

ON THE STABILITY OF RECEPTIVITY-BASED ADAPTIVE SYNAPTOGENESIS

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Abstract: We investigate the stability properties of the receptivity-based adaptive synaptogenesis process. We show that, following convergence, synaptogenesis enters an oscillatory state unless a switching mechanism is employed for its termination. Algorithms that detect changes in the statistics of the input environment can then be used to regulate the resumption of the process.

1 Adaptive Synaptogenesis and Receptivity

Adaptive synaptogenesis is a biologically plausible process of making synaptic connections in an initially unconnected network [4]. In this theory, synaptic connections between a postsynaptic neuron and potential presynaptic neurons are gradually formed until the postsynaptic neuron either quits making chemotactically mediated requests or denies sites, for new innervation.

The postsynaptic neuron j 's receptivity to new innervation is represented by the functional $R_j(\bar{y}_j(t))$ where $\bar{y}_j(t)$ is the average postsynaptic activity at time t . A neurally acceptable receptivity functional $R_j(t) \equiv R_j(\bar{y}_j(t))$ must satisfy the following conditions:

- 1) $R_j(t) \geq 0, \forall t$.
- 2) It is continuous but not necessarily differentiable.
- 3) It is bounded.

4) There exists a constant μ_y such that $R_j(t) = 0$ whenever $\bar{y}_j(t) \geq \mu_y$. This cut-off value is typically some preset or desired postsynaptic activity level, and it is assumed that $\mu_y \leq E[y_j]$.

Let t_j^0 be the time point when the connectivity of the postsynaptic neuron j becomes fixed; that is, $t_j^0 = \min t : \bar{y}_j(t) \geq \mu_y$. At time $\max_j t_j^0$, synaptogenesis is terminated for all postsynaptic neurons and the entire network converges to some fixed state.

Let $P_{ij}(t) \equiv P_{ij}(\bar{y}_j(t))$ be the probability of input neuron i making a connection with output neuron j at time t . This probability is in fact defined as a functional of the average postsynaptic activity [1]:

$$P_{ij}(\bar{y}_j(t)) = \gamma R_j(\bar{y}_j(t)) \quad (1)$$

where γ is a constant that controls the convergence rate of the synaptogenesis process. Clearly, $R_j(t) \leq 1/\gamma, \forall t$. From equation (1), synaptogenesis terminates for postsynaptic neuron j when $P_{ij}(t_j^0) = 0$, and hence the condition (4) above.

The calculation of the average postsynaptic activity is performed through a running averager such as

$$\bar{y}_j(t+1) = (1-\epsilon)\bar{y}_j(t) + \epsilon y_j(t+1) \quad (2)$$

where $0 < \epsilon < 1$ [1]. The constant coefficient ϵ eliminates any counting requirements for the neuron. Moreover, for large ϵ , recent observations carry more weight in the calculation of equation (2); hence the running averager is capable of handling small nonstationarities in $y_j(t)$ as well.

2 Neuronal Properties and Associative Synaptic Modification

All input neurons are assumed to produce $\{0, 1\}$ -binary outputs corresponding to $\{\text{not firing, firing}\}$, respectively. At time step t , the activity $y_j(t)$ of the postsynaptic neuron j is determined according to the inner

product

$$y_j(t) = f \left\{ \sum_{i \in S_j}^N x_i(t) w_{ij}(t) \right\} \quad (3)$$

where $x_i(t)$ is the activity of the input neuron i and $w_{ij}(t)$ is the synaptic weight between the input neuron i and the output neuron j , both at time t . S_j is the set of input neurons that are connected to neuron j . The threshold function f is defined as

$$f(\zeta) = \begin{cases} 1, & \text{if } \zeta \geq \theta \\ 0, & \text{otherwise,} \end{cases} \quad (4)$$

where θ is a suitable threshold. Hence, $y_j(t) \in \{0, 1\}, \forall j$.

The weights of the existing connections in equation (3) are adjusted via an adaptive process called the associative synaptic modification. One synaptic modification rule with desirable convergence properties is the following:

$$w_{ij}(t + 1) = w_{ij}(t) + \epsilon y_j(t) [x_i(t) - w_{ij}(t)]. \quad (5)$$

The positive constant ϵ controls the modification rate. In this paper, we will set $\epsilon = 0.05$ to ensure that the synaptic weights converge very slowly.

