Models of Perception:
Predictive Coding

Alex Hess

Computational Psychiatry Course Zurich
06.09.2023

“Bayesian brain” hypothesis

Bayes’ rule

$$\underbrace{p(x|y,m)}_{\text{posterior}} = \frac{\overbrace{p(y|x,m)}^{\text{likelihood}}\overbrace{p(x|m)}^{\text{prior}}}{\underbrace{p(y|m)}_{\text{model evidence}}}$$

x: state of the world
y: sensory data
m: model

“Bayesian brain” hypothesis

Bayes’ rule

$$\overbrace{p(x|y,m)}^{\text{posterior}} = \frac{\overbrace{p(y|x,m)}^{\text{likelihood}}\overbrace{p(x|m)}^{\text{prior}}}{\underbrace{p(y|m)}_{\text{model evidence}}}$$

$$p(y|m) = \int p(y|x,m)p(x|m)dx$$

x: state of the world
y: sensory data
m: model

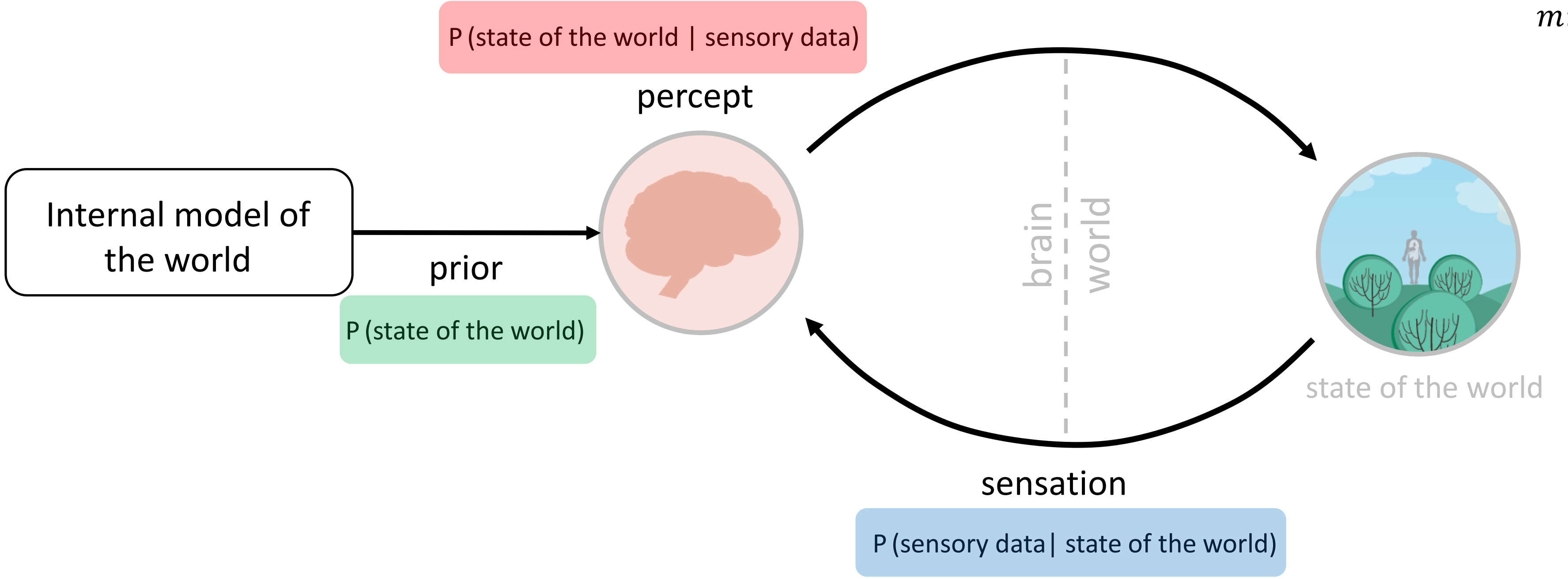


Figure based on slide by Rike Petzschner

(Bayesian) Predictive Coding

what?	(approximate) Bayesian inference
how?	predictive coding
implementation?	(predictive coding in the brain)

Adapted from slide by Lilian Weber

(Bayesian) Predictive Coding

Marr's levels of analysis

Marr 1982

computational — (approximate) Bayesian inference

algorithmic — predictive coding

implementational — (predictive coding in the brain)

Side note

predictive coding can serve different computational goals

approximate Bayesian inference can be realised by other representations

Aitchison & Lengyel 2017, *Curr Op Neurobiol*

Adapted from slide by Lilian Weber

PC in engineering and information theory

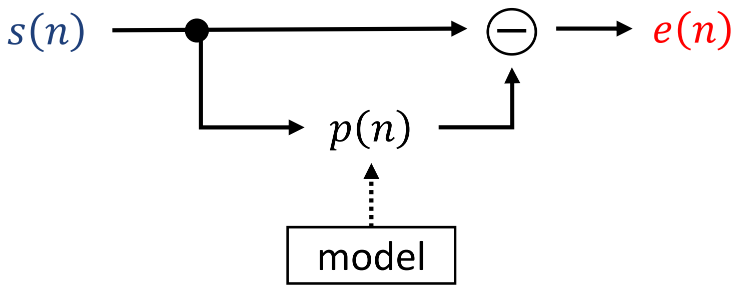
$$e(n) = s(n) - p(n)$$

Redundancy reduction

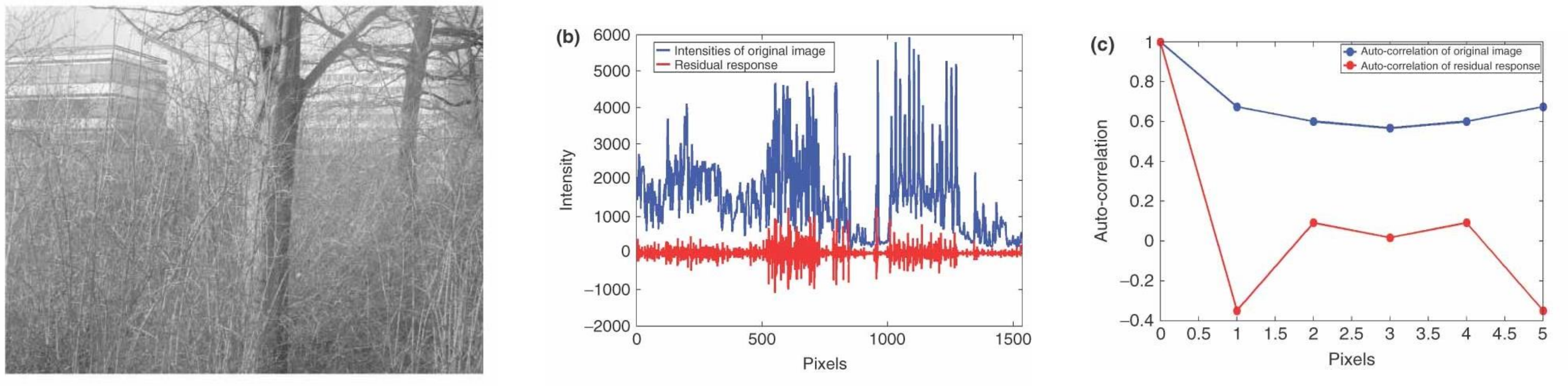
(Barlow, 1961)

- Efficient way to transmit a signal $s(n)$:
  - Model $\Rightarrow$ prediction $p(n)$
  - Residual error $e(n)$

  $\left.\right\}$ reconstruct signal $s(n)$
- Decorrelation



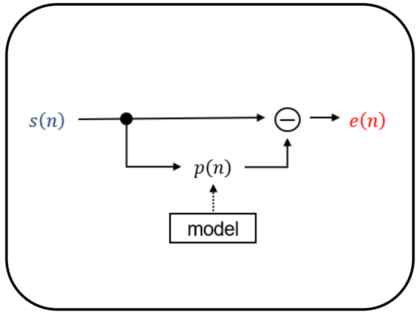
Adapted from O'Shaughnessy 1988, *IEEE Potentials*



Huang & Rao 2011, *WIREs Cogn Sci*

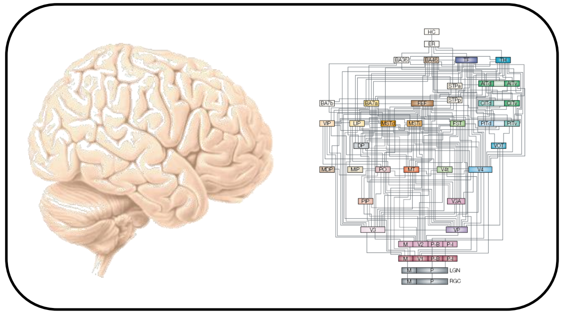
Predictive Coding as neuroscientific theory

