Repetition Suppression, Neural Synchronization, and Behavioral Priming: Mechanisms Underlying Improved Efficiency in Networks of Spiking Neurons

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Introduction

Human subjects tend to perform tasks faster and more accurately with practice. Cognitive-level explanations of these behavioral changes often involve some form of threshold modification to node activity or changes in connection strengths such that representations become active faster, at higher levels, and/or with greater precision. However, the changes in neural activity associated with stimulus repetition and improved performance are most often decreases rather than increases - a phenomenon known as "repetition suppression" (Desimone, 1996). We propose that the behavioral improvement following stimulus repetition involves greater neural synchronization and more efficient neural processing that arises from a reduction of activity. We show that artificial networks of spiking neurons with "synaptic depression" (an automatic reduction in synaptic efficacy following pre-synaptic activity), can account for many of the empirical findings associated with repetition suppression in humans and monkeys. Synaptic depression leads to reductions in both the mean and variance of neural firing rates which dynamically enhances neural synchronization. As neurons synchronize, processing efficiency increases because fewer spikes are required to fire post-synaptic neurons. This can improve the rate of information transmission, allowing earlier propagation of individual spikes throughout an entire processing pathway.
Repetition Priming

The enhanced perception and identification of a stimulus as the result of previous exposure to the stimulus; measured as decreases in reaction time and increases in correct performance

General Characteristics
- Long-lasting (e.g. months: Cave, 1997), although shows immediate decreases over seconds (e.g. McKone, 1998)
- Incremental with additional repetition (e.g. Brown et al., 1996; Ostergaard, 1998)
- Relatively automatic: less influenced by attentional/task demands (e.g. Szymanski & MacLeod, 1996); can occur when subjects are anesthetized during initial exposure (Kihlstrom & Schacter, 1990); spared in amnesia (e.g. Cave & Squire, 1992)
- Robust to small alterations of stimulus form (e.g. Biederman & Cooper, 1991; 1992)

Repetition Priming (novel-repeated RT) in Word Naming (McKone, 1998)
Repetition Suppression

Decrease in neural firing rate following stimulus repetition (e.g. Desimone, 1996; Miller et al., 1993); observed originally in extracellular neural recordings in primates, but also observed in the hemodynamic responses acquired in PET and fMRI studies with humans.

General Characteristics

- Stimulus-specific (e.g. Miller et al, 1991; van Turennout et al., 2000)
- Observed in a wide variety of neocortical brain regions
- Long-lasting (e.g. hours: Li et al., 1993; days: van Turennout et al., 2000), although shows immediate recovery over seconds (e.g. Jiang et al., 2000; Miller et al., 1991)
- Incremental with additional repetition (e.g. Li et al., 1993)
- Relatively automatic: less influenced by the behavioral significance of the stimulus (e.g. Jiang et al., 2000; Miller & Desimone, 1994); can occur under anesthesia (e.g. Miller et al., 1991)
- Robust to alterations of stimulus form or position (e.g. recordings in IT cortex: Lueschow et al., 1994)
- Neurons that show the largest firing rate decreases are those that are initially most active (Li et al., 1993)
- Correlates with magnitude of priming effects (van Turennout et al., 2000; Wagner et al., 2000).

Miller et al. (1991): Short-term effects of stimulus repetition on firing rate in IT neurons (by inter-stimulus interval)

Li et al. (1993): Short term (Sample/Match) and long term (1st/2nd) effects of stimulus repetition on firing rate in IT neurons
Theory

Synchrony as an Account of Behavioral Priming
In firing rate neural networks, it is generally difficult for firing rate decreases - particularly with the empirical characteristics of repetition suppression - to lead to enhanced performance because neurons tend to activate each other more slowly and weakly. However, if neurons throughout a processing pathway are synchronizing their spike times as they fire at lower rates, fewer pre-synaptic spikes could actually elicit larger and more reliable post-synaptic depolarizations throughout that pathway. This could lead to a situation where reduced firing rates produce faster reaction times.