3 Stability of Receptivity-Based Adaptive Synaptogenesis

Naturally, it is desirable that synaptogenesis be a stable process. That is, the network should converge to a stationary state of connectivity and stay in that state as long as the input environment does not change. Unfortunately, the simple running averager in equation (2) may drive the synaptogenesis process to instability. Consider Example 1 to see this point:

Example 1: Let $y_j(t) \in \{0, 1\}, \forall t$, and suppose $\bar{y}_j(t_j^0) = 0.52$. When $\mu_y = 0.5$ and $\epsilon = 0.05$, then $\bar{y}_j(t_j^0 + 1) < \mu_y$ if $y_j(t_j^0 + 1) = 0$, and thus synaptogenesis would restart after only one time step.

More formally, the following lemma establishes the instability of a running averager-based synaptogenesis mechanism.

Lemma 1: Let δ be the amount of overshoot of $\bar{y}_j(t_j^0)$ above μ_y . Suppose synaptogenesis is terminated at time t_j^0 for postsynaptic neuron j , and assume that $\mu_y \gg \delta$ and $\epsilon \ll 1$. Synaptogenesis will resume in finite time with non-zero probability. \square

Proof of Lemma 1: For the sake of simplicity, let $t_j^0 = 0$. That is, let $\bar{y}_j(0) = \mu_y + \delta$. Assume further that $\bar{y}_j(t) \geq \mu_y, \forall t > 0$, with probability one. Then,

$$\bar{y}_j(t) = \epsilon^t (\mu_y + \delta) + \sum_{k=1}^t \epsilon (1 - \epsilon)^{t-k} y_j(k) \geq \mu_y.$$

The above equation implies that

$$\underbrace{\sum_{k=1}^t (1 - \epsilon)^{t-k} y_j(k)}_{h(\{y_j(k)\}_{k=1}^t)} \geq \frac{\mu_y - \epsilon^t (\mu_y + \delta)}{\epsilon} \gg 1$$

with probability one. But $h(\{y_j(k)\}_{k=1}^t) < 1$ with non-zero probability for some $t > 0$, and hence, the assumption that $\bar{y}_j(t) \geq \mu_y, \forall t > 0$, with probability one is false by contradiction. \square

It is important to quantify how the instability of synaptogenesis affects the formation of new synapses. If synaptogenesis turns back on very rarely, the chances of new connections being made will be low. Then one may claim that the instability issue is not critical enough to cause any disturbances in the overall balance of the system.

We need the following basic result first.

Proposition 1: Suppose that the learning constant ϵ in equation (5) is small enough so that the synaptic weights converge very slowly and they can be assumed constant in the steady-state. Let $\bar{y}_j(0) = 0$, and let the running averager be defined as in equation (2). Then \bar{y}_j is asymptotically normal with mean $E[y_j]$ and variance $\eta_\epsilon^2 \sigma_y^2$, where $E[y_j]$ and σ_y^2 are respectively the mean and the variance of the postsynaptic activity y_j , and

$$\eta_\epsilon = \sqrt{\frac{\epsilon}{2 - \epsilon}}. \quad \square$$

Proof of Proposition 1: The recursion in equation (2) is equivalent to

$$\bar{y}_j(t) = \epsilon^t \bar{y}_j(0) + \sum_{k=1}^t \epsilon(1 - \epsilon)^{t-k} y_j(k). \quad (6)$$

Because $\bar{y}_j(0) = 0$ and the weights are slowly varying, the right-hand side of equation (6) reduces to the sum of independent postsynaptic firing activities. The result then follows from the central limit theorem. \square

Notice that the asymptotic distribution of \bar{y}_j is tightly centered around $E[y_j]$. However, since $\bar{y}_j(t)$ converges only in the mean, it is clear that synaptogenesis will oscillate between on- and off-states with non-zero probability.