Intellectual antecedents



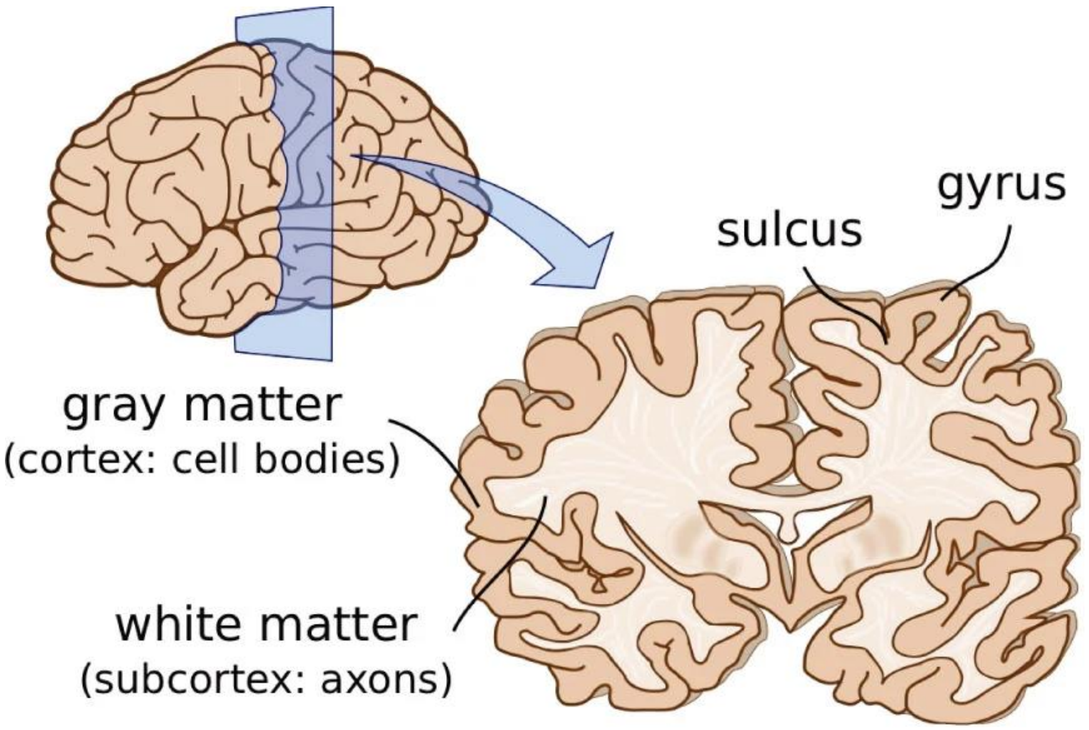
- Redundancy reduction

Neuroanatomy

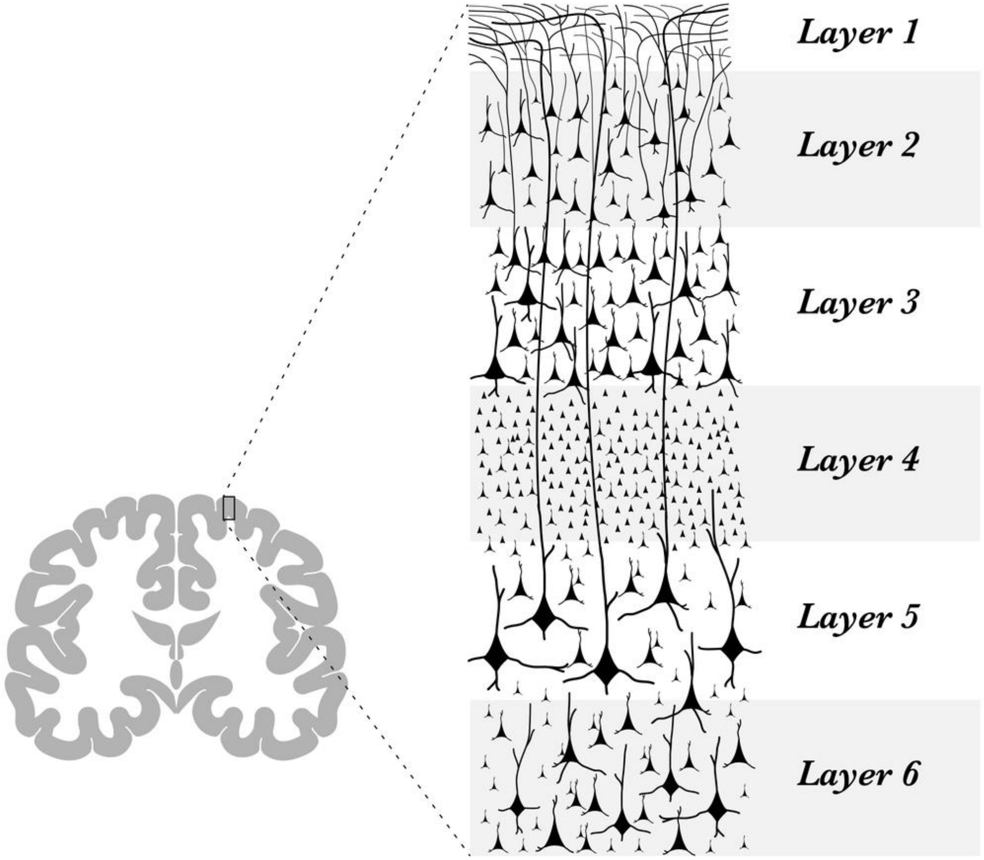


Felleman & Van Essen 1991, *Cereb Cortex*

Cerebral Cortex



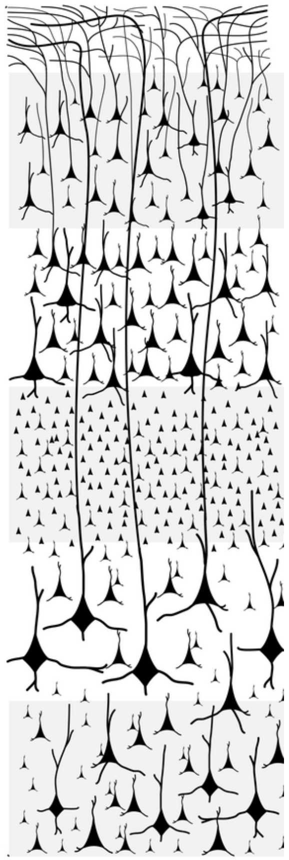
Budday et al. 2014, *Sci Rep*



Barrett 2017

Cell layers of the neocortex

	Lamina …	
	Molecularis	I
Supragranular layers	*Granularis Externa*	II
	Pyramidialis Externa	III
Granular layer	*Granularis Interna*	IV
Infragranular layers	*Pyramidialis Interna*	V
	Multiformis	VI

