Unifying Predictive Coding and Biased Competition into a Model of Visual Attention and V1 Response Properties

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Outline

Part 1
Reconciling Predictive Coding and Biased Competition

Part 2
Improving the Predictive Coding / Biased Competition Model

Part 3
Modelling V1 Response Properties

Part 4
Modelling Visual Attention
Reconciling PC and BC

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Modelling Visual Attention
During visual perception, information propagates through the visual processing hierarchy from primary sensory areas to higher cortical regions.
Lateral connections (both excitatory and inhibitory) enable neurons within the same population to interact, to “process” the incoming information.
Feedforward Theories

Many theories propose a purely serial, feedforward, sequence of processing stages e.g.:
- Hubel & Wiesel
- David Marr
- Donald Broadbent
- Riesenhuber & Poggio (HMAX)
- Simon Thorpe (SpikeNet)
- Edmund Rolls (VisNet)
- Itti & Koch
- Yann LeCun
Inter-Regional Feedback Connections

However, feedback connections are a prominent feature of cortical anatomy, they affect neural responses, and influence perception.
Feedback Theories

How do cortical feedback (FB) connections influence processing?
Feedback Theories

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FB *suppresses* activity in preceding area

  e.g.:  • Rao & Ballard
         • Karl Friston
         • David Mumford
         • Horace Barlow

“Predictive Coding” (PC)
Feedback Theories

How do cortical feedback (FB) connections influence processing?

FB **suppresses** activity in preceding area
- e.g.: • Rao & Ballard
  • Karl Friston
  • David Mumford
  • Horace Barlow
- “Predictive Coding” (PC)

FB **enhances** activity in preceding area
- e.g.: • Gustavo Deco
  • Reynolds & Heeger
  • Fred Hamker
  • Roelfsema & Lamme
- “Biased Competition” (BC)

Predictive coding and biased competition seem incompatible
Biased Competition Model

- **Input (from thalamus or lower cortical region):** 
  - Feeds into two cortical regions.
- **Two Cortical Regions:** 
  - Competition between neurons in each region.
- **Feedback (excitation):** 
  - Enhances responses consistent with top-down expectation: biases outcome of competition.
- **Excitatory**: Implanted arrows.
- **Inhibitory**: Unimplanted arrows.
- **Many-to-Many**: Crossed arrows.
Biased Competition (Standard Mechanism)

Standard mechanism of competition: nodes compete to generate outputs i.e. nodes suppress the response generated by neighbouring nodes
Biased Competition (Alternative Mechanism)

Alternative mechanism of competition: nodes compete to receive inputs i.e. nodes suppress the inputs to neighbouring nodes.

“e” population of neurons represents the inhibited inputs to the region.
Biased Competition Model (Reformulated)

If we implement the biased competition model using this alternative mechanism of competition we get a neural architecture like this
Predictive Coding Model

higher cortical regions predict outputs of lower regions

cortical feedback connections suppress predicted information

residual error ("e") is sent forward
Predictive Coding Model

\[ y^{Si} \leftarrow (1 - \vartheta)y^{Si} + \xi W^{Si} e^{Si-1} - \eta e^{Si} \]

\[ e^{Si} = y^{Si} - (W^{Si+1})^T y^{Si+1} \]

\[ e^{Si-1} = y^{Si-1} - (W^{Si})^T y^{Si} \]

feedback

substitute for \( e^{Si} \) ...
Predictive Coding (Reformulated)

$y^{Si} \leftarrow (1 - \eta - \vartheta) y^{Si} + \zeta W^{Si} e^{Si-1} + \eta (W^{Si+1})^T y^{Si+1}$

...changes the mechanism of feedback between $y$ populations:
- from 2-stage inhibitory mechanism
- to a direct excitatory feedback mechanism

