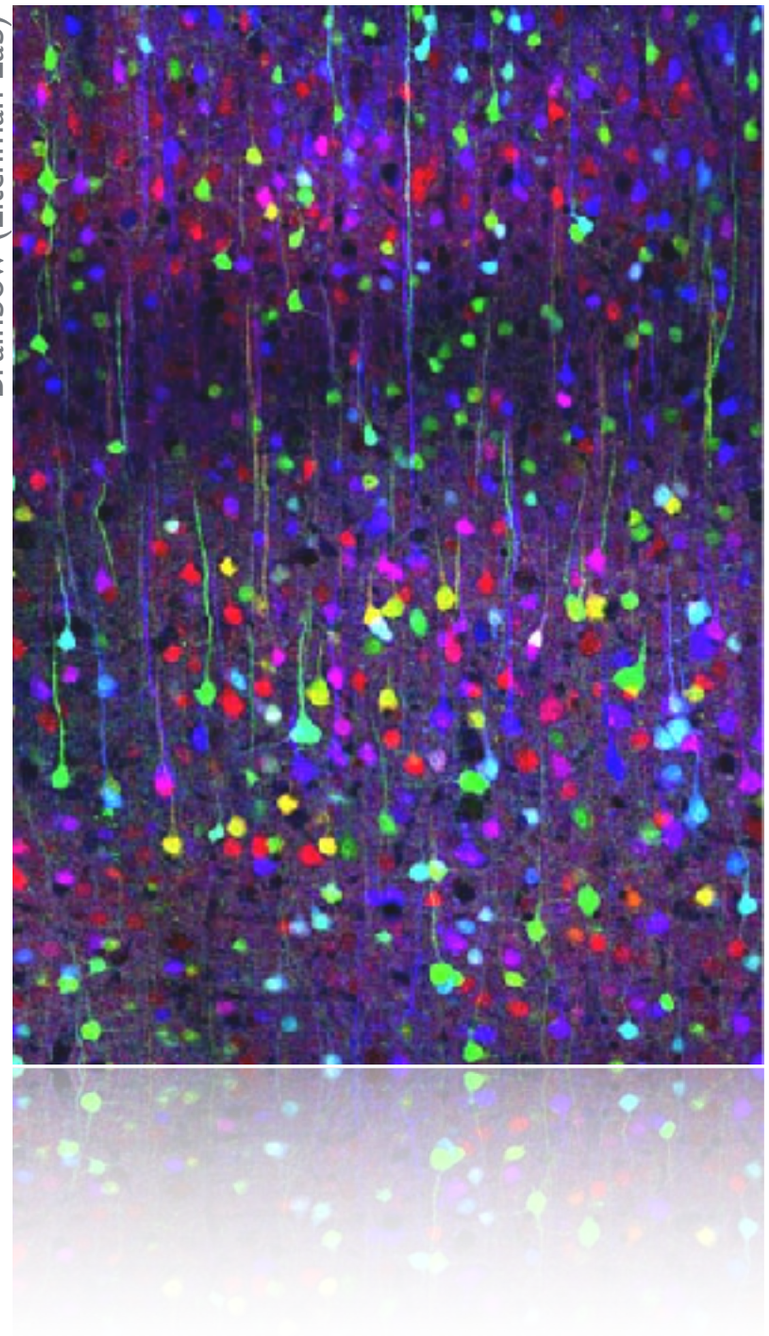
Information Processing & the Brain 2019/2020