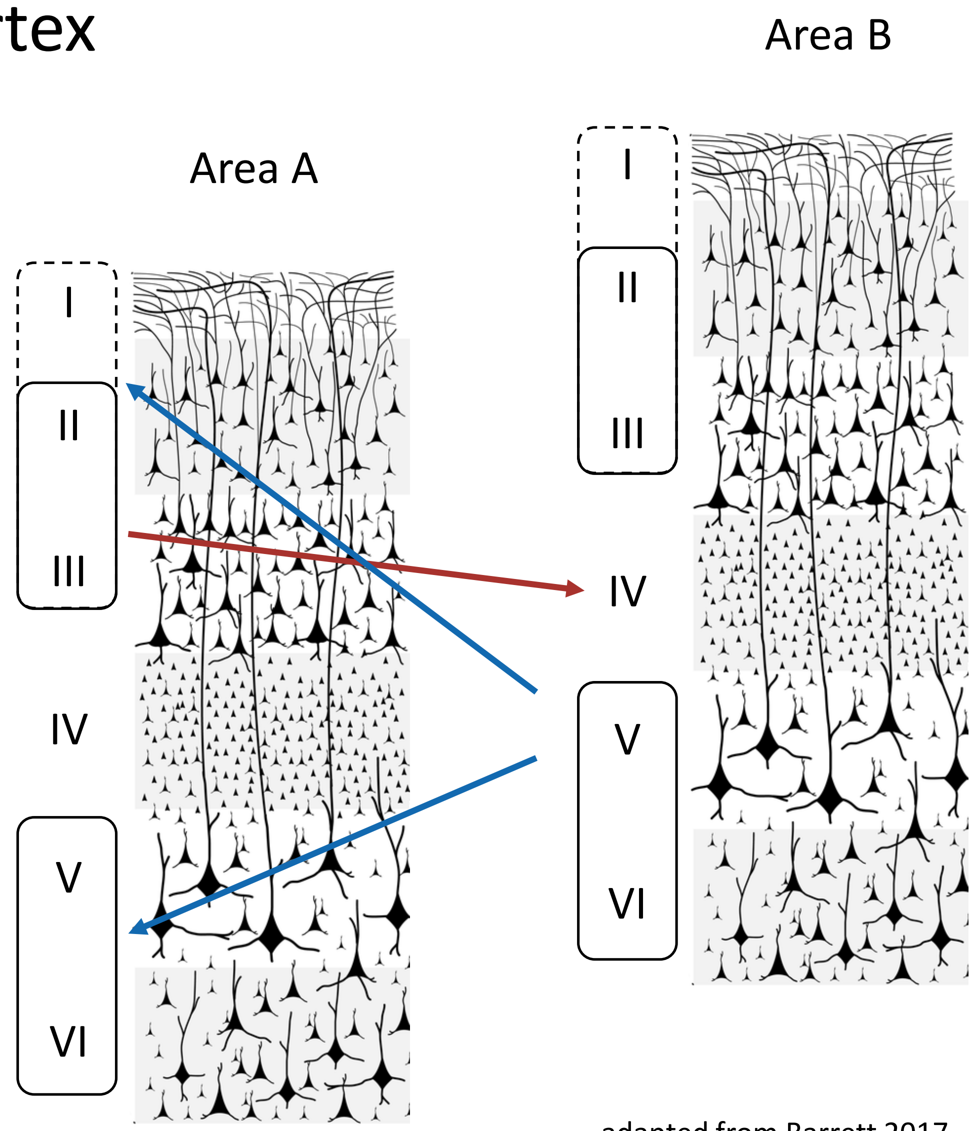


adapted from Barrett 2017

Hierarchical Relationships in the Visual Cortex

Visual cortex of macaque monkeys
Felleman & Van Essen 1991, *Cereb Cortex*

- Reciprocity of cortico-cortical connections
- Laminar patterns
  - Forward connections (ascending pathways):
    - Origin: superficial pyramidal cells (layers II & III)
    - Termination: granular layer (IV)
  - Backward connections (descending pathways):
    - Origin: deep pyramidal cells (layer V)
    - Termination: agranular layers (mainly I & VI)

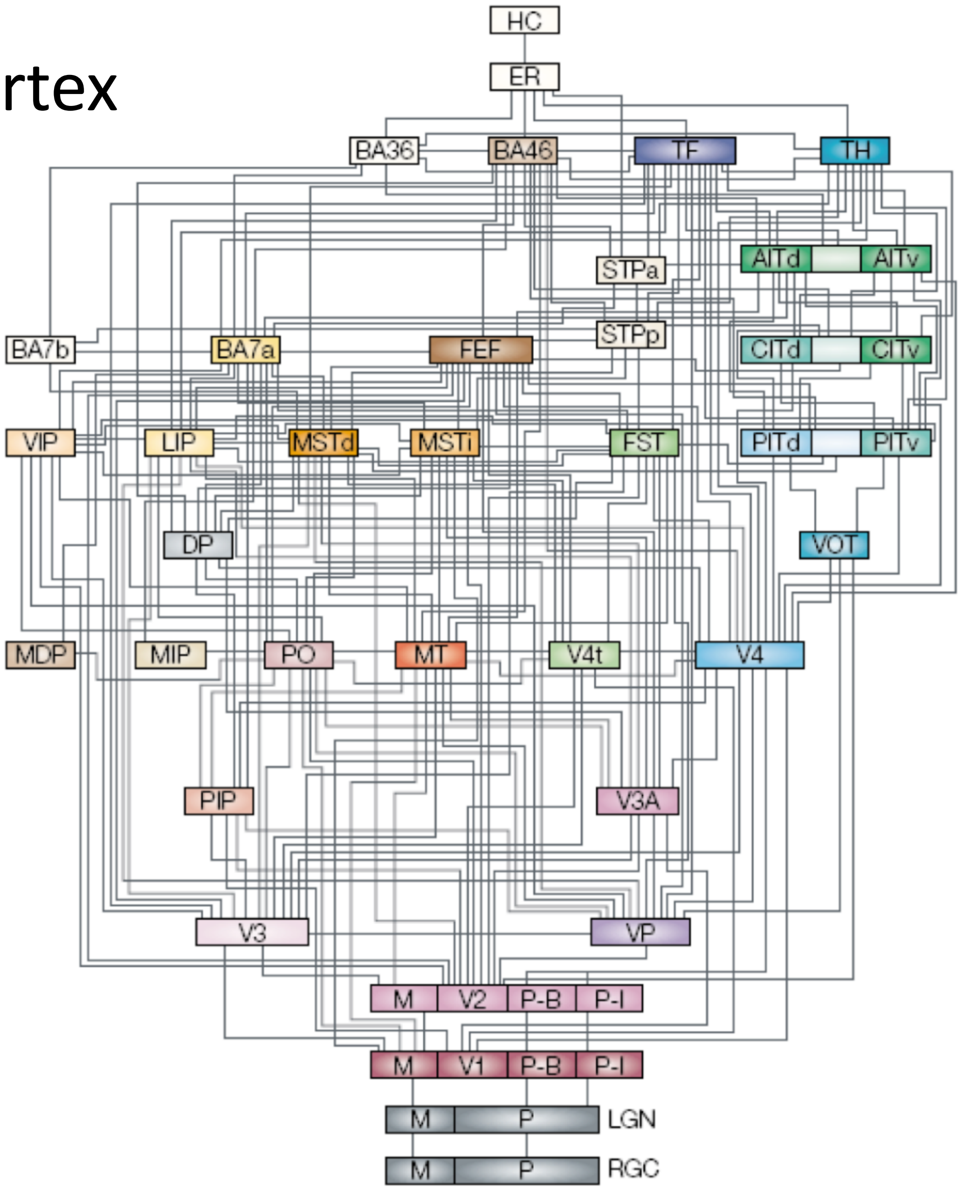


adapted from Barrett 2017

Hierarchical Relationships in the Visual Cortex

Visual cortex of macaque monkeys
Felleman & Van Essen 1991, *Cereb Cortex*

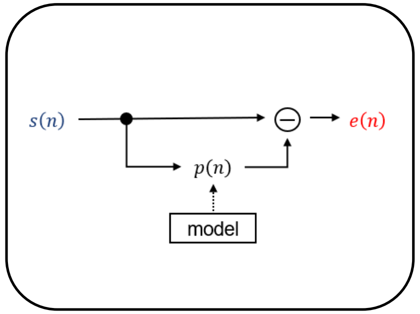
- Reciprocity of cortico-cortical connections
- Laminar patterns
  - Forward connections (ascending pathways):
    - Origin: superficial pyramidal cells (layers II & III)
    - Termination: granular layer (IV)
  - Backward connections (descending pathways):
    - Origin: deep pyramidal cells (layer V)
    - Termination: agranular layers (mainly I & VI)
- Identify hierarchy based on laminar patterns of cortical connectivity (forward & backward connections)
- Hierarchical relationships also…
  - In other regions (somatosensory, auditory cortex, etc.)
  - In other species (other primates, cats, rats, etc.)



Felleman & Van Essen 1991, *Cereb Cortex*

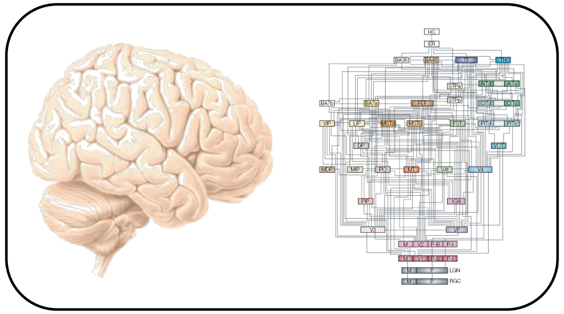
Predictive Coding as neuroscientific theory