Lemma 2: Suppose that all the conditions in Lemma 1 are valid. Let ν_j denote the ratio of the number of times when synaptogenesis is on over the number of times when synaptogenesis is off, after convergence is achieved for postsynaptic neuron j . Then,

$$\nu_j = \frac{\Phi\left(\frac{\mu_y - E[y_j]}{\eta_\epsilon \sigma_y}\right)}{1 - \Phi\left(\frac{\mu_y - E[y_j]}{\eta_\epsilon \sigma_y}\right)}, \quad (7)$$

where $\Phi(\zeta)$ is the cumulative distribution function of the zero-mean, unit-variance Gaussian random variable at point ζ . \square

Proof of Lemma 2: The proof follows directly from Lemma 1. \square

Interestingly enough, $\nu_j = 1$ for $\mu_y = E[y_j]$. That is, synaptogenesis is on half of the time. Below we give a more general example.

Example 2: Let $\mu_y = 0.5$ and $\epsilon = 0.05$. By equations (3) and (4), $y_j(t)$ is a stationary Bernoulli process, and let p_y denote the corresponding Bernoulli parameter. Then, $E[y_j] = p_y$ and $\sigma_y^2 = p_y(1 - p_y)$. The following receptivity functional is employed in all simulations:

$$R_j(t) = \max\{-2\bar{y}_j(t) + 1, 0\}, \quad 0 \leq \bar{y}_j(t) \leq 1, \quad \forall t. \quad (8)$$

From equation (7), one can see that, for $0 < \mu_y < 1$, $\nu_j \rightarrow \infty$ as $p_y \rightarrow 0$ since more synapses are required to reach the desired activity level when the output (and hence the input) firing probability is small. For similar reasons, $\nu_j \rightarrow 0$ as $p_y \rightarrow 1$. In fact, for this particular example, $\nu_j > 10,000$ for $p_y < 0.2$ and $\nu_j < 1.0 \times 10^{-4}$ for $p_y > 0.8$.

For the same example, we also carried out one set of numerical experiments with 64 input neurons receiving 64 distinct input patterns. The threshold θ in equation was set to 2. p_y was controlled by varying

the input activity level. The simulations were run for 409,600 time steps, for ten different input environments. We started keeping track of the running averager as soon as synaptogenesis stopped for the first time. Table 1 lists averages of the theoretical (equation(7)) and experimental values for ν_j , as well as the number of new synapses accrued due to the instability of synaptogenesis, for various values of p_y .

We ignored trivial situations where $p_y < \mu_y$. The relative discrepancy between the theoretical and experimental ν_j values is due to the extremely tight asymptotic distribution of \bar{y}_j . As the table indicates, the number of new synapses formed during on-times (following convergence) is not negligible when the cut-off value μ_y is close to the average postsynaptic activity, and thus a regulatory mechanism is necessary.

Table 1: Theoretical and experimental values of ν_j as a function of p_y , for $\mu_y = 0.5$ and $\epsilon = 0.05$. Numbers in table are averages over ten distinct input environments.

p_y	ν_j (theoretical)	ν_j (experimental)	New synapses accrued
0.50	1.000	1.002	8
0.58	0.185	0.168	11
0.63	0.048	0.040	2
0.64	0.036	0.016	1

4 Stabilizing Mechanisms

In this section, we propose two alternatives to regulate synaptogenesis after convergence. Both methods turn off synaptogenesis as soon as the receptivity functional becomes zero, and then start monitoring the running averager to detect a change in the input environment. (A change in the statistics of the input environment will result in a change in the output firing level.) In particular, we model the latter change by a drop in the neurons' firing probability as there is ample biological evidence in support of this premise. The first mechanism uses a statistical change detection algorithm due to Page [6], while the second one is based on tracking the number of times the running averager falls below the cut-off threshold μ_y .

