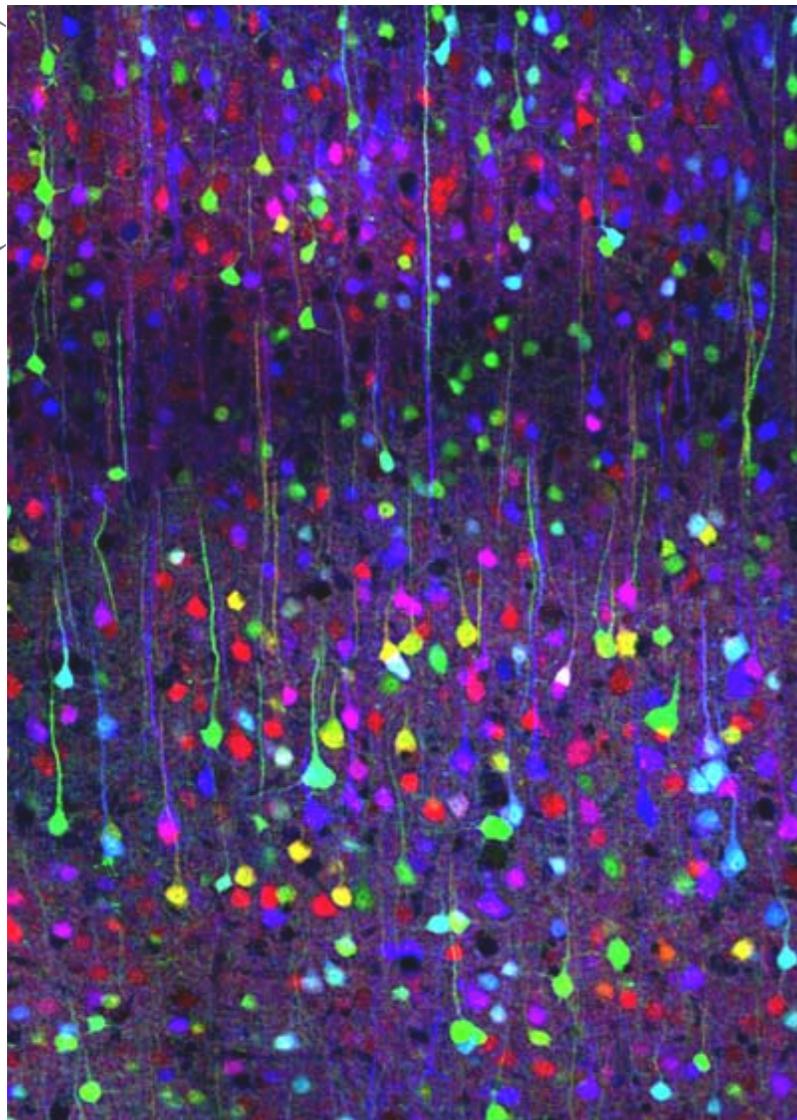


Information Processing & the Brain 20/21



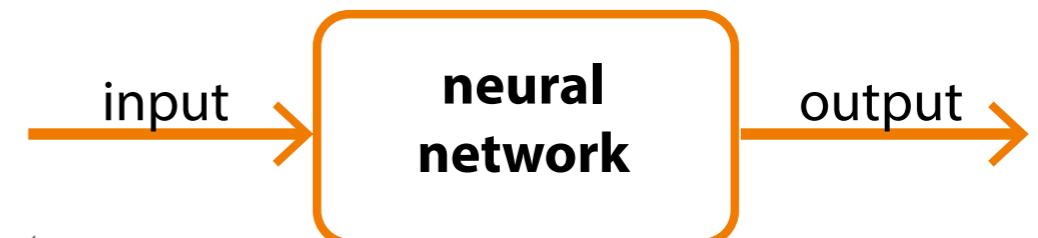
Brainbow (Litchman Lab)



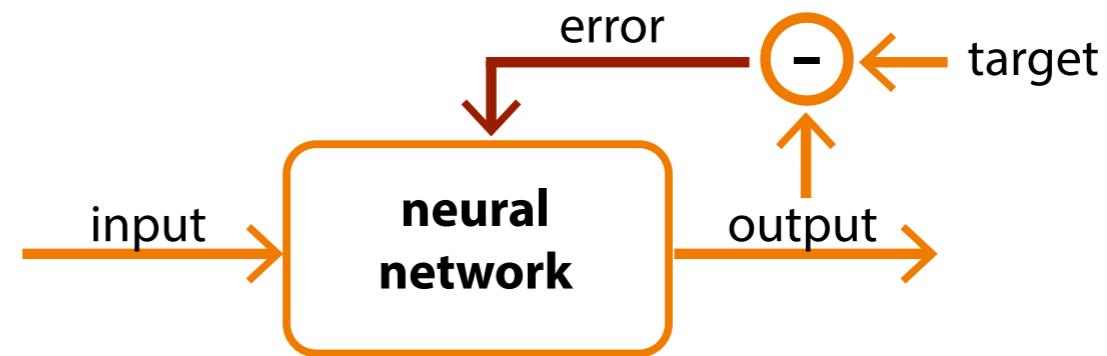
Lecture 2 Neural circuits and learning: Supervised learning: backprop & cerebellum

Previously on *IPB*...

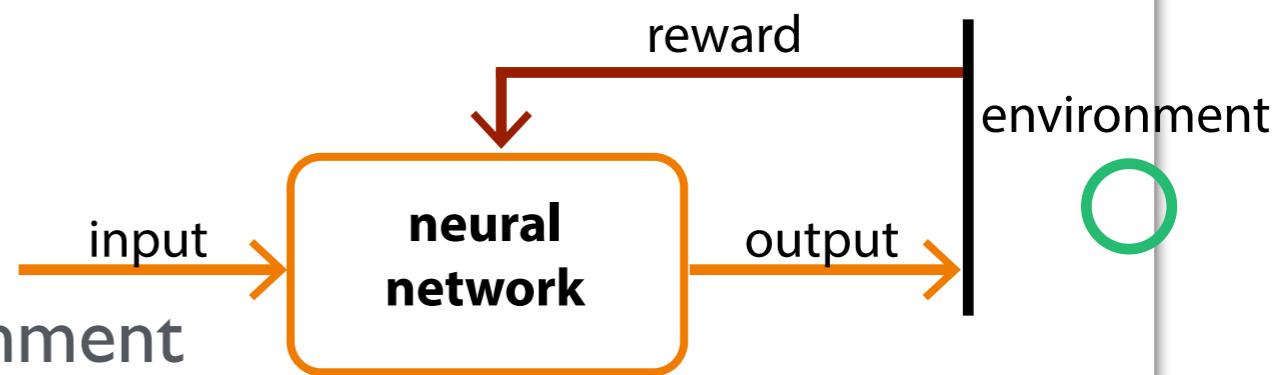
Unsupervised Learning:
Extracts useful representations of input



Supervised Learning:
Relies on a teaching signal

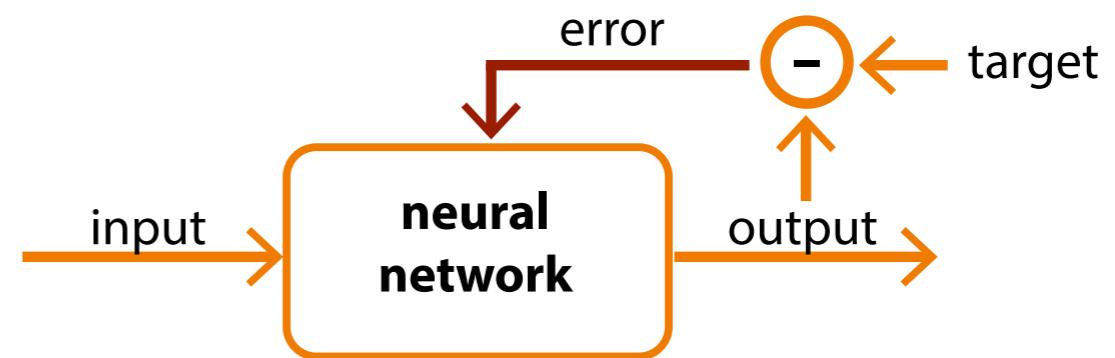


Reinforcement Learning:
Learn to navigate/survive an environment



But, how to exactly train neural networks?

Supervised Learning:
Relies on a teaching signal



Solution: The backprop algorithm which is the workhorse of deep learning!

Note: Backprop is a general optimization algorithm, that can also be used in unsupervised and reinforcement learning

Outline

- I. The backpropagation algorithm**
- 2. Backprop in the brain**
- 3. Does the cerebellum implement supervised learning?**

The backpropagation of errors algorithm

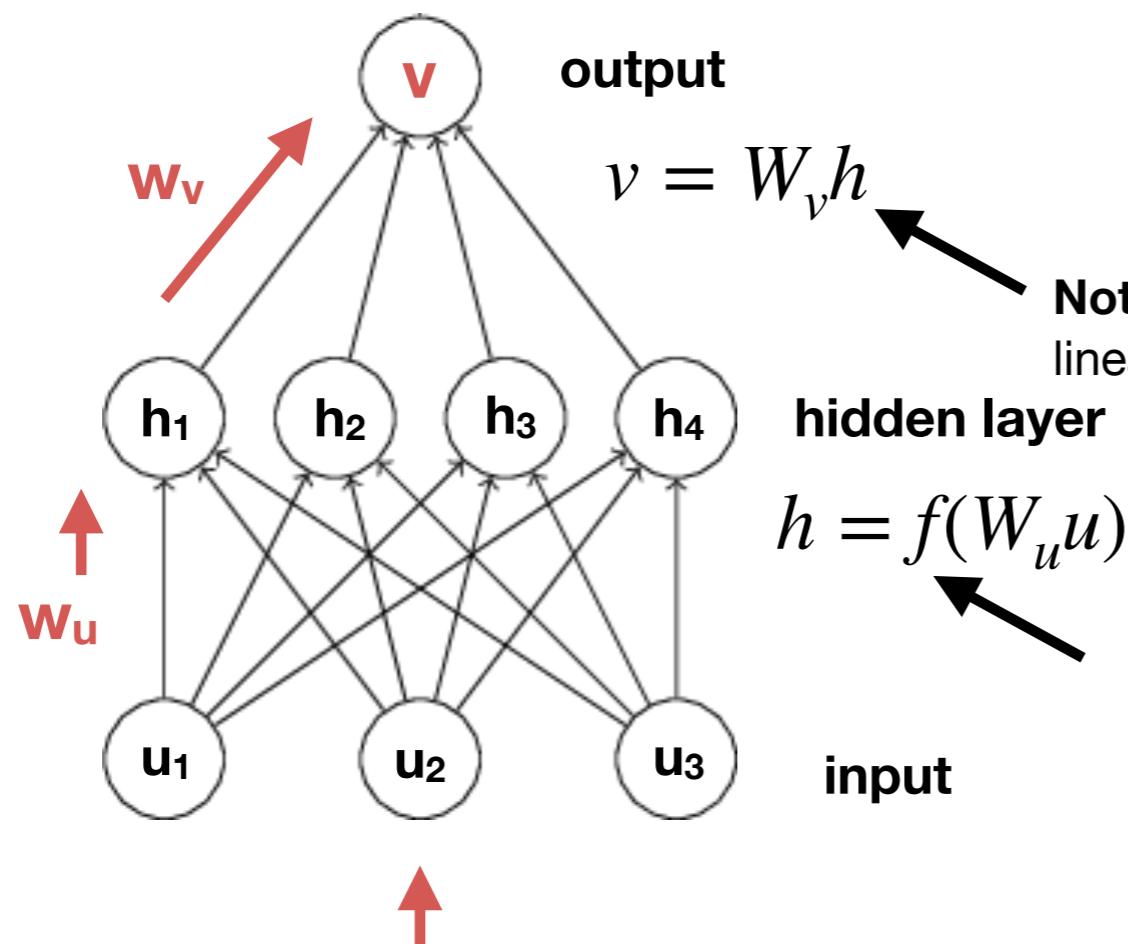
- **Backpropagation** is an algorithm used to train artificial neural networks. It calculates a gradient from the error function with respect to a given parameter (i.e. weight). With this gradient errors are effectively back propagated during training throughout the network.

$$\Delta w = \eta(v - \text{target})u$$

- It is a generalisation of the **delta rule** (above) to deep feedforward networks, which relies on the use of the chain rule to compute gradients for each layer (see next slides).
- **Backpropagation** is typically used to perform gradient descent optimisation, adjusting the weights of neurons while optimising a desired loss function (error).

Rumelhart et al. 1986 PDP

The backpropagation algorithm



The backpropagation algorithm:

1. Calculate forward activity

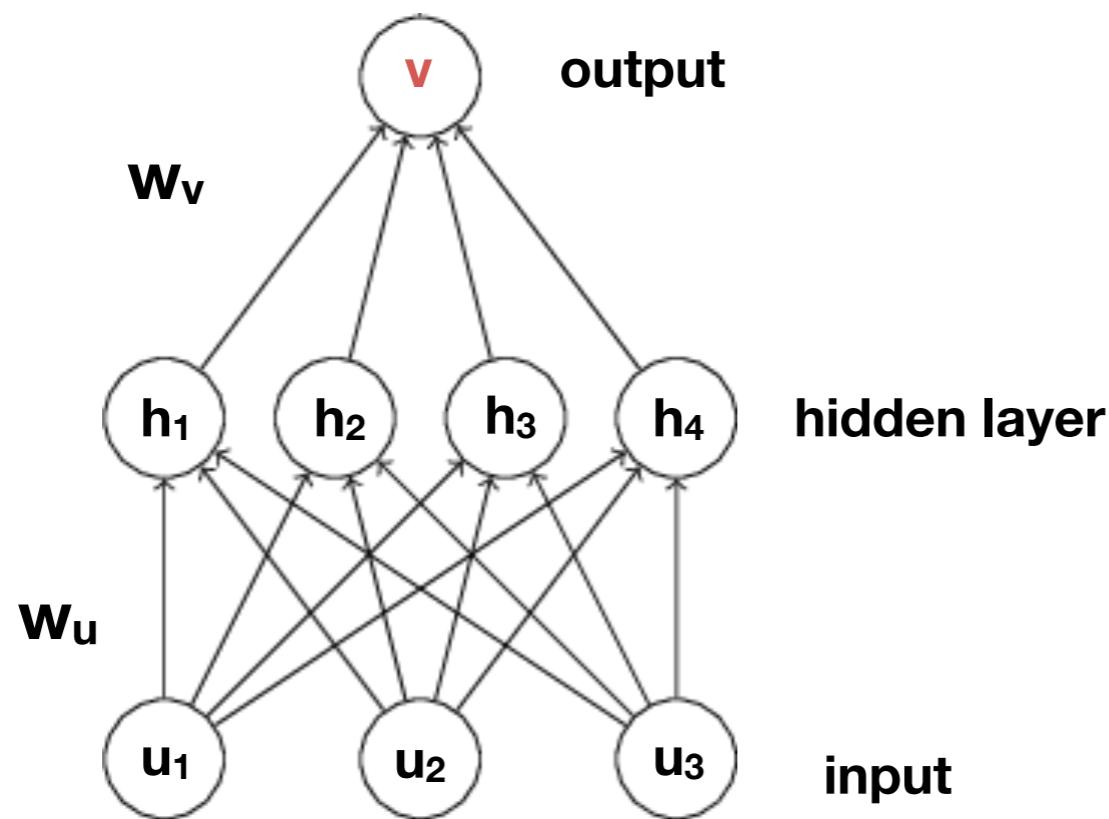
Note: Here, we are assuming a linear activation for v

f denotes the activation function (i.e. input-output function), which is typically modelled as a sigmoid or rectifying linear unit function (ReLU)

Rumelhart et al. 1986 PDP

The backpropagation algorithm

$$\text{error} = \frac{1}{2}(v - \text{target})^2$$

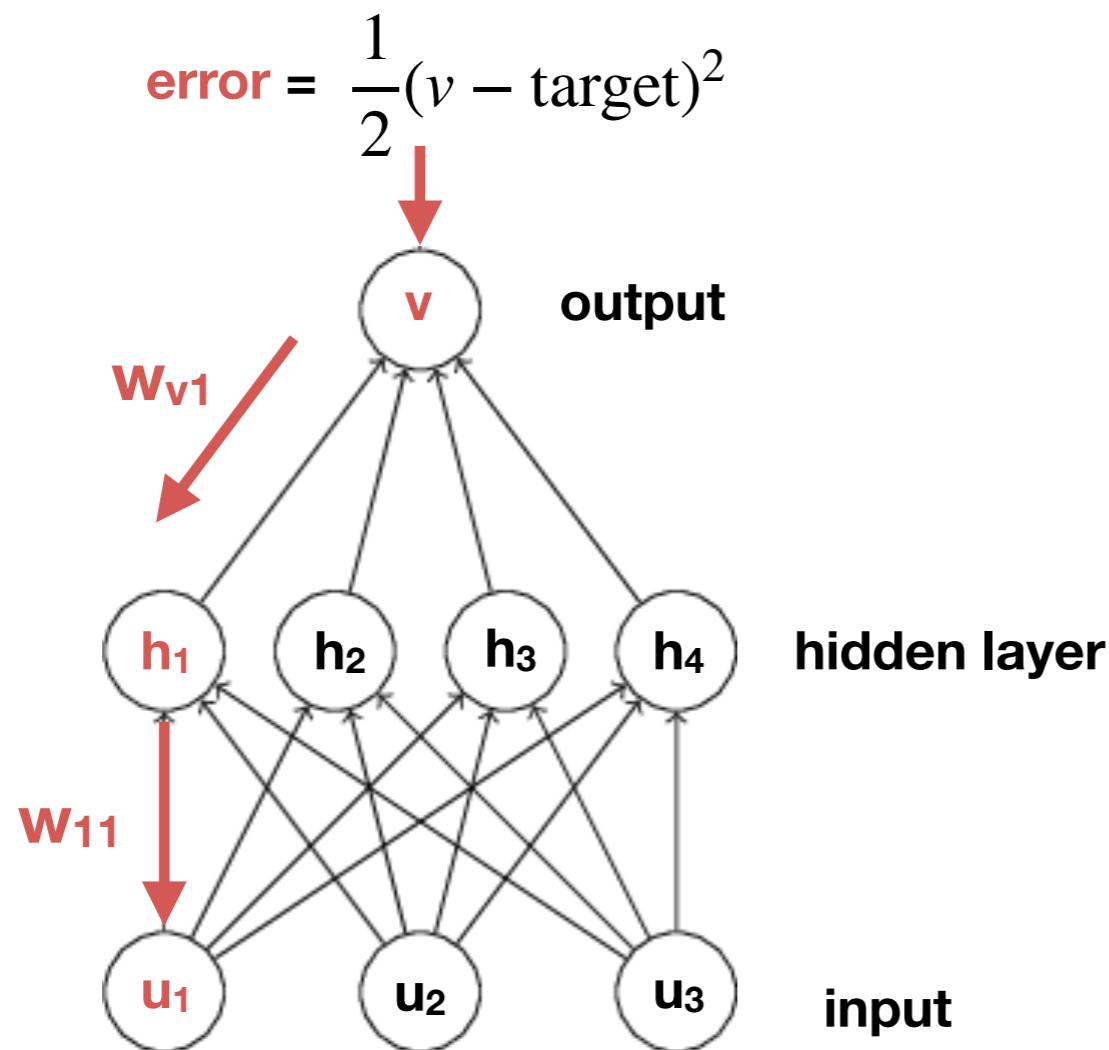


The backpropagation algorithm:

1. Calculate forward activity
2. Calculate **error**

Rumelhart et al. 1986 PDP

The backpropagation algorithm



$$\text{error} = \frac{1}{2}(v - \text{target})^2$$

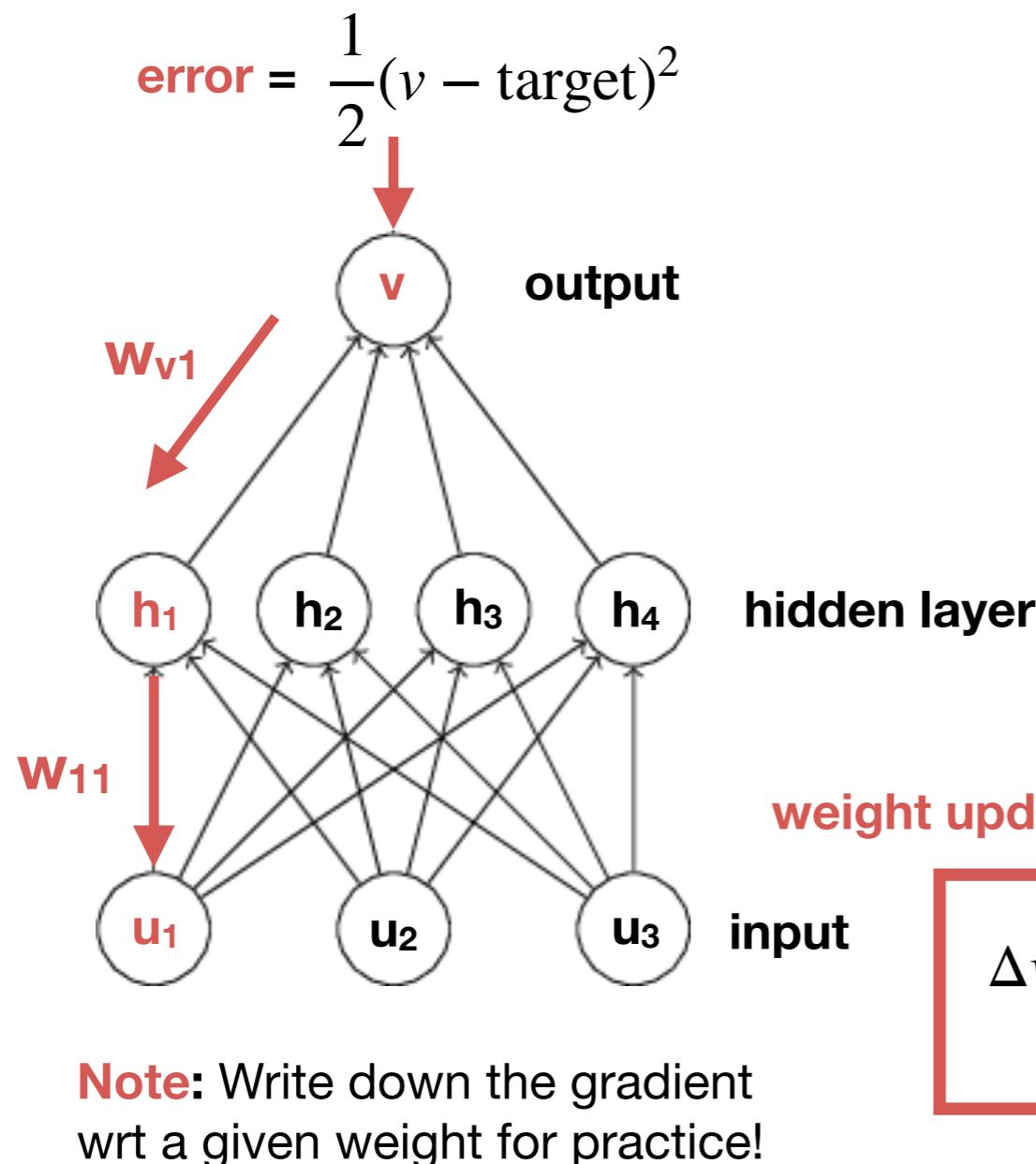
The backpropagation algorithm:

1. Calculate forward activity
2. Calculate error
3. **Backpropagate** error, e.g. how to calculate the gradient wrt w_{11} :

$$\frac{\partial \text{Error}}{\partial w_{11}} = \underbrace{\frac{\partial \text{Error}}{\partial v} \frac{\partial v}{\partial h_1} \frac{\partial h_1}{\partial w_{11}}}_{\text{chain rule}}$$

Rumelhart et al. 1986 PDP

The backpropagation algorithm



The backpropagation algorithm:

1. Calculate forward activity
2. Calculate error
3. **Backpropagate** error, e.g. how

to calculate the gradient wrt w_{11} :

$$\frac{\partial \text{Error}}{\partial w_{11}} = \underbrace{\frac{\partial \text{Error}}{\partial v} \frac{\partial v}{\partial h_1} \frac{\partial h_1}{\partial w_{11}}}_{\text{chain rule}}$$

$$\Delta w_{11} = -\eta \frac{\partial \text{Error}}{\partial w_{11}} = \underbrace{(v - \text{target})}_{\text{error}} w_{v1} f'_h u_1$$

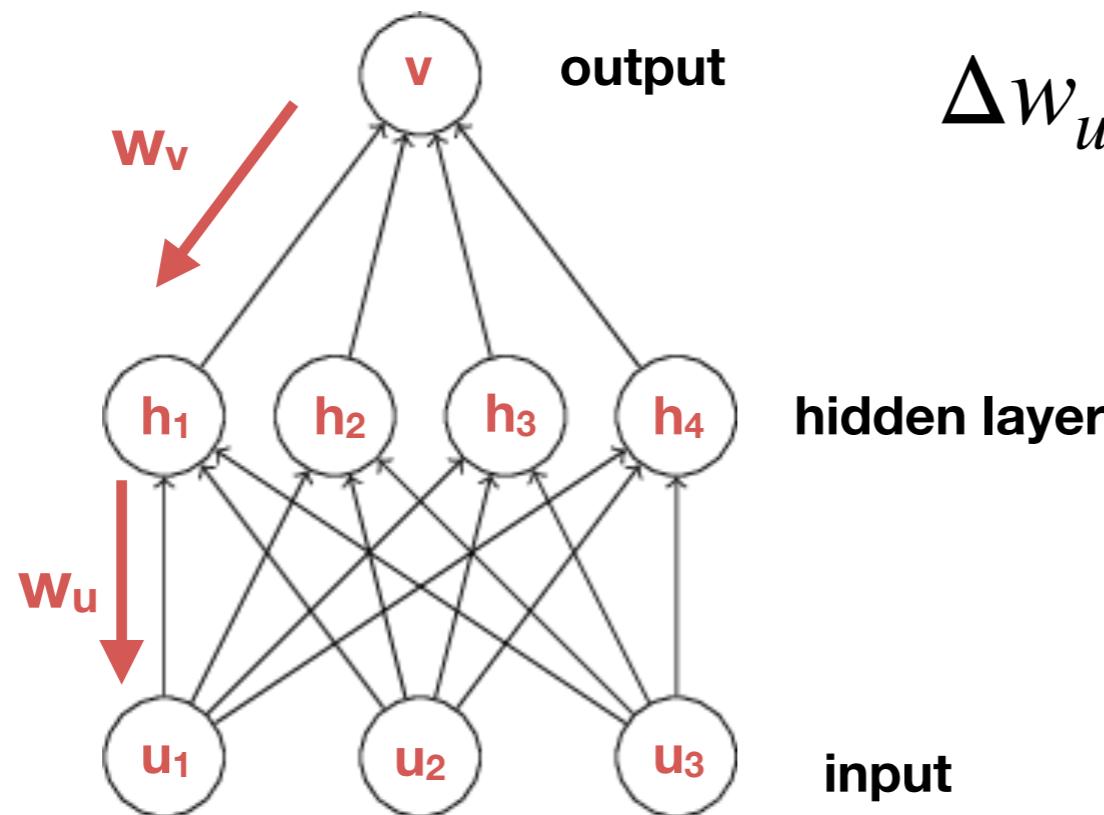
Rumelhart et al. 1986 PDP

The backpropagation algorithm general weight update

$$\text{error} = \frac{1}{2}(v - \text{target})^2$$

The general form for the weight update:

$$\Delta w_u = -\eta \underbrace{(v - \text{target})}_{\text{error}} w_v^T f'_h u$$

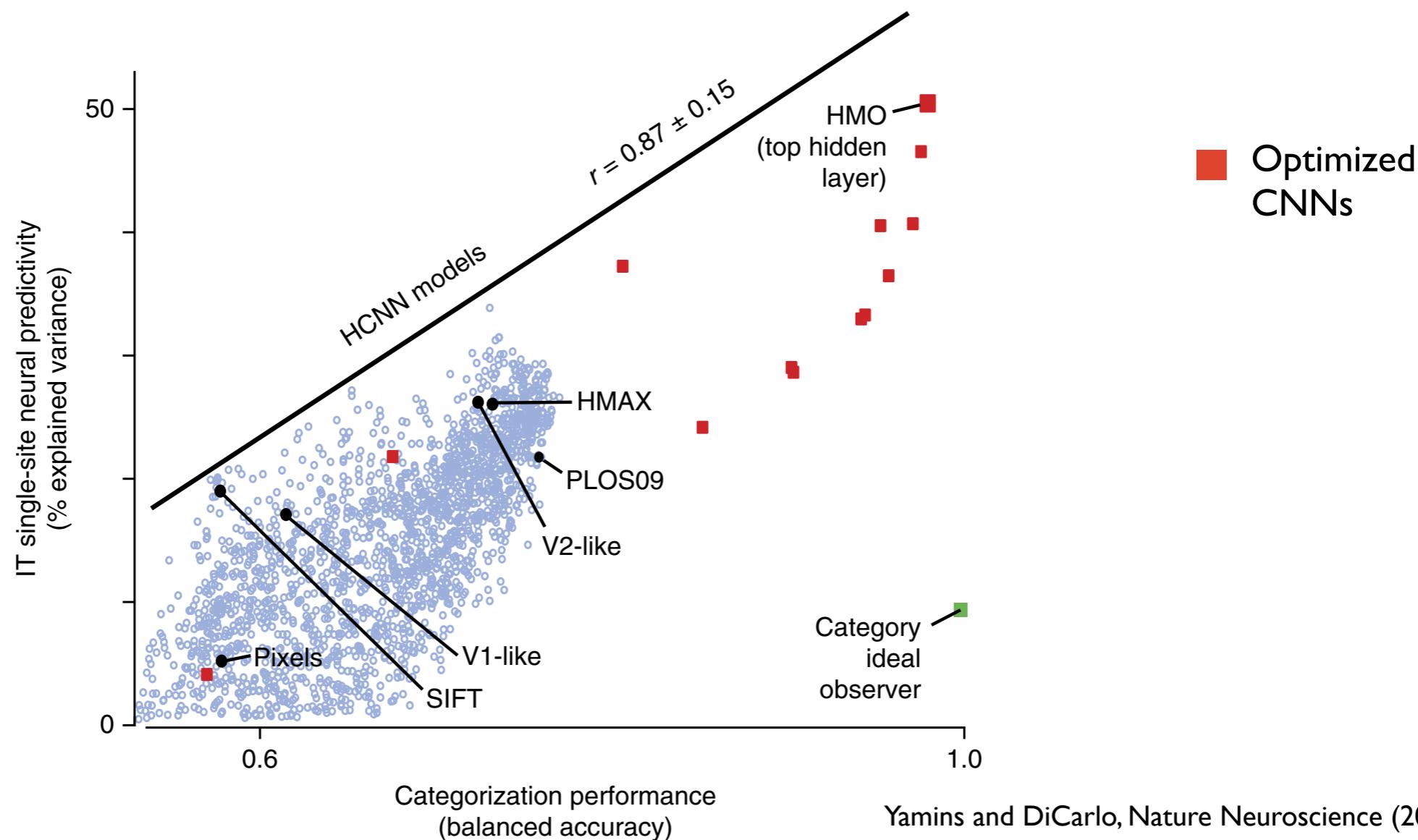


Note: Write down the gradient wrt a weight for practice!

Rumelhart et al. 1986 PDP

The backpropagation algorithm in the brain

Next lecture: Neural nets trained with backprop can predict neural data to a high degree!
So should we consider backprop as a potential mechanism for learning in the brain?



Backprop in the brain and why should we care?

This would provide for the **first time a good model of learning in the brain!**

Once we have done this mapping, we can then use the brain as **inspiration** for better/**more robust optimisation algorithms!**

The backpropagation algorithm is **NOT** = backpropagating action potential

In biology there is a phenomenon known as action potential backpropagation. This does **NOT** directly relate to the backpropagation algorithm!

Backpropagating action potential \neq Backpropagation algorithm

see Stuart et al. TiNS (1997) for more info

The backpropagation algorithm in the brain

However, at a first glance the backpropagation algorithm seems to not be biologically plausible.

Key issues:

1. **Weight transport problem**: Suggests that feedback weights = feedforward weights
2. **Derivative of activation functions**: Relies on calculating derivatives of the activation functions
3. **Two phase learning**: (1) feedforward propagation of activity and (2) error backpropagation
4. **Separate error network**: Suggest the need for a separate biological network computing the learning rules
5. **Non-local learning rules**: The weight update depends on non-local information
6. **Target**: The target label guides supervised learning

Useful references:

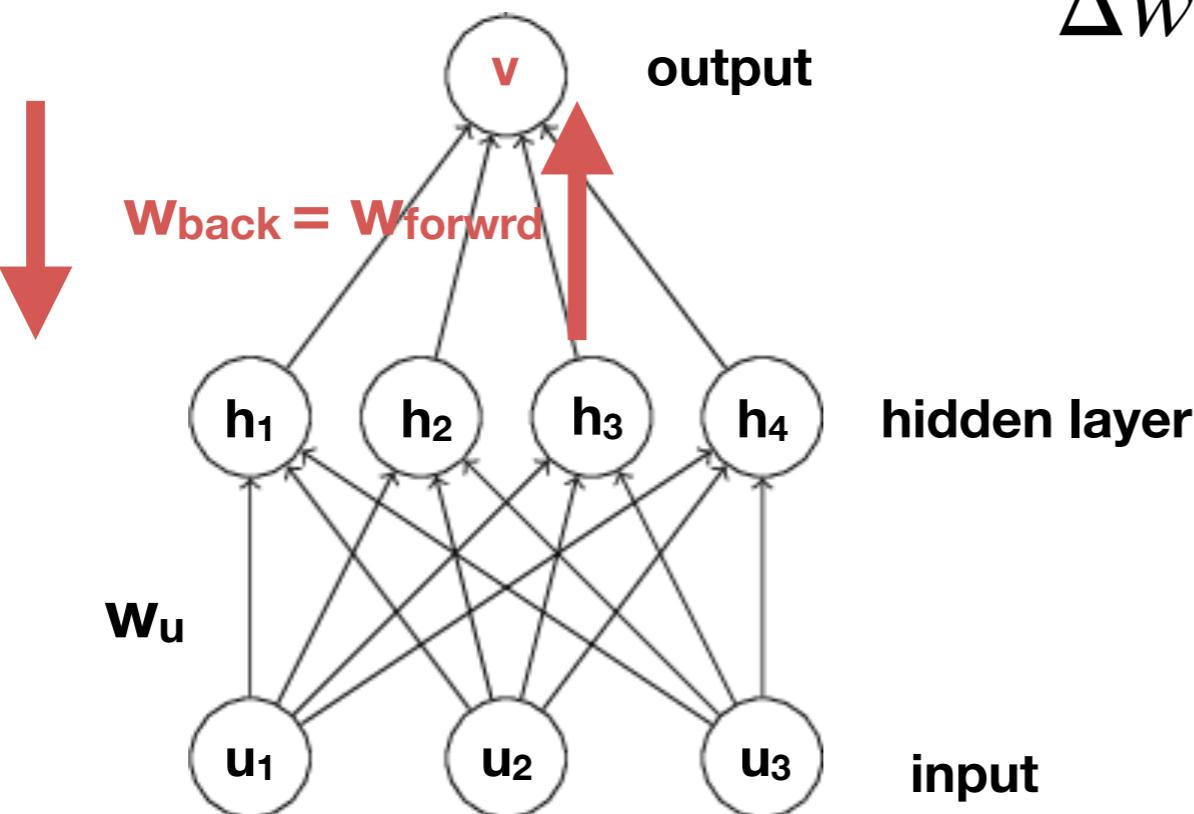
Roelfsema and Holtmaat, Nature Neuroscience Rev (2018)
Richards and Lillicrap, Current Opinion in Neurobiology (2019)

The backpropagation algorithm and why it is at odds with biology

I. Weight transport problem

Backprop: The chain rule predicts feedback weights that are equal to feedforward weights: $\mathbf{W}_v^T = \mathbf{W}_v$

Biology: No evidence that feedback connections exactly mirror feedforward ones.

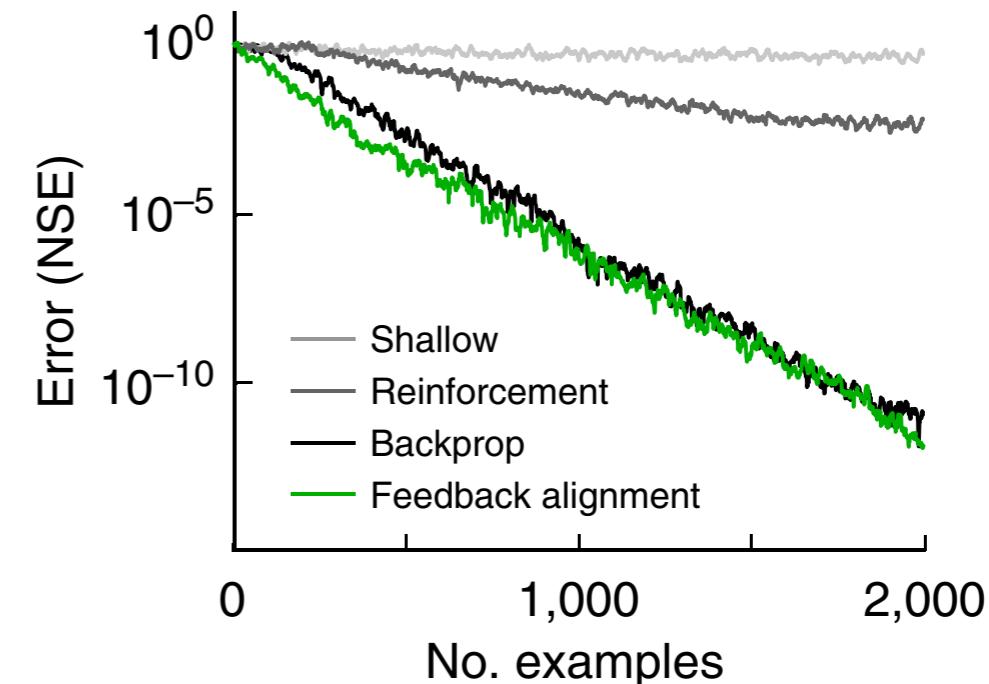
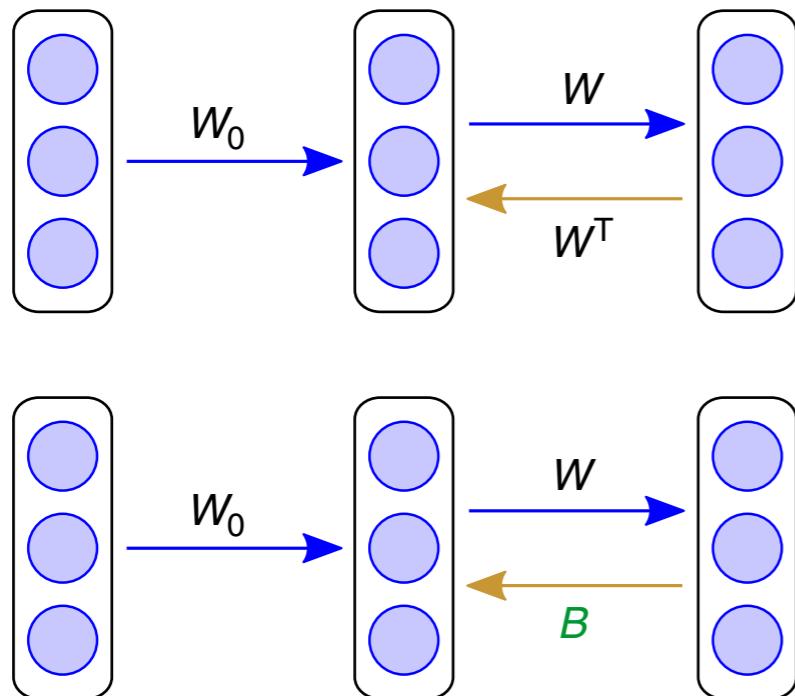


$$\Delta w_{uv} = -\eta \underbrace{(v - \text{target})}_{\text{error}} \underbrace{\mathbf{w}_v^T f'_h u}_{\begin{array}{l} \text{Backprop/Feedback weights} \\ = \\ \text{Feedforward weights} \end{array}}$$
$$v = \mathbf{W}_v h$$

The backpropagation algorithm and why it is at odds with biology

I. Weight transport problem

Solution: Unclear; but *Lillicrap et al.* found that exact feedback weights can be replaced by random weights, without a major impact on performance. This method is known as **feedback alignment**, and suggests that the brain may not need an exact feedback signal to implement ‘backprop’.



