

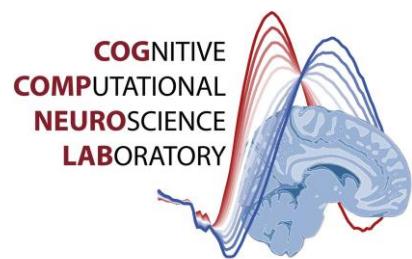


# Predictive Coding

Computational Psychiatry Course

09.09.2020

Lilian A. Weber



Translational Neuromodeling Unit

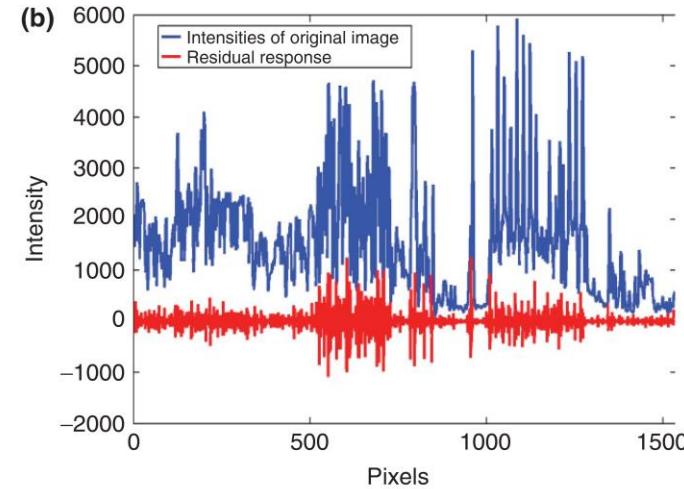
# Predictive coding

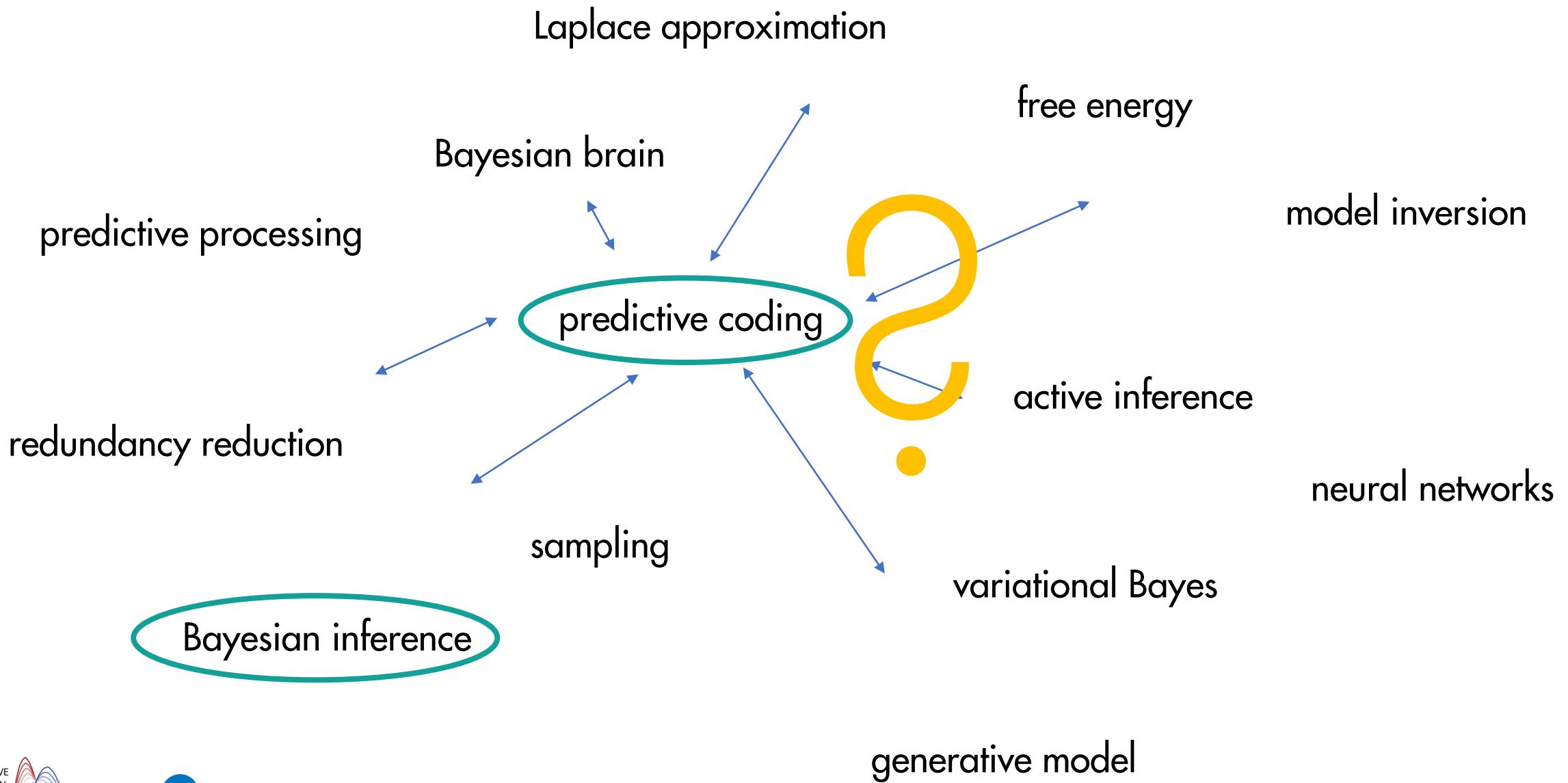
$$\text{prediction error} = \text{prediction} - \text{input}$$

(a)

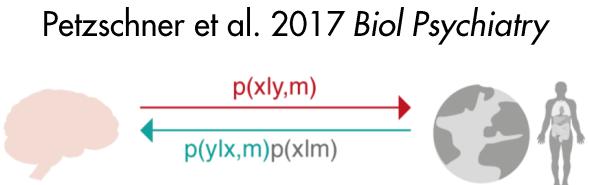
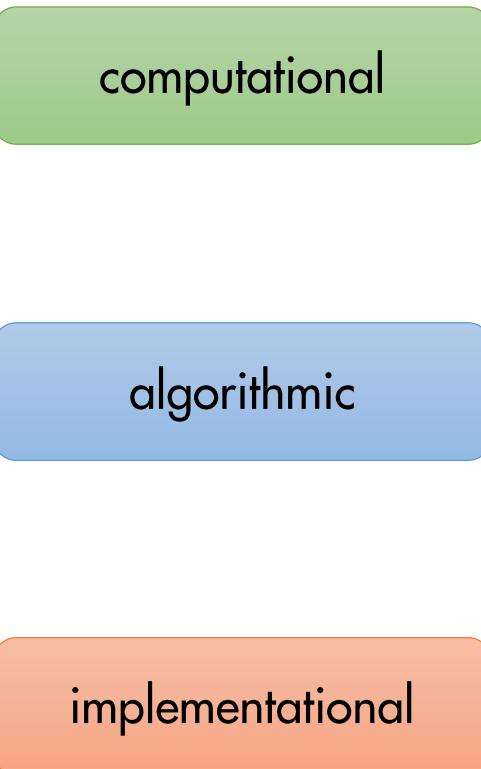


(b)





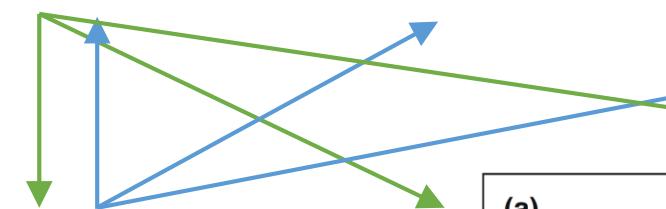
# Levels of analysis



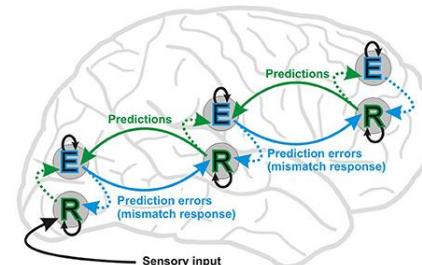
(approximate)  
Bayesian inference

redundancy  
reduction

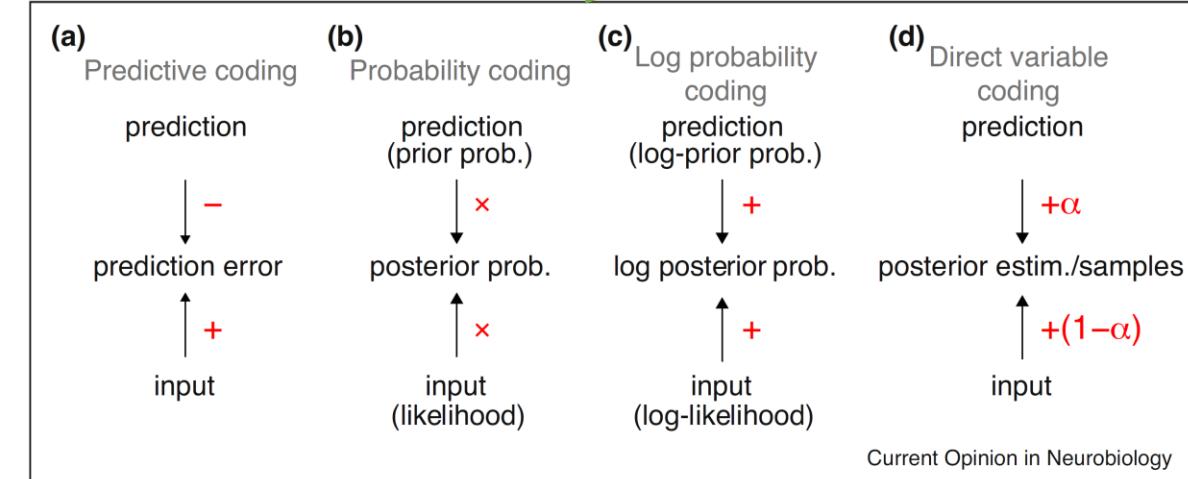
...



**predictive coding**



Stefanics et al. 2014  
*Front Hum Neurosci*



Aitchison & Lengyel 2017 *Curr Op Neurobiol*

**"Bayesian predictive coding"**

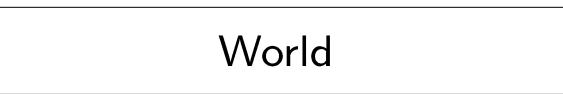


Translational Neuromodeling Unit

# Bayesian observers

today

yesterday

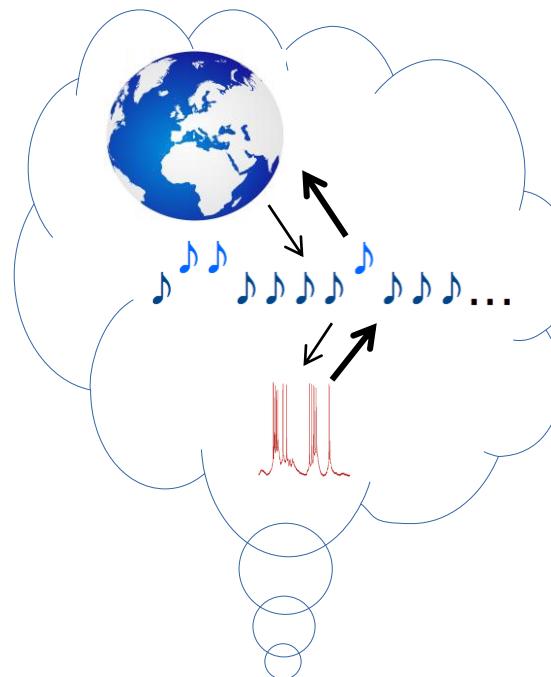


$\text{environmental state } x$

perception  
 $p(x|y,m)$

$\text{neuronal activity } y$

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



beliefs  $b$



statistical inference  
 $p(b|a,m)$



actions  $a$

model of the agent  
 $p(a|b,m)p(b|m)$

# I. Bayesian predictive coding

From redundancy reduction in signal processing to approximate Bayesian inference in the visual cortex: *Rao & Ballard, 1999*



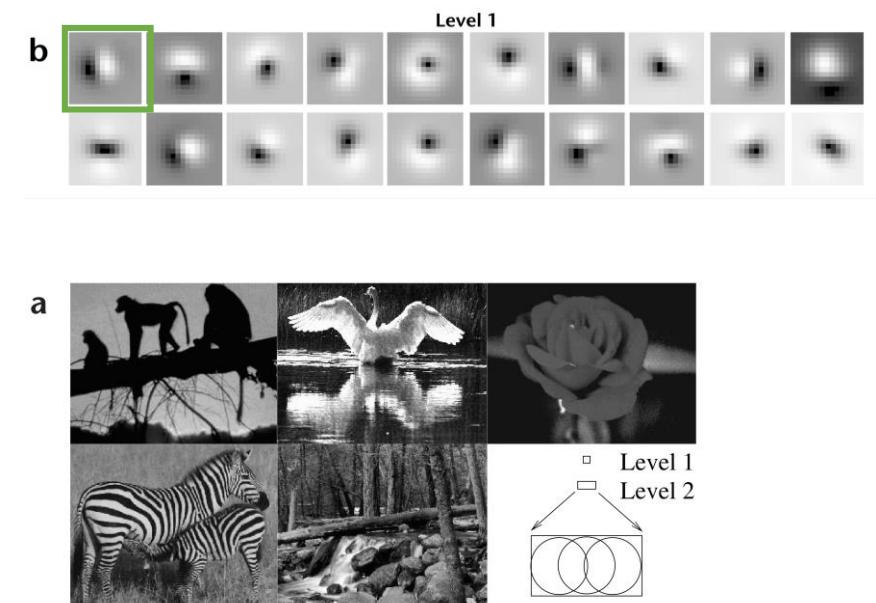
Translational Neuromodeling Unit

# 1. Predicting the input

Firing rates/  
Pixel values      Model (possible  
patterns)      noise

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

$$\begin{bmatrix} i_1 \\ i_2 \\ i_3 \\ \vdots \\ i_K \end{bmatrix} = f\left(\begin{bmatrix} u_{1,1} & u_{1,2} & \cdots & u_{1,N} \\ u_{2,1} & u_{2,2} & \cdots & u_{2,N} \\ u_{3,1} & u_{3,2} & \cdots & u_{3,N} \\ \vdots & \ddots & & \vdots \\ u_{K,1} & u_{K,2} & \cdots & u_{K,N} \end{bmatrix} \begin{bmatrix} r_1 \\ r_2 \\ \vdots \\ r_N \end{bmatrix}\right) + \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ \vdots \\ n_K \end{bmatrix}$$