$e^{Si-1} = y^{Si-1} - (W^{Si})^T y^{Si}$

change mapping onto cortical regions...
Predictive Coding (Reconciled)

\[ y^{Si} \leftarrow (1 - \eta - \vartheta) y^{Si} + \zeta W^{S_i} e^{S_i} + \eta (W^{S_i+1})^T y^{S_i+1} \]

...shifting assignment of neural populations to cortical regions:
  * add 1 to the processing stage label for each e population

\[ e^{S_i} = y^{S_i-1} - (W^{S_i})^T y^{S_i} \]

This implementation of PC is identical to BC using the alternative mechanism of competition.
The same model can be interpreted in two ways:

1. Predictive Coding (a hierarchy of generative models)
   
   \( y \) represents the prediction of the causes which underlie the input.

2. Biased Competition (a hierarchy of discriminative models)
   
   \( y \) encodes the similarity between the input and the neural representations.
The same model can be interpreted in two ways:

1. Predictive Coding (a hierarchy of *generative* models)
   - $e$ represents the *residual error* between the actual input and the predicted input.

2. Biased Competition (a hierarchy of *discriminative* models)
   - $e$ represents the *inhibited input* to a population of competing nodes.
The same model can be interpreted in two ways:

1. Predictive Coding (a hierarchy of generative models)
   
   the dynamics operate to minimise the error between the input and the top-down reconstruction of the input.

2. Biased Competition (a hierarchy of discriminative models)
   
   the dynamics operate to determine the outcome of the competition between the neural representations.
Reconciliation

The same model can be interpreted in two ways:

1. Predictive Coding (a hierarchy of *generative* models)

   **cortical feedback** provides *priors* that modify the prediction of the generative model.

2. Biased Competition (a hierarchy of *discriminative* models)

   **cortical feedback** generates *biases* which effect the outcome of the competition between neural representations.
Improving PC/BC

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Reconciliation (recap)

Predictive Coding

Biased Competition

Mathematical reorganisation

Replace mechanism of competition

re-map onto cortical regions
Reconciliation (recap)

Predictive Coding (Original)

Two ways of implementing a single mathematical model

Replace mechanism of competition

re-map onto cortical regions

Linear PC/BC
Implementational Differences

Two ways of implementing a single mathematical model... make different predictions about how the same underlying model could be implemented in cortical circuitry.
Implementational Differences

Predictive Coding (Original)

• Cortical feedback inhibitory

Linear PC/BC

• Cortical feedback excitatory
Implementational Differences

Predictive Coding (Original)

- Cortical feedback inhibitory
- Firing rates negative (essential)

• Cortical feedback excitatory
• Firing rates negative (undesirable)

Linear PC/BC
**Improving the mechanism of competition**

Avoiding negative firing rates:
- biologically implausible
- results in instability

The “alternative mechanism of competition” within each stage of the PC/BC hierarchy is the linear generative model proposed by Harpur and by Olshausen and Field.

\[ e^{Si} = y^{Si-1} - (W^{Si})^T y^{Si} \]
\[ y^{Si} \leftarrow y^{Si} + \mu W^{Si} e^{Si} \]
Improving the mechanism of competition

Avoiding negative firing rates:
  • biologically implausible
  • results in instability

\[ e^{Si} = y^{Si-1} - (W^{Si})^T y^{Si} \]
\[ y^{Si} \leftarrow y^{Si} + \mu W^{Si} e^{Si} \]

Harpur / Olshausen and Field linear generative model
Improving the mechanism of competition

Avoiding negative firing rates:
  • biologically implausible
  • results in instability

\[
e_{Si} = y_{Si-1} - (W_{Si})^T y_{Si}
\]

\[
y_{Si} \leftarrow y_{Si} + \mu W_{Si} e_{Si}
\]

Harpur / Olshausen and Field linear generative model
Improving the mechanism of competition

Avoiding negative firing rates:
- biologically implausible
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\[ e^{S_i} = y^{S_i-1} - (W^{S_i})^T y^{S_i} \]

\[ y^{S_i} \leftarrow y^{S_i} + \mu W^{S_i} e^{S_i} \]

