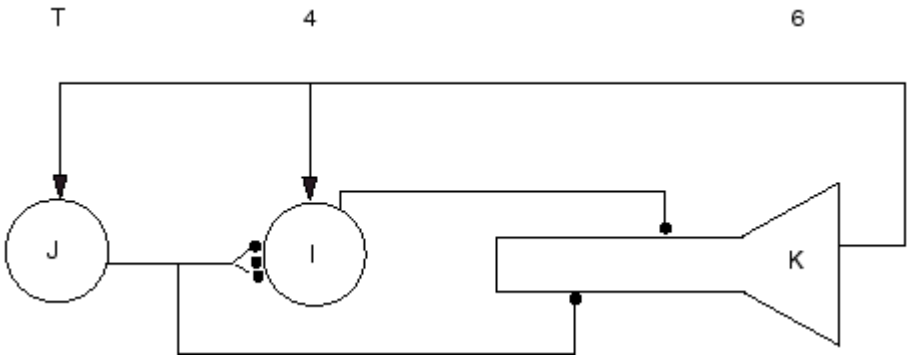
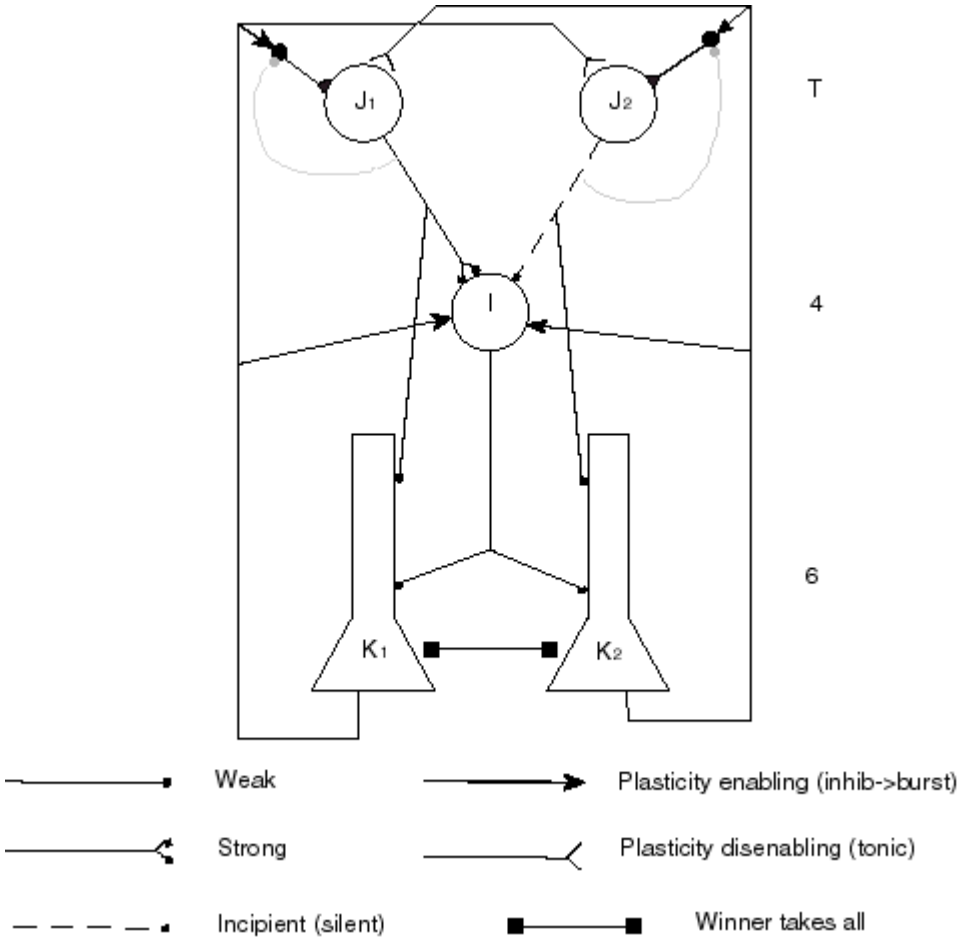
Simple Proofreading Circuit