Translational Neuromodeling Unit

Rao & Ballard 1999 Nat Neurosci

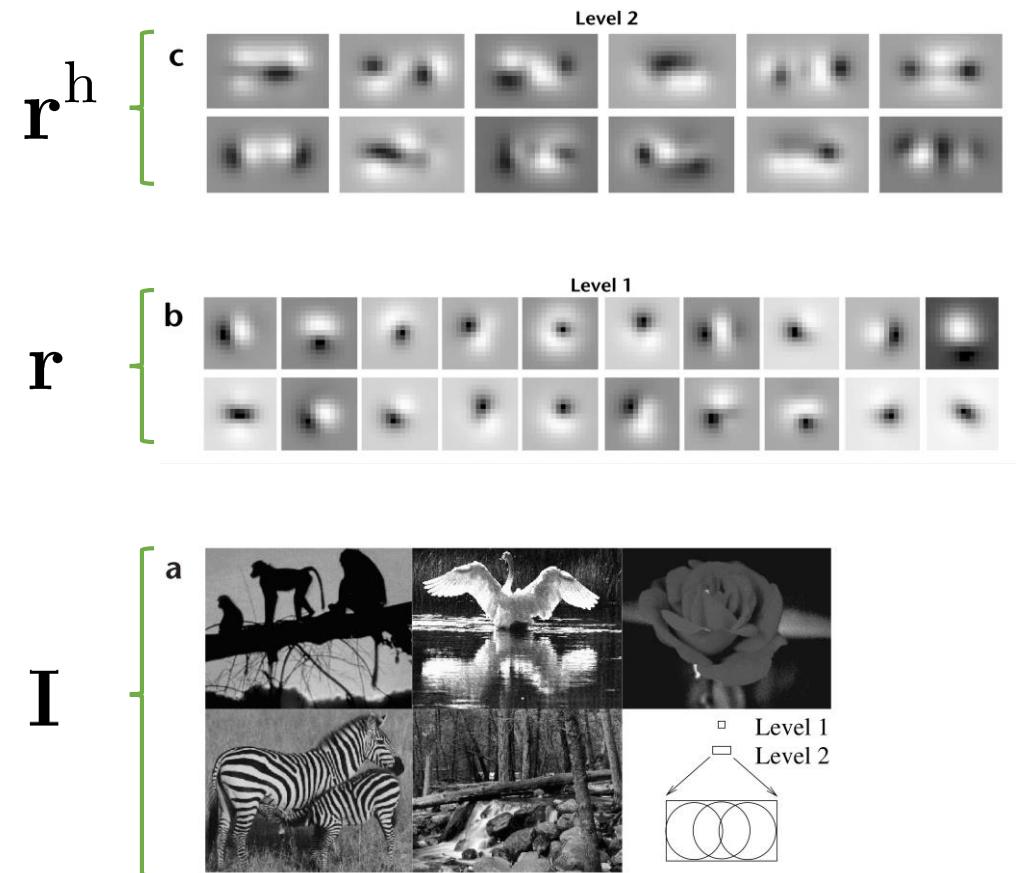
# 1. Predicting the input

Introducing hierarchy

$$\mathbf{r} = \mathbf{r}^{\text{td}} + \mathbf{n}^{\text{td}}$$

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

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



Translational Neuromodeling Unit

Rao & Ballard 1999 *Nat Neurosci*

# 1. Predicting the input

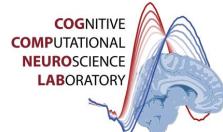
## Implementation

$$\mathbf{r} = \mathbf{r}^{\text{td}} + \mathbf{n}^{\text{td}}$$

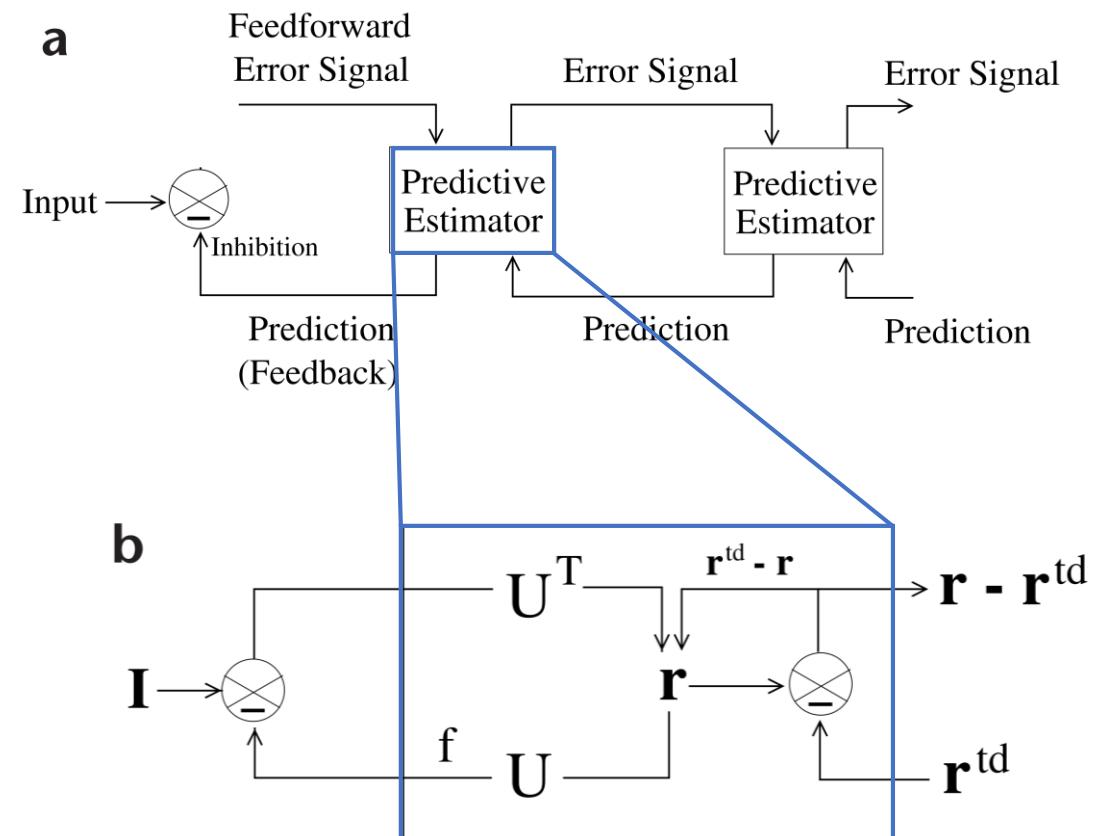
$$= f(\mathbf{U}^{\text{h}} \mathbf{r}^{\text{h}}) + \mathbf{n}^{\text{td}}$$

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

Question: How to find  $\mathbf{r}$  and  $\mathbf{U}$ ?



Translational Neuromodeling Unit



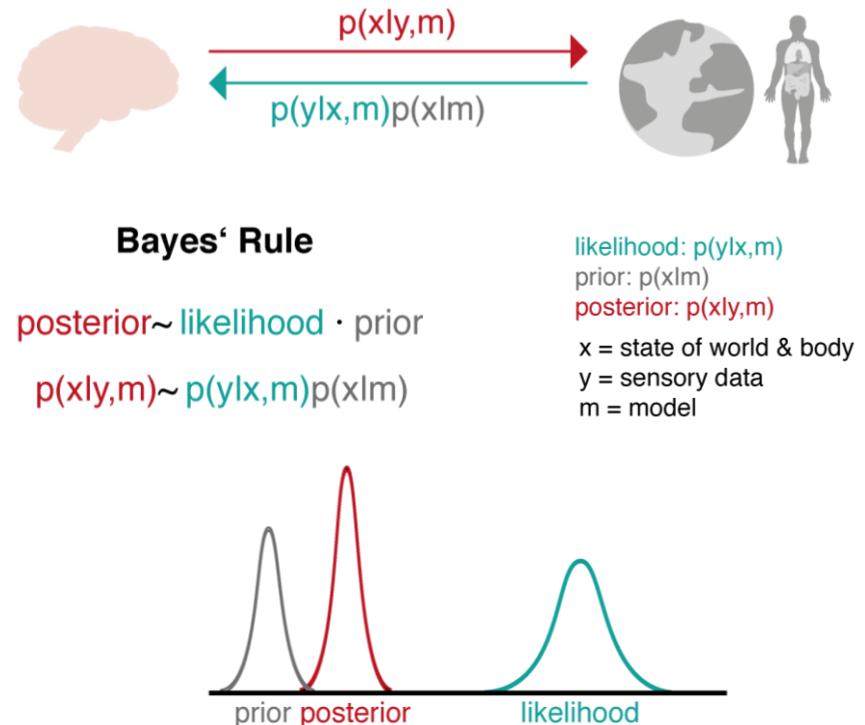
Rao & Ballard 1999 *Nat Neurosci*

## 2. Inverting the model

Optimization: Finding causes and associations

$$\begin{aligned}
 E &= E_1 - \log p(\mathbf{r}) - \log p(U) \\
 E_1 &= \underbrace{\frac{1}{\sigma^2}(\mathbf{I} - f(U\mathbf{r}))^\top(\mathbf{I} - f(U\mathbf{r})) + \frac{1}{\sigma_{\text{td}}^2}(\mathbf{r} - \mathbf{r}^{\text{td}})^\top(\mathbf{r} - \mathbf{r}^{\text{td}})}_{-\log p(\mathbf{I}|\mathbf{r}, U) + C} \\
 E &= -\log p(\mathbf{I}|\mathbf{r}, U) - \log p(\mathbf{r}) - \log p(U) \\
 &= -\log(p(\mathbf{I}|\mathbf{r}, U) p(\mathbf{r}) p(U))
 \end{aligned}$$

Optimization looks like finding the most likely cause (MAP estimate) in Bayesian inference.



### 3. (Precision-weighted) Prediction errors

**Inference:** Estimating the causes based on inputs and expectations

**Learning:** Improving the model to reflect the statistics of the environment

$$\frac{d\mathbf{r}}{dt} = -\frac{k_1}{2} \frac{\partial E}{\partial \mathbf{r}}$$

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

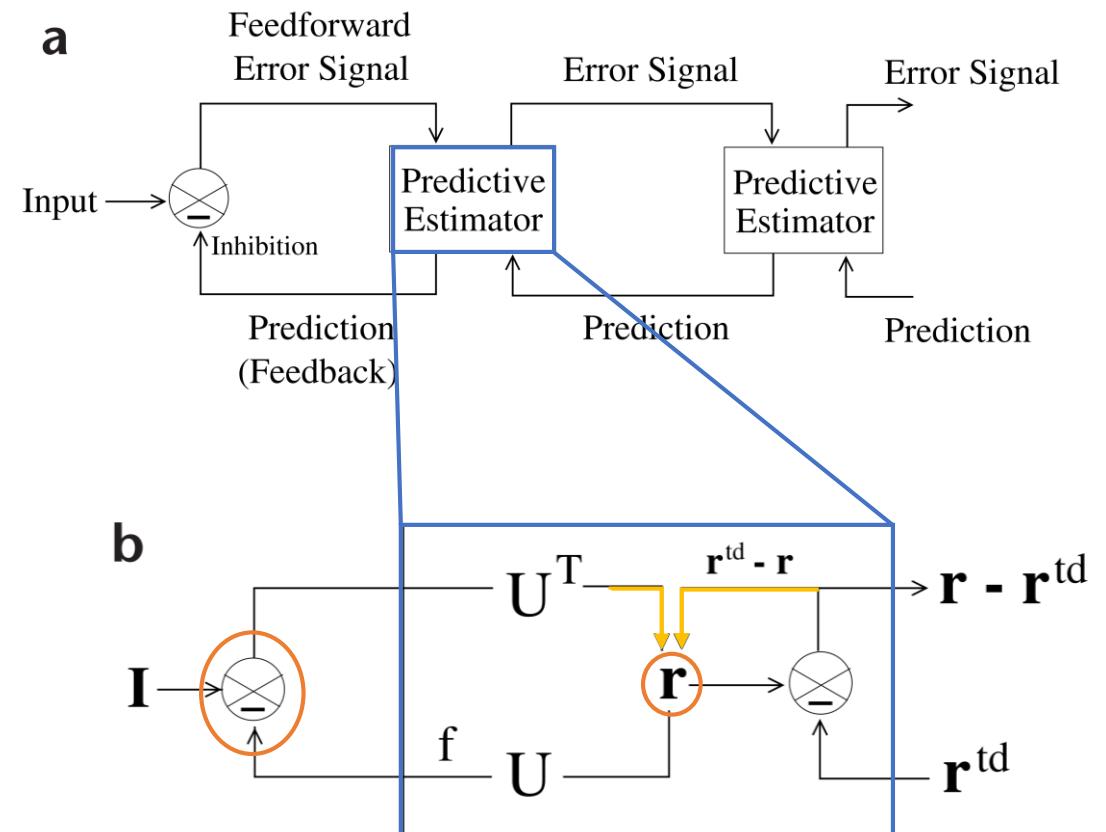
Inputs                      Expectations  
precision-weighting

$$\frac{dU}{dt} = -\frac{k_2}{2} \frac{\partial E}{\partial U} = \frac{k_2}{\sigma^2} \frac{\partial f}{\partial U \mathbf{r}}^\top (\mathbf{I} - f(U\mathbf{r})) \mathbf{r} - \frac{k_2}{2} \lambda U$$