Intellectual antecedents



- Redundancy reduction

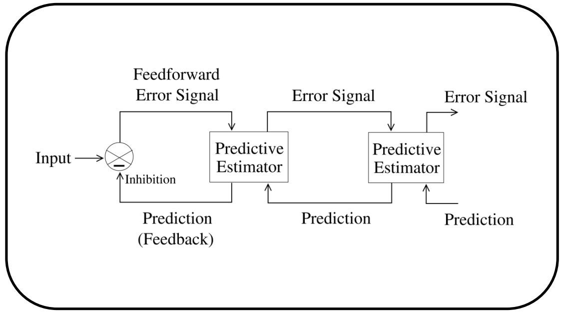
Neuroanatomy



Felleman & Van Essen 1991, *Cereb Cortex*

- Hierarchical organization of cortex
- Laminar patterns of connectivity

Hierarchical PC model

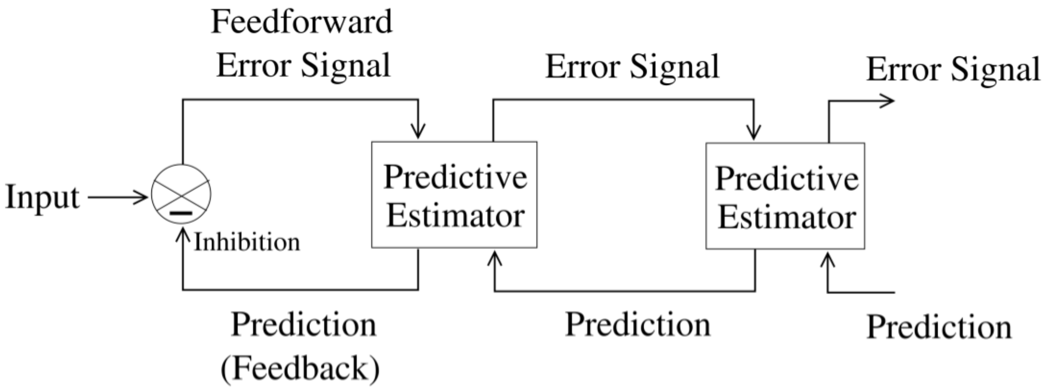


Rao & Ballard 1999, *Nat Neurosci*

On the computational architecture of the neocortex
D. Mumford 1992, *Biol Cybern*

Hierarchical predictive coding model

- Hierarchical network
  - Feedback connections: predictions
  - Feedforward connections: error signal
  - Predictive estimator: use error signal to generate next prediction



$$\boldsymbol{I} = f(U\boldsymbol{r}) + \boldsymbol{n}$$

$$\mathbf{r} = \boldsymbol{r}^{td} + \boldsymbol{n}^{td} = f\left(U^h \boldsymbol{r}^h\right) + \boldsymbol{n}^{td}$$

$\boldsymbol{I}$: inputs

$\boldsymbol{r}$: causes

U: weights

f: activation function

$\boldsymbol{n}$: noise

U^h: higher-level weights

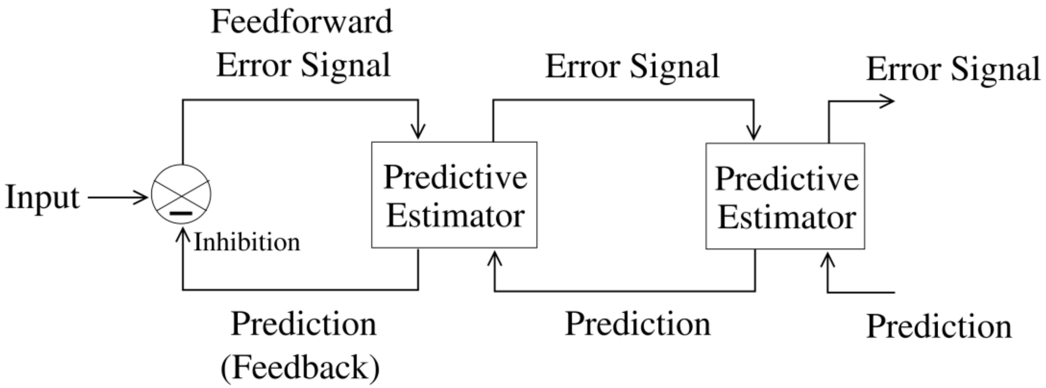
$\boldsymbol{r}^h$: higher-level causes

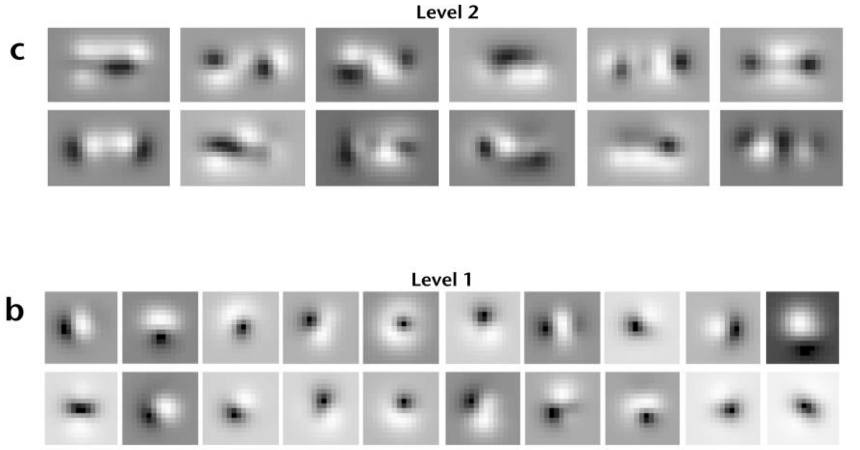
$\boldsymbol{n}^{td}$: noise

Rao & Ballard 1999, *Nat Neurosci*

Hierarchical predictive coding model

- Hierarchical network
  - Feedback connections: predictions
  - Feedforward connections: error signal
  - Predictive estimator: use error signal to generate next prediction
- Train network on patches of static natural images
  - Learned synaptic weights resemble cell-like receptive fields
  - Receptive field sizes: lower vs. upper levels

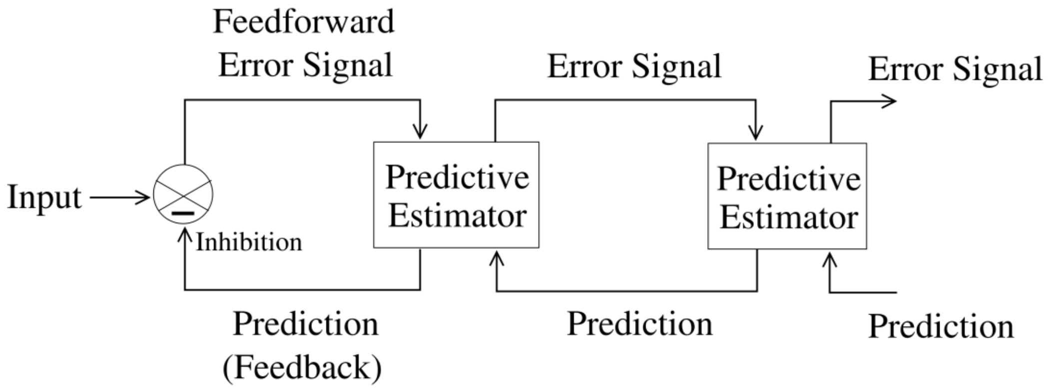


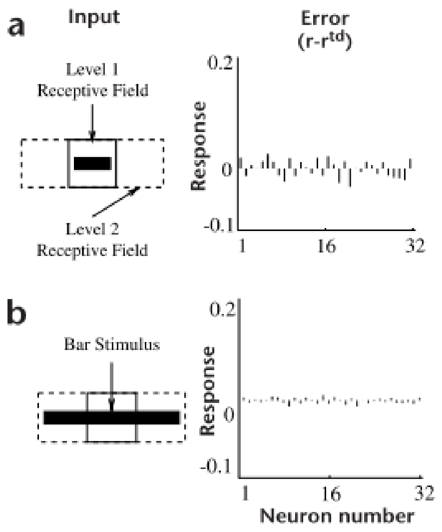


Rao & Ballard 1999, *Nat Neurosci*

Hierarchical predictive coding model

- Hierarchical network
  - Feedback connections: predictions
  - Feedforward connections: error signal
  - Predictive estimator: use error signal to generate next prediction
- Train network on patches of static natural images
  - Learned synaptic weights resemble cell-like receptive fields
  - Receptive field sizes: lower vs. upper levels
- Functional explanation for extra-classical receptive field effects:
  - Endstopping: error-detecting model neurons