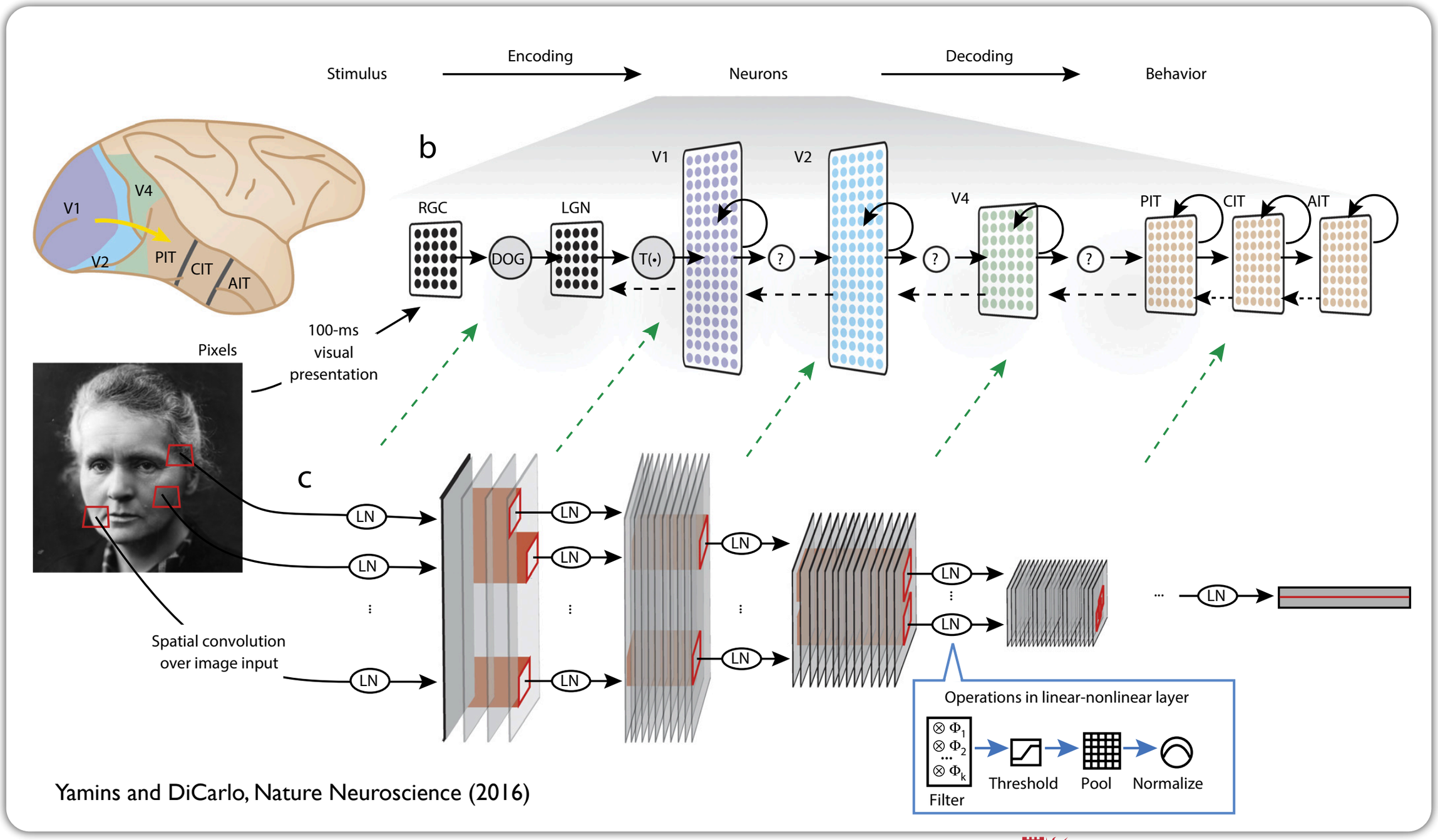
University of BRISTOL



Brainbow (Litchman Lab)

Lecture 13
Neural circuits and learning:
Supervised learning:
backprop & cerebellum