Hebbian learning



Translational Neuromodeling Unit



Rao & Ballard 1999 Nat Neurosci

### 3. (Precision-weighted) Prediction errors

**Inference:** Estimating the causes based on inputs and expectations

**Learning:** Improving the model to reflect the statistics of the environment

$$\frac{d\mathbf{r}}{dt} = -\frac{k_1}{2} \frac{\partial E}{\partial \mathbf{r}}$$

**Inputs**                    **Expectations**

$$= \frac{k_1}{\sigma^2} U^\top \frac{\partial f}{\partial U \mathbf{r}}^\top (\mathbf{I} - f(U \mathbf{r})) + \frac{k_1}{\sigma_{\text{td}}^2} (\mathbf{r}^{\text{td}} - \mathbf{r}) - k_1 \alpha \mathbf{r}$$

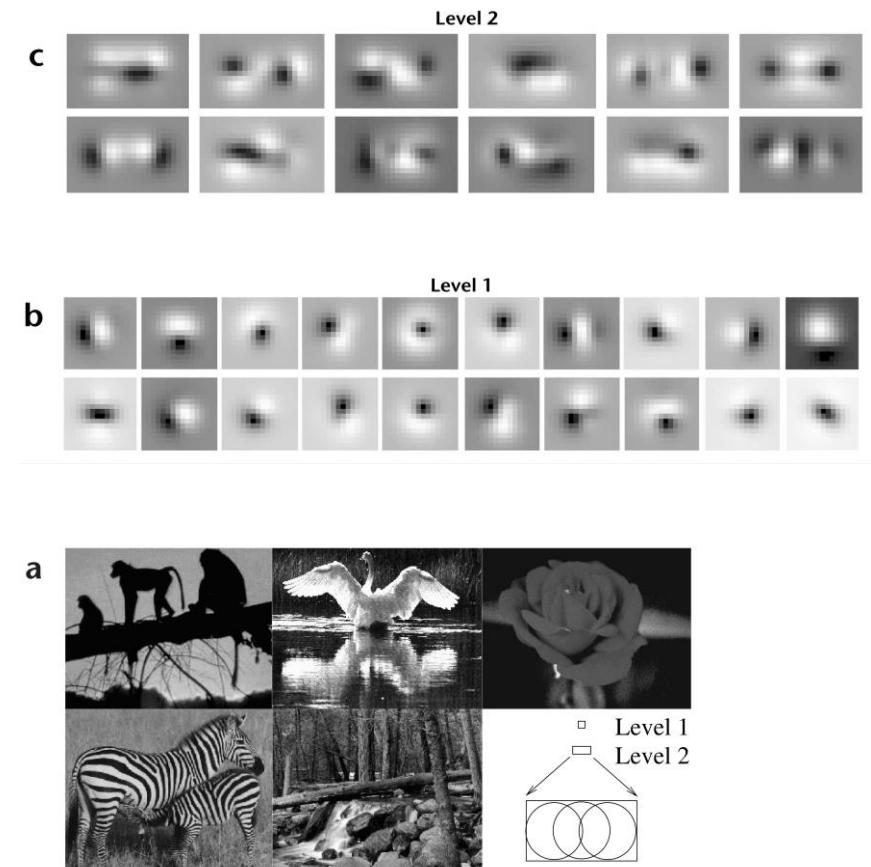
precision-weighting

$$\frac{dU}{dt} = -\frac{k_2}{2} \frac{\partial E}{\partial U} = \frac{k_2}{\sigma^2} \frac{\partial f}{\partial U \mathbf{r}}^\top (\mathbf{I} - f(U \mathbf{r})) \mathbf{r} - \frac{k_2}{2} \lambda U$$

Hebbian learning



Translational Neuromodeling Unit



Rao & Ballard 1999 Nat Neurosci

# Predictive coding as approximate inference

**Inference:** Estimating the causes based on inputs and expectations

**Learning:** Improving the model to reflect the statistics of the environment

$$\frac{d\mathbf{r}}{dt} = -\frac{k_1}{2} \frac{\partial E}{\partial \mathbf{r}}$$

$$= \frac{k_1}{\sigma^2} U^\top \frac{\partial f}{\partial U \mathbf{r}}^\top (\mathbf{I} - f(U \mathbf{r})) + \frac{k_1}{\sigma_{\text{td}}^2} (\mathbf{r}^{\text{td}} - \mathbf{r}) - k_1 \alpha \mathbf{r}$$

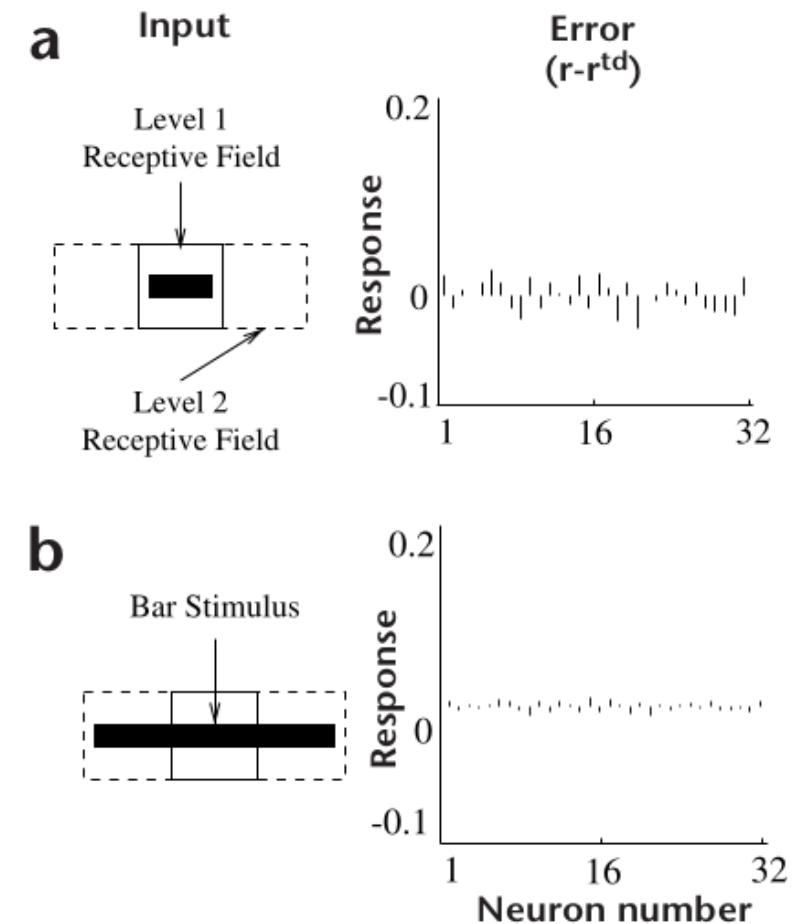
Inputs                      Expectations  
precision-weighting

$$\frac{dU}{dt} = -\frac{k_2}{2} \frac{\partial E}{\partial U} = \frac{k_2}{\sigma^2} \frac{\partial f}{\partial U \mathbf{r}}^\top (\mathbf{I} - f(U \mathbf{r})) \mathbf{r} - \frac{k_2}{2} \lambda U$$

Hebbian learning



Translational Neuromodeling Unit

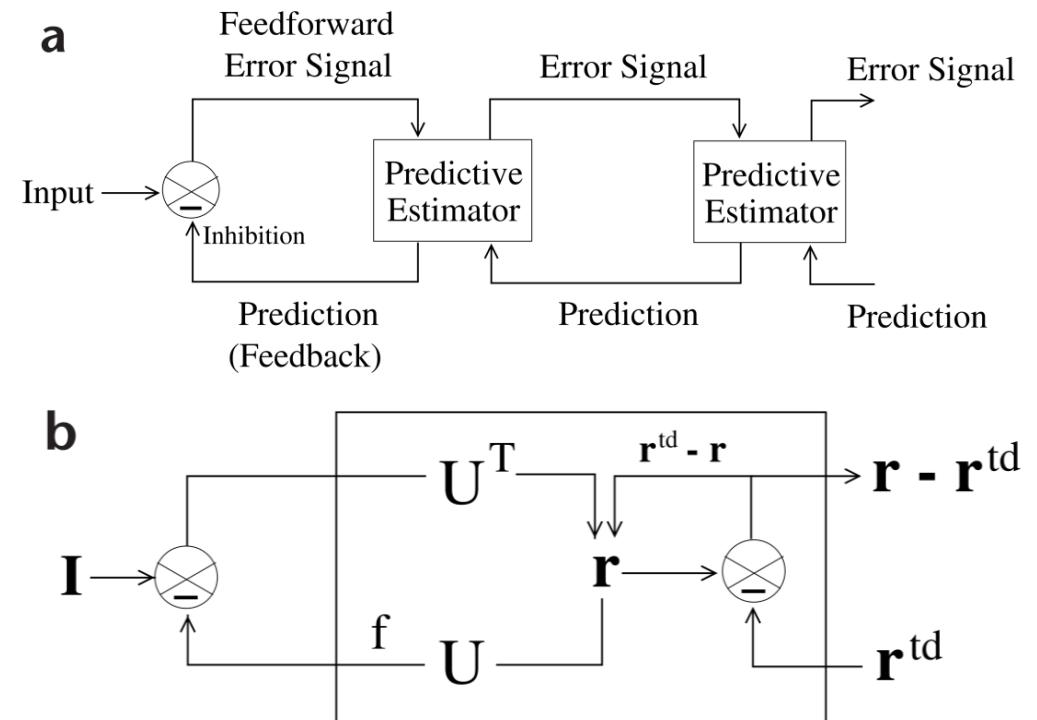


Rao & Ballard 1999 Nat Neurosci

# Predictive coding as approximate inference

Summary

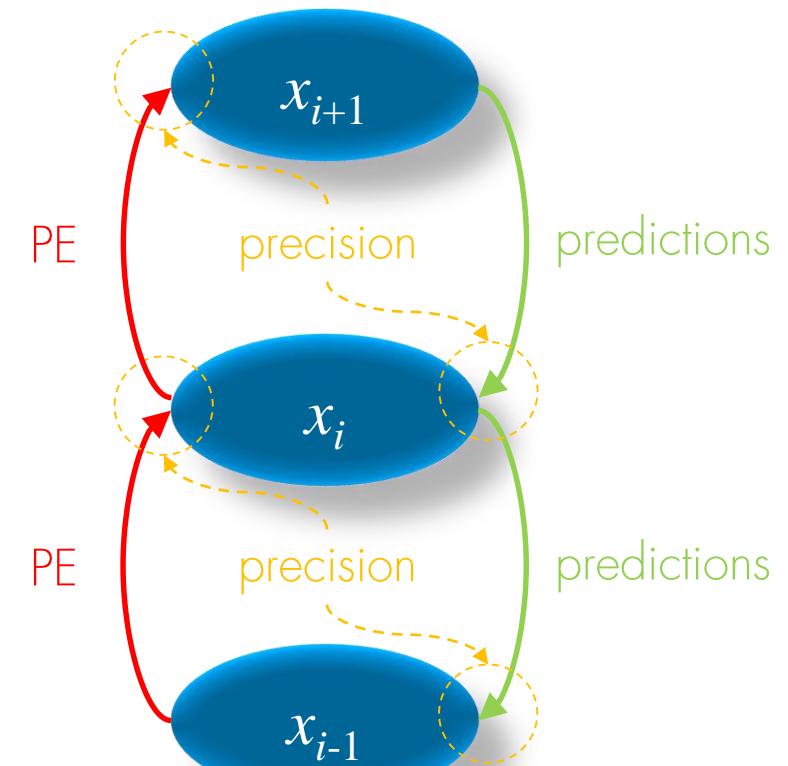
- A hierarchy of causes (predictive estimators and PE units)
- **Recurrent message passing:** PEs are signaled upwards (bottom-up) and predictions are signaled top-down
- **Inference:** finding the most appropriate causes to describe the data
- **Learning:** finding the most appropriate model to describe the data
- Both involve **minimizing precision-weighted prediction errors**
- This looks like **Bayesian inference** for finding the most likely causes of sensory inputs (**MAP estimates**) and like Hebbian learning, respectively



# The main ingredients of predictive coding (from a computational point of view)

- A hierarchical generative model of sensory inputs
- The estimates of the causes generate predictions of sensory input
- The estimates of causes are updated in response to prediction errors (mismatches)
- The relative influence of PEs and predictions is determined by their relative precision (certainty)
- These computations underlie both perception (inference) and learning (model update)