Rao & Ballard 1999, *Nat Neurosci*

Hierarchical predictive coding model

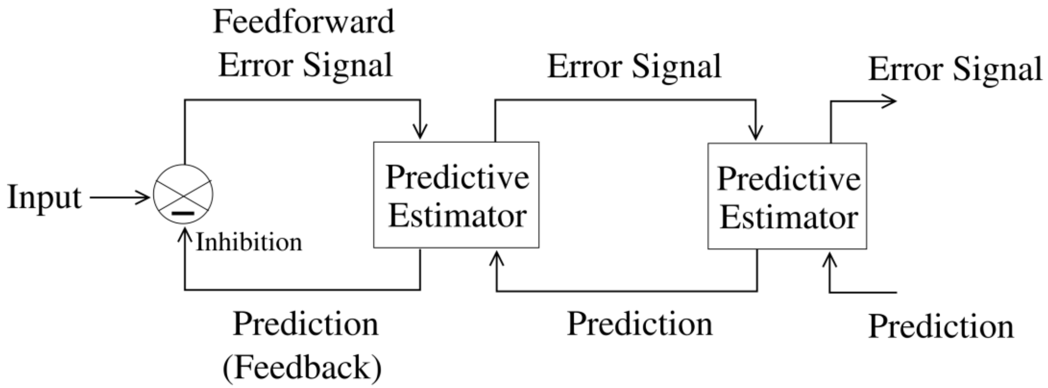
- Assume probabilistic hierarchical generative model for images
  - Cost function: negative log joint (⇒ MAP estimation)

$$E = \underbrace{-\log p(\boldsymbol{I}|\boldsymbol{r},U) - \log p(\boldsymbol{r}) - \log p(U)}_{\frac{1}{\sigma^2}(\boldsymbol{I}-f(U\boldsymbol{r}))^T(\boldsymbol{I}-f(U\boldsymbol{r})) + \frac{1}{\sigma_{td}^2}(\boldsymbol{r}-\boldsymbol{r}^{td})^T(\boldsymbol{r}-\boldsymbol{r}^{td})}$$

$$= -\log(p(\boldsymbol{I}|\boldsymbol{r},U)\, p(\boldsymbol{r})\, p(U))$$

posterior ∝ likelihood * prior

$$p(x|y,m) \propto p(y|x,m)p(x|m)$$



$$\boldsymbol{I} = f(U\boldsymbol{r}) + \boldsymbol{n} \qquad \mathbf{r} = \boldsymbol{r}^{td} + \boldsymbol{n}^{td}$$

$$\Rightarrow p(\boldsymbol{I}|\boldsymbol{r},U)$$

$\boldsymbol{I}$: inputs

$\boldsymbol{r}$: causes

U: weights

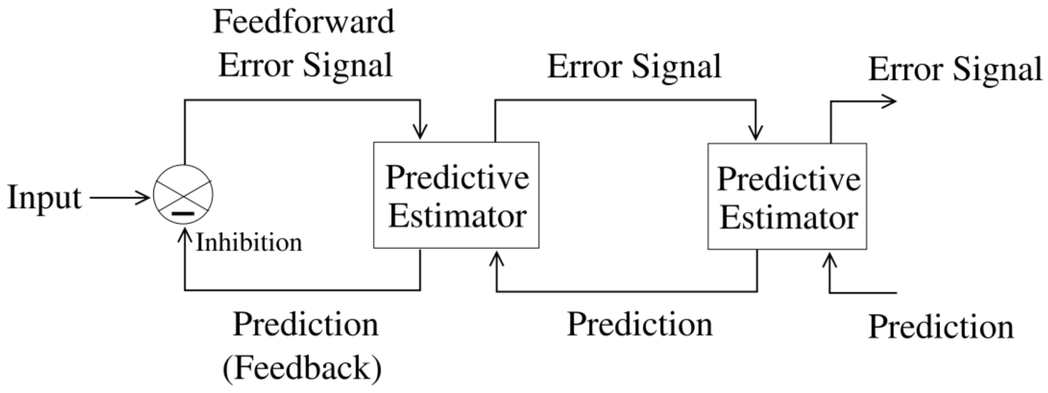
f: activation function

$\boldsymbol{n}$: noise

Rao & Ballard 1999, *Nat Neurosci*

Hierarchical predictive coding model

- Assume probabilistic hierarchical generative model for images
  - Cost function: negative log joint (⇒ MAP estimation)
- Network dynamics & synaptic learning rules
  - Error signal weighted by inverse variances (precisions)
  - Single cost function accounts for inference (updating $\boldsymbol{r}$) & learning (updating U)



$$\boldsymbol{I} = f(U\boldsymbol{r}) + \boldsymbol{n} \qquad \mathbf{r} = \boldsymbol{r}^{td} + \boldsymbol{n}^{td}$$

Δbelief ~ precision × PE

$$\frac{\mathrm{d}\boldsymbol{r}}{\mathrm{d}t} = -\frac{k_1}{2}\frac{\partial E}{\partial \boldsymbol{r}}$$

$$= \frac{k_1}{\sigma^2} U^T \frac{\partial f}{\partial U\boldsymbol{r}}^T \big(\boldsymbol{I} - f(U\boldsymbol{r})\big) + \frac{k_1}{\sigma_{td}^2}(\boldsymbol{r}^{td} - \boldsymbol{r}) - k_1 \alpha \boldsymbol{r}$$

$$\frac{\mathrm{dU}}{\mathrm{d}t} = -\frac{k_2}{2}\frac{\partial E}{\partial U} = \frac{k_2}{\sigma^2}\frac{\partial f}{\partial U\boldsymbol{r}}^T \big(\boldsymbol{I} - f(U\boldsymbol{r})\big)\boldsymbol{r}^T - \frac{k_2}{2}\lambda U$$

$\boldsymbol{I}$: inputs

$\boldsymbol{r}$: causes

U: weights

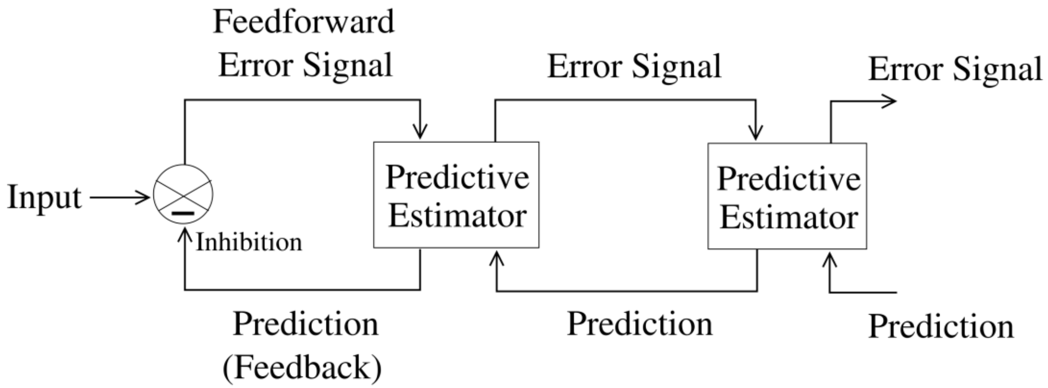
f: activation function

$\boldsymbol{n}$: noise

Rao & Ballard 1999, *Nat Neurosci*

Hierarchical predictive coding model

- Assume probabilistic hierarchical generative model for images
  - Cost function: negative log joint (⇒ MAP estimation)
- Network dynamics & synaptic learning rules
  - Error signal weighted by inverse variances (precisions)
  - Single cost function accounts for inference (updating $\boldsymbol{r}$) & learning (updating U)
  - Separation of timescales



$$\boldsymbol{I} = f(U\boldsymbol{r}) + \boldsymbol{n} \qquad \mathbf{r} = \boldsymbol{r}^{td} + \boldsymbol{n}^{td}$$

$$\frac{\mathrm{d}\boldsymbol{r}}{\mathrm{d}t} = -\frac{k_1}{2}\frac{\partial E}{\partial \boldsymbol{r}}$$

$$= \frac{k_1}{\sigma^2} U^T \frac{\partial f}{\partial U\boldsymbol{r}}^T \left(\boldsymbol{I} - f(U\boldsymbol{r})\right) + \frac{k_1}{\sigma_{td}^2}(\boldsymbol{r}^{td} - \boldsymbol{r}) - k_1 \alpha \boldsymbol{r}$$

$$\frac{\mathrm{dU}}{\mathrm{d}t} = -\frac{k_2}{2}\frac{\partial E}{\partial U} = \frac{k_2}{\sigma^2}\frac{\partial f}{\partial U\boldsymbol{r}}^T \left(\boldsymbol{I} - f(U\boldsymbol{r})\right)\boldsymbol{r}^T - \frac{k_2}{2}\lambda U$$

$\boldsymbol{I}$: inputs

$\boldsymbol{r}$: causes

U: weights

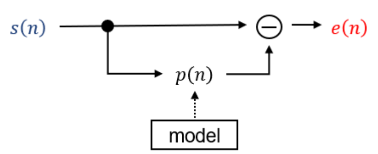
f: activation function

$\boldsymbol{n}$: noise

Rao & Ballard 1999, *Nat Neurosci*

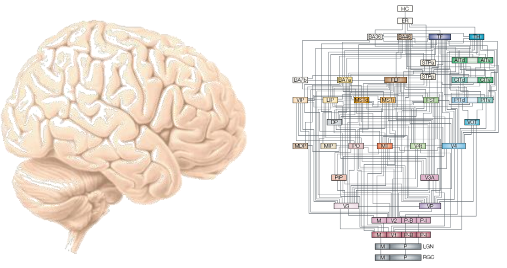
Predictive Coding as neuroscientific theory