Previously on *IPB*…

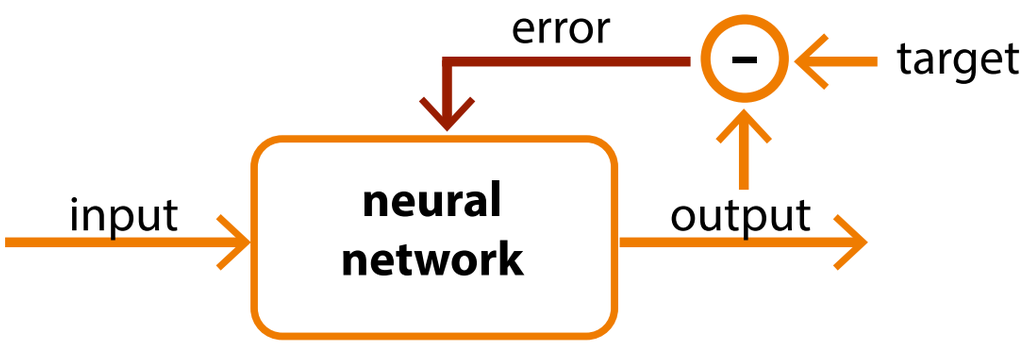


Yamins and DiCarlo, Nature Neuroscience (2016)

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

1. **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.

