Plasticity in the Brain
A Physicist’s Perspective on Learning and Memory

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Frontiers in the Interaction
Between Physics and Biology
web.bryant.edu/~bblais/research.html
Abstract

When approaching a new problem, as a physicist, one starts writing down the simplest possible theories. “Things should be made as simple as possible, but not any simpler” is the motto, attributed to Albert Einstein, but describing the methods used throughout the history of physics. The theories are then modified when new data are available, when predictions are falsified, and when simpler descriptions are shown to work.

In this presentation, I will begin with some basic observations of plasticity in the brain, and present some theories which explain them. Through the mutual interaction of theory and experiment, I will demonstrate the methods by which one can test theories of the brain, and when to modify them. The journey will take us from phenomenological descriptions of learning down to the cellular and molecular processes underlying learning and memory.
Outline

1. Receptive Field Plasticity
   - Introduction
   - Deprivation and Plasticity

2. Theories of Learning
   - Model Neurons
   - Hebbian Synaptic Modification
   - BCM Synaptic Modification
   - Consequences

3. Model of the Mouse
   - Normal Rearing
   - Natural Images to Photoreceptors
   - Architecture
   - Normal Development

4. Deprivation in Mouse
   - Deprivation
   - Deprivation with Structure
Visual System

Architecture

Properties

- Retina
  - light → electrical signals

- LGN
  - relay signals
  - eye inputs kept separate

- Visual Cortex
  - binocular
  - selective to input patterns
Visual System

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Orientation Selectivity
Ocular Dominance
Mioche and Singer, 1989

Normal Rearing, Cats

![Bar Chart](chart.png)

- **Contra**: 16 cells
- **Both**: 15 cells
- **Ipsi**: 2 cells

- Total: 33 cells

**Ocular Dominance Class**

- Contra
- Both
- Ipsi

**Number of Cells**

- Y-axis: Number of Cells
- X-axis: Ocular Dominance Class

**Legend**

- Red: Contra
- Pink: Both
- Purple: Ipsi

**Note**: The chart shows the distribution of cells in different ocular dominance classes for normally reared cats. The data includes 33 cells in total, with 16 in the Contra class, 15 in the Both class, and 2 in the Ipsi class.
Why the Visual System for *Learning and Memory*?

- Experience dependent modification
- Nature reuses mechanisms
- Intuitive and convenient input
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Orientation Preference
Sharma, Angelucci, and Sur, 2000

Orientation Preference Across Visual Cortex
Orientation Preference
Sharma, Angelucci, and Sur, 2000

Orientation Preference, Another Example
Orientation Preference Across Rewired **Auditory** Cortex

Sharma, Angelucci, and Sur, 2000
Monocular Deprivation Shifts Ocular Dominance

- Not just an intensity difference
- Requires *patterned* input: shift occurs with diffuse lens
  (Blakemore and Van Sluyters, 1974)
Visual Cortex Receptive Field Plasticity
Wiesel and Hubel, 1969

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**Normal Rearing, Cats**

- Contra
- Both
- Ipsi

- N=33

**Monocular Deprivation, Cats**

- Contra
- Both
- Ipsi

- N=33
Visual Cortex Receptive Field Plasticity
Blakemore and VanSluyters, 1974

Reverse Suture Gives Recovery to Monocular Deprivation

Initial state

After 1 day RS

After 2 days RS

Right eye response:

Left eye response:
Visual Cortex Receptive Field Plasticity
Movshon and Blakemore, 1974

- MD from eye opening
- RS at 5 weeks

Reverse Suture Gives Recovery to Monocular Deprivation
BD has a slower timescale than MD

Binocular Deprivation, Cats

(adapted from Freeman et.al. 1981)

N=42
Strabismus yields monocular cells with unaffected responses to each eye.
Visual System: Environment to Synapses

**Architecture**

- **Retina**: light → electrical signals
- **LGN**: relay signals, eye inputs kept separate
- **Visual Cortex**: binocular, selective to input patterns

**Properties**

- **Retina**: light → electrical signals
- **LGN**: relay signals, eye inputs kept separate
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**Visual**

- **Cortex**
- **LGN**
- **Retina**

**Visual System**

- **Retina**
- **LGN**
- **Visual Cortex**

**Visual Pathway**

- Light input from retina
- Relay signals through LGN
- Binocular input to visual cortex