Harpur / Olshausen and Field linear generative model

increasing network size
Improving the mechanism of competition

Avoiding negative firing rates:
• biologically implausible
• results in instability

\[ e^{Si} = y^{Si-1} \odot \left( (\hat{W}^{Si})^T y^{Si} \right) \]
\[ y^{Si} \leftarrow y^{Si} \otimes W^{Si} e^{Si} \]
Nonlinear PC/BC

\[ e^{Si} = y^{Si-1} - (W^{Si})^T y^{Si} \]

\[ y^{Si} \leftarrow y^{Si} + \mu W^{Si} e^{Si} \]

\[ e^{Si} = y^{Si-1} \odot ((\hat{W}^{Si})^T y^{Si}) \]

\[ y^{Si} \leftarrow y^{Si} \odot W^{Si} e^{Si} \]

use modulatory rather than additive feedback

\[ y^{Si} \leftarrow y^{Si} + \nu (W^{Si+1})^T y^{Si+1} \]

\[ y^{Si} \leftarrow y^{Si} \odot \left( 1 + \eta (W^{Si+1})^T y^{Si+1} \right) \]
Improving Predictive Coding

Predictive Coding (Original)

- Cortical feedback inhibitory
- Firing rates negative
- Unstable

Nonlinear PC/BC

just “PC/BC” from now on...

• Cortical feedback excitatory
• Firing rates positive
• Stable
Modelling V1 Response Properties

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Modelling V1 Response Properties

PC/BC makes specific predictions about the mechanism of competition operating within each cortical area.

The effects of competitive interactions between cortical neurons have been most extensively studied in primary visual cortex (V1).

Simulating V1 response properties thus provides a good test to see if the mechanism of competition proposed for PC/BC (i.e. DIM) is consistent with the mechanism of competition used by cortex.
Modelling V1 Response Properties

Model will consider one processing stage in isolation.

Need to define synaptic weights to simulate V1 receptive fields.
Modelling V1 Response Properties

**LGN Model**
- on- and off-centre
- centre-surround
- RFs = LoG functions

**V1 Model**
- RFs = Gabor functions split into on and off channels
- 32 nodes (8 orientation and 4 phases)
  - centred at each image pixel
Orientation Tuning

Tuning:
- narrow (no response to orthogonal orientation)
- contrast invariant
Orientation Tuning

Nonlinear PC/BC simulation
Spatial Frequency Tuning


Tuning:
• contrast invariant

Response vs. Spatial Freq. (cycles/degree)
Spatial Frequency Tuning

Nonlinear PC/BC simulation
Temporal Frequency Tuning

Freeman, Durand, Kiper, Carandini (2002) Neuron

![Graph showing temporal frequency tuning](image)

- **Response** along the y-axis.
- **Drift Rate (cycles/second)** along the x-axis.

PC/BC, FIAS 2010
Temporal Frequency Tuning

Nonlinear PC/BC simulation
Cross-Orientation Suppression

Bonds (1989) Visual Neuroscience
Cross-Orientation Suppression

Nonlinear PC/BC simulation
Cross-Orientation Suppression Temporal

Freeman, Durand, Kiper, Carandini (2002) Neuron

Note, y-axis suppression index:
• strong suppression even at high mask frequencies
Cross-Orientation Suppression Temporal

Nonlinear PC/BC simulation

Suppression Index

Drift Rate (cycles/second)

Response

Drift Rate (cycles/iteration)
Surround Suppression

Suppression depends on:
- orientation of surround
- size of centre

Surround Suppression


Nonlinear PC/BC simulation

Increasing size of centre
Dynamics of Suppression

Smith, Bair, Movshon (2006) Journal of Neuroscience

Onset of surround suppression delayed compared to onset of cross-orientation suppression.
Dynamics of Suppression

Smith, Bair, Movshon (2006) Journal of Neuroscience
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Modelling Visual Attention

Lots of attention data consistent with BC.