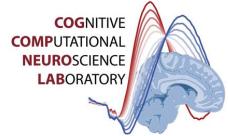
$$\Delta \text{belief} \sim \text{precision} \times \text{PE}$$



Adapted from Stephan et al. 2016 *Brain*

## II. Implementing (and testing) PC

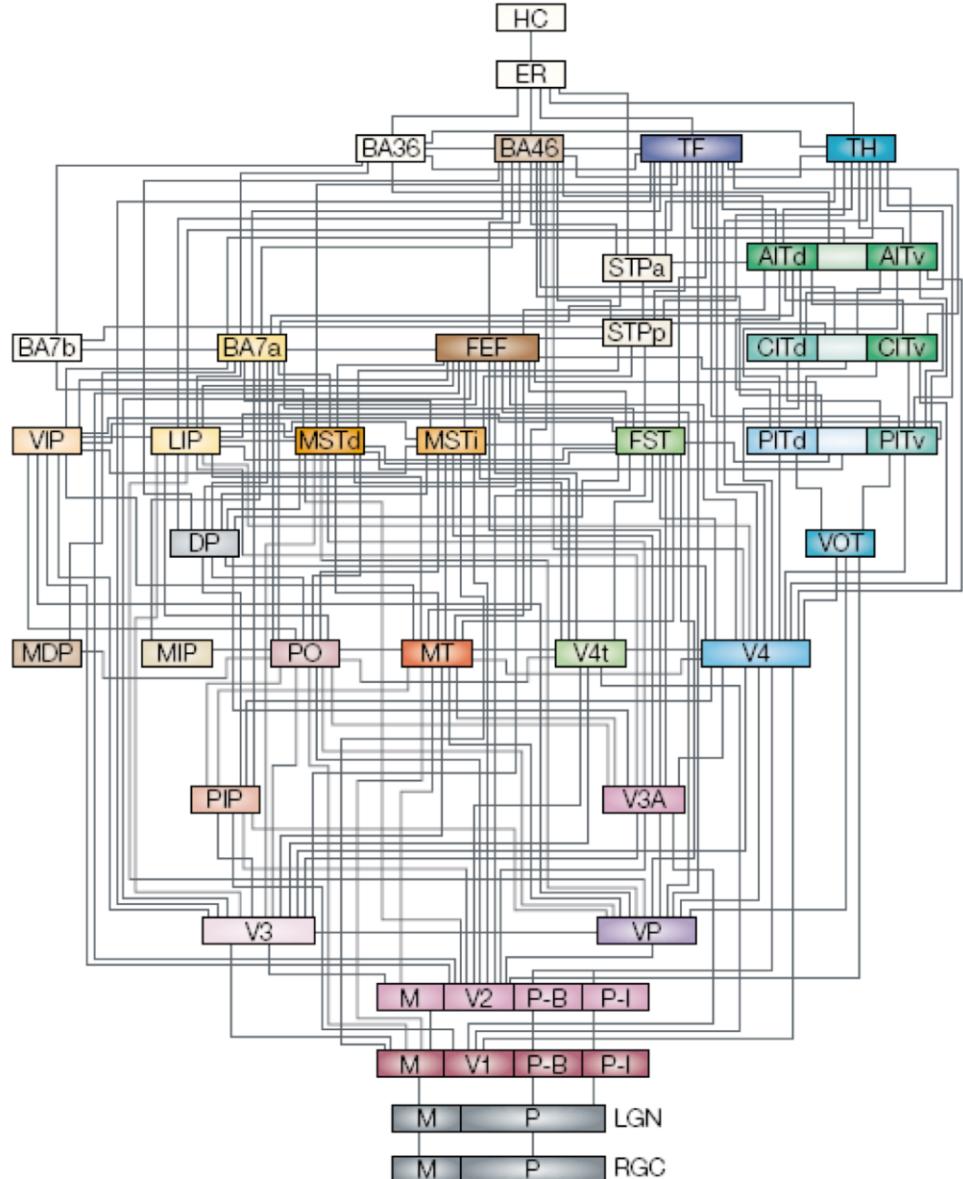
Mapping the ingredients of predictive coding onto neuroanatomy and  
neurophysiology



Translational Neuromodeling Unit

# Mapping predictive coding onto the brain

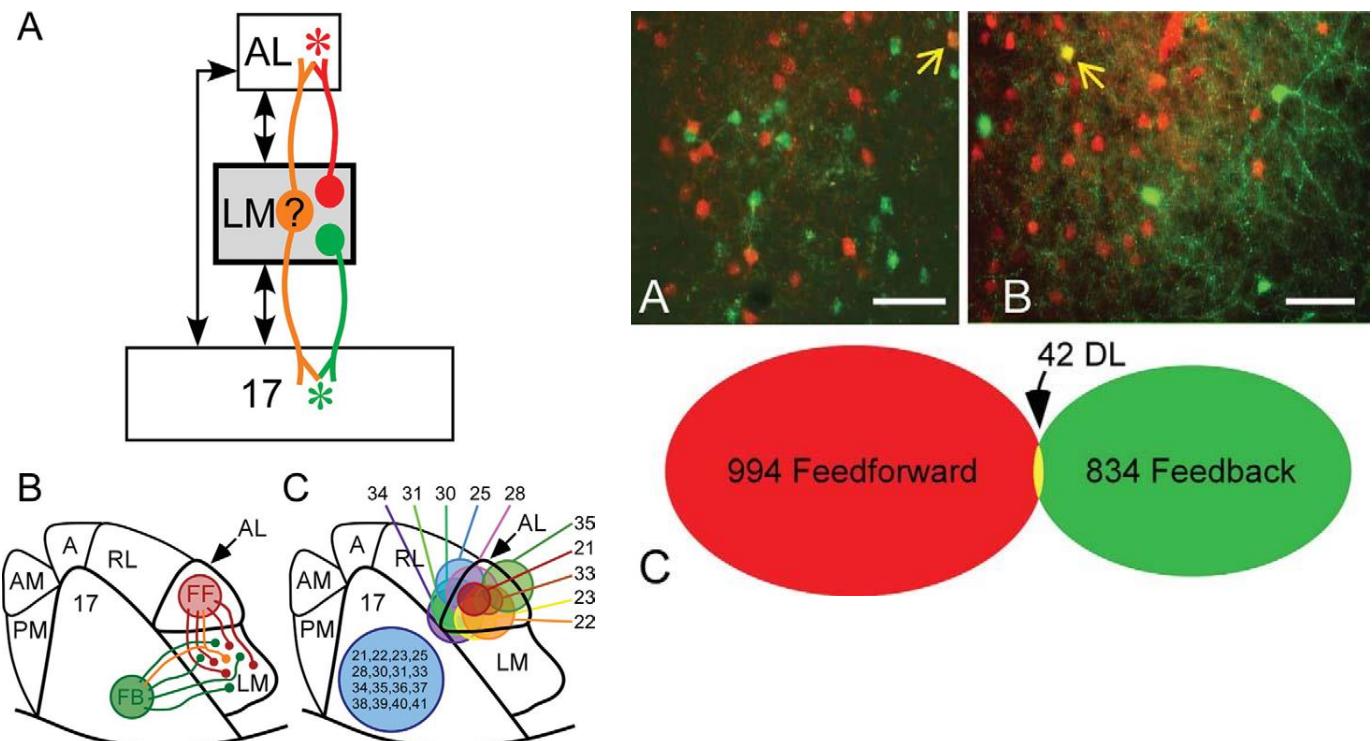
- A hierarchical generative model of sensory inputs
- The estimates of the causes generate predictions of sensory input
- The estimates of causes are updated in response to prediction errors (mismatches)
- The relative influence of PEs and predictions is determined by their relative precision (certainty)
- These computations underlie both perception (inference) and learning (model update)



# Mapping predictive coding onto the brain

- A hierarchical generative model of sensory inputs
- The estimates of the causes generate predictions of sensory input
- The estimates of causes are updated in response to prediction errors (mismatches)
- The relative influence of PEs and predictions is determined by their relative precision (certainty)
- These computations underlie both perception (inference) and learning (model update)

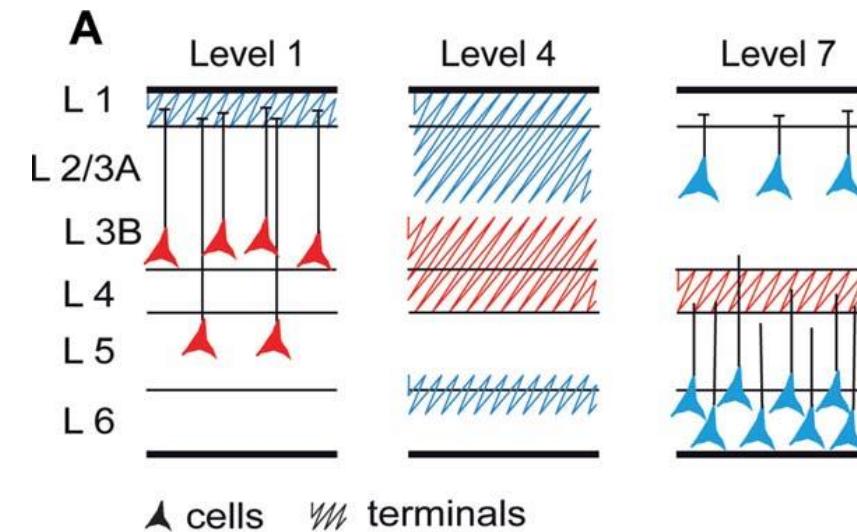
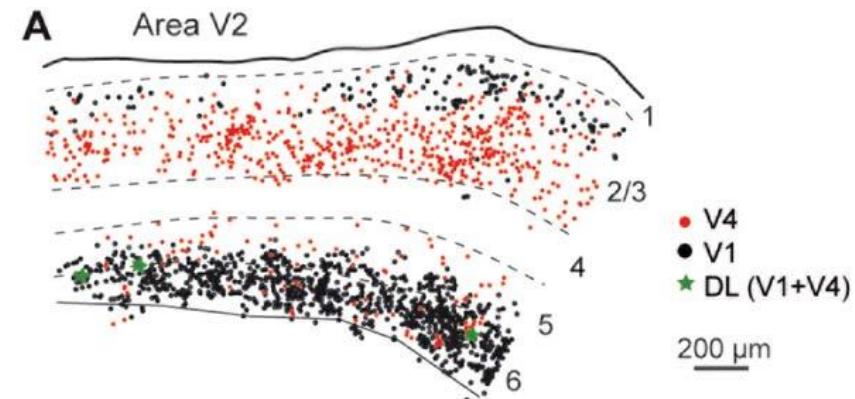
1. The source populations of forward and backward pathways should be completely separate, given their functional distinction.



# Mapping predictive coding onto the brain

- A hierarchical generative model of sensory inputs
- The estimates of the causes generate predictions of sensory input
- The estimates of causes are updated in response to prediction errors (mismatches)
- The relative influence of PEs and predictions is determined by their relative precision (certainty)
- These computations underlie both perception (inference) and learning (model update)

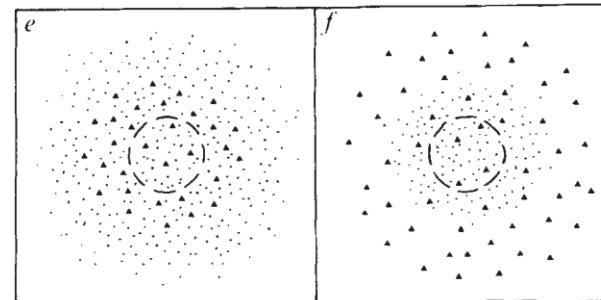
1. The source populations of forward and backward pathways should be completely separate, given their functional distinction.