Intellectual antecedents



- Redundancy reduction

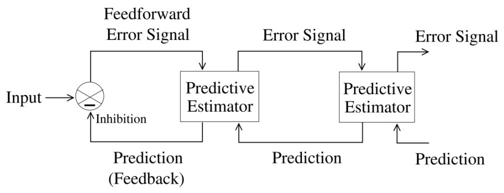
Neuroanatomy



Felleman & Van Essen 1991, *Cereb Cortex*

- Hierarchical organization of cortex
- Laminar patterns of connectivity

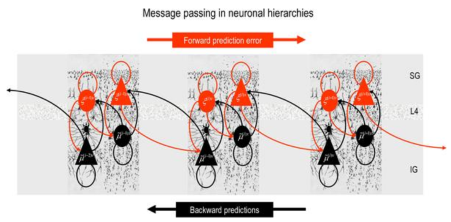
Hierarchical PC model



Rao & Ballard 1999, *Nat Neurosci*

- Visual cortex
- Point estimate of posterior
- Static representations

PC as variational inference

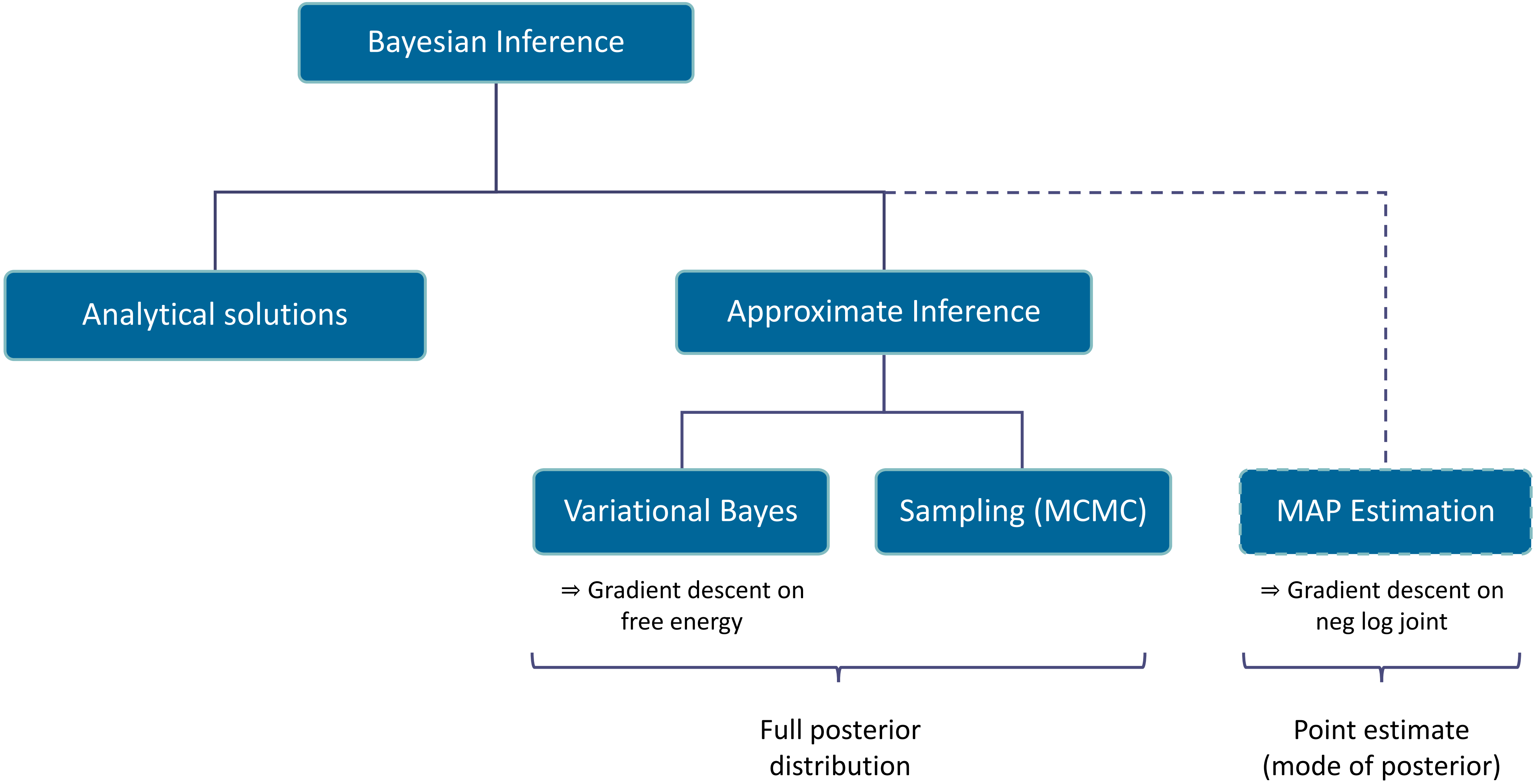


Friston 2003, 2005, 2008

On the computational architecture of the neocortex
D. Mumford 1992, *Biol Cybern*

Recap: Methods for Bayesian inference

Generative Models: Lecture (*Tue*)



Recap: Variational inference

VB & MCMC: Lecture (*Tue*)

posterior, likelihood, prior, model evidence

$$\underbrace{p(x|y,m)}_{\text{posterior}} = \frac{\overbrace{p(y|x,m)}^{\text{likelihood}}\overbrace{p(x|m)}^{\text{prior}}}{\underbrace{p(y|m)}_{\text{model evidence}}} \qquad p(y|m) = \int p(y|x,m)p(x|m)dx$$

Approximate posterior $q(x|y;\phi)$ e.g. for q Gaussian, $\phi = \{\mu, \Sigma\}$

Find best proxy $q^*(x|y;\phi) = argmin_\phi D_{KL}[q(x|y;\phi)||p(x|y,m)]$

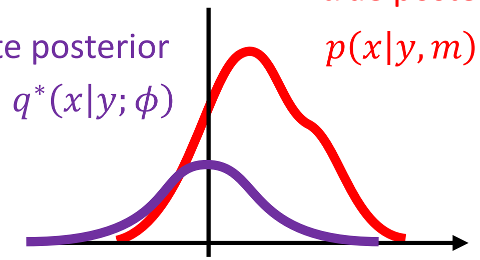


Figure adapted from slide by Yu Yao

Beal 2003, *PhD Thesis*; Blei et al. 2017, *J Am Stat Assoc*

Recap: Variational inference

VB & MCMC: Lecture (*Tue*)

$$\underbrace{p(x|y,m)}_{\text{posterior}} = \frac{\overbrace{p(y|x,m)}^{\text{likelihood}}\overbrace{p(x|m)}^{\text{prior}}}{\underbrace{p(y|m)}_{\text{model evidence}}} \qquad p(y|m) = \int p(y|x,m)p(x|m)dx$$

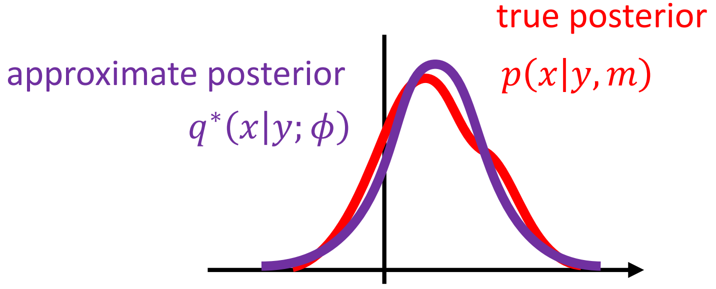


Figure adapted from slide by Yu Yao

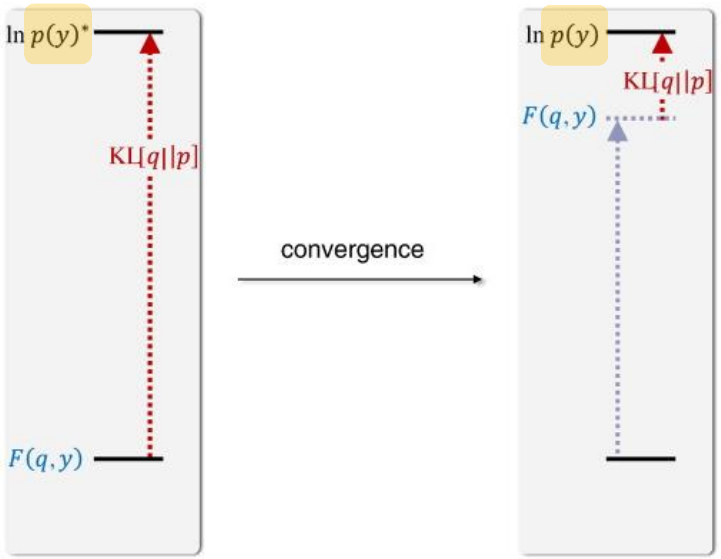
Approximate posterior $\quad q(x|y;\phi) \qquad$ e.g. for q Gaussian, $\phi = \{\mu, \Sigma\}$