B is a random matrix, replacing W^T

Lillicrap et al., Nature Comms (2016)

The backpropagation algorithm and why it is at odds with biology

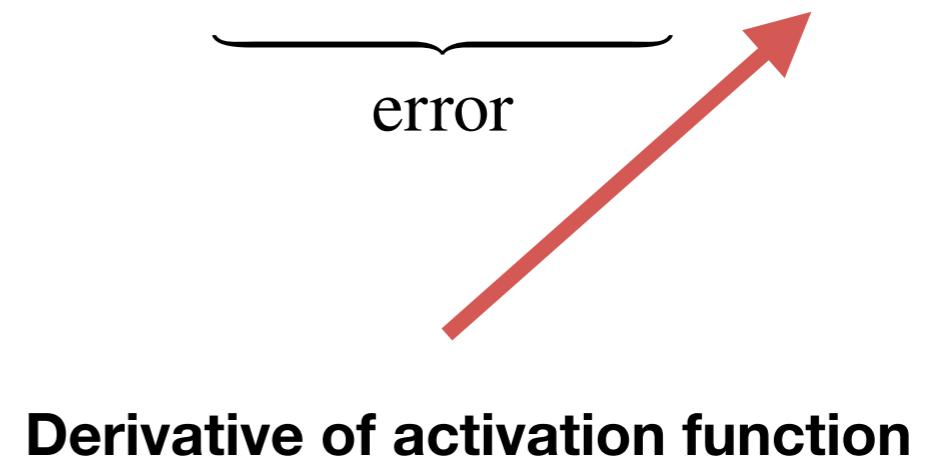
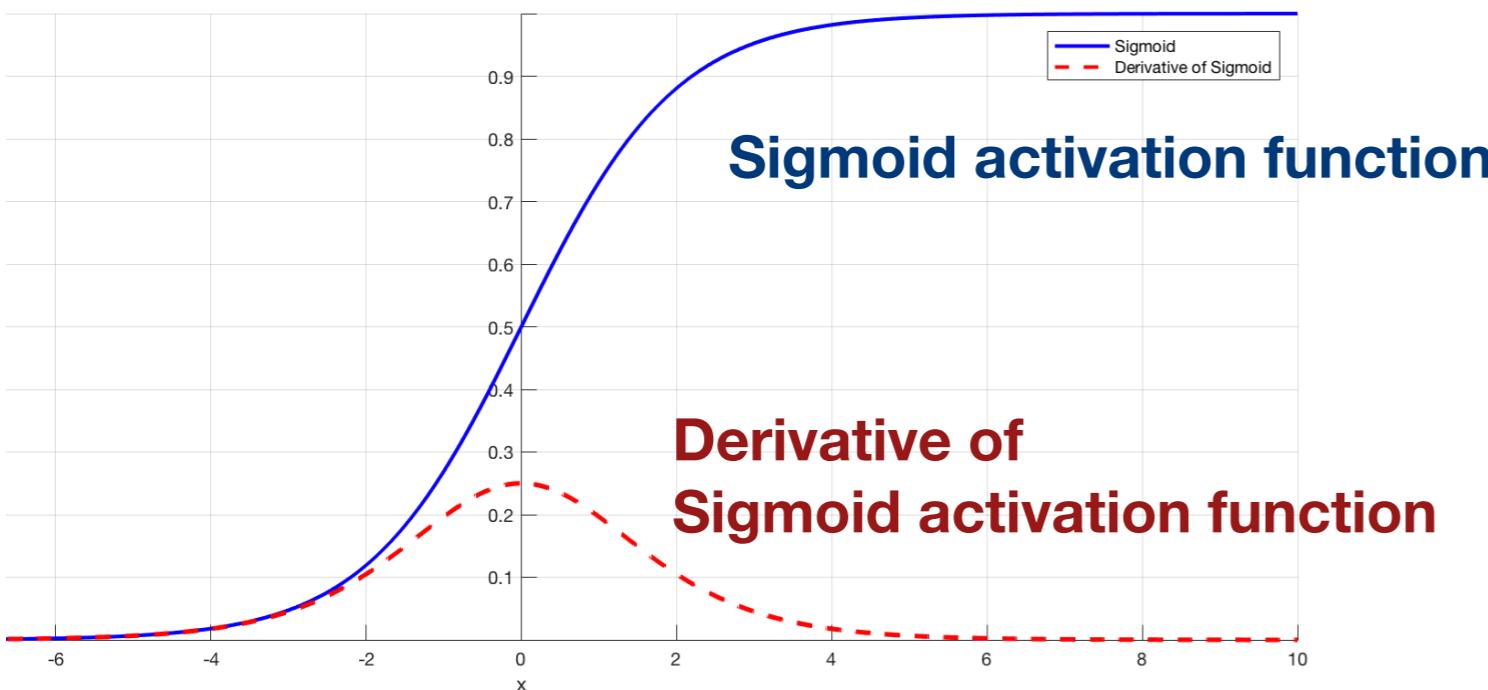
2. Derivative of activation function

Backprop: Relies on the derivative of the activation function.

Biology: Not clear how neurons could calculate their own derivative.

Solution: Unclear; but as long as it doesn't impact on the gradient direction this derivative is not critical for performance (similar to feedback alignment).

$$\Delta w_u = -\eta (v - \text{target}) w_v^T f'_h u$$



The backpropagation algorithm and why it is at odds with biology

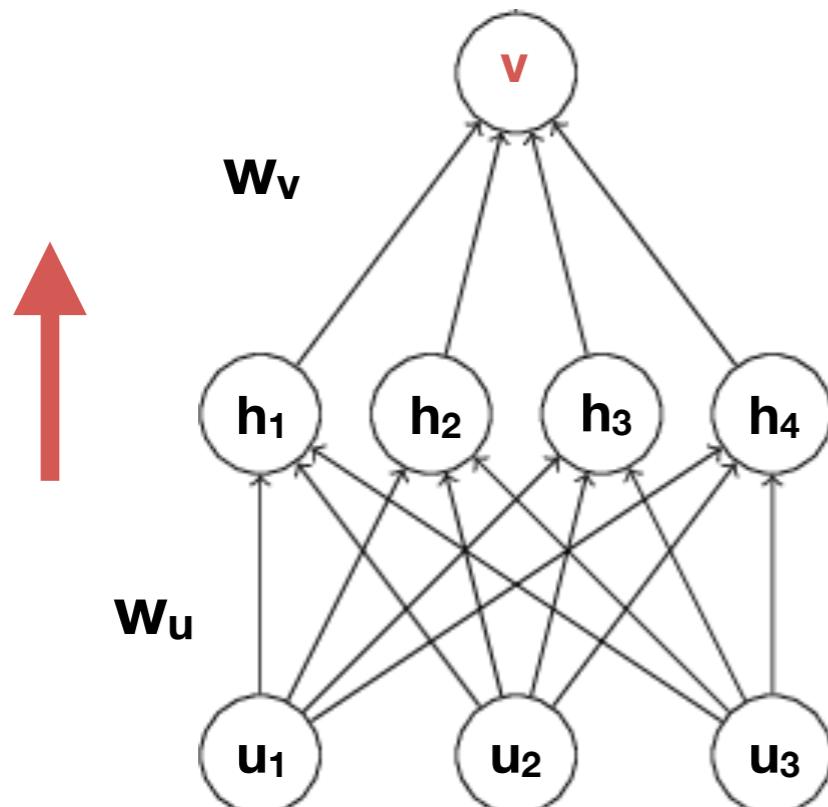
3. Two-phase learning

Backprop: The backprop relies on **two phases**, first a feedforward pass of the activity and then a backward pass of errors.

Biology: In the brain there is no clear separation between perception and learning.

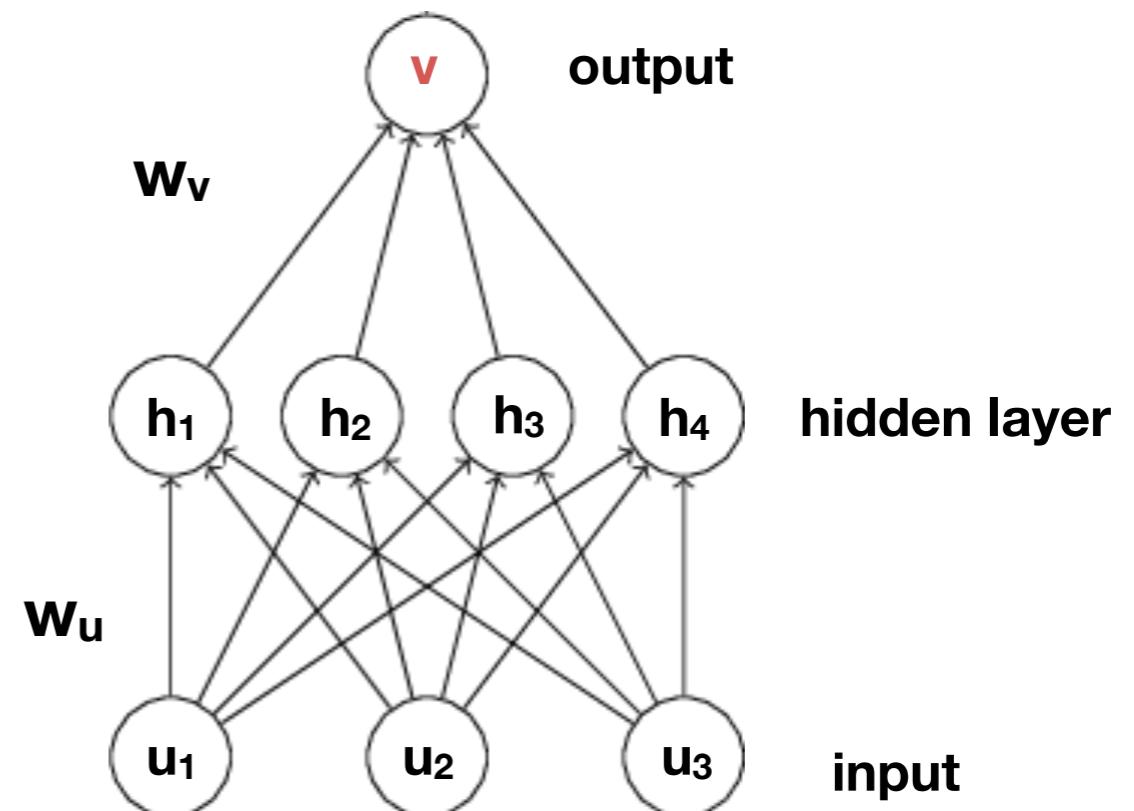
Forward phase

(perception/inference)



Backward phase (learning)

$$\text{error} = \frac{1}{2}(v - \text{target})^2$$



The backpropagation algorithm and why it is at odds with biology

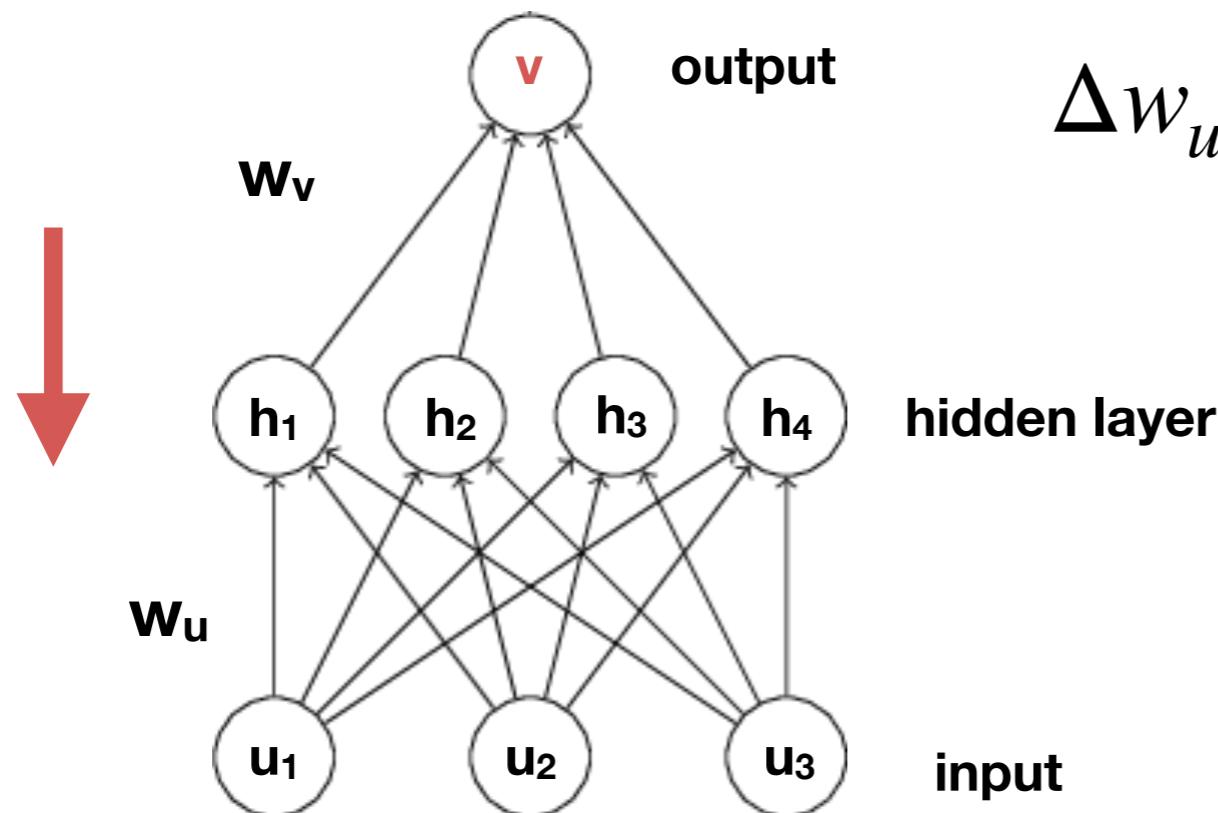
4. Separate error network

Backprop: The chain rule can be seen as a separate (error/gradients) network.

Biology: Minimal evidence for the existence of such gradient or error networks.

Backward phase ~ error network (EN)

$$\text{error} = \frac{1}{2}(v - \text{target})^2$$



$$\Delta w_u = -\eta \underbrace{(v - \text{target})}_{\text{error}} \overbrace{w_v^T f'_h u}^{\text{EN activation function}}$$

EN weights

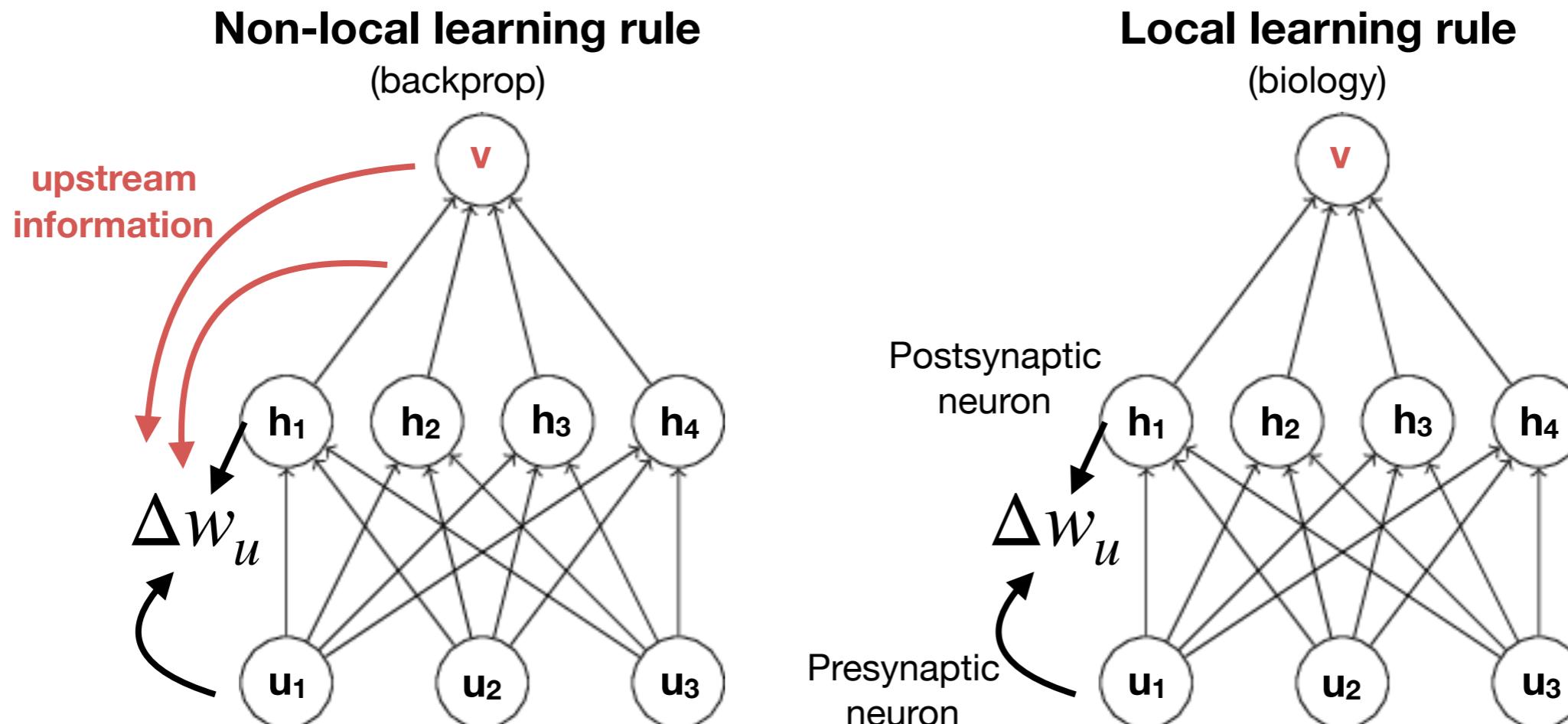
EN activation function

The backpropagation algorithm and why it is at odds with biology

5. Non-local learning rules

Backprop: Relies on non-local learning rules (i.e. a given neuron needs information about other neurons and layers).