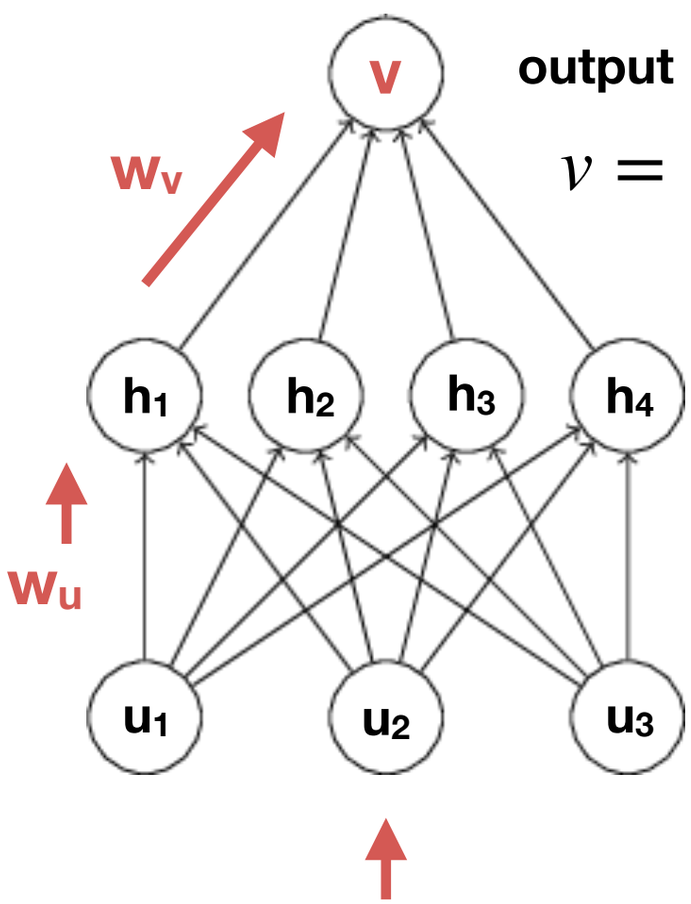
$$\Delta w = \eta(v - \text{target})u$$

- 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

$$v = W_v h$$

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

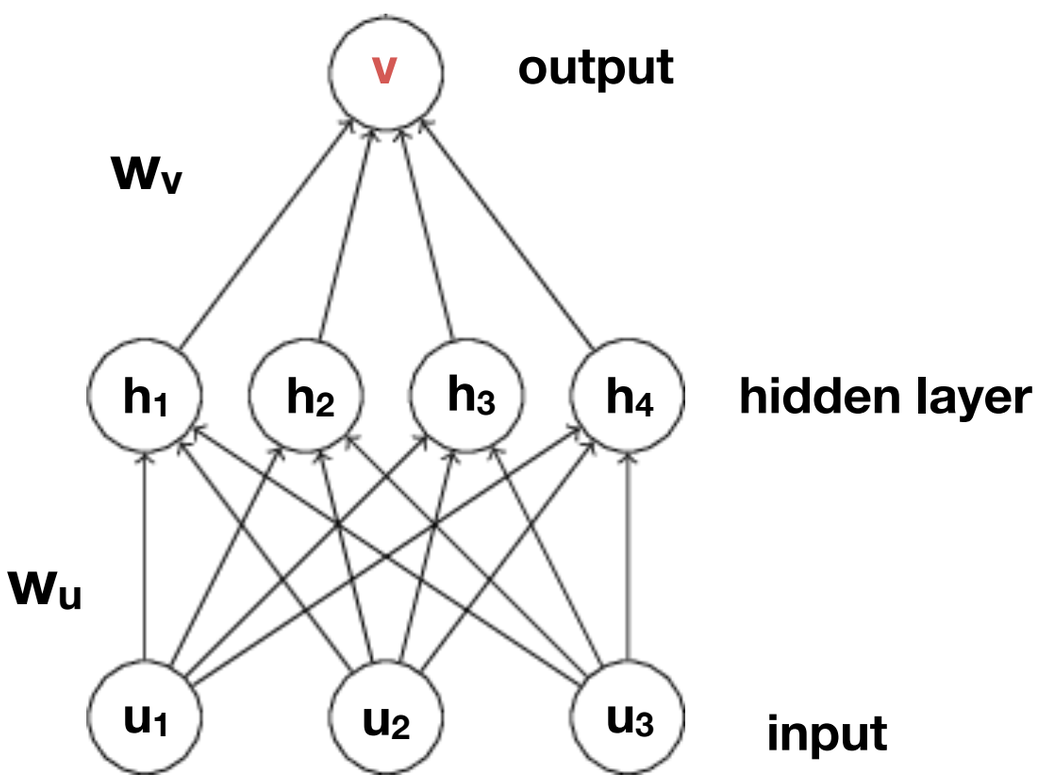
$$h = f(W_u u)$$

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