Find best proxy $\quad q^*(x|y;\phi) = argmin_\phi D_{KL}[q(x|y;\phi)||p(x|y,m)]$

$$D_{KL}[q(x|y;\phi)||p(x|y,m)] = \ln p(y|m) - \int q(\mathrm{x}|\mathrm{y};\phi)\,\frac{p(x,y|m)}{q(x|y;\phi)}dx$$

$$= \ln p(y|m) - F$$

$$\ln p(y|m) = D_{KL}[q(x|y;\phi)||p(x|y,m)] + F(q(x|y;\phi), p(x,y|m))$$



Stephan et al. 2017 *NeuroImage*

Beal 2003, *PhD Thesis*; Blei et al. 2017, *J Am Stat Assoc*

Predictive coding as variational inference

The free energy formulation of predictive coding

Friston 2003, 2005, 2008

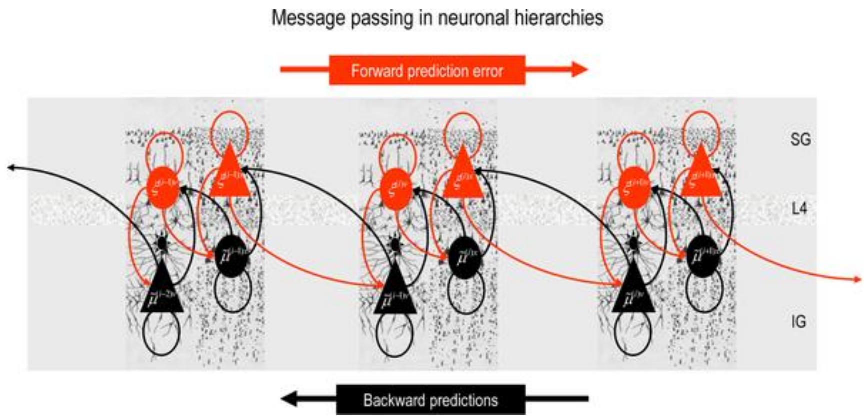
- Minimal neuronal model
  - PE units (SG layers)
  - Prediction units (IG layers)

  at each level of the hierarchy

  ⇒ canonical microcircuit model Bastos et al. 2012, *Neuron*

- Model dynamics
  - Differential equations
  - Gradient descent on free energy F
- Importance of precision
- Extension to …
  - Temporal sequences (dynamic environment) ⇒ minimize free action $\bar{F}$
  - Action (active inference) Friston et al. 2010, *Biol Cybern*; Adams et al. 2013, *Brain Struct Funct*

Active Inference: Lecture (*Today*)



Friston 2008, *PLoS Comput Biol*

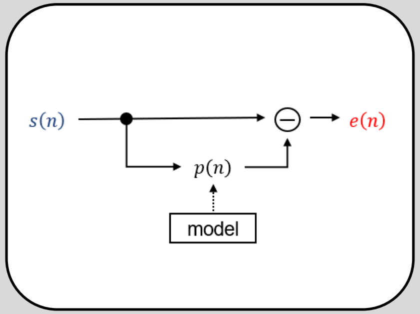
$$F = \int q(x|y;\phi)\,\frac{p(x,y|m)}{q(x|y;\phi)}\,dx$$

$$\bar{F} = \int F_t\,dt$$

Predictive Coding as neuroscientific theory

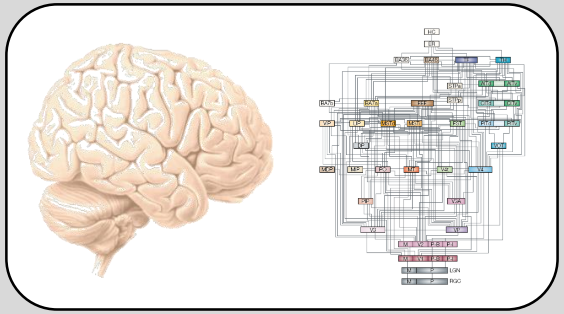
Non-Bayesian

Intellectual antecedents



- Redundancy reduction

Neuroanatomy



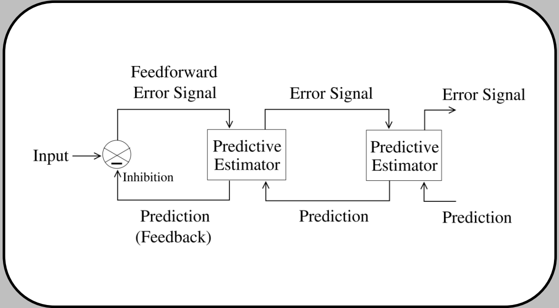
Felleman & Van Essen 1991, *Cereb Cortex*

- Hierarchical organization of cortex
- Laminar patterns of connectivity

On the computational architecture of the neocortex
D. Mumford 1992, *Biol Cybern*

PC as approximate Bayesian inference

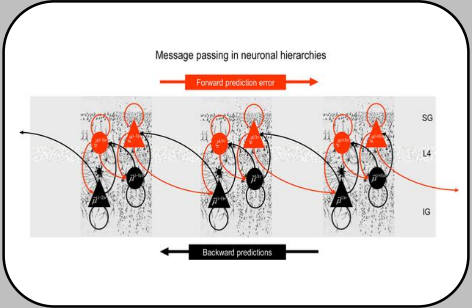
Hierarchical PC model



Rao & Ballard 1999, *Nat Neurosci*

- Visual cortex
- Point estimate of posterior
- Static representations

PC as variational inference



Friston 2003, 2005, 2008

- Cortical function
- Estimate full posterior
- Dynamic representations

Predictive coding in computational psychiatry

Predictive coding in computational psychiatry

Schizophrenia: Lecture (*Mon*)

Schizophrenia/Psychosis

(Stephan et al. 2006, *Biol Psychiatry*; Corlett et al. 2011, *NPP*; Adams et al. 2013, *Front Psychiatry*; Friston et al. 2016, *Schizophr Res*; Sterzer et al. 2018, *Biol Psychiatry*)

Autism: Lecture (*Mon*)

Autism Spectrum Disorder

(Pellicano & Burr 2012, *TiCS*; Van de Cruys et al. 2014, *Psychol Rev*; Lawson et al. 2014, *Front Hum Neurosci*; Haker et al. 2016, *Front Psychiatry*; Lawson et al. 2017, *Nat Neurosci*)

The role of precision

- Finding the right balance
- Disorders of precision?

From exteroception …

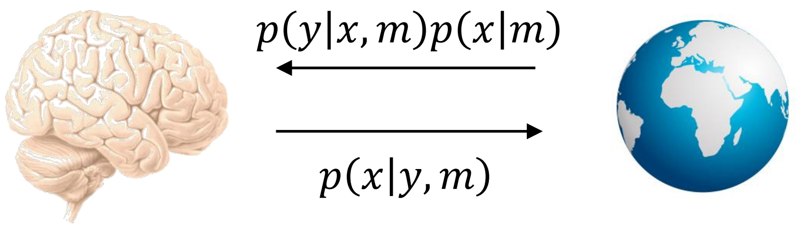


Figure based on slide by Klaas Enno Stephan

Predictive coding in computational psychiatry

Schizophrenia: Lecture (*Mon*)

Autism: Lecture (*Mon*)

The role of precision

- Finding the right balance
- Disorders of precision?