Biology: Learning is believed to occur through local changes at synapses, a process known as synaptic plasticity which can only access locally available information (i.e. within the pre and postsynaptic neuron).



Quiz time!

**Please go to BB
and solve quiz 2.**

It should take you just a couple of minutes.

The backpropagation algorithm in the brain

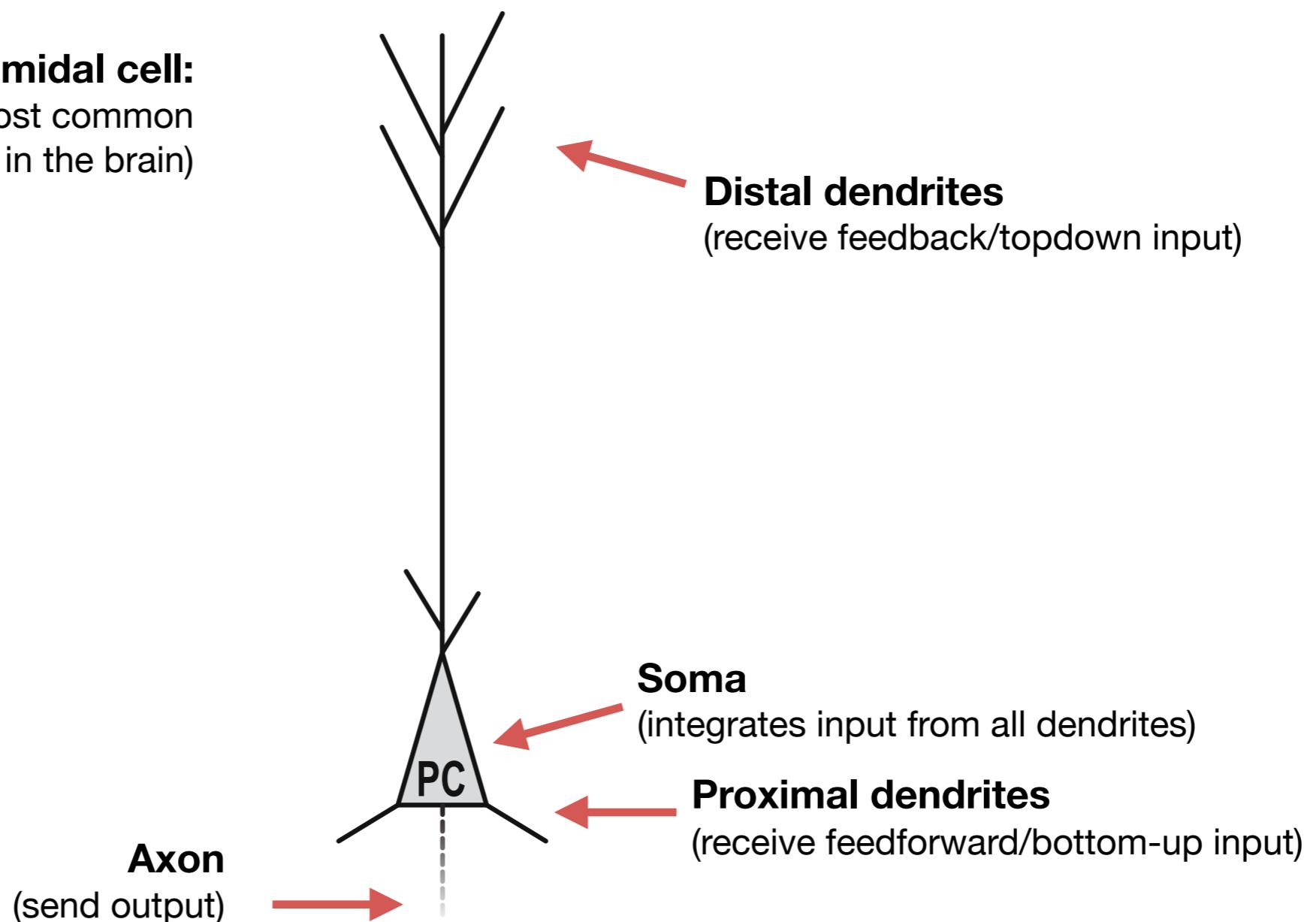
How to solve:

1. **Weight transport problem:** It proposes feedback weights equal to feedforward
2. **Derivative of activation functions:** Relies on calculating derivatives of the activation functions
3. **Two phase learning:** (1) feedforward propagation of activity and (2) error backpropagation
4. **Separate error network:** Suggest the need for a separate biological network computing the learning rules
5. **Non-local learning rules:** The weight update depends on non-local information
6. **Target:** The target label guides supervised learning

The backpropagation algorithm in the brain

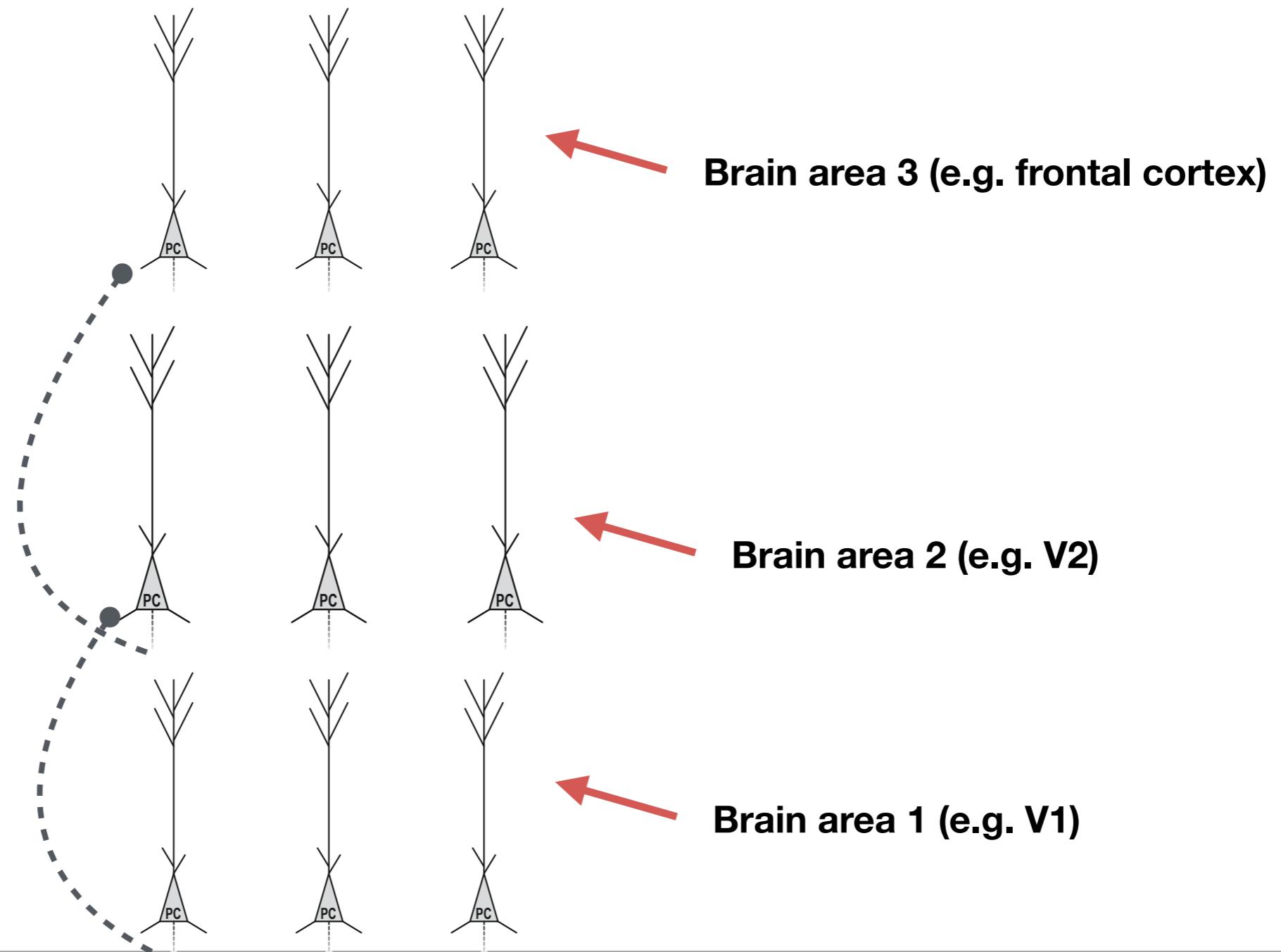
Inspiration from real neurons: pyramidal cells

Pyramidal cell:
(one of the most common
neurons in the brain)

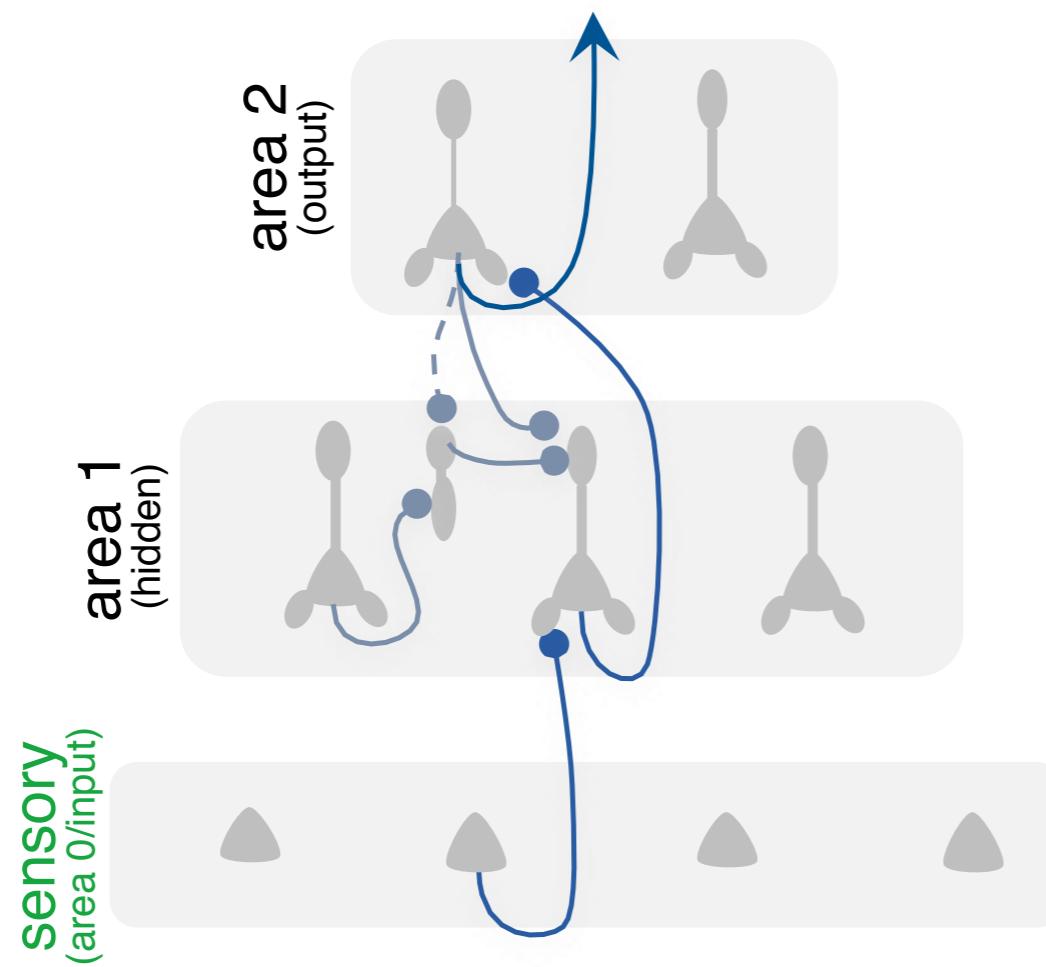


The backpropagation algorithm in the brain

Inspiration from real neurons: pyramidal cells

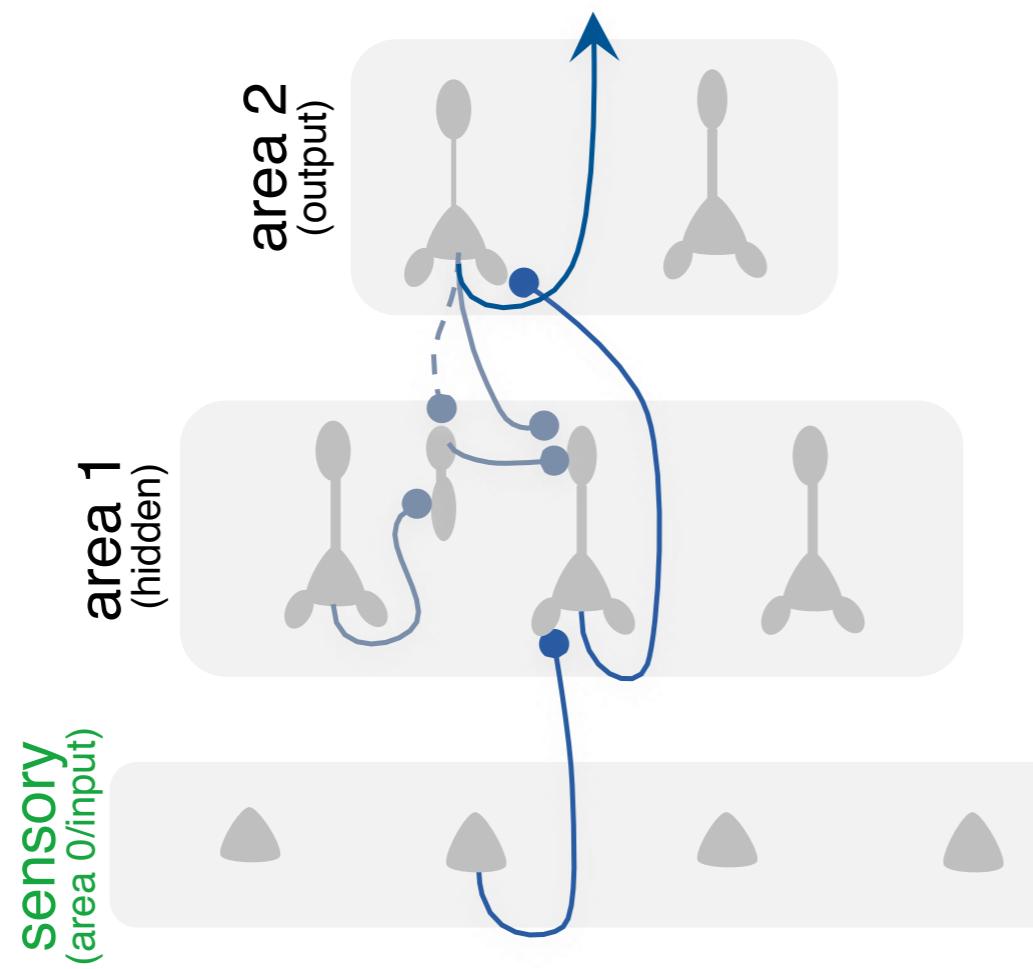


Dendritic microcircuits approximate backprop



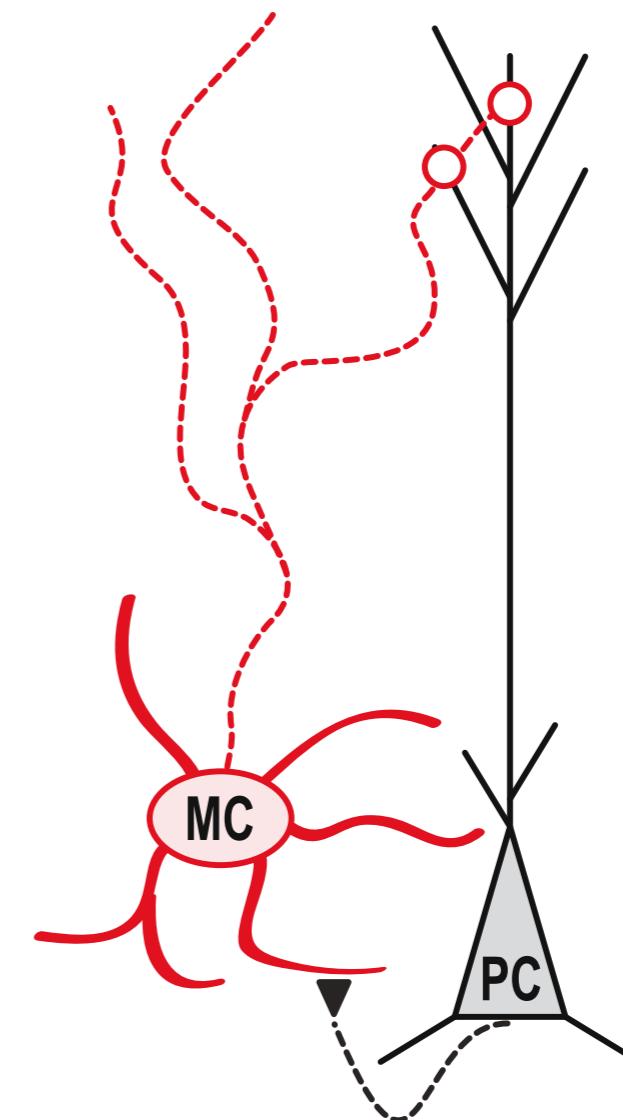
Sacramento et al. 2018 (NIPS)

Dendritic microcircuits approximate backprop



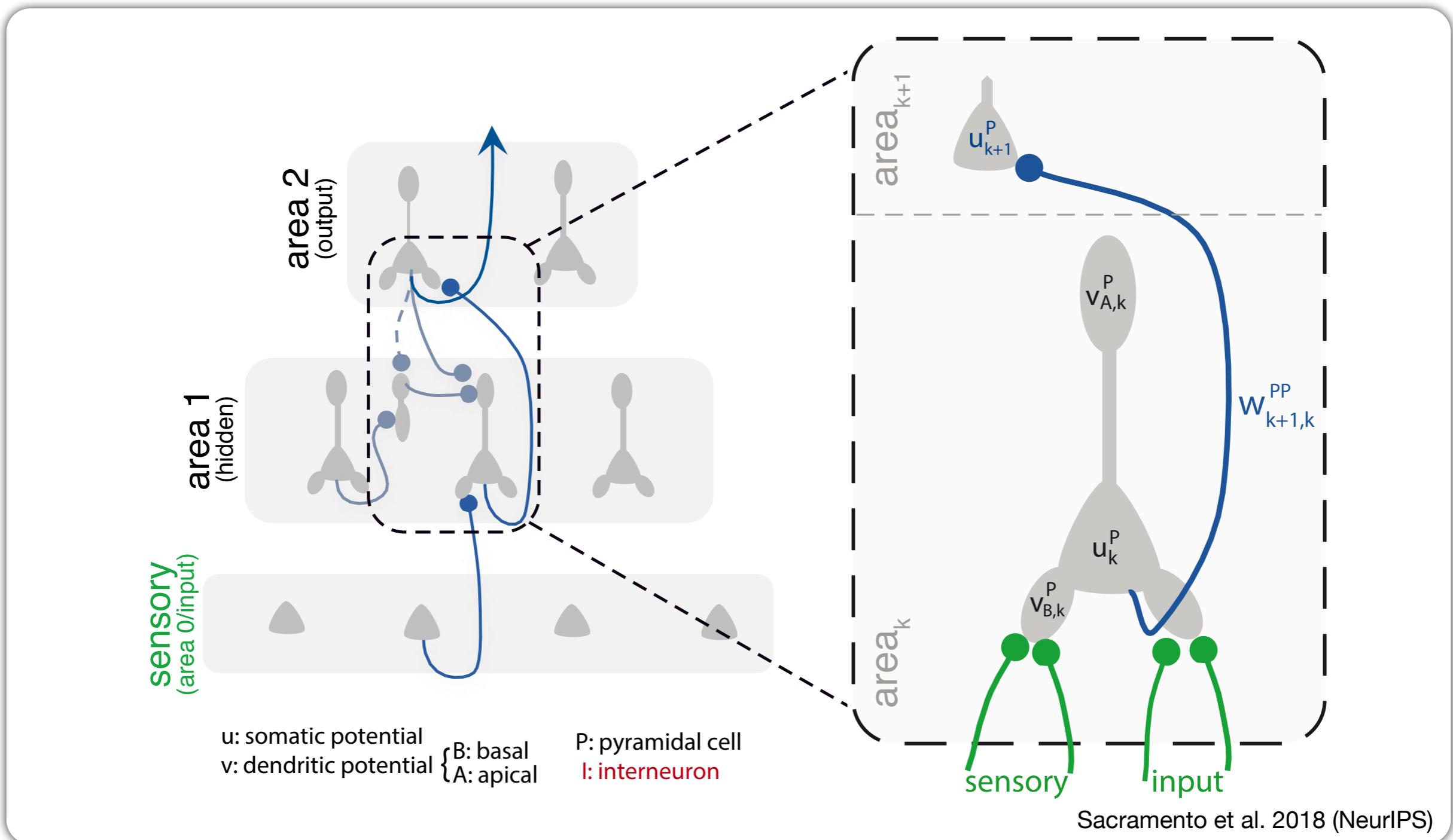
Inspired by two key cell types in the cortex:

- **Pyramidal cells** (excitatory cell)
- **Martinotti cells** (inhibitory cell)

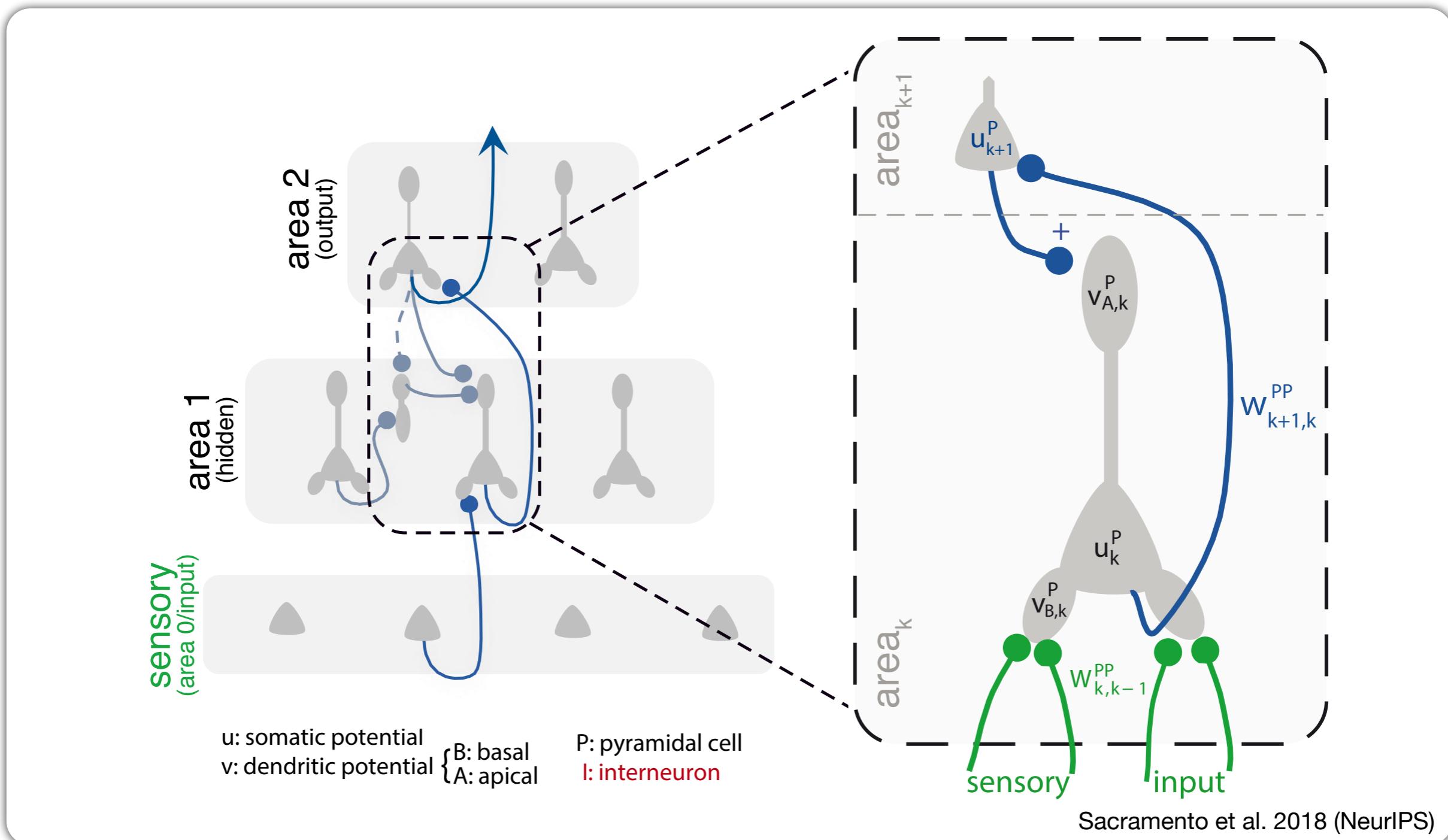


Sacramento et al. 2018 (NeurIPS)

Dendritic microcircuits approximate backprop

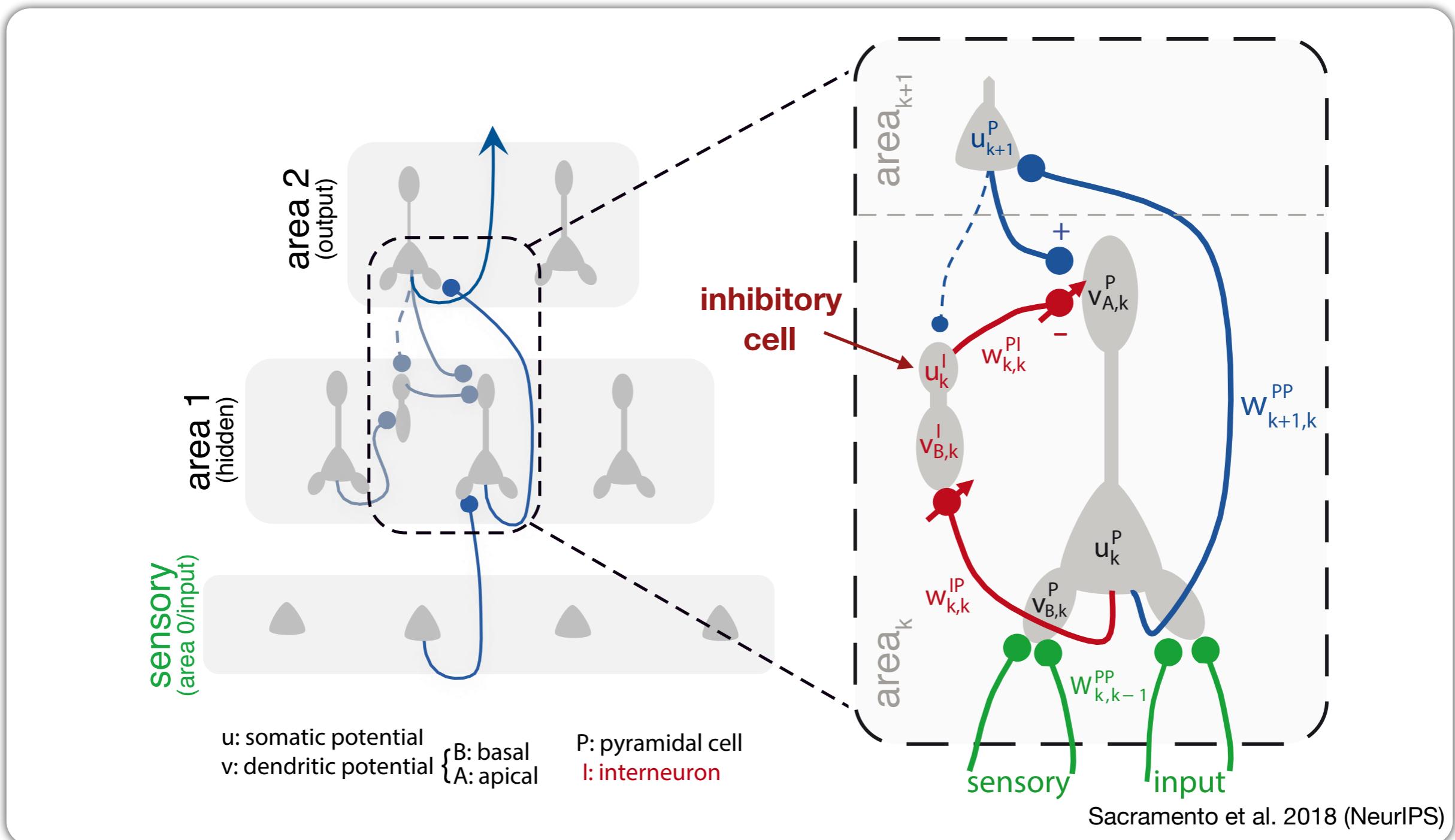


Dendritic microcircuits approximate backprop



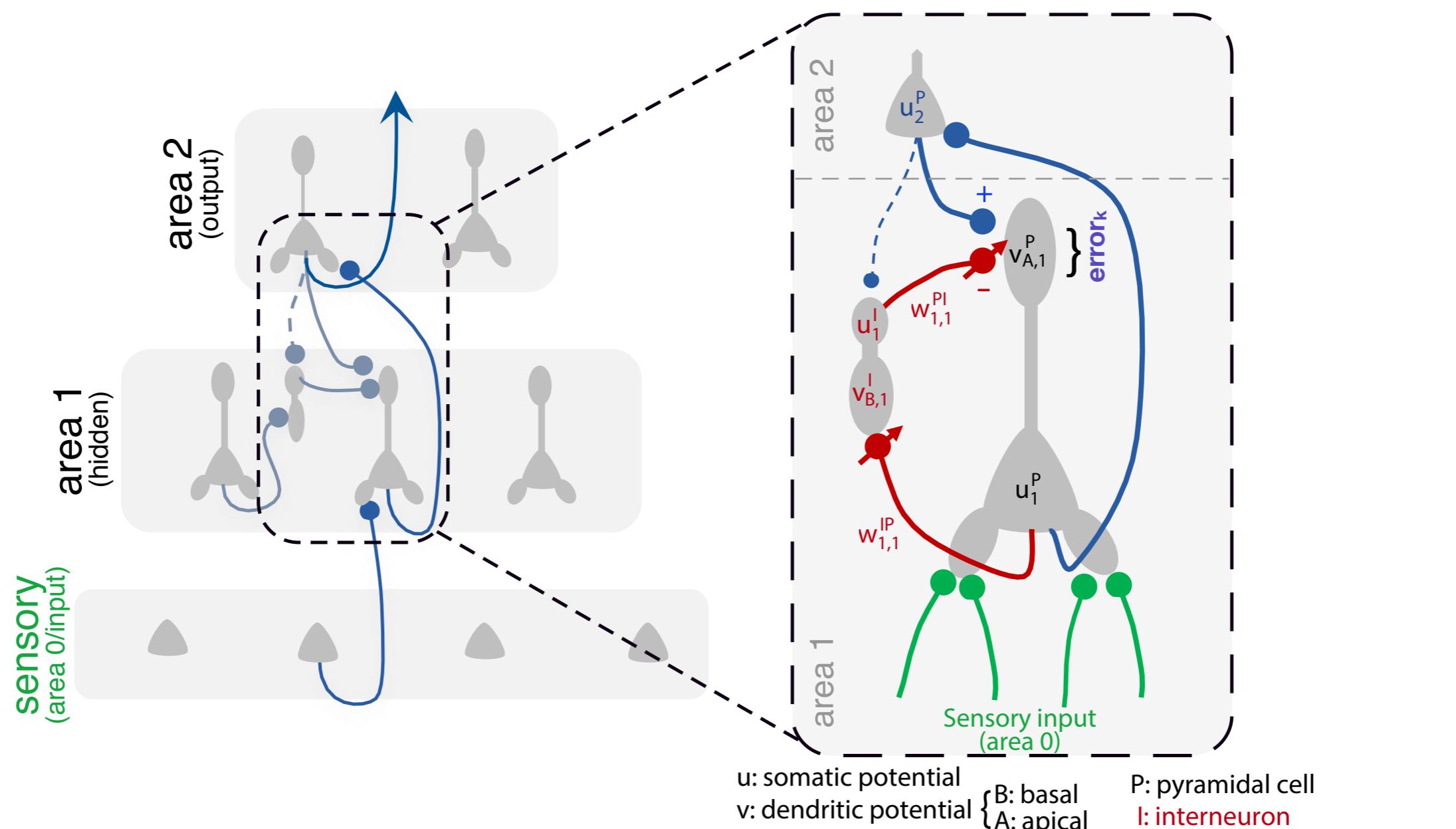
Sacramento et al. 2018 (NeurIPS)

Dendritic microcircuits approximate backprop



Sacramento et al. 2018 (NeurIPS)

Dendritic microcircuits approximate backprop

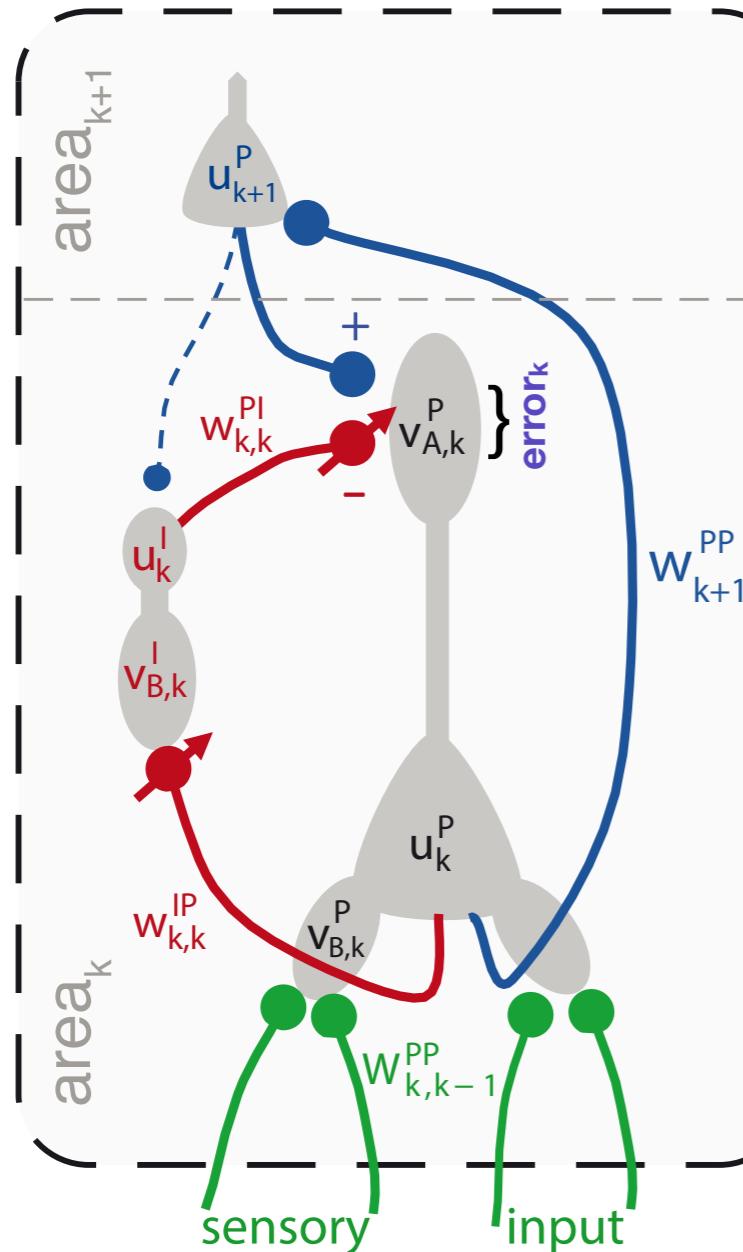


Sacramento et al. 2018 (NeurIPS)

Dendritic error microcircuits

local error-correcting learning rules

Important note: For this model u and v have a different meaning from before!



General idea:

1. Difference between topdown activity from u_{k+1}^P and lateral inhibition u_k^I generates an **error** signal:

$$v_{A,k}^P \sim u_{k+1}^P - u_k^I$$

The **error** signal triggers changes in bottom weights:

$$w_{k,k-1}^{PP}$$

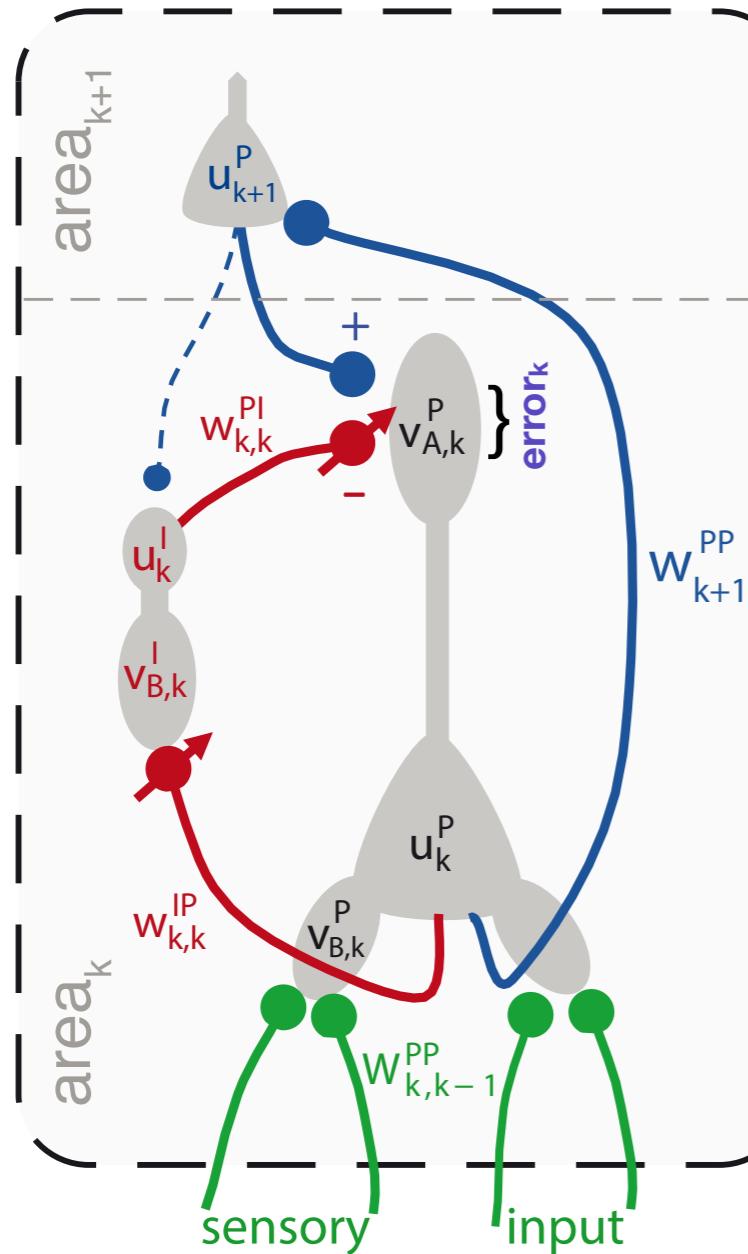
2. The model learns recursively across areas/layers (as in backprop) to correctly predict an output.