# Mapping predictive coding onto the brain

- A hierarchical generative model of sensory inputs
- The estimates of the causes generate predictions of sensory input
- The estimates of causes are updated in response to prediction errors (mismatches)
- The relative influence of PEs and predictions is determined by their relative precision (certainty)
- These computations underlie both perception (inference) and learning (model update)

2. Backward connections encode predictions and expected precision, so they should be more divergent.



Zeki & Shipp 1988 *Nature*

3. Causes interact non-linearly to generate data, so backward connections should be more modulatory.

Self et al. 2012 *PNAS*  
Olsen et al. 2012 *Nature*  
Zilles et al. 2004 *J Anat*

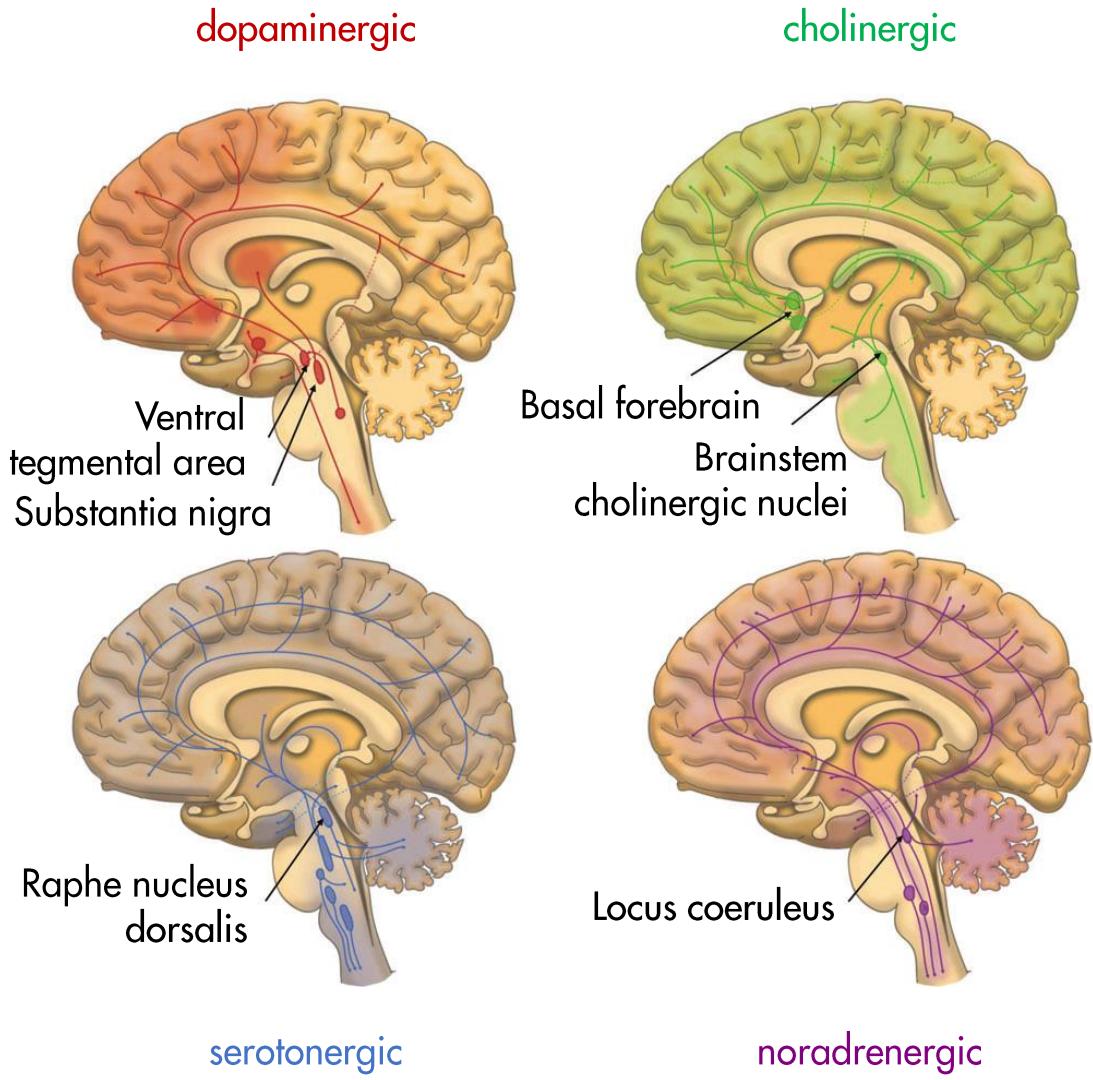
4. Predictions are generated more slowly than prediction errors, suggesting a spectral asymmetry.

Roopun 2006 *PNAS*  
Roopun et al. 2008  
*Front. Cell. Neurosci*

Buffalo et al. 2011 *PNAS*  
Bosman et al. 2012 *Neuron*  
Bastos et al. 2015 *NeuroImage*

# Mapping predictive coding onto the brain

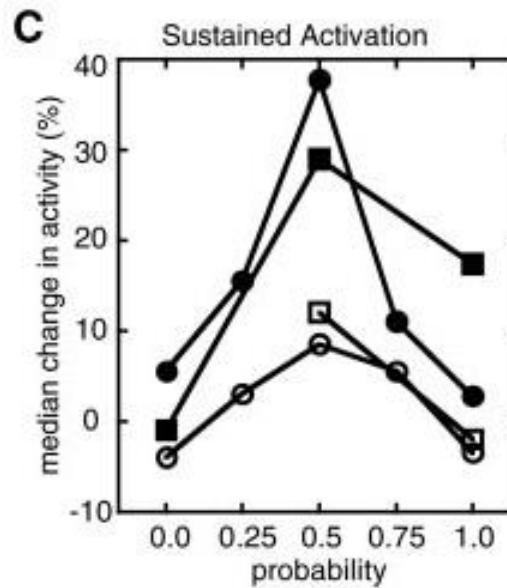
- A hierarchical generative model of sensory inputs
- The estimates of the causes generate predictions of sensory input
- The estimates of causes are updated in response to prediction errors (mismatches)
- **The relative influence of PEs and predictions is determined by their relative precision (certainty)**
- These computations underlie both perception (inference) and learning (model update)



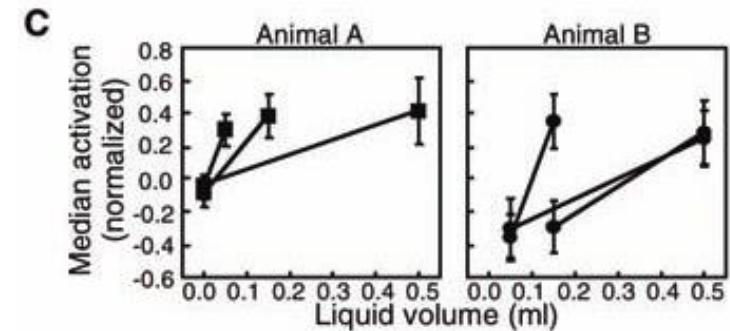
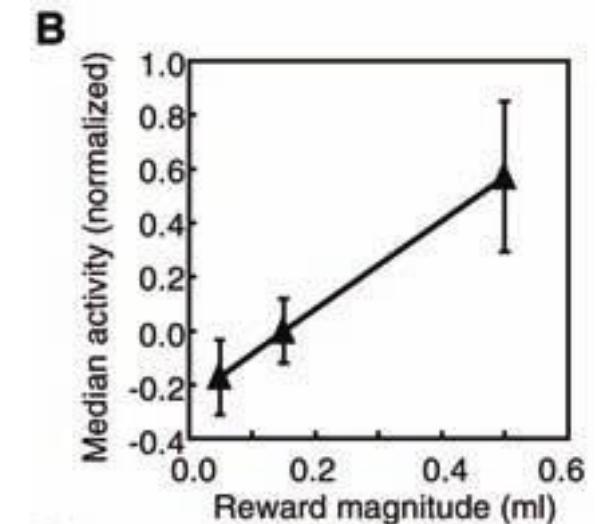
Adapted from Iglesias et al. 2017 *WIRE Cogn Sci*

# Mapping predictive coding onto the brain

- A hierarchical generative model of sensory inputs
- The estimates of the causes generate predictions of sensory input
- The estimates of causes are updated in response to prediction errors (mismatches)
- **The relative influence of PEs and predictions is determined by their relative precision (certainty)**
- These computations underlie both perception (inference) and learning (model update)



Fiorillo et al. 2003 *Science*

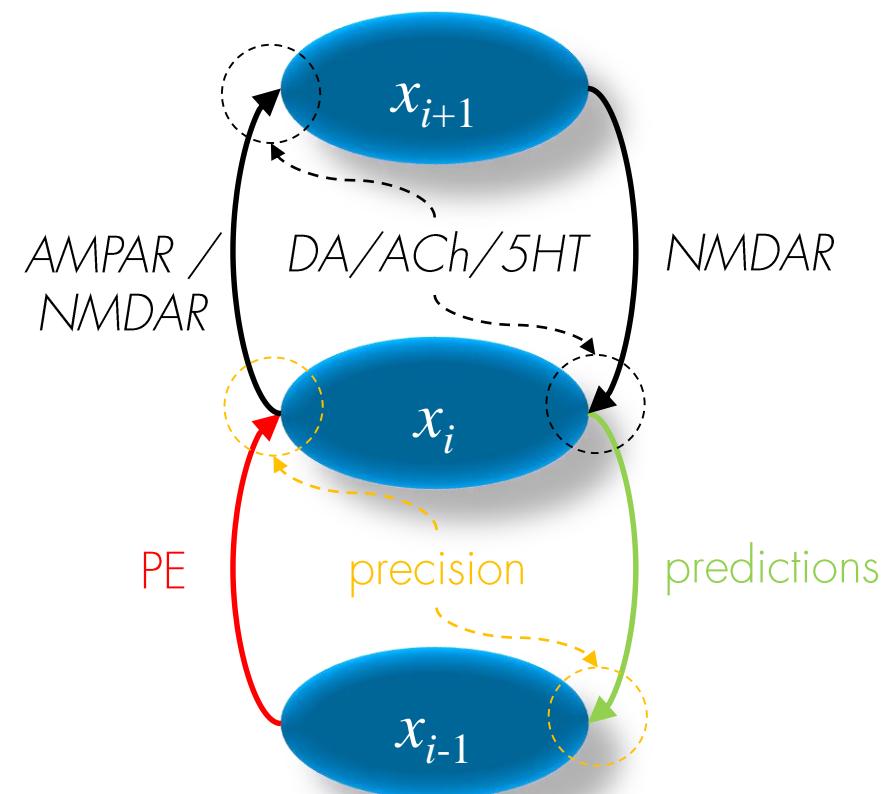


Tobler et al. 2005 *Science*

Achieved via cholinergic modulation?  
Naudé et al. 2018 *bioRxiv*

# Mapping predictive coding onto the brain

- A hierarchical generative model of sensory inputs
- The estimates of the causes generate predictions of sensory input
- The estimates of causes are updated in response to prediction errors (mismatches)
- The relative influence of PEs and predictions is determined by their relative precision (certainty)
- These computations underlie both perception (inference) and learning (model update)

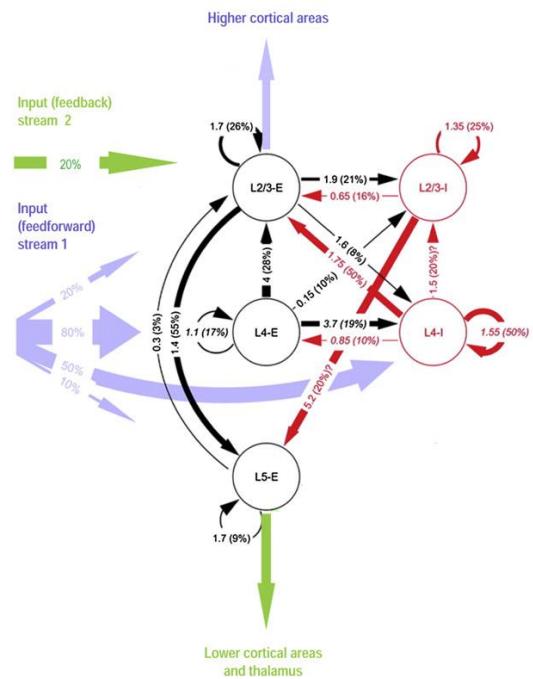




# Is predictive coding theory articulated enough to be testable?

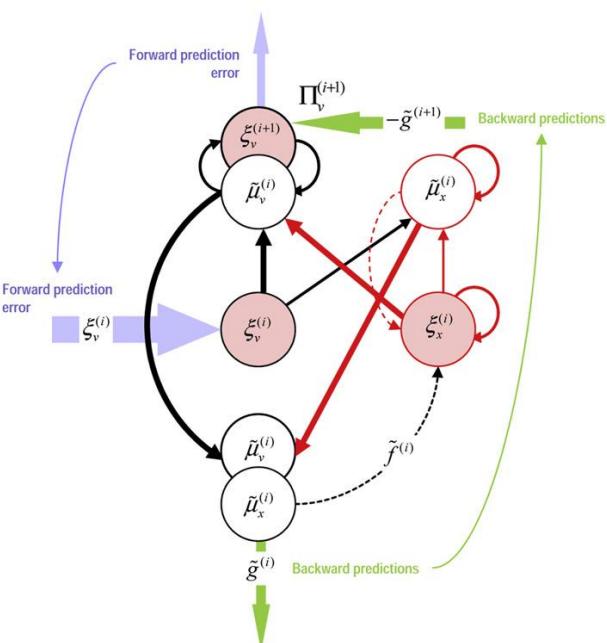
*Naoki Kogo \* and Chris Trengove*

Haeusler and Maass (2007)