Schizophrenia/Psychosis

(Stephan et al. 2006, *Biol Psychiatry*; Corlett et al. 2011, *NPP*; Adams et al. 2013, *Front Psychiatry*; Friston et al. 2016, *Schizophr Res*; Sterzer et al. 2018, *Biol Psychiatry*)

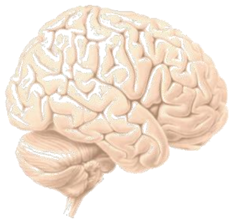
Autism Spectrum Disorder

(Pellicano & Burr 2012, *TiCS*; Van de Cruys et al. 2014, *Psychol Rev*; Lawson et al. 2014, *Front Hum Neurosci*; Haker et al. 2016, *Front Psychiatry*; Lawson et al. 2017, *Nat Neurosci*)

From exteroception to interoception

- Interoceptive predictive coding
  Seth et al. 2012, *Front Psychol*; Seth 2013, *TiCS;* Barrett & Simmons 2015, *Nature Rev Neurosci*
- Crucial role in mental health disorders
- Fatigue & depression Stephan et al. 2016, *Front Hum Neurosci*

Fatigue: Lecture (*Mon*)



$p(y|x,m)p(x|m)$

$p(x|y,m)$

Figure based on slide by Klaas Enno Stephan

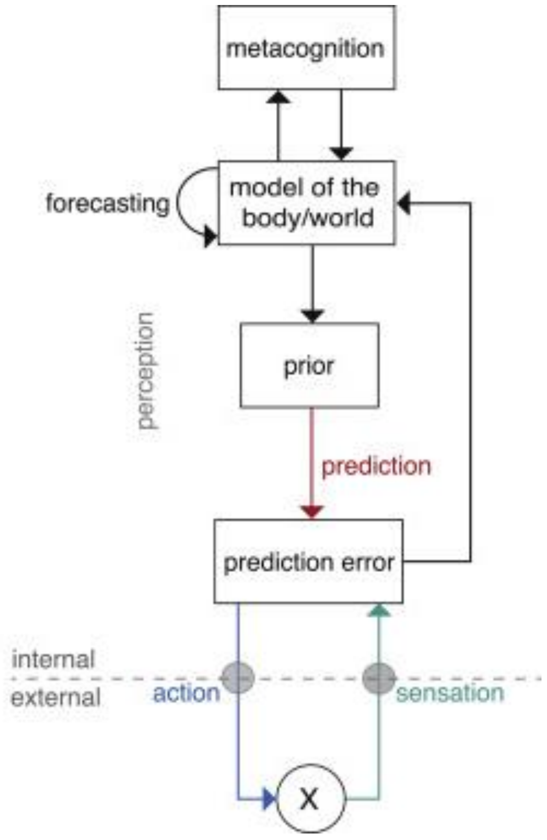
Hierarchical Bayesian Inference in Computational Psychiatry

Petzschner et al. 2017, *Biol Psychiatry*

Framework for modelling adaptive behaviour

- Possible primary disruption at:
  - Sensory inputs (sensations)
  - Inference (perception)
  - Forecasting
  - Control (action)
  - Metacognition
- At any of the above, possible disturbance of:
  - predictions
  - prediction error computation
  - Estimation of precision

⇒ guide differential diagnosis



Petzschner et al. 2017, *Biol Psychiatry*

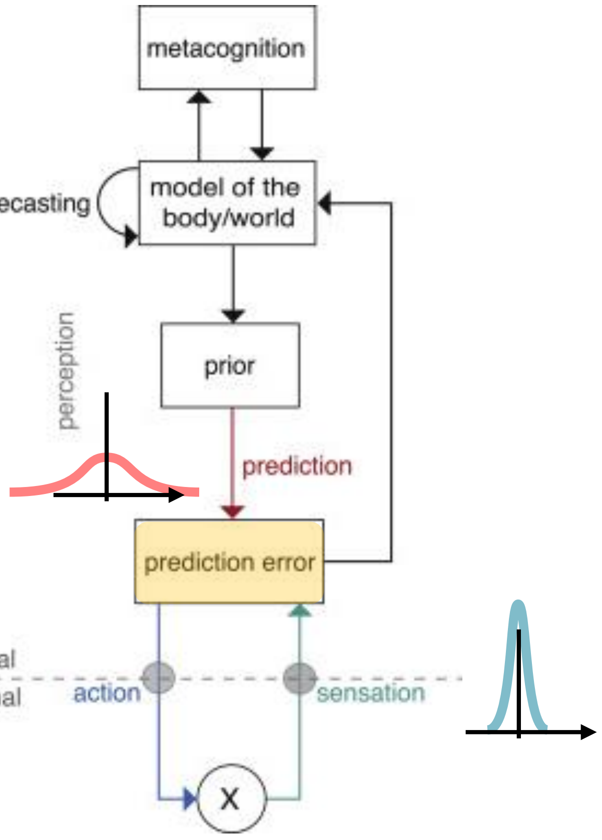
Hierarchical Bayesian Inference in Computational Psychiatry

Petzschner et al. 2017, *Biol Psychiatry*

Example: Autism Spectrum Disorder

- Patients: excessive processing of irrelevant details
- 2 competing explanations
  - Sensory inputs of overwhelming precision
  - Too imprecise higher-order beliefs

  ⇒ large PEs during perception
- Disambiguate 2 hypotheses:
  - Assess individual sensory processing (experiment + model)
  - Detect (sub)groups

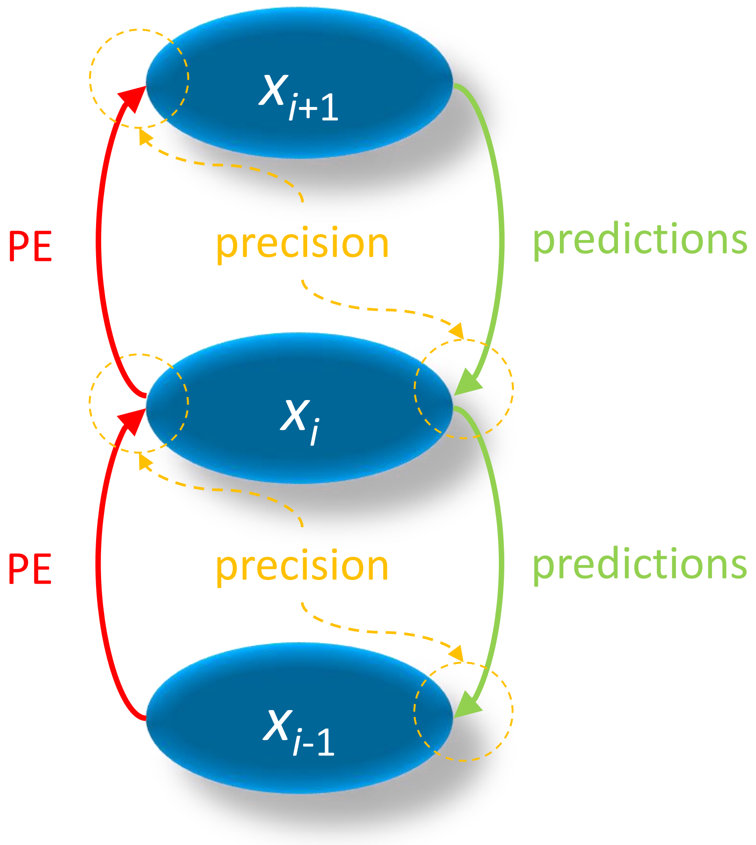


Petzschner et al. 2017, *Biol Psychiatry*

Predictive coding in a nutshell

Δbelief $\sim$ precision $\times$ PE

- Possible way of implementing Hierarchical Bayesian inference in the brain
- Based on
  - Redundancy reduction
  - Hierarchical organization of cortex
- Computational quantities:
  - Each layer makes **predictions** about activity in layer immediately below
  - Predictions are compared with inputs of each layer
  - **Prediction errors (PE)** signalled upwards
  - Relative influence of PEs and predictions is determined by their relative **precision** (certainty)
- Goal of the brain:
  - minimize PE at each level of the hierarchy
- Utility of this framework for Computational Psychiatry & Computational Psychosomatics



Adapted from Stephan et al. 2016, *Brain*

Further reading

REVIEWS

Theoretical & experimental review Millidge et al. 2021, *arXiv:2107.12979*

Experimental evidence for PC in the brain Walsh et al. 2020, *Ann N Y Acad Sci*

PC algorithms Spratling et al. 2017, *Brain Cogn*

TUTORIALS

PC as variational inference Bogacz 2017, *J Math Psychol*; Buckley 2017, *J Math Psychol*

OTHER

PC & laminar fMRI Stephan et al. 2019, *NeuroImage*

PC networks and backpropagation of error algorithm Whittington & Bogacz 2017, *Neural Comput*; Song et al. 2020, *Adv Neural Inf Process Syst*

PC, variational autoencoders & normalizing flows Marino 2020*, arXiv:2011.07464*

Universität Zürich[UZH] ETH zürich

Translational Neuromodeling Unit

Thank you!

Lilian Weber
Matthias Müller-Schrader
Stefan Frässle
Sandra Iglesias
Klaas Enno Stephan

Alex Hess

Translational Neuromodeling Unit

University of Zurich & ETH Zurich

E-Mail: hess@biomed.ee.ethz.ch

/ @alex_j_hess