During this process lateral inhibition learns to predict the top-down input, leading to a zero error after learning, i.e.:

$$u_k^I \sim u_{k+1}^P$$

Dendritic error microcircuits local error-correcting learning rules

Important note: For this model u and v have a different meaning from before!

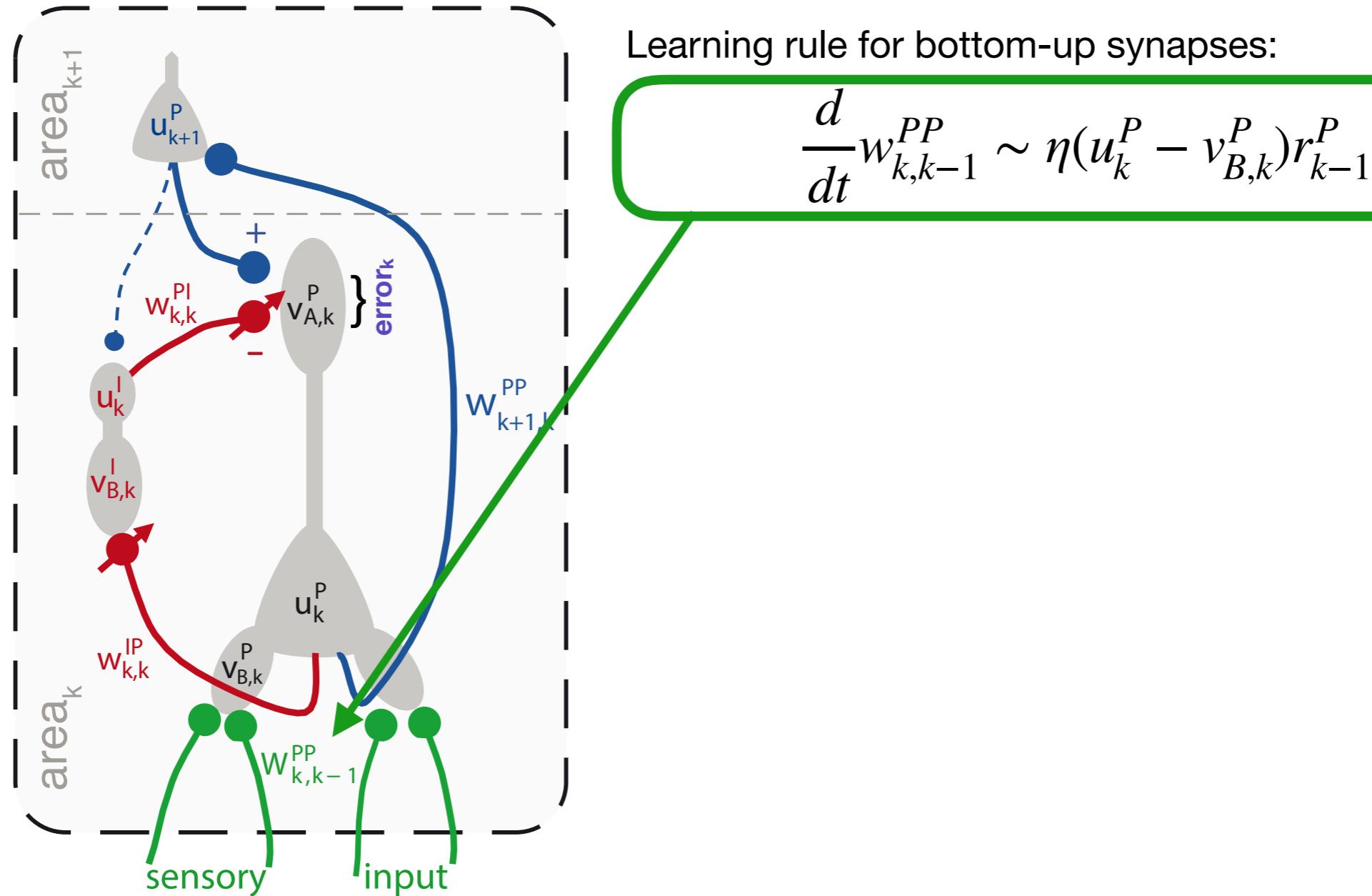


General form of the (local) learning rule:

$$\frac{d}{dt}w \sim \eta(u - v)r$$

Dendritic error microcircuits local error-correcting learning rules

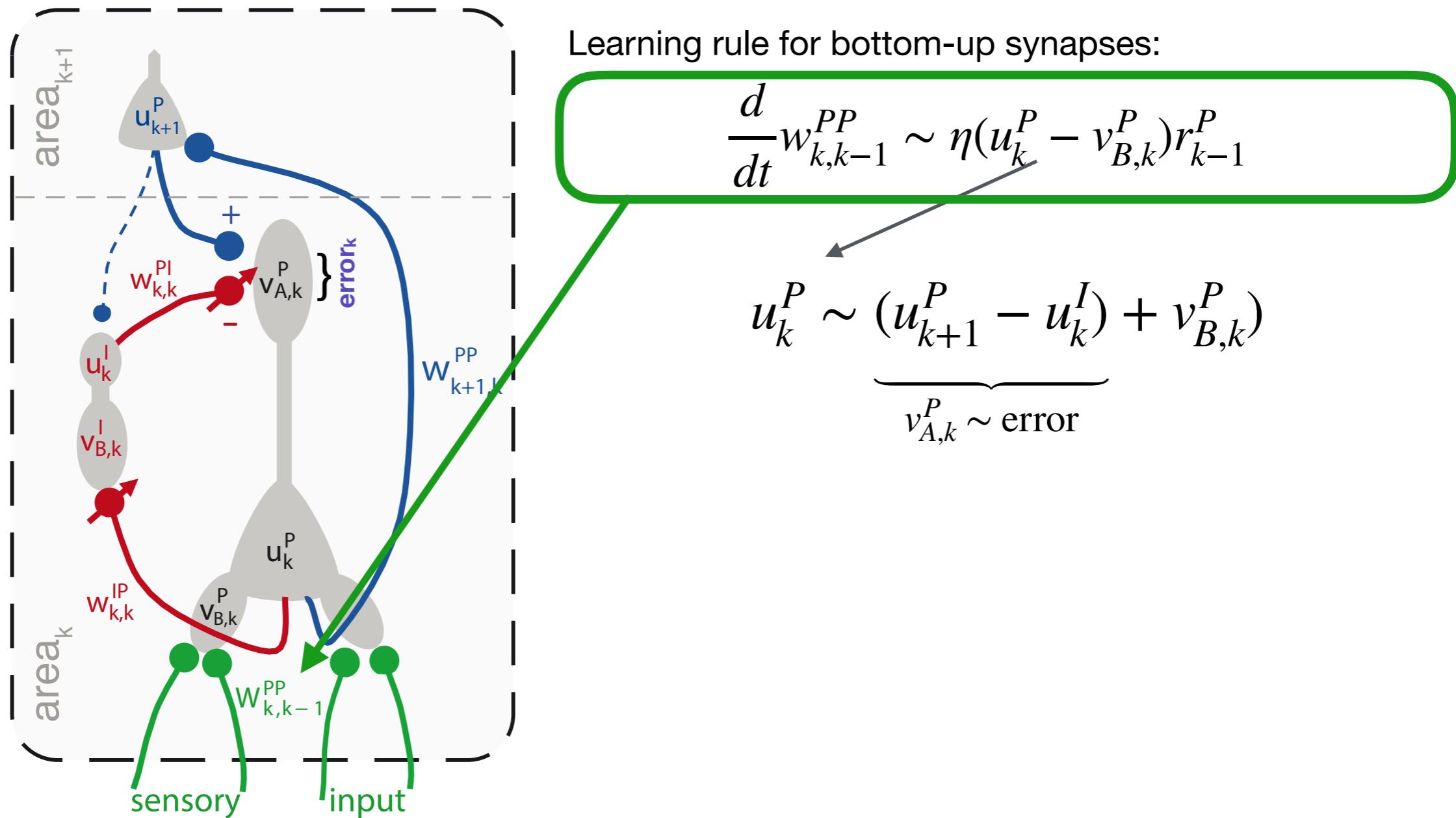
Important note: For this model u and v have a different meaning from before!



Sacramento et al. 2018 (NeurIPS)

Dendritic error microcircuits

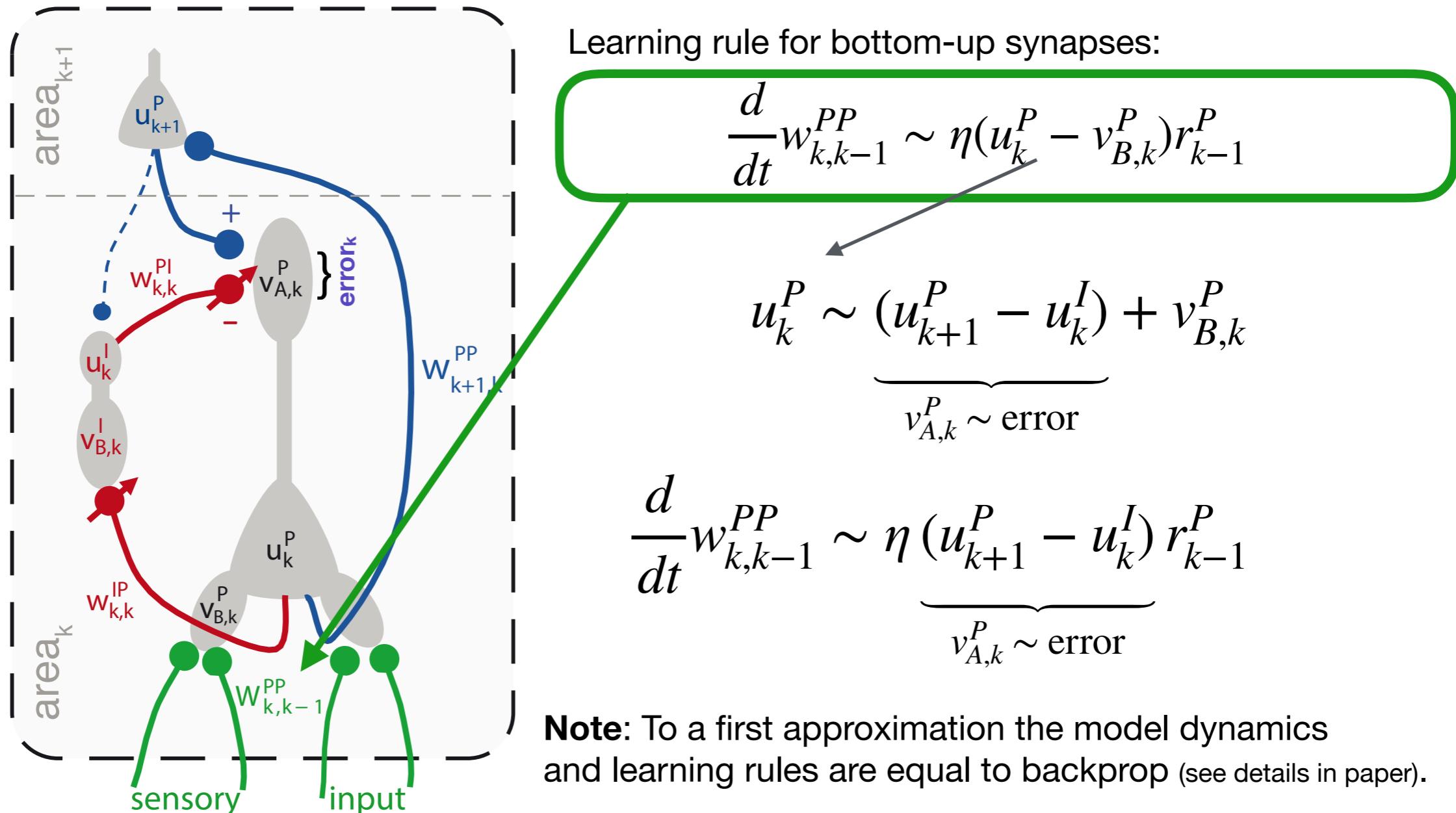
local error-correcting learning rules



Sacramento et al. 2018 (NeurIPS)