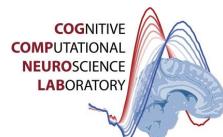
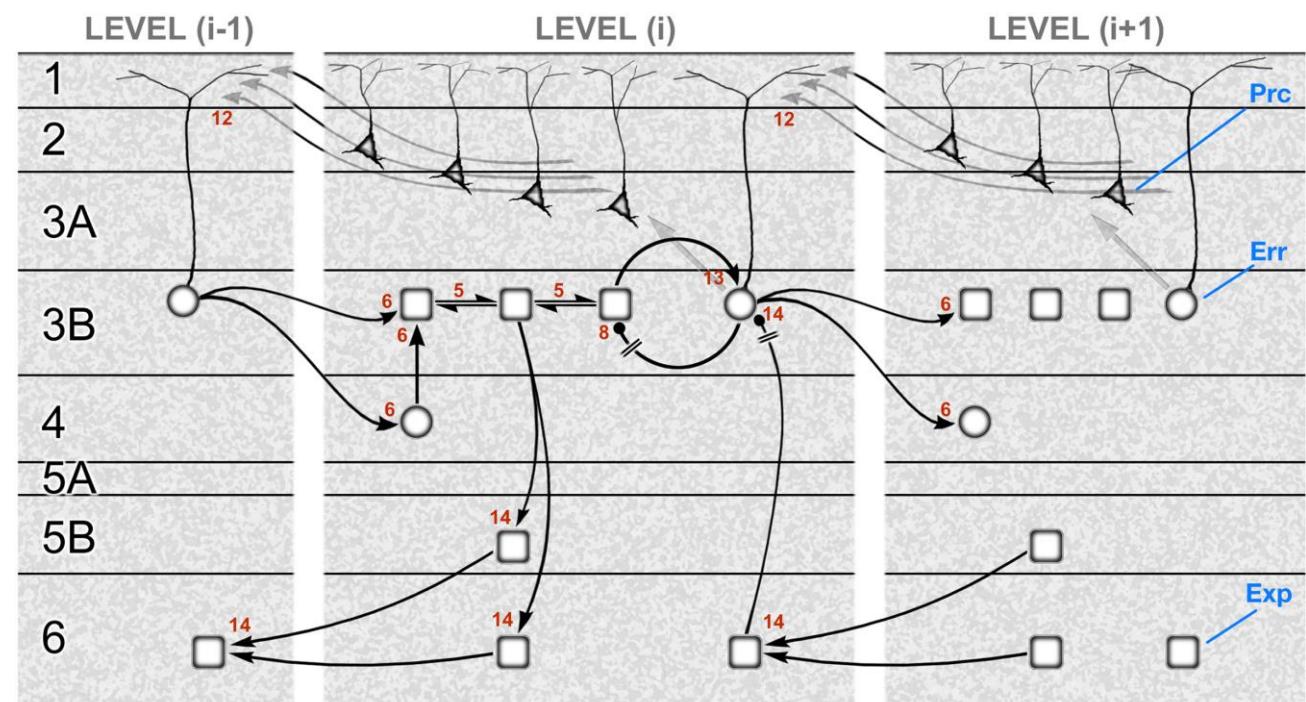


Bastos et al. 2012 *Neuron*

Canonical microcircuit for predictive coding



# Mapping predictive coding onto the brain ... advanced



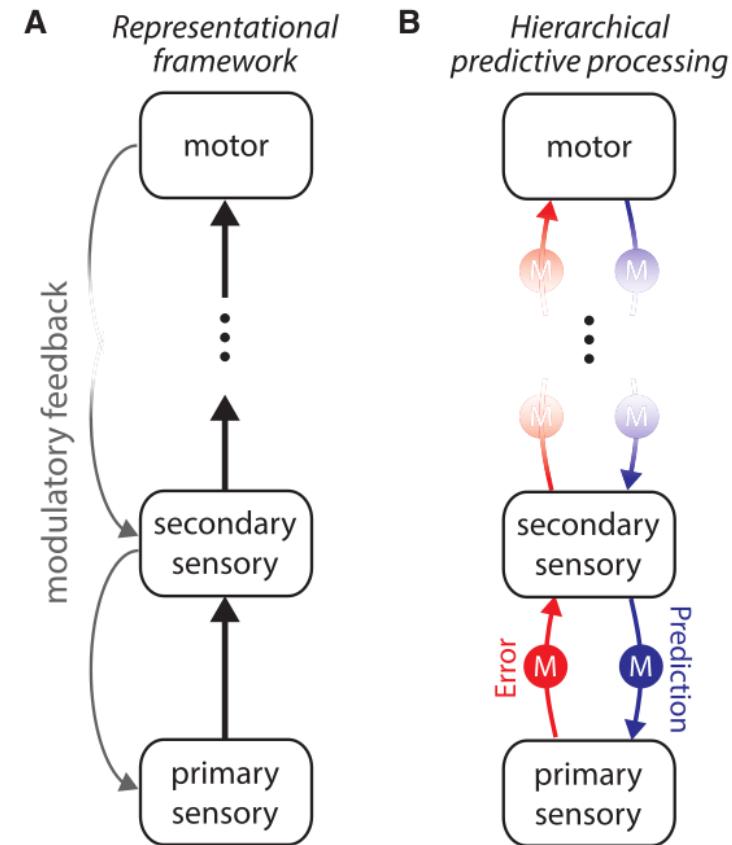
Translational Neuromodeling Unit

Shipp 2016 *Frontiers in Psychology*

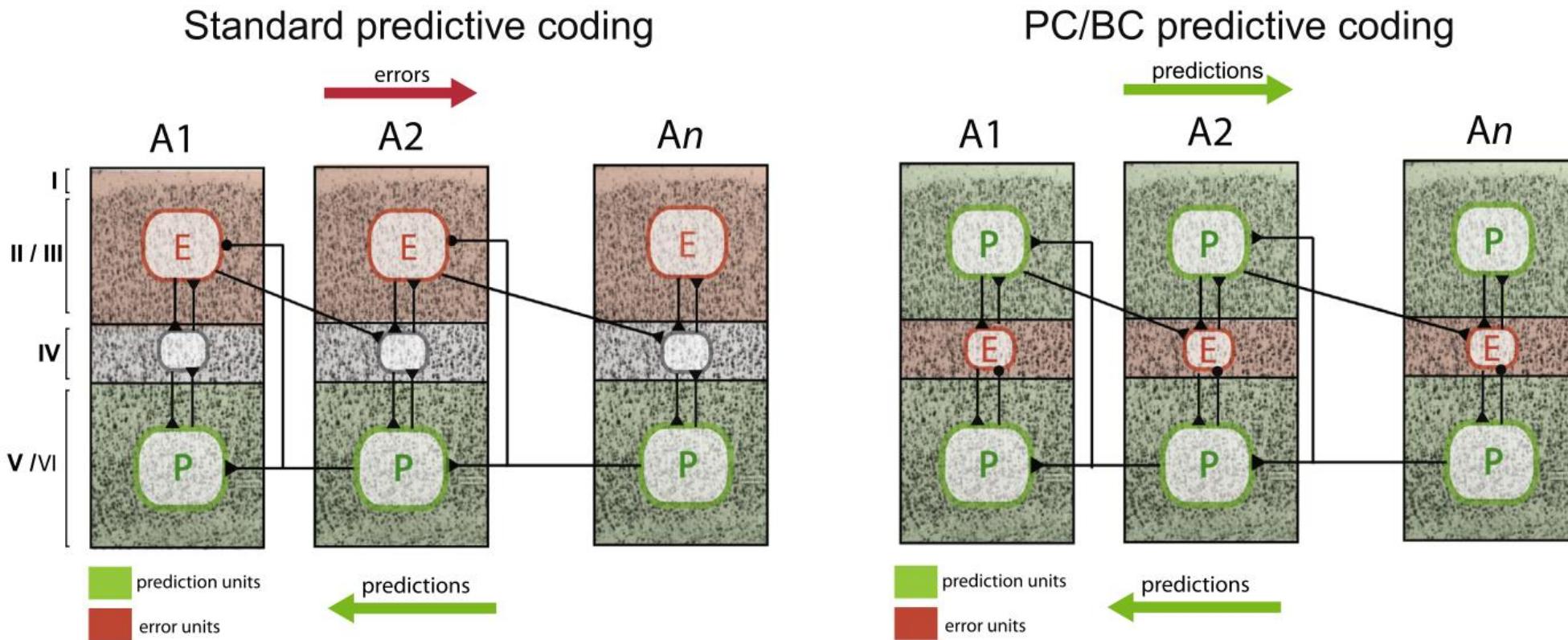
25

# Testing the *relevant* predictions

- locomotion is sufficient to drive activity in mouse V1, even in the complete absence of visual input (**Keller et al., 2012, Saleem et al., 2013**)
- layer 2/3 of sensory cortices signals a mismatch between predicted and actual sensory feedback (**Eliades and Wang, 2008, Keller et al., 2012**)
- this results from a comparison of an excitatory motor-related input and an inhibitory visual input (**Attinger et al., 2017, Zmarz and Keller, 2016**)
- A24b/M2 provides a strong and dense projection to V1, which conveys motor-related signals that depend on the mouse's visuomotor experience. This projection fulfills all the criteria necessary to be interpreted as a prediction of visual flow given a motor output (**Leinweber et al., 2017**)



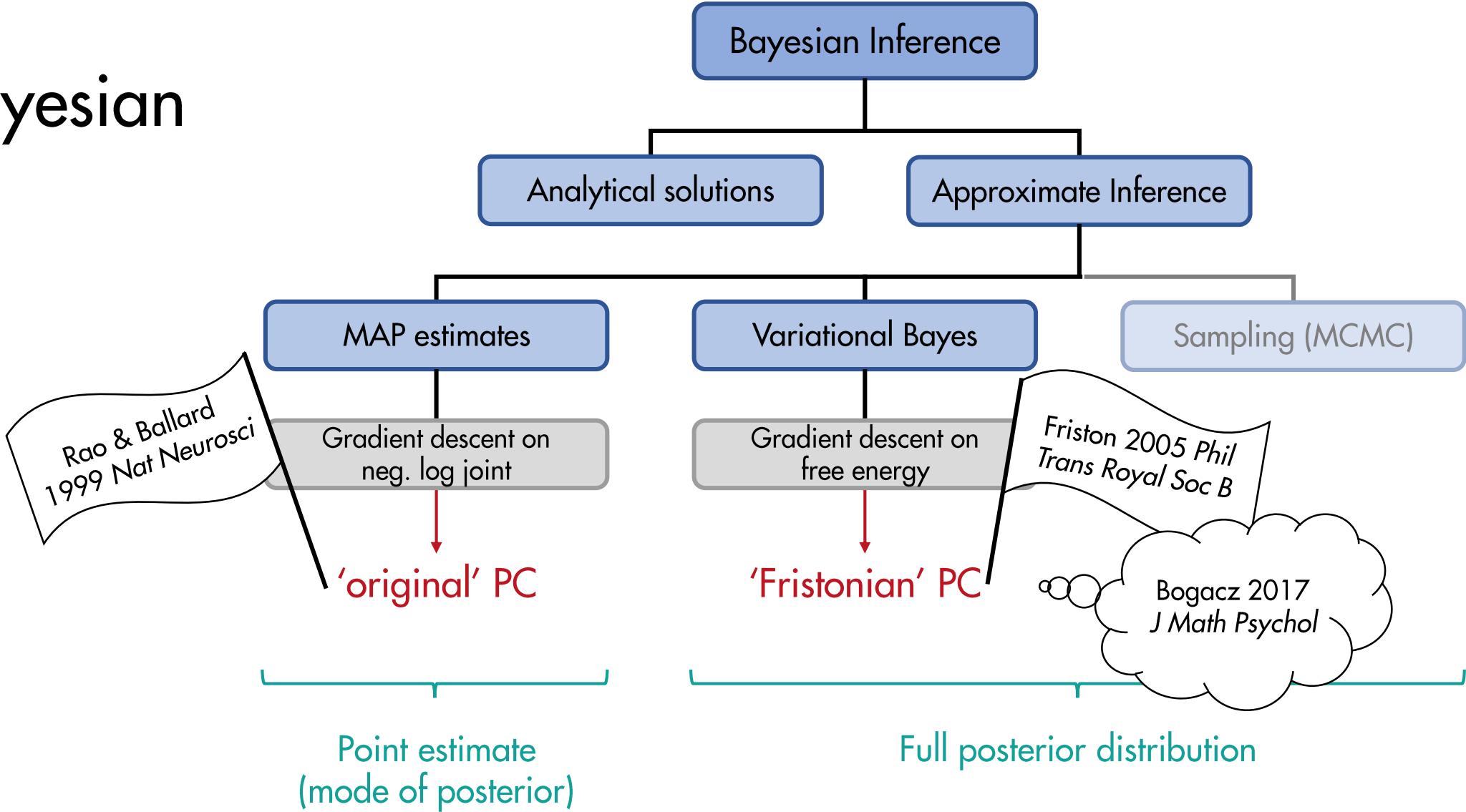
# Testing the *relevant* predictions



# III. Predictive coding and free-energy

From representing probability distributions (and uncertainty) and the Laplace assumption to predictions on cortical infrastructure and plasticity: *Friston, 2005*

# The Bayesian Brain



$$p(x|y) = \frac{p(x)p(y|x)}{p(y)} \quad p(y) = \int p(x)p(y|x) \, dx$$

# Representing uncertainty

So far, we've only computed the MAP.  
To be fully Bayesian: care about your uncertainty!