Low, Homogenous Firing Rates Promote Synchrony
Interestingly, analyses of the dynamical interactions of networks of excitatory neurons suggest that lower firing rates are important for synchronization (e.g. Chow, 1998; Hansel et al., 1995; Van Vreeswijk et al., 1994). Other factors which slow firing rates such as spike adaptation and/or inhibition can also promote better synchronization (e.g. Crook et al., 1998; Ermentrout & Kopell, 1998). If the mean or variance of neural firing rates become too large, synchronization tends to break down.

Synaptic Depression Promotes Low, Homogenous Firing Rates
We propose that synaptic depression, a temporary reduction in synaptic efficacy following pre-synaptic activity (e.g. Abbott et al., 1997; Tsodyks & Markram, 1997), underlies the short-term firing rate decreases observed under stimulus repetition. Because synaptic depression is roughly proportional to the pre-synaptic firing rate, it can reduce both the mean and variance in firing rates, leading to dynamic enhancement of neural synchronization.
Analyses

IAF network:
\[ e^s: \frac{dV}{dt} = I - V - g_e(t)(V-V_e) - g_i(t)(V-V_i) \]

Phase model:
\[ \frac{d\theta_i}{dt} = \omega_i + H(\theta_j - \theta_i) \]
\[ \frac{d\theta_j}{dt} = \omega_j + H(\theta_i - \theta_j) \]

Let \( \psi = \theta_i - \theta_j \),
\[ \frac{d\psi}{dt} = \omega_i - \omega_j + H(-\psi) - H(\psi) \]

A phase-locked solution is stable if the slope of \( H_{odd} \) is positive where it crosses \( \omega_i - \omega_j \). The synchronous solution corresponds to \( H_{odd} \) crossing \( \omega_i - \omega_j \) at \( t=0 \), and can only exist strictly if \( \omega_i - \omega_j = 0 \) (i.e. neurons i and j are firing at identical rates).
The synchronous solution breaks down at higher firing rates (~ 60 Hz for this system):

It also breaks down if inhibition is removed, controlling for firing rate:
Simulation

Network of conductance-based neurons with fast AMPA and GABA synapses and the Varela et al. (1999) model of synaptic depression.

For each neuron,
\[ \frac{dV}{dt} = -g_L (V-V_{\text{rest}}) - g_E n^4 (V-V_E) - g_{\text{Na}} m^3 h (V-V_{\text{Na}}) + I_{\text{syn}} + I_{\text{ext}} \]

\[ I_{\text{syn}} = -\sum_j g_{\text{ex}} D_j(t) s_j(t) (V-V_{\text{ex}}) - \sum_k g_{\text{in}} D_k(t) s_k(t) (V-V_{\text{in}}) \]

where \( V_{\text{rest}} = -65 \text{mV}, V_{\text{ex}} = 0 \text{mV}, V_{\text{in}} = -80 \text{mV}, D \) is the synaptic depression scaling term which ranges 0 to 1 (see below), and \( I_{\text{ext}} = 0 \) for neurons in the coupled pool. For excitatory neurons, \( g_{\text{ex}} = .2 \) and \( g_{\text{m}} = .2 \), and for inhibitory neurons, \( g_{\text{ex}} = .15 \) and \( g_{\text{m}} = .2 \). Excitatory synaptic currents recover with a \( \tau \) of 4ms, and inhibitory currents recover with a \( \tau \) of 10ms.
Synaptic Depression
We implemented the Varela et al. (1999) model of synaptic depression (based on intracellular recordings from slices of rat primary visual cortex).

At excitatory synapses, $D = D_{ex\text{fast}} D_{ex\text{slow}}$, and at inhibitory synapses, $D = D_{in\text{slow}}$, where

$$\frac{dD_{kj}}{dt} = H(t) (d_{kj} - 1) D_{kj} + (1 - H(t)) \left(1 - D_{kj}\right)/\tau_{kj}$$

where $H(t)$ is a Heaviside function that takes a value of 1 at the peak of a pre-synaptic spike (0 otherwise), $d_{kj}$ determines the amount of depression at each pre-synaptic spike ($d_{ex\text{fast}} = 0.75$, $d_{ex\text{slow}} = 0.97$, $d_{in\text{slow}} = 0.94$), and $\tau_{kj}$ determines the rate of recovery between pre-synaptic spikes ($\tau_{ex\text{fast}} = 0.634 \text{ sec}$, $\tau_{ex\text{slow}} = 9.3 \text{ sec}$, $\tau_{in\text{slow}} = 1.9 \text{ sec}$).