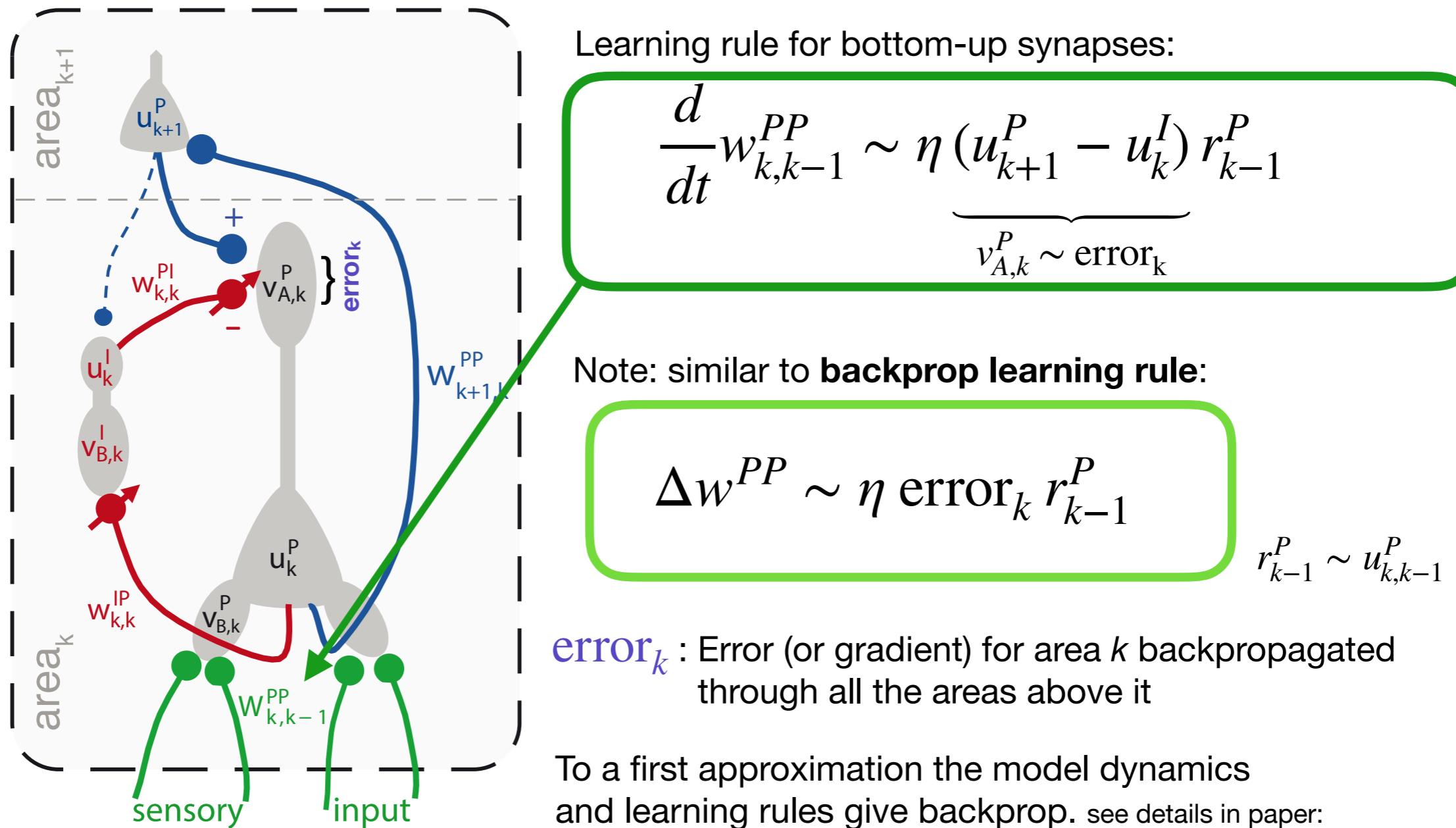
Dendritic error microcircuits

local error-correcting learning rules

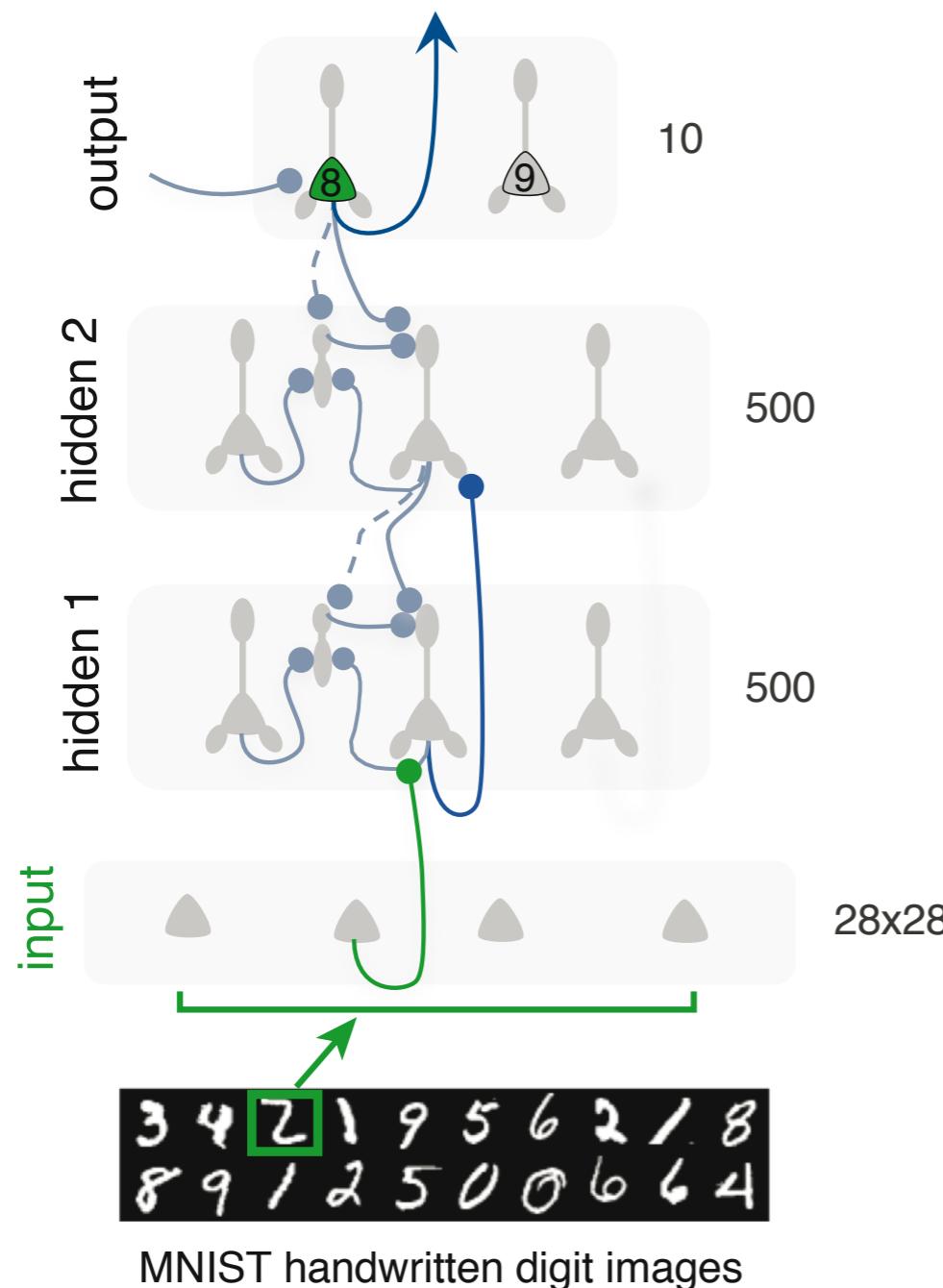


Dendritic error microcircuits

local error-correcting learning rules



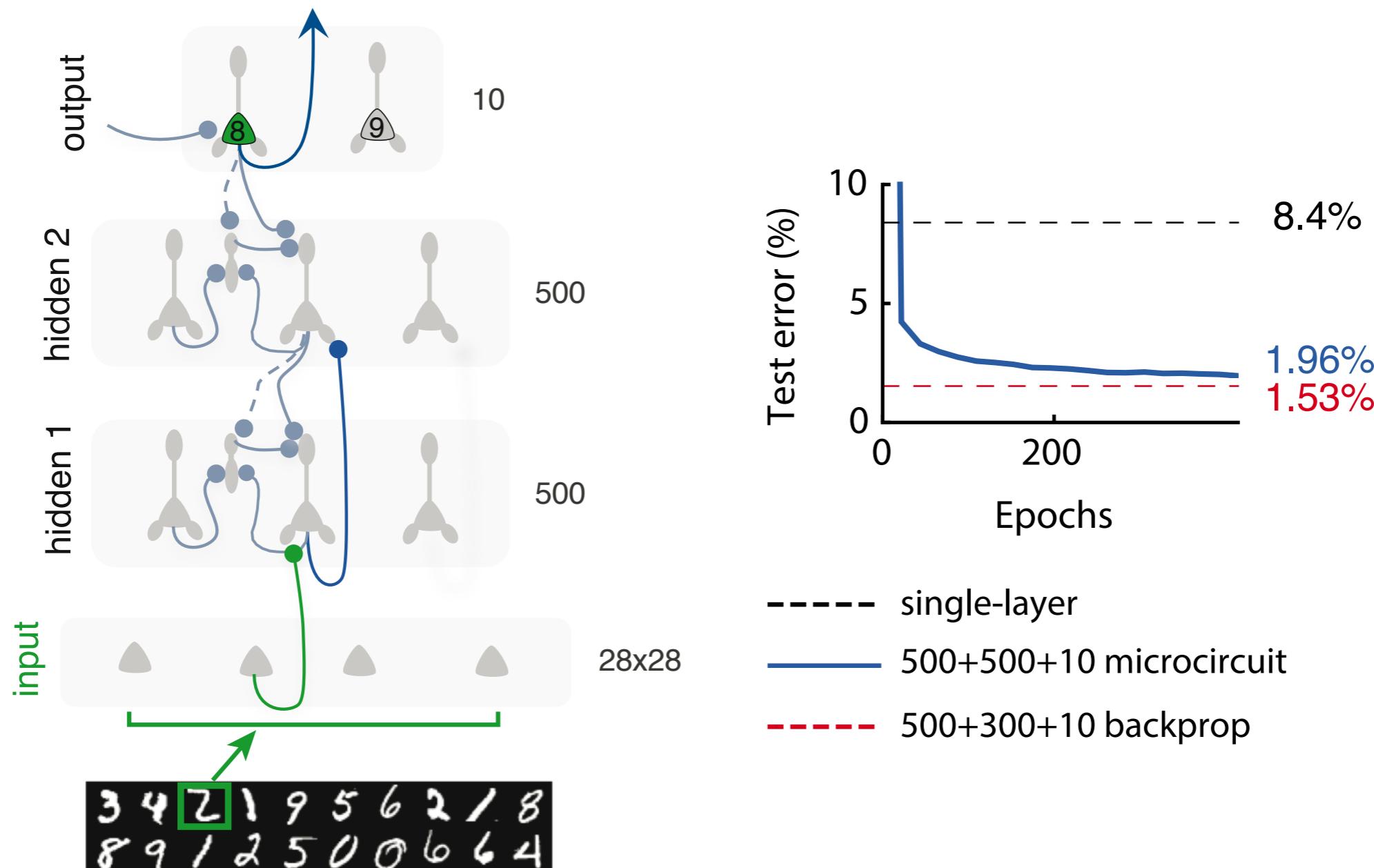
Dendritic error microcircuits learn to classify hand-written digits



MNIST handwritten digit images

Sacramento et al. 2018 (NeurIPS)

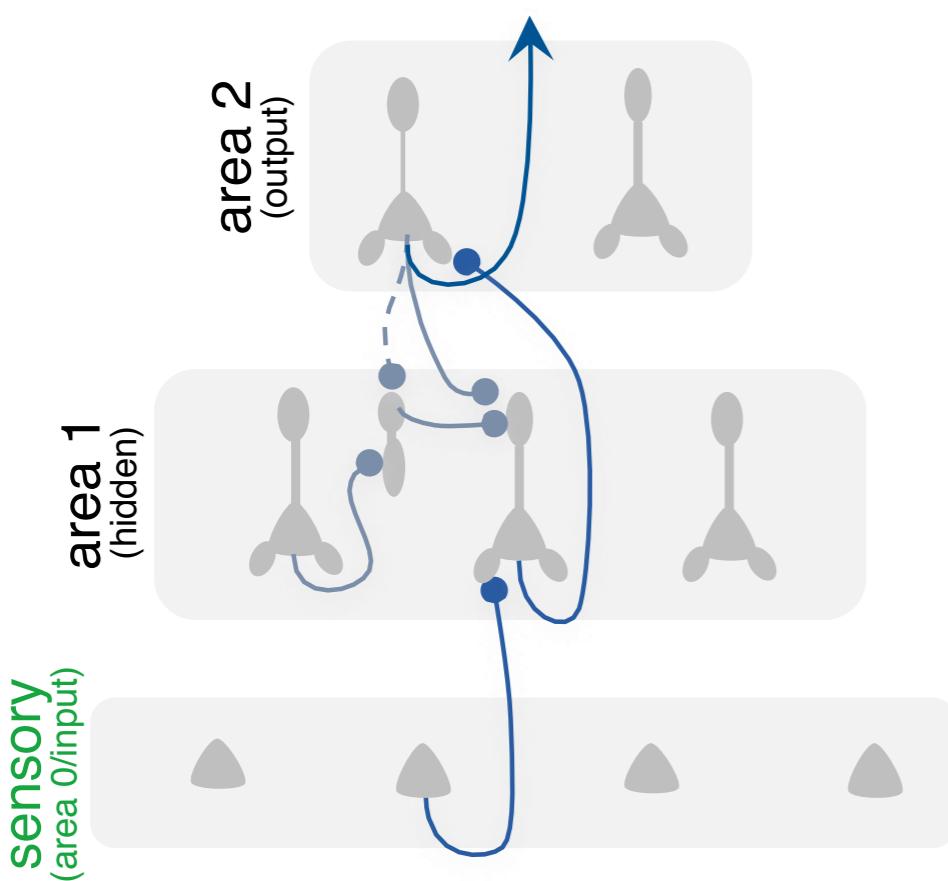
Dendritic error microcircuits learn to classify hand-written digits



MNIST handwritten digit images

Sacramento et al. 2018 (NeurIPS)

Dendritic error microcircuits approximate backprop



Sacramento et al. 2018 (NeurIPS)

**By being closer to biology neural networks
'solve' three key problems:**

3. **Two phase learning:** No need for two separate phases
4. **Separate error network:** Neuron encodes both activity and errors
5. **Non-local learning rules:** Learning rules are local

see also Guergiev et al. eLife 2017

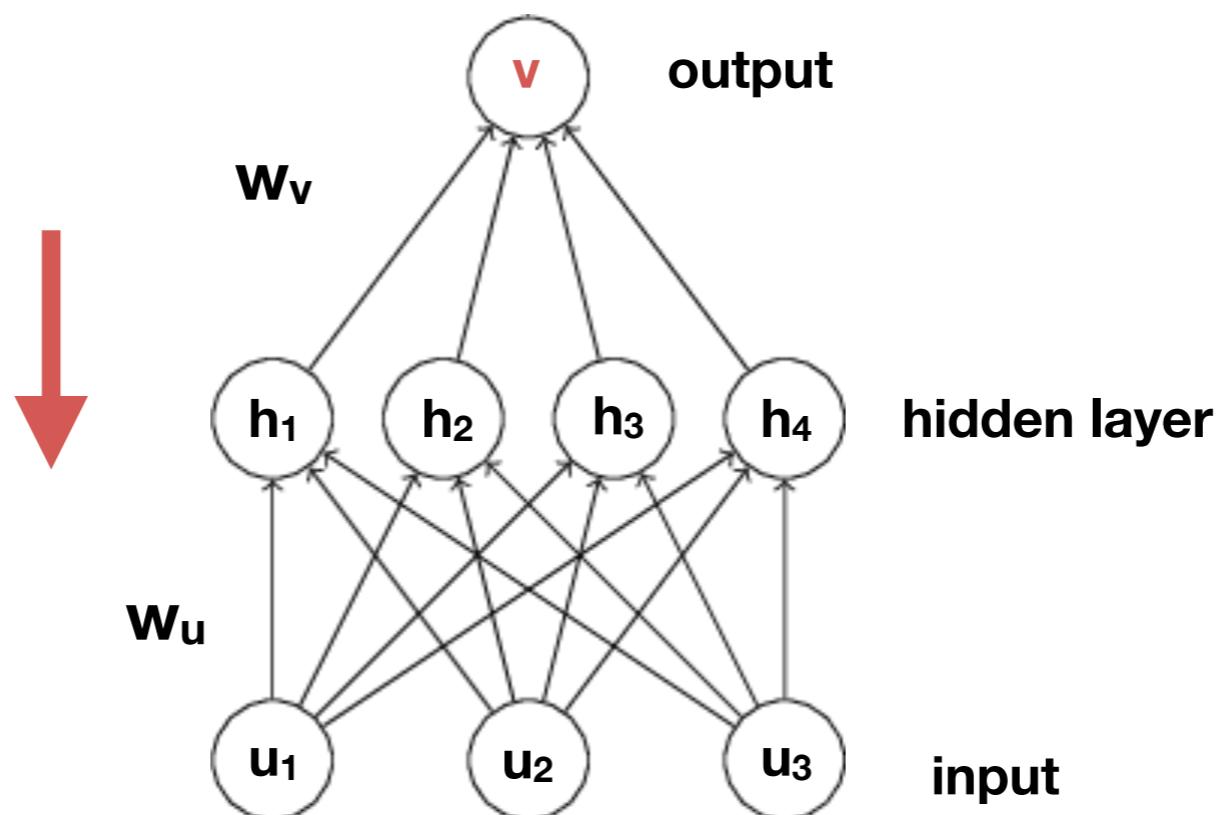
The backpropagation algorithm and why it is at odds with biology

6. Target

Backprop: Supervised learning needs a specific target (teaching signal).

Biology: It is far from clear how such target signals could be generated.

$$\text{error} = \frac{1}{2}(v - \text{target})^2$$



The backpropagation algorithm and why it is at odds with biology

6.Target

Solution 1: Backprop also works in the context of unsupervised (e.g. autoencoders) and reinforcement learning (e.g. deep Q-learning). We are going to cover some of this in the coming lectures.

Solution 2: Specific brain areas (e.g. cerebellum) may be calculating teaching signals, which are then used for internal supervised learning at other brain areas (see end of this lecture).

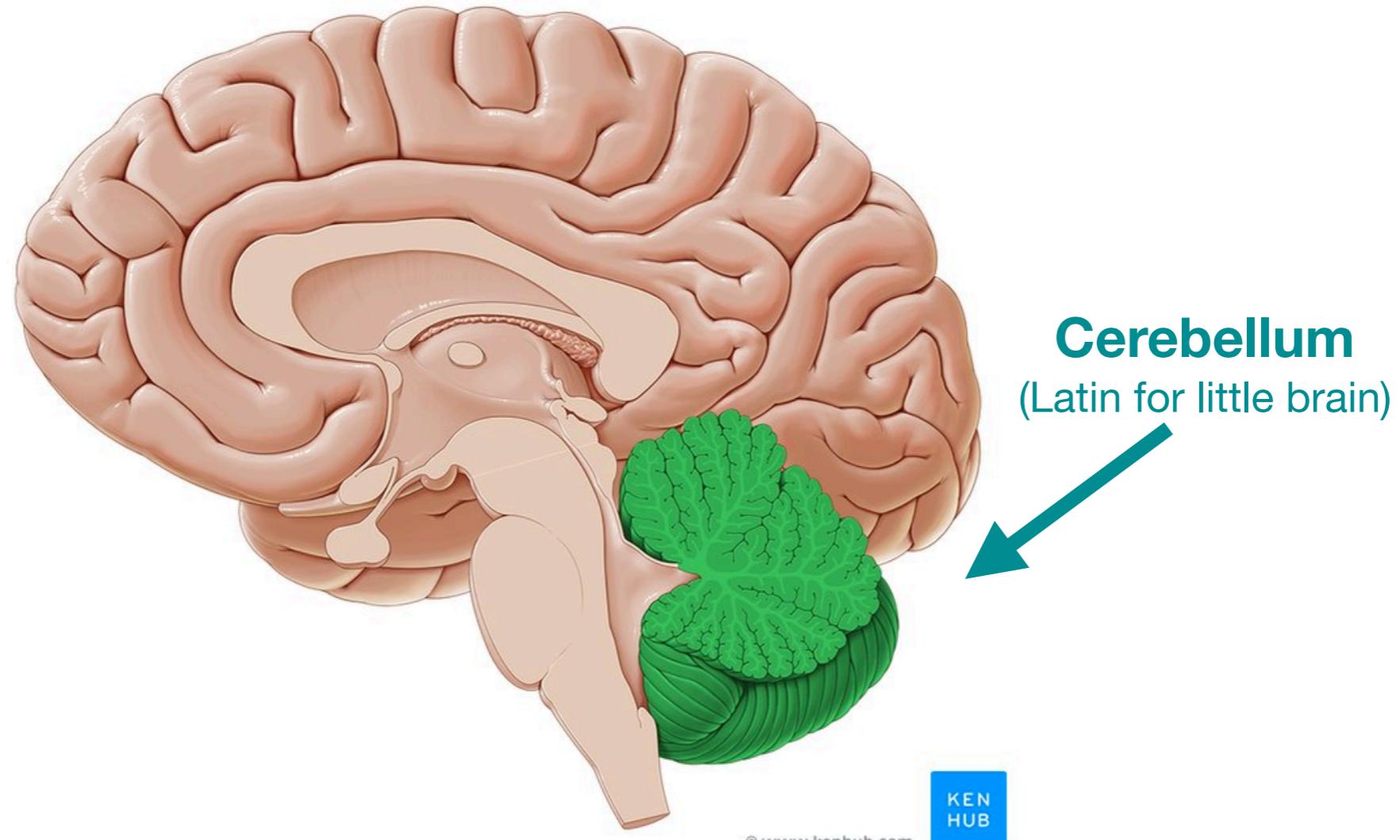
Quiz time!

**Does this make you reconsider your answers in quiz 2?
If so try it again.**

Note, however, that is no *correct* order.

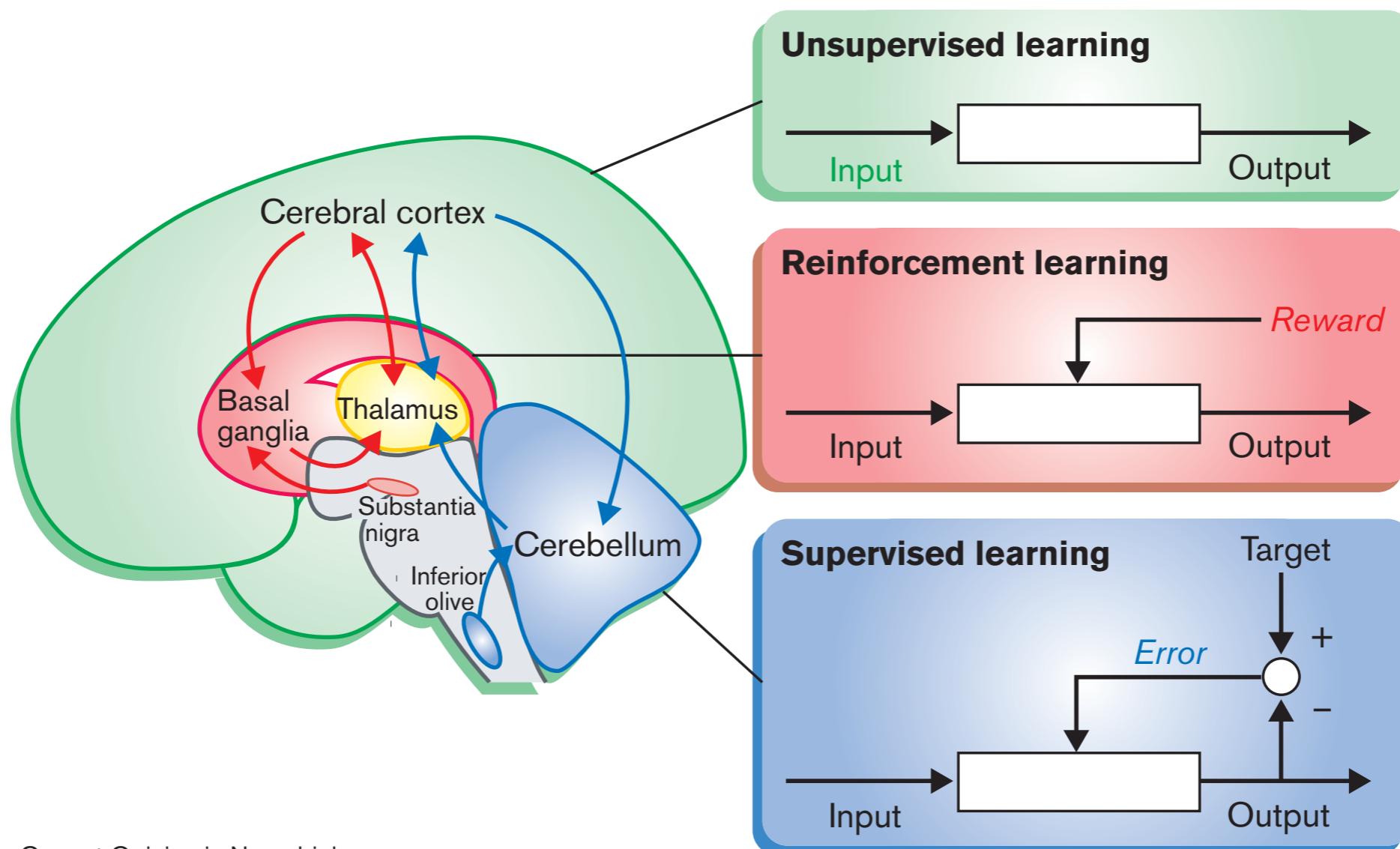
Supervised learning in the Cerebellum

The **cerebellum** (small brain in Latin) has a stereotypical structure, and contains more neurons than the rest of the brain! It is classically involved in motor error correction, but growing evidence suggests to be also involved in regulating many other aspects of behaviour.