**Properties**

- **Retina**: converting light to electrical signals
- **LGN**: relaying signals from eyes
- **Visual Cortex**: processing binocular inputs

**Diagram**

- Schematic representation of the visual system
  - Light input to retina
  - Relay signals through LGN
  - Binocular input to visual cortex

**Legend**

- **Visual Cortex**
- **LGN**
- **Retina**

**Educational Concept**

- Receptive Field Plasticity
- Theories of Learning
- Model of the Mouse
- BCM Synaptic Modification
- Consequences
Visual System: Environment to Synapses

Electrical Signal Changed to Chemical Signal at the Synapse

- Electrical Signal (action potential)
- Chemical Signal (neurotransmitter, receptors)
- Synaptic Vesicle
- Synaptic Gap
- Dendrite of Cortical Neuron
- LGN Neuron
- Cortical Neuron
- Inputs (dendrites)
- Output (axon)
- Synapse

Inputs (dendrites):

(axon)

Output (axon):

(axon)
Simple Model of a Neuron
Theories of Learning
As simple as possible...

Some things we are including
- Single neuron
- Rate code
- Effective synapses

Things we know are important but are not including
- different types of cells/synapses
- feedback to LGN
- lateral connectivity
- layer/area differences
- spike timing and temporal codes
Theories of Learning
As simple as possible...

Some things we are including
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Things we know are important but are not including
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Theories of Learning
Theme of Structure and Noise

Structure
- Open Eye Inputs
  - Normal Rearing (Selectivity): Finding Structure
  - Strabismus: Structure versus Structure

Noise
- Closed Eye Inputs
  - Monocular Deprivation: Structure versus Noise
  - Reverse Suture: Structure versus Noise
  - Binocular Deprivation: Noise versus Noise

Questions
- What is Structure?
- What is Noise?
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# Theories of Learning

**Theme of Structure and Noise**

## Structure
- Open Eye Inputs
- Normal Rearing (Selectivity): Finding Structure
- Strabismus: Structure versus Structure

## Noise
- Closed Eye Inputs
- Monocular Deprivation: Structure versus Noise
- Reverse Suture: Structure versus Noise
- Binocular Deprivation: Noise versus Noise

## Questions
- What is Structure?
- What is Noise?
Model Architecture (Binocular)

Equations

inputs: \( x = (x_1, x_2, \cdots) \)

weights: \( w = (w_1, w_2, \cdots) \)

output: \( y = \sigma(x_1 \cdot w_1 + x_2 \cdot w_2 + \cdots) = \sigma(x \cdot w) \)
Hebb’s Rule

Hebb, 1949

*When an axon in cell A is near enough to excite cell B and repeatedly and persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A’s efficiency in firing B, is increased.*

“What those that fire together wire together”

\[
\frac{dw}{dt} = yx
\]

Unstable!
Hebb’s Rule

Hebb, 1949

When an axon in cell A is near enough to excite cell B and repeatedly and persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A’s efficiency in firing B, is increased.

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Unstable!
Hebbian Synaptic Modification
Objective Function Formulation

Maximize Variance in Output Distribution

- **definition of variance**

\[
V_w(y) = E[y^2]
\]

\[
y = w \cdot x
\]

- **weights modify to maximize** \(V\)

\[
\frac{dw}{dt} = \frac{\partial}{\partial w} V_w = E[yx]
\]

- Directions of maximum variance \(\equiv\) directions of strongest 2-point correlations

- Still needs stabilization
Maximize Variance in Output Distribution

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Synaptic Stabilization

Mathematical method implies Biological Mechanism

- Saturation Limits (Miller 1994)
  \[ w_{\text{min}} < w < w_{\text{max}} \]

- Normalization (Linsker, 1986; Miller 1994)
  \[ \sum_i w_i^2 = \text{constant} \]

- Decay Terms (Oja, 1982; Blais et.al. 1998)
  \[ \frac{dw}{dt} = yx - y^2w \]

- Moving Threshold (Bienenstock, et.al. 1982; Blais et.al. 1999)
BCM Learning Rule
Bienenstock, Cooper, Munro, 1982

\[
\frac{dw_i}{dt} = \phi(y, \theta_M) x_i \\
\theta_M \sim E[y^2]
\]