$q(x)$ : our best guess about  $p(x|y)$

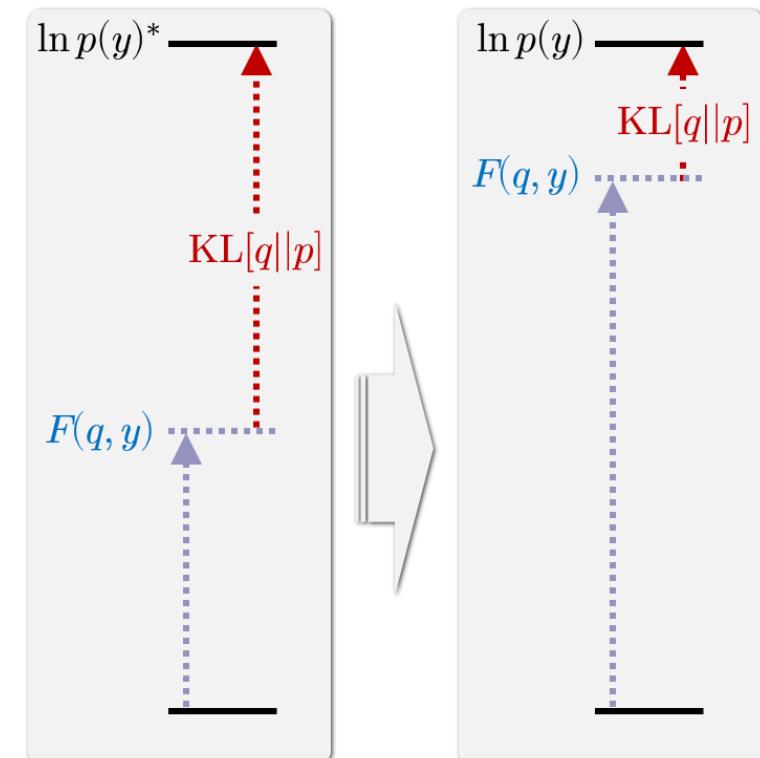
$$\begin{aligned} \text{KL}(q(x), p(x|y)) &= \ln p(y) - \int q(x) \ln \frac{p(y, x)}{q(x)} \, dx \\ &= \ln p(y) - F \end{aligned}$$



$$\ln p(y|m) = \text{KL}(q(x), p(x|y, m)) + F(q(x), p(x, y|m))$$



$$F = \int q(x) \ln \frac{p(y, x)}{q(x)} \, dx$$



# 'Fristonian' PC

The free energy formulation of predictive coding

$$F = \int q(x) \ln \frac{p(y, x)}{q(x)} dx$$

**Inference:** maximizing F to find the approximate posterior

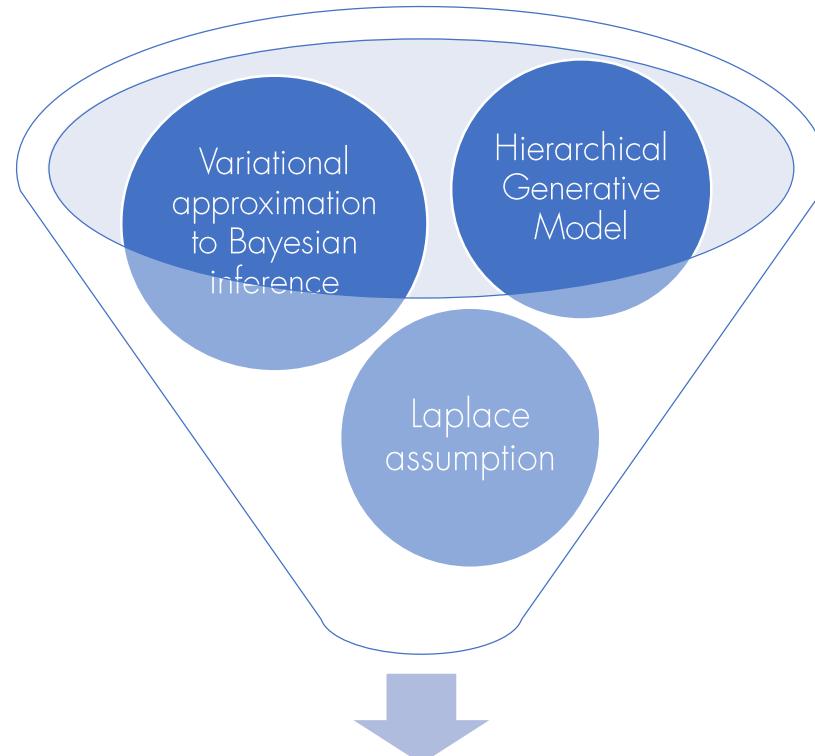
**Learning:** maximizing F to improve the model and thereby reduce average surprise over time.

Additional assumption:  $q(x)$  is a Gaussian.

We only need to represent the mean and the variance.

→ *precision-weighted prediction errors*

Predictive Coding can be viewed as the implementation of a particular scheme of approximate Bayesian inference in the brain.



Predictive Coding

## PREDICTIVE CODING

# Does predictive coding have a future?

In the 20th century we thought the brain extracted knowledge from sensations. The 21st century witnessed a 'strange inversion', in which the brain became an organ of inference, actively constructing explanations for what's going on 'out there', beyond its sensory epithelia. One paper played a key role in this paradigm shift.

Karl Friston

## IV. PC in CP

Stratifying psychiatric diseases using hierarchical Bayesian models

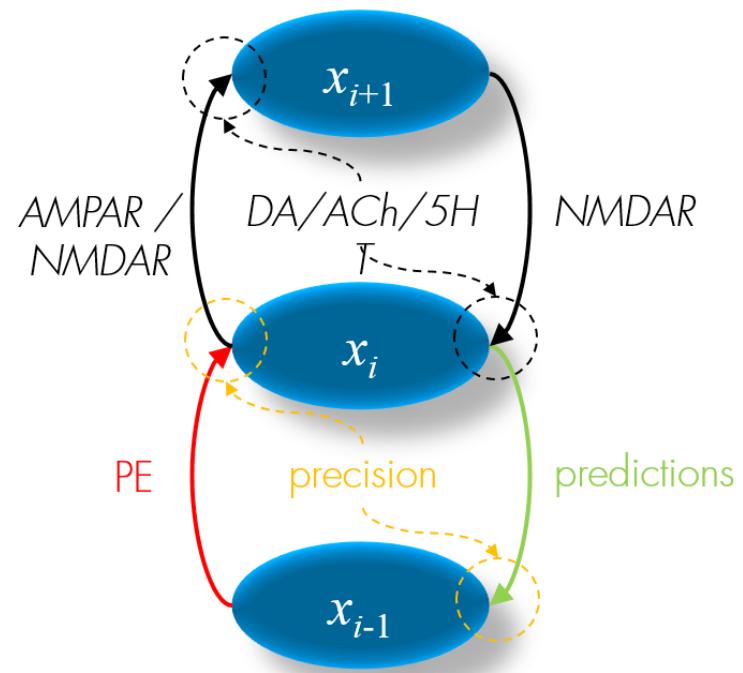
# Hierarchical Bayesian Inference in Computational Psychiatry

Possible primary disruption at:

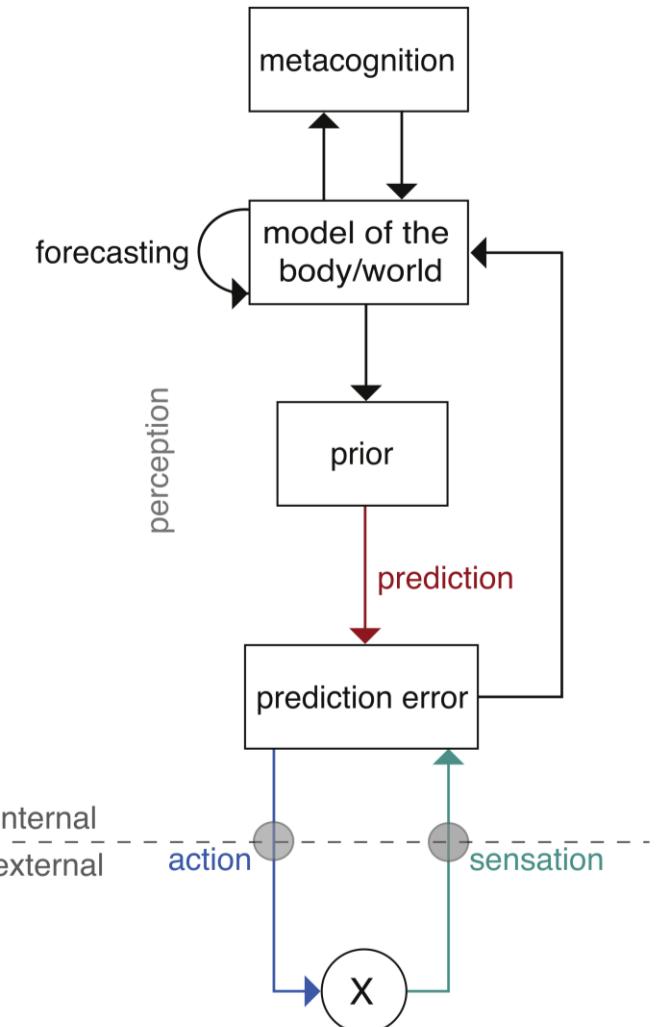
1. Sensory inputs (sensations)
2. Inference (perception)
3. Forecasting
4. Control (action)
5. Metacognition

At any of these, possible disturbance of:

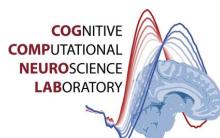
- Prediction error (PE) computation
- Predictions/Expectations
- Estimation of their precision.



Stephan et al. 2016 *Brain*



Petzschnier et al. 2017 *Biol Psychiatry*



Translational Neuromodeling Unit

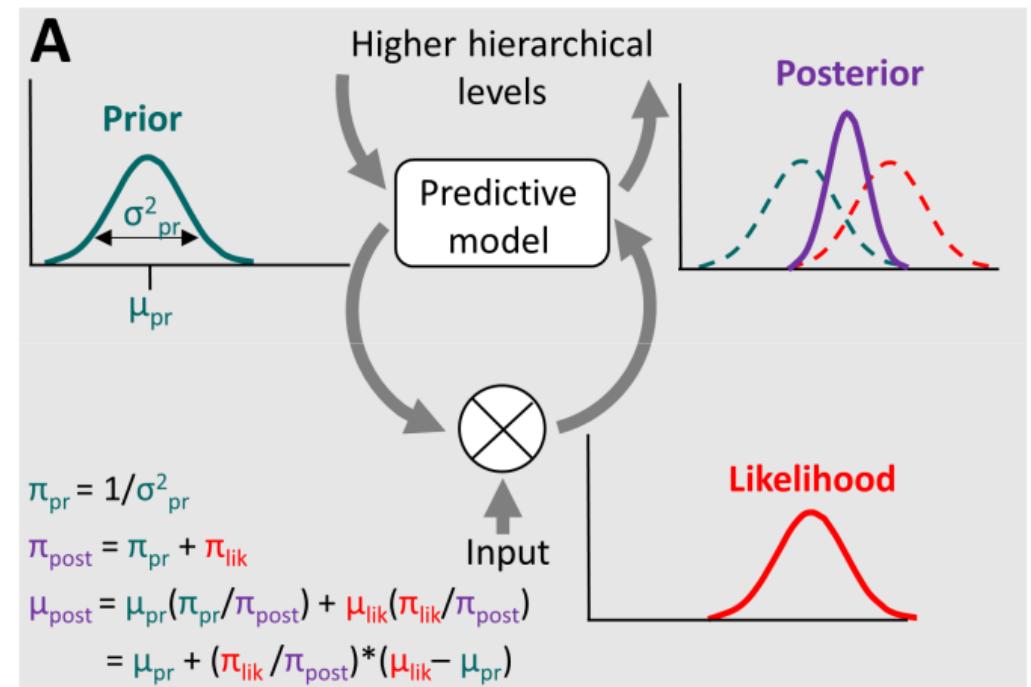
# Precision: The right balance

Schizophrenia/Psychosis

Sterzer et al. 2018 *Biol Psychiatry*; Adams et al. 2013 *Front Psychiatry*; Corlett et al. 2011 *NPP*; Stephan et al. 2006 *Biol Psychiatry*; 2009; Powers et al. 2017 *Science*

Autism spectrum disorder

Pellicano & Burr 2012 *TiCS*; Van de Cruys et al. 2014 *Psychol Rev*; Lawson et al. 2014 *Front Hum Neurosci*; Lawson et al. 2017 *Nat Neurosci*