Hebbian Proofreading – the J-I connection is Hebbian but not completely specific, K is a coincidence detector which gates the plasticity of the Hebbian connection using an outer product ruleThis circuit can apply to any feedforward cortical network that must accurately learn complex input statistics. In the case of the feedforward connections from thalamus to middle layers of cortex, the coincidence-detecting K cell would be a layer 6 "simple" cell. It would show "double simplicity" because it would receive inputs from both a layer 4 simple cell and from the relay cells that form monosynaptic connections on its layer 4 partner, and would only fire when both sets of inputs fire. This arrangement corresponds to that found biologically (e.g. Sherman and Guillery; Callaway). The layer 6 cell would then innervate both the relay cells that generate its simple responses, and the layer 4 simple cell; these feedback pathways would conjunctively enable the plasticity of the relevant relay-to layer 4 connection, by neuromodulatory glutamate release from drumstick synapses. There is anatomical and physiological evidence for these pathways (Sherman Guillery; Callaway etc), but our model goes beyond available evidence.

Push-Pull Proofreading Circuit



Simple proofreading lowers the error rate but cannot guarantee avoidance of an error catastrophe, because even at a reduced error rate, unfavorable input statistics may occur, leading to loss of all previous learning. The cortex has to take everything the environment throws at it, learning when opportunities arise, yet maintaining its existing interpretations (the "stability/plasticity dilemma"). This can be achieved using a more sophisticated version of the basic proofreading circuit, which we call "push-pull proofreading". Push-pull proofreading also fits better with observed anatomy and physiology.

The basic idea is that one needs to compare correlations across current connections (i.e strong connections which have formed in response to previous favorable input statistics, and that capture aspect of the past structure of the world) with correlations across "incipient" connections (existing weak or "silent" connections, which could respond to correlations across them by strengthening; these should be distinguished from "potential" connections, which are synapseless touchpoints across which silent synapses can appear as a result of spine creation). In pushpull proofreading, 2 slightly different types of K cell are postulated, K1 which measures correlations across current connections, and K2 which measures correlations across incipient connections. In order to avoid an error catastrophe, the cortex needs to ensure that correlations across current or incipient connections are strong relative to correlations across incipient or current connections (see Truth Table). This can be done by a winner take all mechanism between layer 6 cells (for example, strong mutual inhibition). There are actually 2 ways to use these competitive correlation signals: relatively strong correlations can enable their own plasticity (as in simple proofreading) or they can disenable the plasticity of connections supporting weak connections. Both of these ideas are incorporated in the Figure. Thus the output of K1 (which fires when correlations across J1-I are strong compared to correlations across J2) disenables the plasticity of the connections to I made by J2 (by releasing glutamate onto the distal dendrites of relay cell, depolarising the cell and shifting it to tonic mode) as well as enabling the plasticity of the J1-I connections (by depolarising a TRN interneuron which hyperpolarises the relay cell, shifting it to burst mode). Note that these actions would also enable/disenable plasticity of inappropriate J-I connections (not shown); however, the "outerproduct" handshake plasticity-enabling signals sent to layer 4 will selectively pick out the right set of J-I connections, as in simple proofreading. Also note, a second tier of proofreading could be added if the TRN interneurons only fired when there are "handshake" action potentials from relay cells (gray lines).

Error Catastrophe Avoidance Scheme

	CS		CW	
IS	**X** **I**	**X** **C**	**Y** **I**	**X** **C**
IW	**X** **I**	**Y** **C**	**X** **I**	**X** **C**

C - Current connection

I - Incipient connection

S - Strong connection

W - Weak connection

Y I - Enable I

Y C - Enable C

X I - Disable plasticity

X C - Disable plasticity