Page's Stopping Rule

This approach is based on the fact that any change in the Bernoulli parameter of the input firing distribution will manifest itself in a somewhat delayed variation in the Bernoulli parameter of the output firing distribution (see equations (3) and (4)). An efficient method to detect a change in the mean (which is the Bernoulli parameter in our model) is Page's stopping rule [3, 6], which is shown to minimize the expected delay of detection for a fixed and non-zero false alarm rate [5]:

Suppose it is necessary to detect a possible change from a Bernoulli process whose parameter is p to a Bernoulli process whose parameter is q where $p > q$, based on the observation sequence $y_j(t)$. Then the test has the following form [7]:

Detect a drop in the mean at the first instant $t > t_j^0$ such that $g_j(t) \geq \lambda$ where

$$g_j(0) = 0, \tag{9}$$

$$g_j(t) = \max\{0, g_j(t-1) - y_j(t) - \eta(\bar{y}_j(t_j^0), \bar{y}_j(t))\}, \tag{10}$$

$$\eta(p, q) = \frac{\log \frac{1-q}{1-p}}{\log \frac{q(1-p)}{p(1-q)}}. \tag{11}$$

In engineering applications, the threshold $\lambda > 0$ is optimized so as to meet a prespecified upper bound on the false alarm probability. However, the detection performance is not very sensitive to the particular choice of this threshold [3].

In our biological model, the change parameter that is monitored by the detector is the average postsynaptic activity. The change detector will activate at time $t_j^0 + 1$, and the Bernoulli parameter p at the

time of convergence of synaptogenesis will have already been calculated by the running averager; that is, $p = \bar{y}_j(t_j^0)$. A change in the input environment will result in a change in the value of the running averager after convergence; hence, $q = \bar{y}_j(t)$, $t > t_j^0$.

The change detector in equations (9), (10) and (11) is biologically plausible because only local information is used. The algorithm is recursive and does not require tracking time steps.

Example 3: Consider the adaptive synaptogenesis and synaptic modification rules described earlier, and let the receptivity functional be as defined in equation (8). Let $\mu_y = 0.5$, $\epsilon = 0.05$ and $\theta = 2$. Two sets of input environments represented by 64 and 128 distinct 64-bit input patterns were created. In each case, the input patterns were randomly fed to the network over 10 times the number of input patterns time steps. The input firing level was brought down from 0.30 to 0.25 in order to simulate the change in the input environment. Synaptogenesis terminated at time t_j^0 as soon as $\bar{y}_j(t_j^0) \geq \mu_y$, and it was turned back on when a change in the input environment was detected for the first time.

Table 2 displays the detection delays for Page's stopping rule under various scenarios.

Table 2: Detection delay of Page's stopping rule as a function of λ and the number of 64-bit input patterns, for $\mu_y = 0.5$ and $\epsilon = 0.05$. The delays are determined by calculating the number of time steps between the occurrence of the change and the first time the change is detected. The numbers in the table are averages over ten distinct input environments.

λ	64 patterns	128 patterns
2	15	3
3	16	5
4	18	6

As Table 2 demonstrates, Page's algorithm detects any changes in the Bernoulli parameter very rapidly. One reason is that the drop in input Bernoulli parameter is amplified by the input-output relation in equation (3) into a larger difference, making the parameter shift more detectable; hence the advantage of monitoring the running averager. Our simulations also verify the claim that the algorithm's performance is relatively independent of the threshold λ . Finally, we notice that the detection delay is smaller for larger number of input patterns.

A simpler, and perhaps more intuitive, method is the following algorithm which is based on monitoring the status of synaptogenesis directly.

Tracking the Threshold Crossings of the Running Averager

Define

$$r(t) = \begin{cases} 1, & \text{if } \bar{y}_j(t) < \mu_y \\ 0, & \text{otherwise,} \end{cases}$$

for $t \geq t_j^0$. In other words, $r(t)$ evaluates the event $\bar{y}_j(t) < \mu_y$ over the time interval $(t_j^0, t]$. The average of this quantity can be calculated recursively by means of the running averager

$$\bar{r}_j(t) = (1 - \xi)\bar{r}_j(t - 1) + \xi r(t),$$

where $0 < \xi < 1$. When the average number of times $\bar{y}_j(t)$ is less than μ_y exceeds a threshold ω , synaptogenesis restarts.

At the time when a change in the input environment is detected, receptivity will be zero. Therefore the running averager has to be reset to some value smaller than μ_y in order to restart synaptogenesis. That is, $\bar{y}_j(t_j^c + 1) = \mu_c$ where t_j^c is the time when the change is detected and $\mu_c < \mu_y$ is the reset value for the running averager.