BCM Rule Properties
- Selective fixed points
- Requires pre-synaptic activity for modification
BCM: Stability
One Dimensional Example

- Quadratic form
  \[
  \frac{dw}{dt} = y(y - \theta_M)x
  \]

- Instantaneous limit
  \[
  \theta_M = y^2
  \]

- Fixed points at 0 and 1
  \[
  \frac{dw}{dt} = y(y - y^2)x = y^2(1 - y)x
  \]

  (unstable)  (stable)

  0  1
BCM Theory

Threshold and Selectivity Movies

Threshold and Selectivity
Functional Forms
Mathematical Convenience versus Theoretical Necessity

- Parabolic

\[ \frac{dw}{dt} = y(y - \theta_M)x \]

- Parabolic, with Scale (Law and Cooper, 1992)

\[ \frac{dw}{dt} = y(y - \theta_M)x / \theta_M \]

Necessary Conditions

1. \( \frac{dw}{dt} > 0 \) for \( y > \theta_M \)
2. \( \frac{dw}{dt} < 0 \) for \( y < \theta_M \)
3. \( \theta_M \sim \) super-linear function of history of \( y \)
Maximize Sparseness in Output Distribution

- definition of sparseness (bimodality, high skewness, etc.)

\[ R_w(y) = \frac{1}{3} E[y^3] - \frac{1}{4} E^2[y^2] \]

\[ y = w \cdot x \]

- weights modify to maximize \( R \)

\[ \frac{dw}{dt} = \frac{\partial}{\partial w} R_w = E[y^2 x] - E[y^2] \left( \underbrace{E[yx]}_{\theta} \right) \]

\[ = E[(y(y - \theta)x)] \]

- Selectivity \( \equiv \) sparse responses, i.e. responding to a small subset of patterns
Maximize Sparseness in Output Distribution

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Receptive Field Plasticity
Theories of Learning
Model of the Mouse
Deprivation in Mouse

BCM Maximizes Sparseness

\[ R_w(y) = \frac{1}{3} E[y^3] - \frac{1}{4} E^2[y^2] \]

\( R = -0.25 \) (noise)

\( R = +0.33 \) (indep. patterns)
BCM Maximizes Sparseness

\[ R_w(y) = \frac{1}{3} E[y^3] - \frac{1}{4} E^2[y^2] \]

- \( R = +0.13 \) (noise)
- \( R = +0.40 \) (natural images)
Approximate Visual System

- ~ 1000 photoreceptors per ganglion cell\(^1\)
- Retina/LGN responses center-surround organization\(^2\)
- Center Diameter\(^2\) cat \(< 1^\circ\)
- Center/Surround ratio\(^2\) \(\sim 1 : 3\)
- Mean V1 RF Widths cat \(\sim 1^\circ\)

---

\(^1\) Sterling 1988; Jeon, et.al. 1998
\(^2\) Stone and Pinto 1993; Grubb and Thompson 2003
Natural Images
 Pixels to Photoreceptors

- On the order of 1000 photoreceptors feeding into 1 ganglion cell
  - 32×32 photoreceptors input to ganglion cell
- A Difference of Gaussians (DoG) filter
  - 3:9 center:surround ⇒ center diameter ~ 13 pixels
  - 1:3 center:surround ⇒ center diameter ~ 4.4 pixels
- Resize Image
  - 13 pixels (or 4.4 pixels) ~ 0.5° (cat)
Cat Ganglion Responses

Response Images

Unprocessed

Cat 1:3

- White → High Response
- Black → Low Response
Model Architecture (Binocular)

Architecture

- Image Plane
- Right Retina
- Left Retina
- LGN
- Cortex (single cell)
- Inputs
- Weights
- Output

Natural Image Patches

Noise Patches
Normal Rearing

Initial Conditions are Random...
Normal Rearing

...Selectivity Develops...
Normal Rearing

...Selectivity Sharpens, Binocular Responses.
Monocular Deprivation
Structure in Open Eye, Noise in Closed Eye

Initial Conditions are Binocular...
Monocular Deprivation
Structure in Open Eye, Noise in Closed Eye

...Responses to Closed Eye Drop...
Monocular Deprivation
Structure in Open Eye, Noise in Closed Eye

