



Theoretical models of synaptic short term plasticity

Matthias H. Hennig*

School of Informatics, Institute for Adaptive and Neural Computation, University of Edinburgh, Edinburgh, UK

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*Correspondence:

Matthias H. Hennig, School of Informatics, Institute for Adaptive and Neural Computation, University of Edinburgh, 10 Crichton Street, Edinburgh EH8 9AB, UK
e-mail: m.hennig@ed.ac.uk

Short term plasticity is a highly abundant form of rapid, activity-dependent modulation of synaptic efficacy. A shared set of mechanisms can cause both depression and enhancement of the postsynaptic response at different synapses, with important consequences for information processing. Mathematical models have been extensively used to study the mechanisms and roles of short term plasticity. This review provides an overview of existing models and their biological basis, and of their main properties. Special attention will be given to slow processes such as calcium channel inactivation and the effect of activation of presynaptic autoreceptors.

Keywords: short term plasticity, synaptic transmission, mathematical model, synaptic depression, synaptic facilitation

INTRODUCTION

Chemical synapses are highly specialized structures that enable neurons to exchange signals, or to send signals to non-neural cells such as muscle fibers. Even though there is a staggering diversity of synapse morphologies and types in the brain, the fundamental process of synaptic transmission is always the same. A presynaptic membrane potential depolarization, typically caused by the arrival of an action potential, triggers the release of neurotransmitter, which then binds to receptors that, in turn, generate a response in the postsynaptic neuron.

A key quantity in neural circuits is the synaptic efficacy or strength, which varies over time. Cellular processes such as long-term potentiation and depression contribute to the patterning of the nervous system during development, and are thought to constitute the basis of learning and memory (Morris, 2003). Slow and long-lasting homeostatic processes adjust synaptic strength to maintain circuit activity within functional regimes (Turrigiano and Nelson, 2004). In addition, a whole range of activity-dependent processes exist that modulate synaptic efficacy continuously on very short time scales ranging from milliseconds to minutes (for reviews, see Zucker and Regehr, 2002; Fioravante and Regehr, 2011). Unlike long-term and homeostatic plasticity, short term plasticity, the topic of this review, has a direct influence on the computation performed by neural circuits as these dynamics take place on the time scale of stimulus-driven activity, neural computations and behavior.

Broadly, short term plasticity can be classified as synaptic depression and facilitation. Depression refers to the progressive reduction of the postsynaptic response during repetitive presynaptic activity, while facilitation is an increase synaptic efficacy. Each of these may be caused by a range of different mechanisms with different time constants, and the two forms are not mutually exclusive. For instance, a particularly well-studied example of a strongly depressing synapse is the calyx of Held, a giant synaptic terminal in the mammalian auditory brainstem (Schneggenburger and Forsythe, 2006). A closer

look at the underlying mechanisms, however, reveals that the response is also modulated by facilitation, which is however, partially masked by depression. In fact, most synapses express some combination of these two mechanisms, but with considerable variability between different neuron types (Wang et al., 2006).

The purpose of this review is to summarize models of short term plasticity, to discuss their biological background and plausibility, and to provide a guide for selecting an appropriate model and level of detail. The focus here is on the mechanistic aspects of these models, for a review of functional implications see Abbott and Regehr (2004). The review begins with a reminder of the main processes involved in synaptic transmission. Next, the vesicle depletion model and its variants will be introduced as a canonical model for short term plasticity. Finally, several additions to this class of models will be discussed that were required to explain more recent experimental findings.

PRINCIPLES OF SYNAPTIC TRANSMISSION

Almost all factors contributing to short term plasticity are located in the presynaptic terminal. To identify the relevant variables required in models, we begin with a brief review of the main events following the arrival of a presynaptic action potential at a synapse, as illustrated in Figure 1. The site where synaptic transmission of neural activity is initiated is called the active zone (AZ), a presynaptic morphological specialization where vesicles containing neurotransmitter and proteins required for the release process are clustered. The AZ is opposed by the postsynaptic density (PSD), an area that contains a large number of different proteins implicated in synapse maintenance and plasticity. In addition to a whole variety of structural and signaling complexes, the PSD contains the bulk of the neurotransmitter receptors mediating the postsynaptic response.

Neurotransmitter release from vesicles located at the AZ is initiated by an elevation of the intracellular calcium concentration $[Ca^{2+}]_i$ due to opening of voltage gated calcium channels

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