5 Summary and Discussion

Adaptive synaptogenesis, when controlled solely by the receptivity of postsynaptic neurons, is unstable in the sense that the process may oscillate indefinitely, resulting in unwanted or unnecessary synaptic connections. In this paper, we introduced a modified model where synaptogenesis is turned off as soon as convergence is achieved, and the postsynaptic activity is subsequently monitored to detect any changes in the input environment. Synaptogenesis is then turned on again in order to cope with these changes.

One definite conclusion of this paper is that receptivity alone may not be enough to regulate synaptogenesis. Future research should include avidity and synapse removal [2] functions in explaining the dynamics of synaptogenesis. On the other hand, one can certainly argue that once the input neuron set S_j has reached fixed connectivity with output neuron j , it is not desirable to break up the existing configuration because the subject may face the same input environment in the future. So, perhaps, there exists some intra-neuronal mechanism where output neuron j calls upon other output neurons to form connectivity in order to learn the new environment.

Ultimately, context-dependent synaptogenesis which requires a very large network may provide the best explanation.

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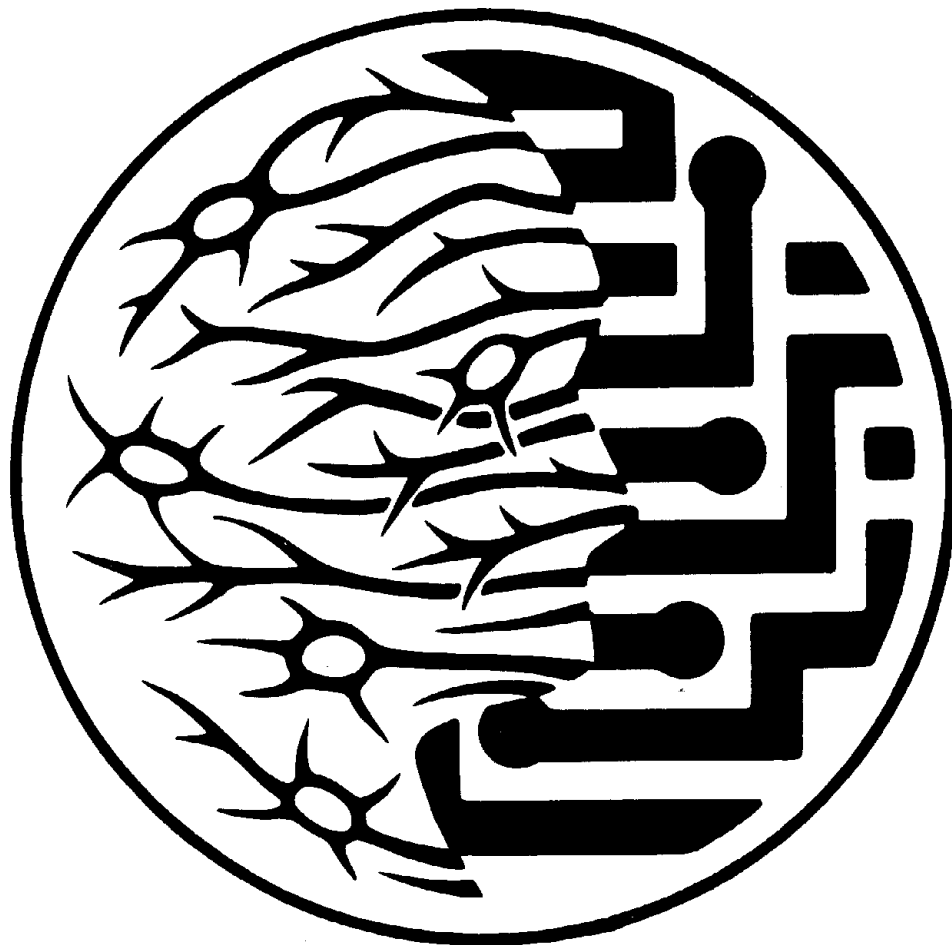
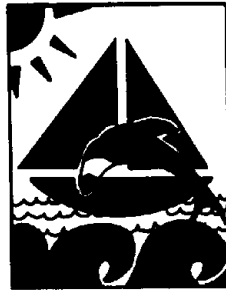
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