# Interoceptive predictive coding

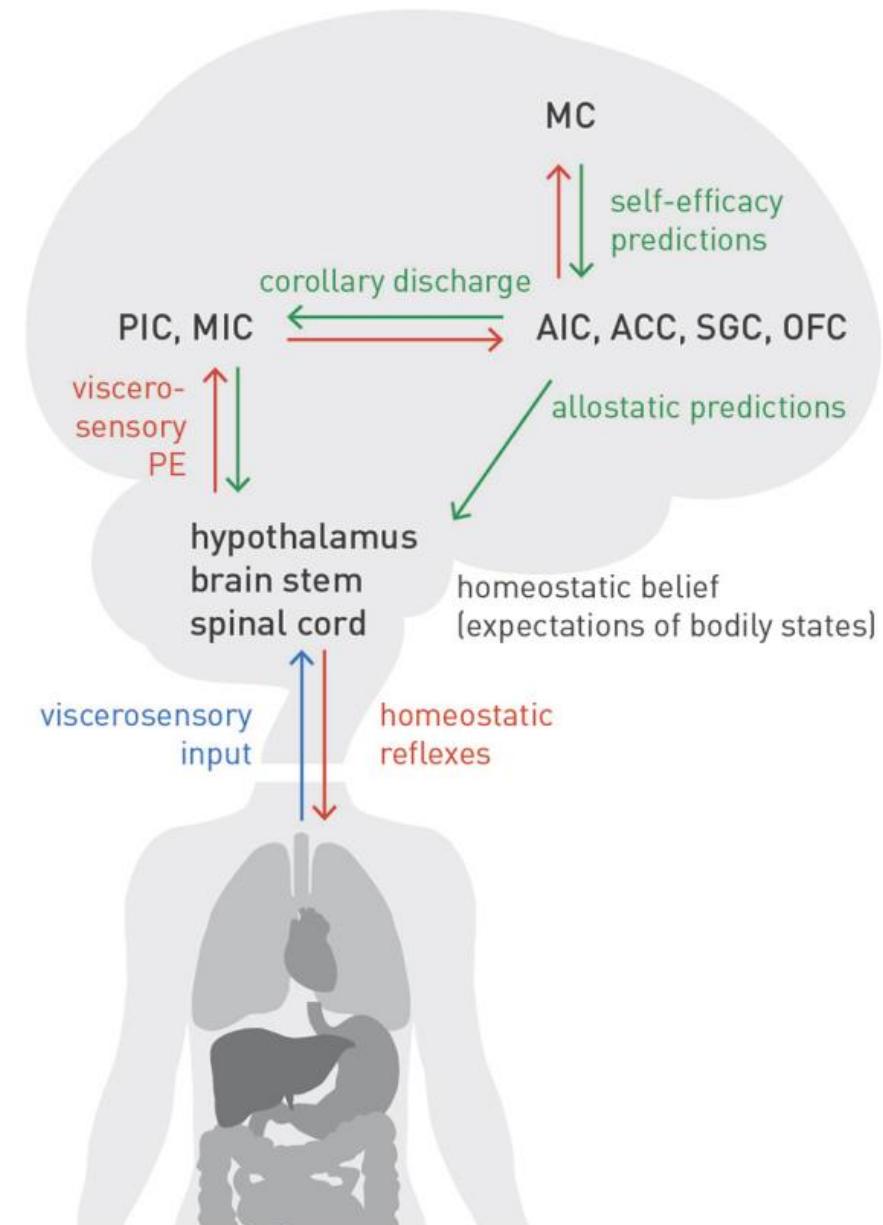
Seth 2013 *TiCS*

Barrett & Simmons 2015 *Nature Rev Neurosci*

Seth & Friston 2016 *Phil Trans Royal Soc B*

**Stephan et al. 2016 *Front Hum Neurosci***

Petzschnier et al. 2017 *Biol Psychiatry*

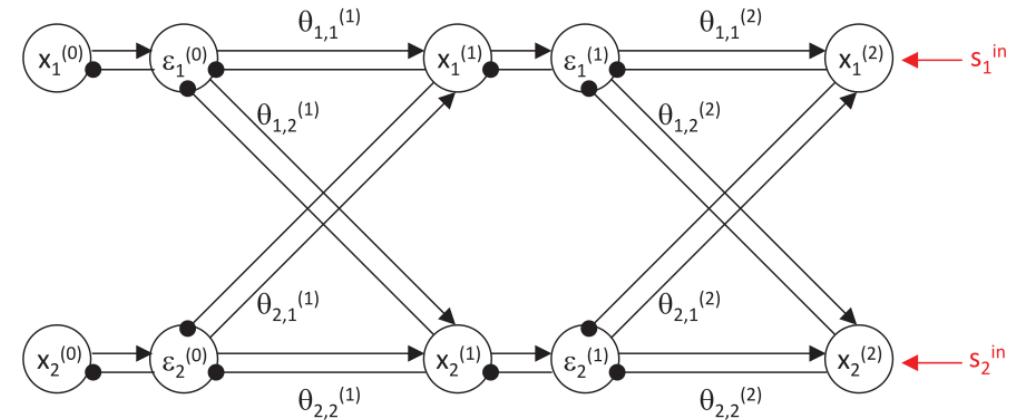


# Testing further

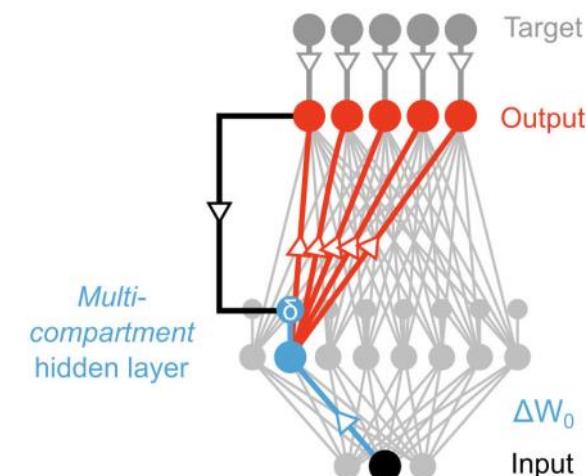
- Sources of modulatory (precision) signals
  - Neuromodulators and how they interact
- Separate error units and prediction (representation) units
  - Laminar resolution, especially in the auditory domain (vision: Kok et al. 2016 *Curr Biol*)
  - High temporal resolution (predictions can precede a stimulus, PEs can only follow)
- Computationally explicit analyses ('model-based')
  - to test crucial theoretical distinctions, e.g. PEs vs. precision-weighted PEs
  - e.g., Iglesias et al. 2013 *Neuron*; Sedley et al. 2016 *eLife*; Bell et al. 2016 *Curr Biol*

# PC and ANNs

- A predictive coding network can perform supervised learning autonomously using simple Hebbian learning and approximates the backpropagation algorithm (Whittington & Bogacz 2017 *Neural Computation*)
- A single pyramidal neuron can implement predictive coding via its apical dendrites (Urbanczik & Senn 2014 *Neuron*; Sacramento et al. 2018 *NIPS*) which can help to solve the credit assignment problem... (Guergiev et al. 2017 *eLife*)



B Segregated dendrites solution

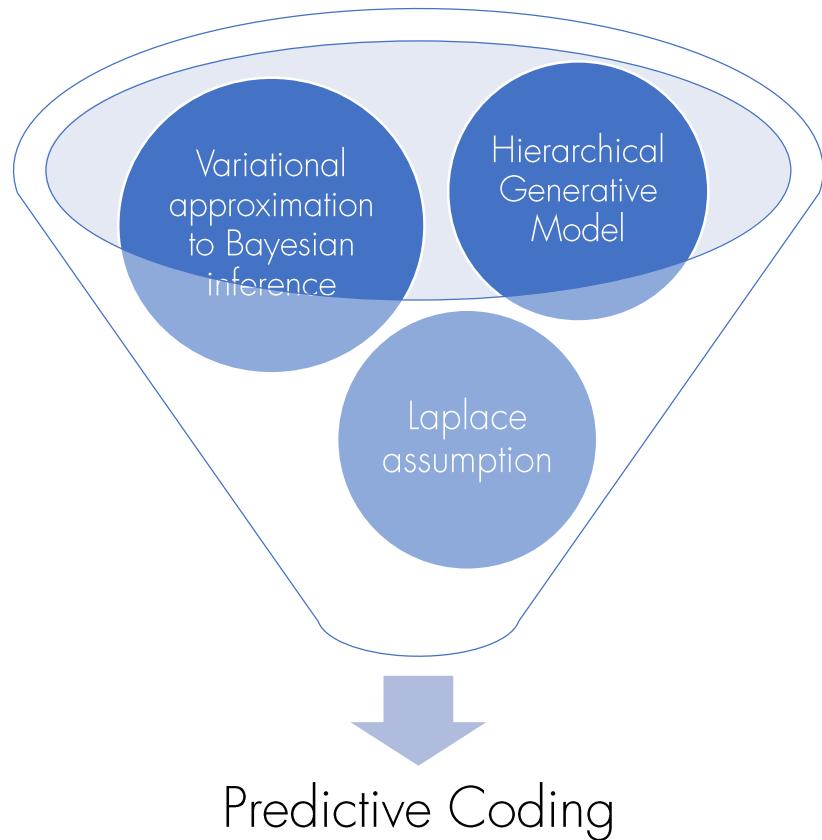


# V. How can I apply this model?

Why there is no predictive coding toolbox (yet)

# Building a model with PC

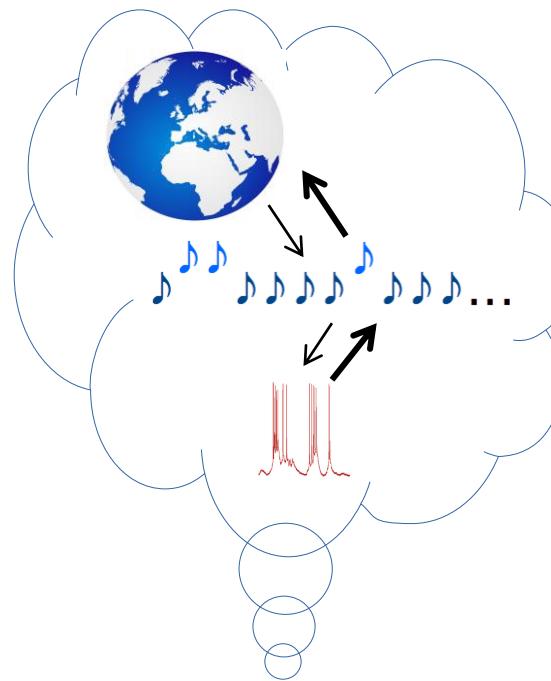
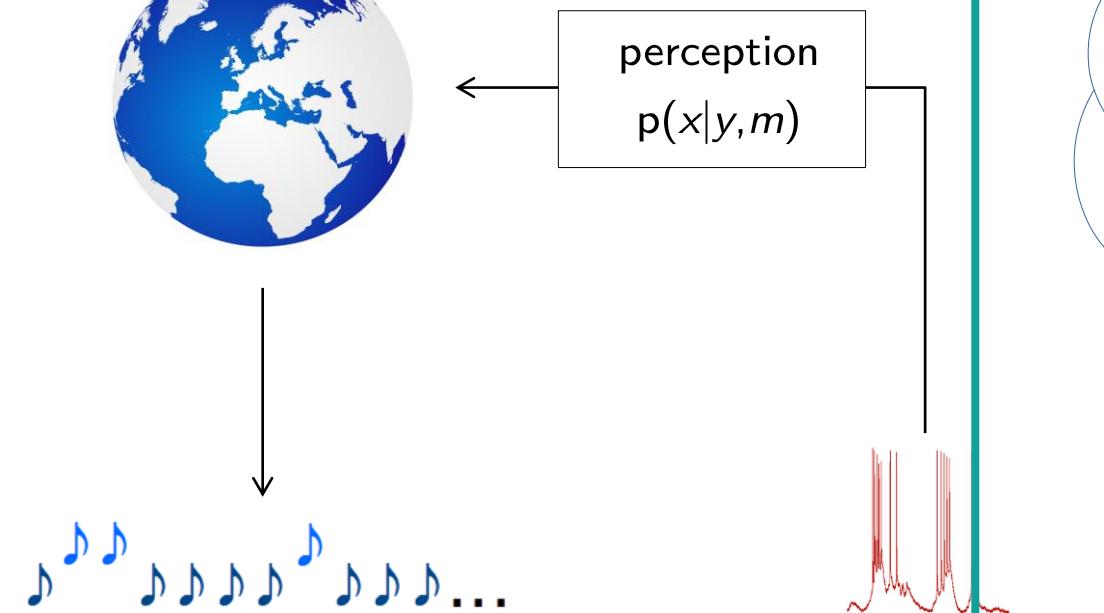
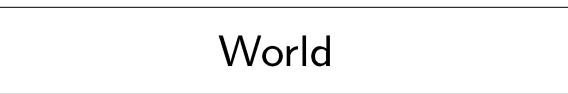
1. Predict the input
  - generative model of the sensory inputs
2. Invert the model
  - gradient descent on the neg. log joint
  - or: be fully Bayesian and use F
3. Simulate!
4. Fitting: Be the scientist
  1. Specify a mapping to observable data
  2. Write down the likelihood, specify your priors
  3. Acquire data & invert your model



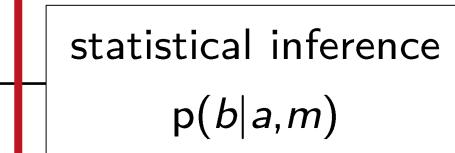
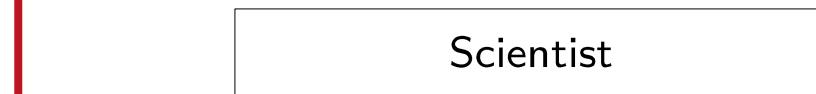
# Bayesian observers

today

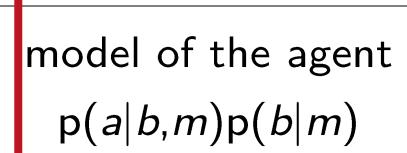
yesterday



beliefs  $b$



actions  $a$

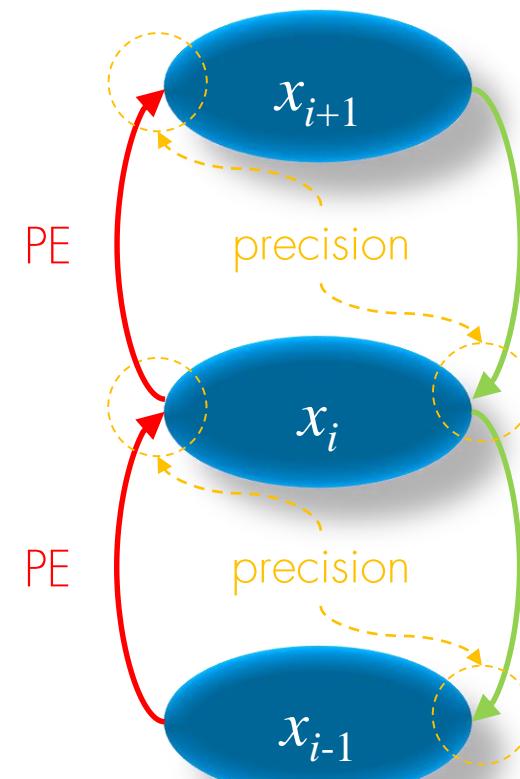


# Thank you



Translational Neuromodeling Unit

Rick Adams  
Rafal Bogacz



$$\Delta \text{belief} \sim \text{precision} \times \text{PE}$$