...Monocular Responses to the Open Eye.
Monocular Deprivation
Structure in Open Eye, Noise in Closed Eye

Structure Versus Noise

Neuron Chooses Structure Over Noise
Reverse Suture
Structure in Previously Closed Eye, Noise in Previously Open Eye

Initial Conditions are Monocular to the Closed Eye...
Reverse Suture
Structure in Previously Closed Eye, Noise in Previously Open Eye

...Responses to Closed Eye Drop...Open Eye Increases...
Reverse Suture
Structure in Previously Closed Eye, Noise in Previously Open Eye

...Monocular Responses to Newly Open Eye.
Reverse Suture
Structure in Previously Closed Eye, Noise in Previously Open Eye

Structure Versus Noise

Neuron Chooses Structure Over Noise
Binocular Deprivation
Noise in both Closed Eyes

Initial Conditions are Binocular...

- Binocular Deprivation
- Noise in both Closed Eyes
- Initial Conditions are Binocular...
Binocular Deprivation
Noise in both Closed Eyes

...Responses to Closed Eyes Drop Slowly...
Binocular Deprivation
Noise in both Closed Eyes

...Binocular Responses with Reduced Selectivity.
Binocular Deprivation
Noise in both Closed Eyes

Noise Versus Noise

Less Competition $\Rightarrow$ Slower Response Reduction
Strabismus
Different, Equal Structure in Each Eye

Initial Conditions are Binocular...

- Left eye
- Right eye

Response vs. Stimulus Angle vs. Time

Synaptic weights

Graph showing response against stimulus angle and time for both eyes.
Strabismus
Different, Equal Structure in Each Eye

...Responses to One of the Eyes Decreases...
Receptive Field Plasticity
Theories of Learning
Model of the Mouse
Deprivation in Mouse


different, equal structure in each eye

...monocular responses to the other eye.
Strabismus
Different, Equal Structure in Each Eye

Structure Versus Structure

Neuron Chooses One Structured Channel
Model of the Mouse

Advantages

- More animals (more data)
- Data more quantitative (chronic recordings)
- Possibility for genetic manipulation

Requires some modifications to the model
Model of the Mouse

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Experimental Results: Visually Evoked Potentials
Frenkel and Bear, 2004

- Contralateral-eye VEP
- Ipsilateral-eye VEP

VEP amplitude (normalized to day 0 ipsi)

- Day 0: Contralateral-eye VEP (n = 7)
- Day 5: Contralateral-eye VEP
Normal Rearing (NR)
Frenkel and Bear, 2004

- contralateral bias magnitude $\sim 2.5$
- VEP includes responses from *populations* of cells

![Graph showing VEP amplitude normalized to day 0 ipsi](image)
Approximate Mouse Visual System

- \( \sim 1000 \) photoreceptors per ganglion cell\(^3\)
- Retina/LGN responses center-surround organization\(^4\)
- Center Diameter\(^2\) \( \sim 7 - 10^\circ \) [cat < 1\(^\circ\)]
- Center/Surround ratio\(^2\) \( \sim 1 : 3\)
- Mean V1 RF Widths\(^5\) \( \sim 6^\circ - 14^\circ\)
- Contralateral bias\(^6\) \( \sim 2.5 \) (functionally)

---

\(^3\) Sterling 1988; Jeon, et.al. 1998
\(^4\) Stone and Pinto 1993; Grubb and Thompson 2003
\(^5\) Gordon, et.al. 1996; Metin, et.al. 1998
\(^6\) Frenkel and Bear, 2004
Pixels to Photoreceptors

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- Resize Image
  - 13 pixels (or 4.4 pixels) ∼ 7° (mouse)
  - 13 pixels (or 4.4 pixels) ∼ 0.5° (cat)
Mouse Ganglion Responses
Response Images 53x81 pix

Unprocessed

Mouse 2:6

Mouse 3:9
Contralateral Bias

- Measurements on populations of monocular and binocular cells
- For simplicity assume
  - pure monocular and binocular cells
  - monocular cells do not modify with deprivation
  - binocular cells with equal contribution from contra and ipsi
Normal Rearing Simulations

**Binocular Cells**

- Response vs. Time
  - Scale: 0 to 30 on the y-axis, 0 to 1e+07 on the x-axis

**Monocular Cells**

- Response vs. Time
  - Scale: 0 to 50 on the y-axis, 0 to 1.5e+07 on the x-axis
Response Histogram