Stimuli
Inputs to the coupled pool were stimulated once a second for ten seconds (duration=350 msec). Each input neuron received a different amount of current during stimulation, leading to a range of input firing rates for each stimulus (20-50 Hz, mean = 35 Hz, sd = 11.3 Hz).

IV’s:
- Repetition (1-10)
- Synaptic Depression (present vs. absent)
- GABA (present vs. absent)

DV’s:
- Firing Rate (Hz)
- Coherence - graded measure of synchrony (0-1) between a pair of spike trains that normalizes for differences in firing rate (White et al., 1998)
Voltage Traces for Coupled Excitatory Neurons
(Synaptic Depression and GABA present)

Repetition 1

Repetition 10
Effect of Stimulus Repetition on Firing Rate

SynDep+GABA (Firing Rate):
Repetition [F(9,45)=36.74, p<.0005]

Effect of Interstimulus Interval on Reduced Firing Rate (Syn Dep + GABA)
Effect of Stimulus Repetition on Firing Rate Variability

![Graph showing the effect of stimulus repetition on firing rate variability. The x-axis represents stimulus number, and the y-axis represents the standard deviation of firing rate in Hertz. The graph includes three conditions: Syn Dep + GABA, No Syn Dep, and No GABA.]

Effect of Stimulus Repetition on Coherence

![Graph showing the effect of stimulus repetition on coherence. The x-axis represents stimulus number, and the y-axis represents the average coherence. The graph includes three conditions: Syn Dep + GABA, No Syn Dep, and No GABA.]

Coherence of Input Neurons:
- Mean = 0.154
- Std Dev = 0.06

SynDep+GABA (Coherence):
- Repetition [F(9,126)=52.66, p<.0005]
  - vs. No GABA [F(1,14)=50.53, p<.0005]
  - vs. No SynDep [F(1,14)=6.609, p<.025]
Effect of Input Heterogeneity, Matched Mean Rate

Heterogeneity [F(1,9)=50.84, p<.0005]

Effect of Synchrony on Output Currents

Repetition 1

Repetition 10
Synchrony Can Enhance Processing Efficiency

**Presynaptic Neurons**

- **Not Synchronized**
  - N1
  - N2

- **Synchronized**
  - N1
  - N2

**Postsynaptic Neuron**

- Voltage
- Threshold

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**Effect of Repetition**

- P (post spike | pre spike)

- P (post spike)/msec

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http://www.cnbc.cmu.edu/~gotts/synchPrime/
Synchrony Can Facilitate Reaction Times

In order to speed responding, motor neurons must be driven to fire either earlier or at higher rates. Synchrony could potentially aid both effects:

- Increased $P$ (post spike | pre spike) leads to earlier propagation of individual spikes from sensory to motor, eliciting faster motor responses

- Elevated, coordinated motor neuron firing due to synchronized cortical activity leads to faster muscle contraction
Effect of Pre-Synaptic Firing Rate and Synchronized Spiking on the Firing Rate of a Single Output Neuron

As long as depolarizations from individual pre-synaptic neurons are well below spiking threshold, synchronized input activity can yield higher firing rates in an output cell, even when input firing rates decrease substantially. This can lead to faster Reaction Times if the output cell represents motor activity.

- 100 spiking neurons (80 e, 20i) project to a single IAF neuron ($\epsilon_{ex} = .02$, $\epsilon_{in} = .05$)
- Input spike times are governed by Poisson statistics (homogenous rates), with rates ranging from 5 to 60 Hz
- 4 different levels of correlated spiking generated by assigning each input neuron one of a certain number of independent Poisson processes (N=100: Coh=0.17, N=20: Coh=0.20, N=5: Coh=0.33, N=1: Coh=1.0)

![Graph of Effect of Repetition](image-url)
Summary

• Priming is associated with reduced neural activity

• We propose that short-term repetition-related activity decreases are due to synaptic depression

• Decreased firing rate enhances spike-time synchrony

• Increased synchrony leads to faster reaction times
References