Supervised learning in the Cerebellum

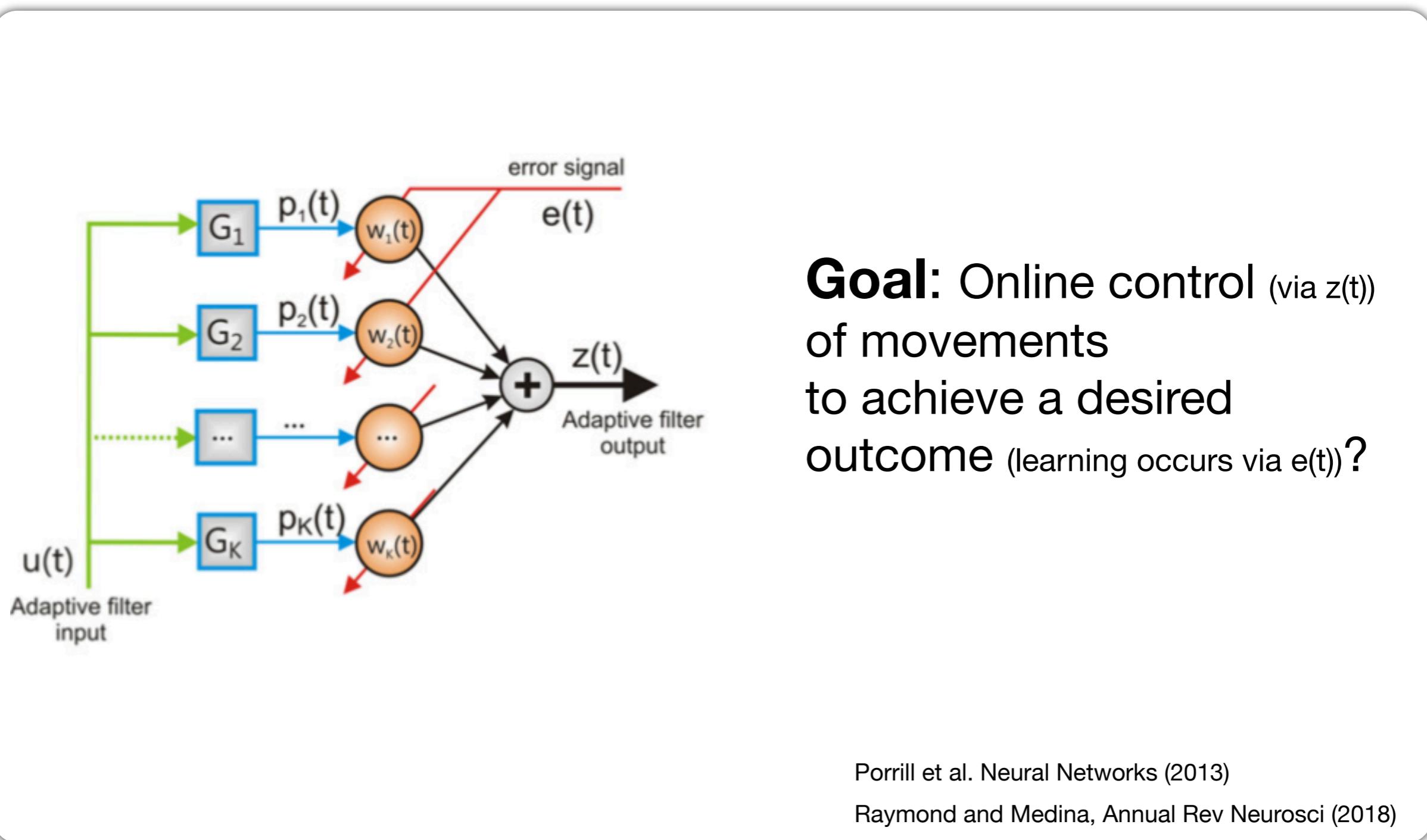
The **cerebellum** itself seems to use a form of supervised learning, but may also provide teaching signals to the cerebral cortex.



Current Opinion in Neurobiology

Doya, Curr Opin Neurobiol (2000)

Cerebellum as a adaptive filter/controller

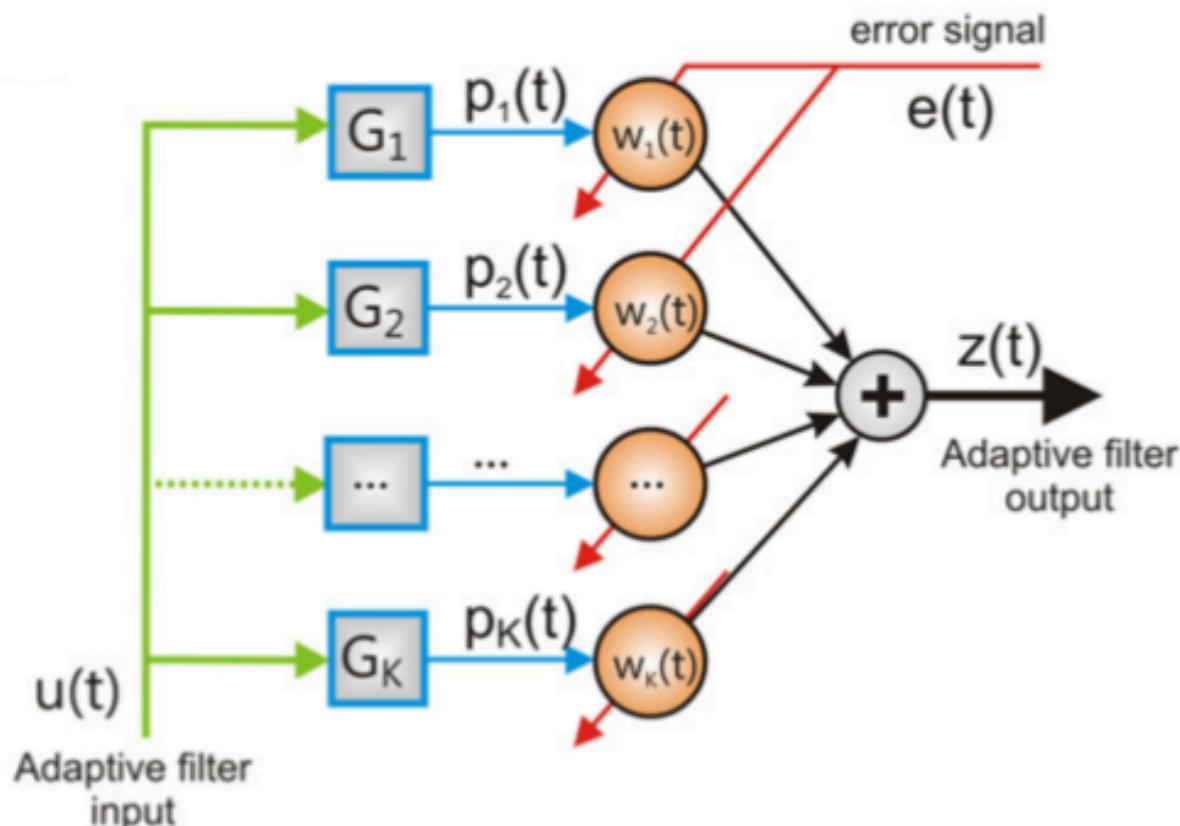


Porrill et al. Neural Networks (2013)

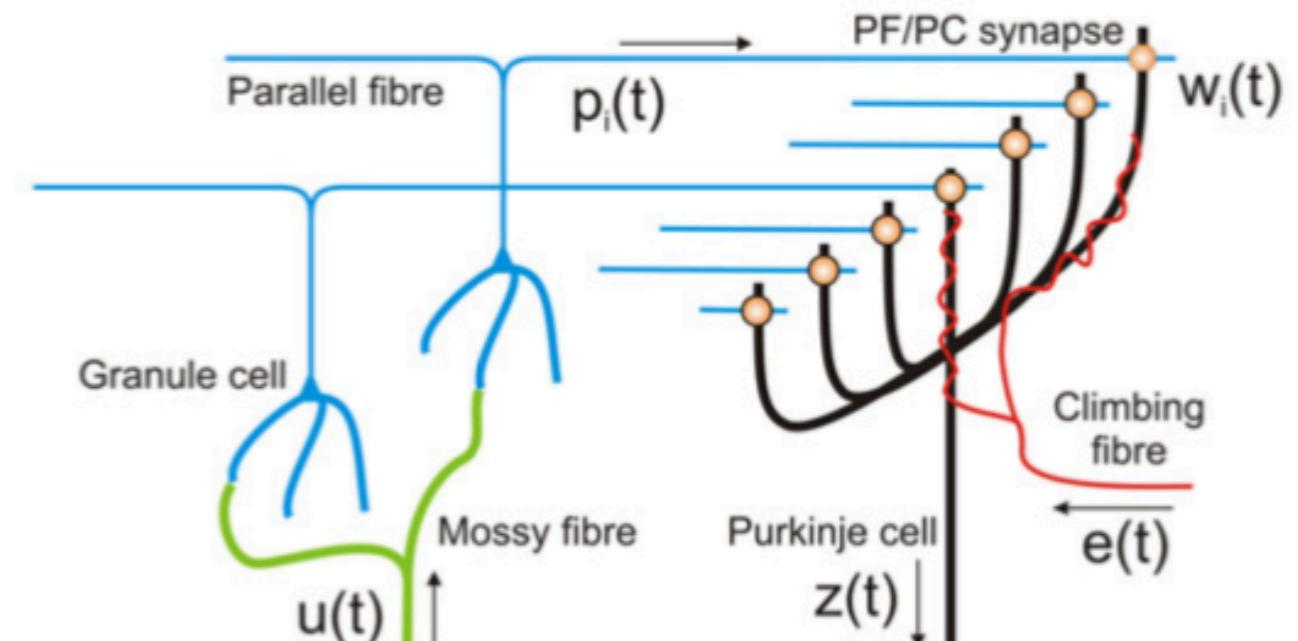
Raymond and Medina, Annual Rev Neurosci (2018)

Cerebellum as a adaptive filter

Controller/filter model



Neurobiology of the cerebellum



Sensory input/
motor copy

Prediction

Porrill et al. Neural Networks (2013)

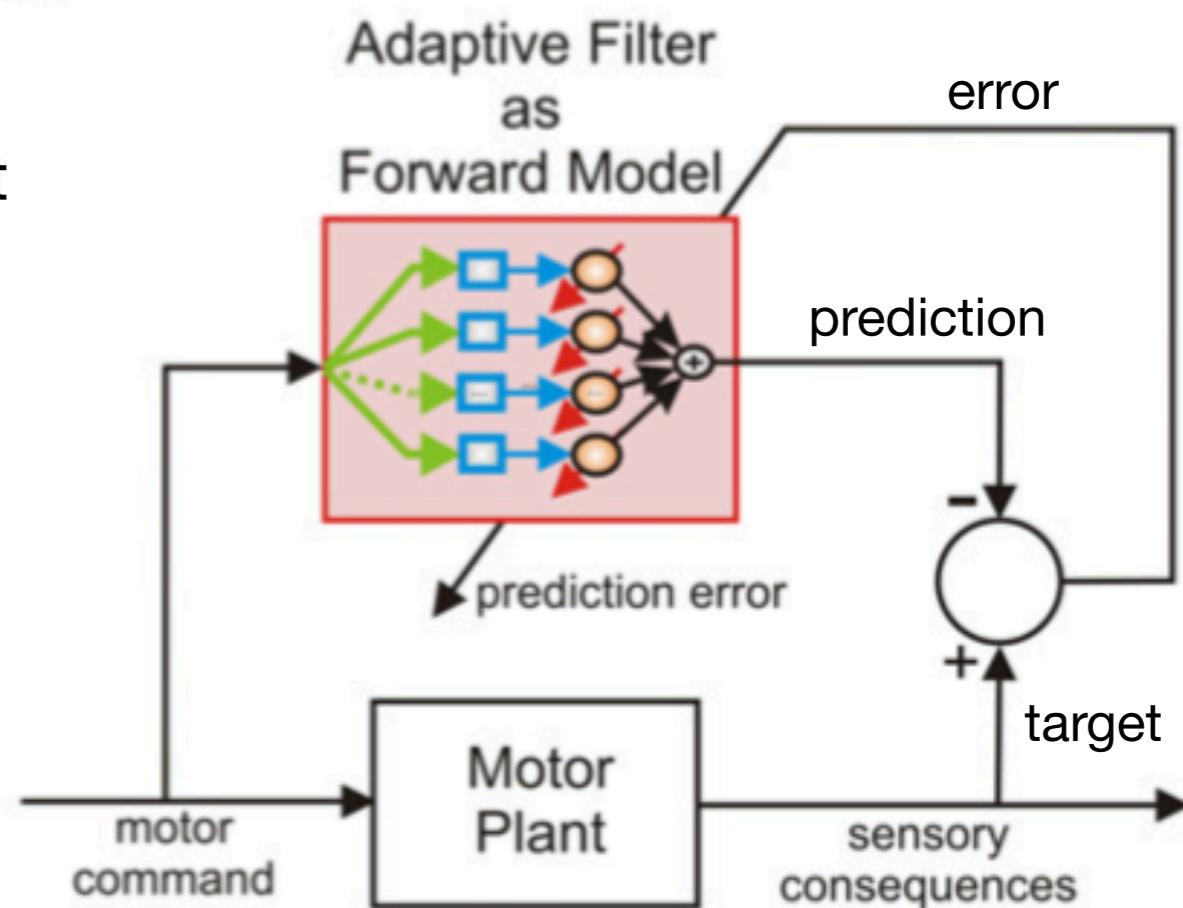
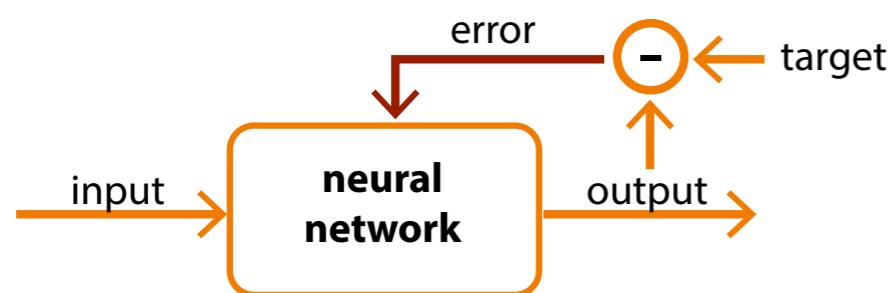
Raymond and Medina, Annual Rev Neurosci (2018)

Forward model of the cerebellum

Forward model:

Given a motor command predict its outcome in the environment (using sensory info).

Note that this is similar to:

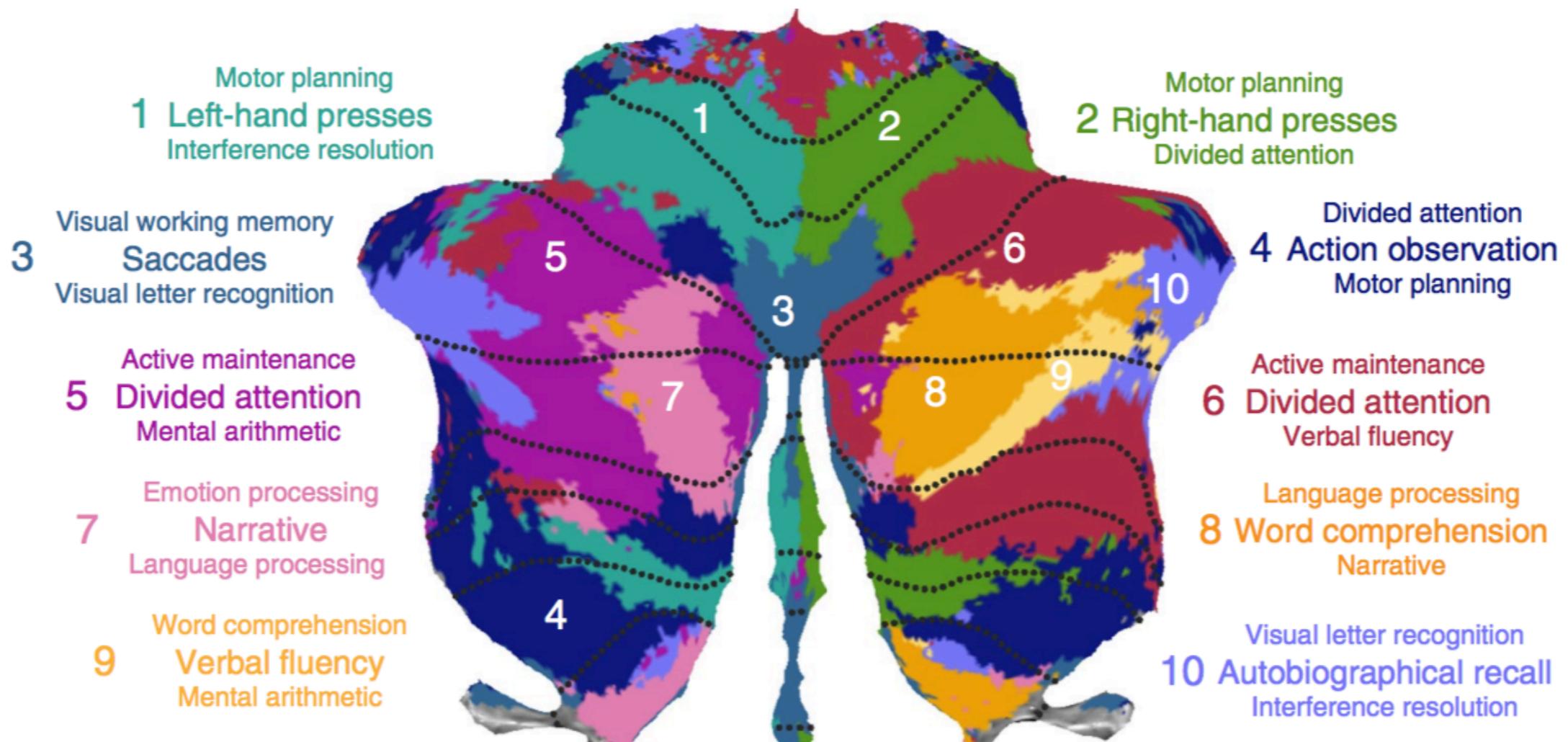


Porrill et al. Neural Networks (2013)

Raymond and Medina, Annual Rev Neurosci (2018)

The cognitive cerebellum

A new emerging field showing that the cerebellum is involved in much more than simple motor control. 2D cognitive map of the cerebellum showing activations to many different tasks:



King et al. NatNeurosci (2019)

Summary

- I. Deep learning successes relies on the backprop algorithm**
- 2. Backprop is slowly becoming a possible model for learning in the brain, but several issues remain unsolved**
- 4. Dendritic microcircuits provide a powerful model of learning in the brain that approximates backprop**
- 6. Cerebellum seems to use supervised learning**

Exercise: Practice writing down the gradient wrt a given weight in a simple neural network!

Questions?

[reddit.com/r/comsm0075/](https://www.reddit.com/r/comsm0075/)

References

Text books:

Parallel Distributed Processing, Rumelhart et al. 1986 (classical book on neural networks)

Relevant papers:

- Roelfsema and Holtmaat, Nature Neuroscience Rev (2018) (recent review on the credit assignment problem in the brain)
- Doya, Curr Opin Neurobiol (2000) (review on how different brain areas learn)
- Richards and Lillicrap, Current Opinion in Neurobiology (2019) (recent review on dendritic credit assignment)
- Sacramento et al., NeurIPS (2018) (shows how dendritic microcircuits may approximate backprop)

Upcoming lectures

- L1^[4]: Neural circuits and learning: introduction
- L2^[4]: Supervised learning & backprop
- L3^[5]: **Visual system: deep learning?**
- L4^[5]: Reinforcement learning
- L5^[6]: Unsupervised learning
- L6^[6]: Temporal processing
- L7^[7]: Recurrent neural networks
- L8^[7]: Guest lecture

Lab I

On Github IPB page:
comsm0075.github.io/2020-21.html

- Implement and study the behaviour and biological plausibility of supervised learning/backprop.
- Teaching assistants: Joe Pemberton
Dabal Pedamonti