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Multiple forms of metaplasticity at a single hippocampal synapse during late postnatal development

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ABSTRACT

Metaplasticity refers to adjustment in the requirements for induction of synaptic plasticity based on the prior history of activity. Numerous forms of developmental metaplasticity are observed at Schaffer collateral synapses in the rat hippocampus at the end of the third postnatal week. Emergence of spatial learning and memory at this developmental stage suggests possible involvement of metaplasticity in the final maturation of the hippocampus. Three distinct metaplastic phenomena are apparent. (1) As transmitter release probability increases with increasing age, presynaptic potentiation is reduced. (2) Alterations in the composition and channel conductance properties of AMPARs facilitate the induction of postsynaptic potentiation with increasing age. (3) Low frequency stimulation inhibits subsequent induction of potentiation in animals older but not younger than 3 weeks of age. Thus, many forms of plasticity expressed at SC-CA1 synapses are different in rats younger and older than 3 weeks of age, illustrating the complex orchestration of physiological modifications that underlie the maturation of hippocampal excitatory synaptic transmission. This review paper describes three late postnatal modifications to synaptic plasticity induction in the hippocampus and attempts to relate these metaplastic changes to developmental alterations in hippocampal network activity and the maturation of contextual learning.
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1. Introduction

What is the difference between synaptic plasticity and metaplasticity? Synaptic plasticity refers to a change in synaptic function following patterned input activity (Fig. 1). Forms of synaptic plasticity vary in how long they persist after induction, ranging from milliseconds to weeks, and different forms of synaptic plasticity are supported by different underlying molecular and biophysical mechanisms. This review focuses on homosynaptic long-term potentiation (LTP) and long-term depression (LTD) of synaptic efficacy, where the plasticity-inducing stimulus impacts the synaptic population that is stimulated (in contrast to heterosynaptic plasticity where stimulation of one synaptic population alters the strength of another synaptic population). LTP and LTD are individually defined by the direction of change in synaptic efficacy after patterned stimulation but both persist for many tens of minutes to hours in acutely prepared slice preparations (Malenka and Bear, 2004; Collingridge et al., 2010). LTP is a lasting increase in synaptic efficacy following moderate to high input activation frequencies. LTD is a lasting decrease in synaptic efficacy following low to moderate input activation frequencies.

Metaplasticity is the dynamic regulation of the ability to induce activity-dependent synaptic plasticity and is

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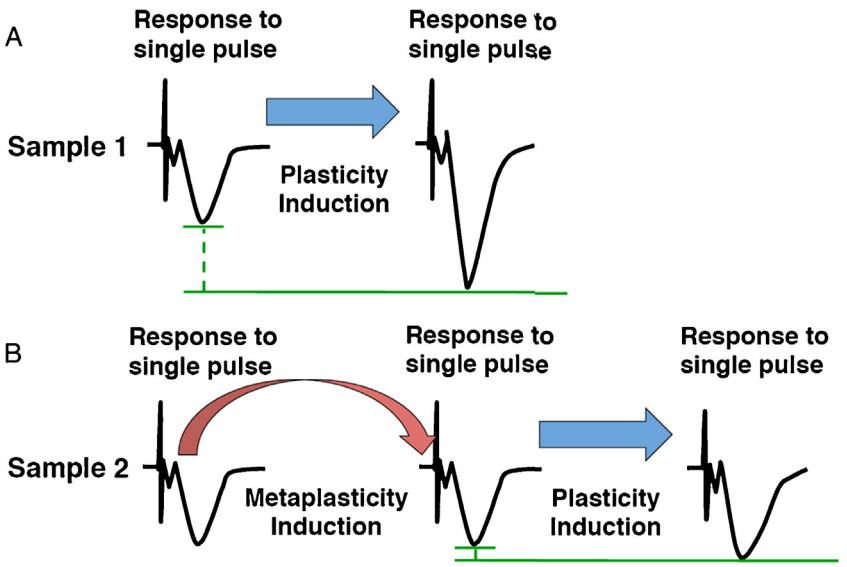

Fig. 1. Illustration of the basic difference between synaptic plasticity and metaplasticity. (A) In a naïve sample (Sample 1), a plasticity-inducing stimulus results in potentiation of the synaptic response. (B) During Sample 2, following a metaplastic event, the same plasticity-inducing stimulus no longer alters synaptic efficacy. Green bars depict the difference in the amplitude of the evoked synaptic event before and after the plasticity-inducing stimulus. This example does not reflect all types of metaplasticity.

governed by the prior history of activity (i.e. the plasticity of synaptic plasticity, Abraham and Bear, 1996). In empirical tests, synaptic metaplasticity is commonly defined as a shift in the threshold activity level to induce lasting alterations in LTP or LTD due to alterations in baseline activity levels (Bienenstock et al., 1982; Mockett and Hulme, 2008). During the maturation of Schaffer collateral to CA1 pyramidal cell (SC-CA1) synapses, alterations to both presynaptic and postsynaptic elements of synaptic transmission produce separate forms of metaplasticity. Presynaptic metaplasticity can be observed as a function of increased baseline transmitter release probability that impacts the constraints for induction of presynaptic LTP. On the postsynaptic side, a change in the types of ionotropic glutamate receptors that are present enhances postsynaptic excitation and shifts the threshold for induction of postsynaptic LTP (Fig. 2). Unlike sensory systems, where the causes for increased input activity are easily defined (i.e. birth enriches olfactory/gustatory/somatosensory input, parting of the eyelids enhances visual input, opening of the auditory meatus augments auditory input), the trigger for increased input activity in the hippocampus is

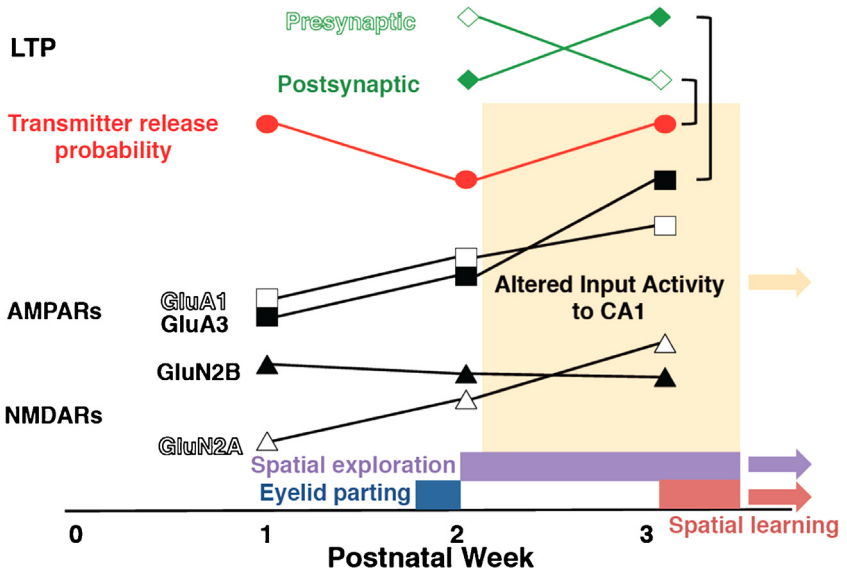

Fig. 2. Summary of pertinent developmental events in the hippocampus. Age related changes in LTP, transmitter release probability, and postsynaptic glutamate receptors are shown in relation to eyelid parting, spatial exploration, and spatial learning. Brackets denote relationships between alterations in synaptic plasticity and baseline transmission.

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