and another and those which merely relay information without transforming it (Knudsen, du Lac, and Esterly (1987) defined the former as "Computational maps"). The topographic maps created by the model presented in this paper serve mainly to relay information; it may be that broad topographic mappings between two areas serve as a basis for computational transformations at a finer scale, but this will not be demonstrated in this paper.

2.2.1. Activity dependence vs. independence

Models of topographic map formation can be divided into those which require activity of the participant cells (that is to say, electrical or spiking activity) in order to form the map and those which do not. Sperry (1963) proposed that the target area be labelled by two orthogonal gradients of chemicals which ingrowing axons could use to be guided to the correct location