**Contra** Binocular + Monocular Responses

**Ipsi** Only Binocular Responses

C/I = 2.2
Monocular Deprivation (MD)
Frenkel and Bear, 2004
Monocular Deprivation (MD) and Inactivation (MI)
Frenkel and Bear, 2004
Monocular Deprivation (MD) and Inactivation (MI)

**MD**
- contra responses decrease

**MI**
- contra responses constant
- ipsi responses increase faster than MD

![Graphs showing MD and MI responses](image)
Extended Monocular Deprivation (MD)
Frenkel and Bear, 2004

Rapid, deprivation-induced response depression

Delayed response potentiation
no significant changes in response
Monocular followed by Binocular Deprivation
Frenkel and Bear

contra response *recovers*

Record C and I VEPs
Ipsi eye
Contra eye
MD

Record C and I VEPs
MD

3d MD (n=8)

3+4 BD (n=5)
Can we account for these results in terms of the theme of structure versus noise?
Deprivation
Prior Work

Normal Input
- Structure

Deprived
- Noise
Deprivation with Structure

Proposed Idea

Normal Input
- Structure

Deprived Input
- Gaussian Blur + Noise
BCM Learning Rule

Competition between pattern and noise

- Blurring lowers the intensity of selected patterns
- Blurring raises the probability of selected patterns (more similar patterns)

<table>
<thead>
<tr>
<th>intensity of patterned input</th>
<th>↓</th>
<th>weights</th>
<th>↑</th>
</tr>
</thead>
<tbody>
<tr>
<td>probability of selected pattern</td>
<td>↑</td>
<td>weights</td>
<td>↓</td>
</tr>
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<td>intensity of noise input</td>
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Binocular Deprivation (BD) Simulations

- no significant changes in response
Monocular followed by Binocular Deprivation Simulations

contra response *recovery*
Extended Monocular Deprivation (MD) Simulations

- contra responses decrease (3d) and then increase (7d)
- ipsi responses increase

Time = $2 \cdot 10^7$

\[ \text{C/I} = 1.1 \]

Time = $4 \cdot 10^7$

\[ \text{C/I} = 1.3 \]
Structure versus Noise
Working Parameters

- **normal DoG filter size**: 2:6
- **size of the blur filter**: 2
- **noise standard deviation**: 0.1 (low noise)
- **scale of the blur filter**: 0.8 (high intensity)
<table>
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<th>Structure versus Noise</th>
<th>Role of Parameters</th>
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<tbody>
<tr>
<td><strong>lower intensity, lower noise</strong></td>
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<tr>
<td><img src="image1.png" alt="Image" /> + <img src="image2.png" alt="Image" /></td>
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<tr>
<td>- BD increases after NR</td>
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</tr>
<tr>
<td><strong>higher intensity, lower noise</strong></td>
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</tr>
<tr>
<td><img src="image5.png" alt="Image" /> + <img src="image6.png" alt="Image" /></td>
<td><img src="image7.png" alt="Image" /> + <img src="image8.png" alt="Image" /></td>
</tr>
<tr>
<td>- MD contra increases</td>
<td>- no MD recovery</td>
</tr>
<tr>
<td>- MD ipsi drops</td>
<td>- BD drops after NR</td>
</tr>
<tr>
<td>- BD increases after NR</td>
<td>- BD drops after NR</td>
</tr>
</tbody>
</table>
Summary

- Interpret neural dynamics as a competition between structure and noise to explain a wide range of experimental results
- Use experiments in mice to constrain the possible theories
  - MD+MI → presynaptic activity needed (BCM)
  - 7d MD contra increase → structure in the deprived input
  - BD no change → noise level, scale
  - rate of MD ipsi increase → ratio of binocular/monocular cells

Unresolved Issues

- magnitude of the contra response decrease in MD
- magnitude of the contra response increase in sustained MD
- magnitude of the ispi response increase in MD
Questions?
Experiments
Frenkel and Bear

MD, TTX, BD, and DR

Normalized VEP Amplitude

3d MD (n=8) 7d MD (n=11) 3+4 TTX (n=6) 3+4 BD (n=5)

3d MD + 4 DR (n=8) 3d Norm + 4 DR (n=6)