PC has been criticised for being inconsistent with single-cell data showing an increase in the amplitude of the neural activity generated in response to an attended (i.e., predicted) stimulus.

Hence, using PC/BC to simulate such data provides a good demonstration that PC can be interpreted as a model of BC.
Modelling Visual Attention

Attention modelled as an additional source of feedback: treated in exactly the same way as feedback from higher stages in the hierarchy.

No attempt made to simulate temporal dynamics.
Spatial Selectivity

Reynolds, Chelazzi, & Desimone (1999) Journal of Neuroscience

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Response

Time

pref attend away

V2

RF

(Attn)
Spatial Selectivity

Reynolds, Chelazzi, & Desimone (1999) Journal of Neuroscience

- pref attend away
- poor attend away

Response vs. Time

V2

RF

(Attn)
Spatial Selectivity

Reynolds, Chelazzi, & Desimone (1999) Journal of Neuroscience

- pref attend away
- poor attend away
- pair attend away

Response

Time

V2

RF

Attn

PC/BC, FIAS 2010
Spatial Selectivity

Reynolds, Chelazzi, & Desimone (1999) Journal of Neuroscience

- pref attend away
- poor attend away
- pair attend away
- pair attend pref

V2

Response vs. Time

PC/BC, FIAS 2010
Spatial Selectivity

Nonlinear PC/BC simulation

- pref attend away
- poor attend away
- pair attend away
- pair attend pref

Response vs. Time

PC/BC, FIAS 2010
Spatial Selectivity


Response to pair:
- without attention; intermediate
- with attention; more similar to attended stimulus in isolation
Spatial Selectivity

Nonlinear PC/BC simulation

Pref attend away
Poor attend away
Pair attend away
Pair attend poor
Spatial Selectivity and Contrast


As poor stimulus contrast *increases*:
- response to poor stimulus in isolation *increases*
- response to stimulus pair *decreases*
Spatial Selectivity and Contrast


Increasing contrast of the poor stimulus

Nonlinear PC/BC simulation
Featural Selectivity

Chelazzi, Miller, Duncan, & Desimone (2001) Cerebral Cortex

Response to pair:
• similar to attended stimulus in isolation
Featural Selectivity

Nonlinear PC/BC simulation

- pref attend pref
- poor attend poor
- pair attend pref
- pair attend poor
Spatial Facilitation and Tuning

McAdams and Maunsell (1999) Journal of Neuroscience

- Response varies with stimulus orientation.
- Attention to stimulus location multiplicatively increases response at all orientations.
Spatial Facilitation and Tuning

Nonlinear PC/BC simulation

Response vs. Orientation

PC/BC, FIAS 2010
Featural Facilitation and Tuning


- Response varies with direction of motion.
- Attention to stimulus motion increases response near cell's preferred direction, decreases response far from cell's preferred direction.
Featural Facilitation and Tuning

Nonlinear PC/BC simulation

“feature similarity gain” can be modelled without the need for attention to have direct suppressive effects
Summary

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Summary

Linear mechanism of competition.

Suffers from:
- negative firing rates
- instability
- poor competition

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Summary

Nonlinear mechanism of competition in place of linear mechanism

Multiplicative modulation in place of additive feedback
Summary

Nonlinear mechanism of competition consistent with competition in V1

Part 4
Modelling Visual Attention
Summary

Nonlinear mechanism of competition consistent with competition in V1

Nonlinear PC/BC consistent with visual attention
Conclusions

1. A unified interpretation of models that are currently considered distinct (e.g. biased-competition and predictive coding).

2. A unified account of phenomena which are currently considered distinct (e.g. surround suppression, cross-orientation suppression, attention).

3. A single computational explanation for this diverse range of neurophysiological findings.