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

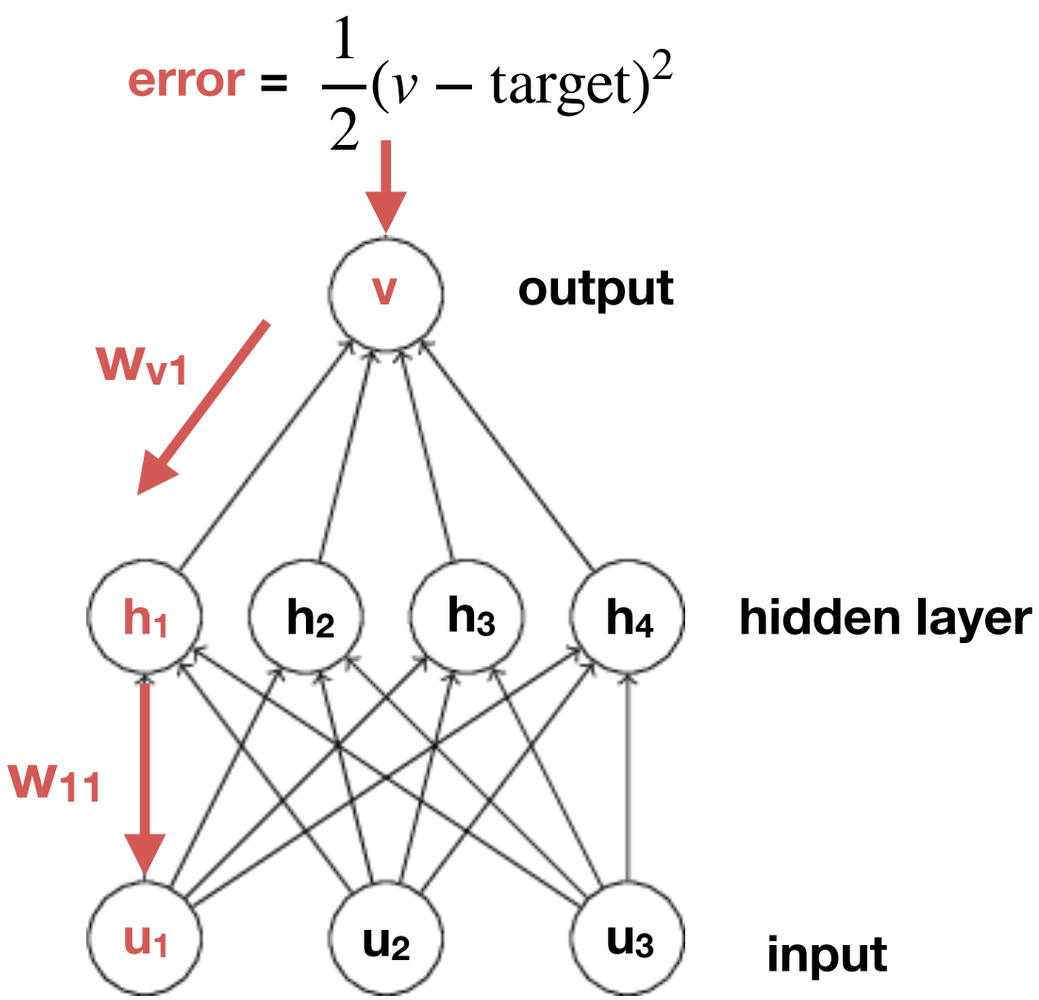


The backpropagation algorithm:

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

Rumelhart et al. 1986 PDP

The backpropagation algorithm



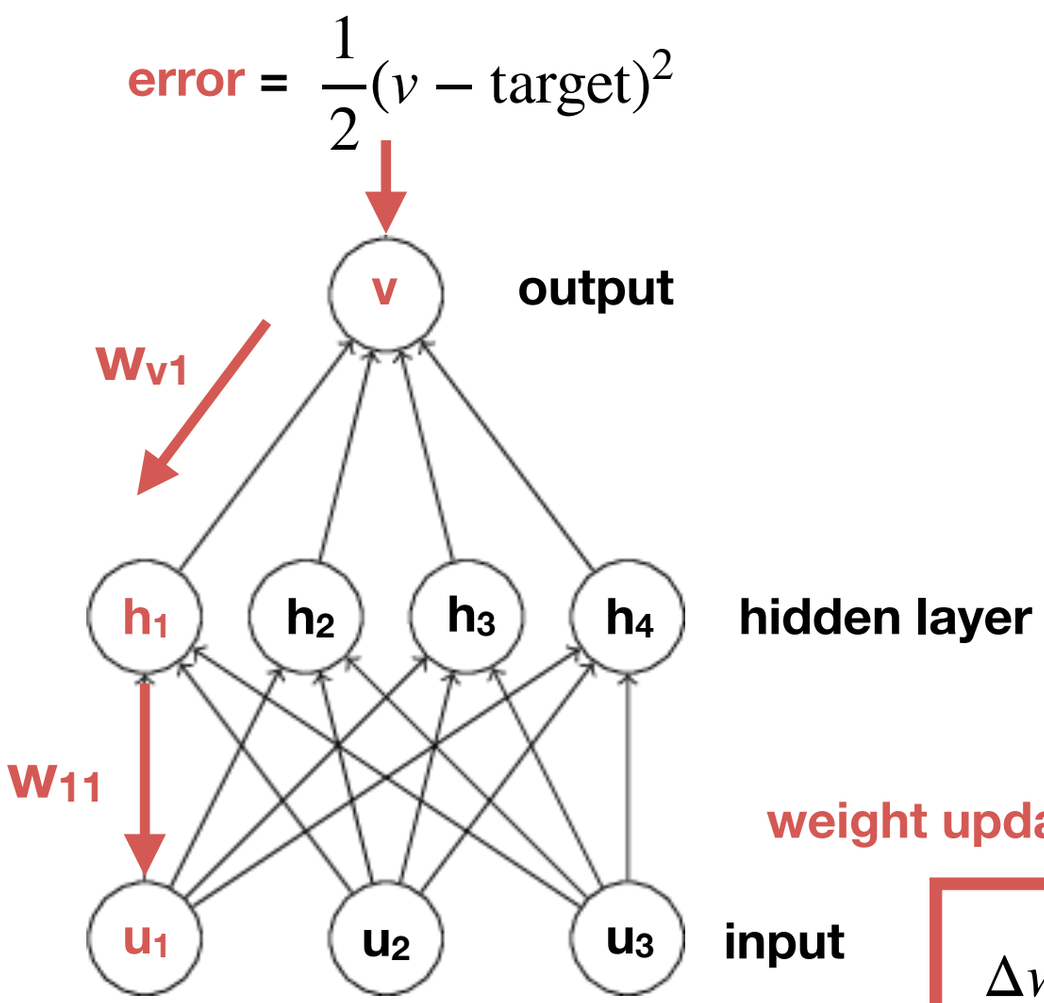
The backpropagation algorithm:

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



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

The backpropagation algorithm:

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

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

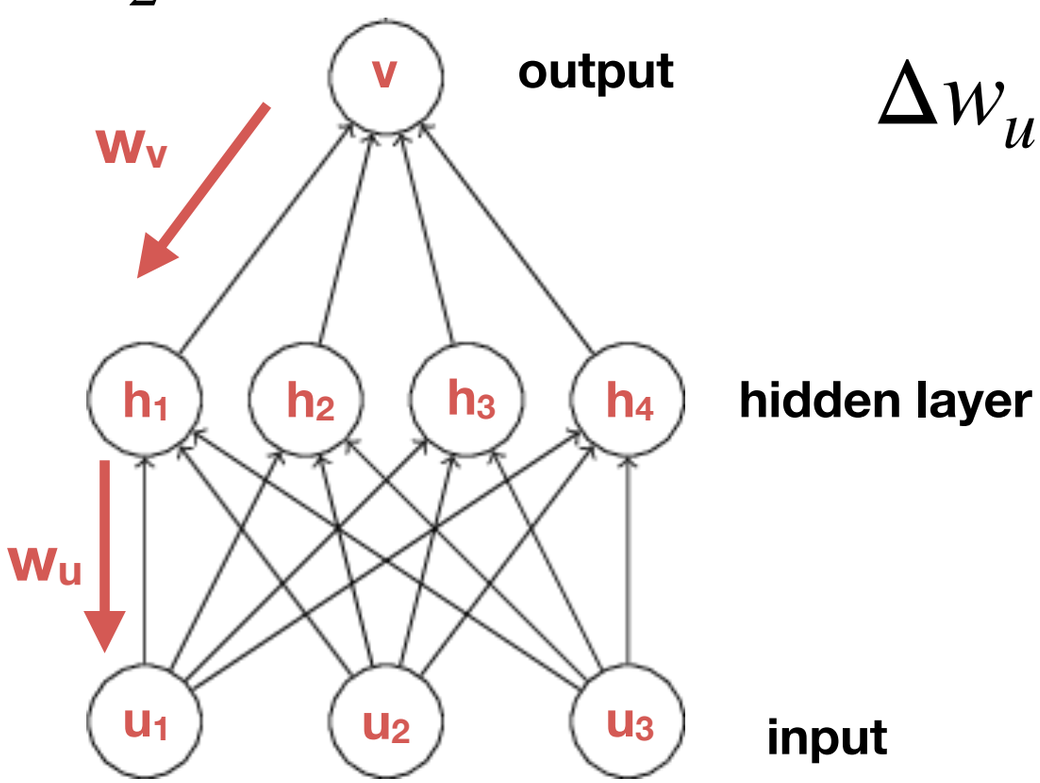
weight update:

$$\Delta w_{11} = -\eta \frac{\partial \text{Error}}{\partial w_{11}} = \underbrace{(\text{v} - \text{target})}_{\text{error}}\ w_{v1} f'_{h_1} u_1$$

Rumelhart et al. 1986 PDP

The backpropagation algorithm
general weight update

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



The general form for the weight update:

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

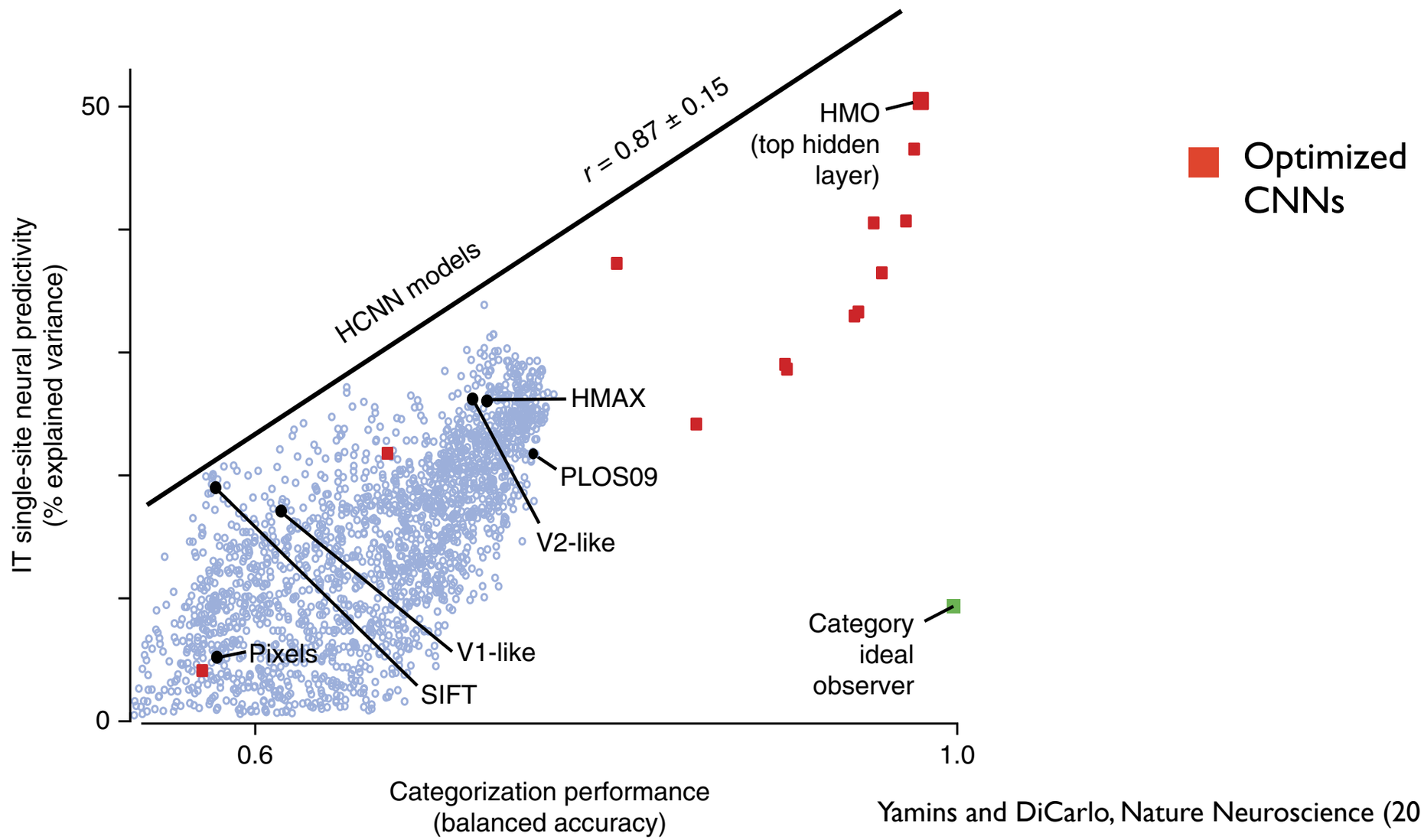
Note: Write down the gradient wrt a weight for practice!

Rumelhart et al. 1986 PDP

The backpropagation algorithm in the brain

Reminder: CNNs 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?



Yamins and DiCarlo, Nature Neuroscience (2016)

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 ≠ 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:

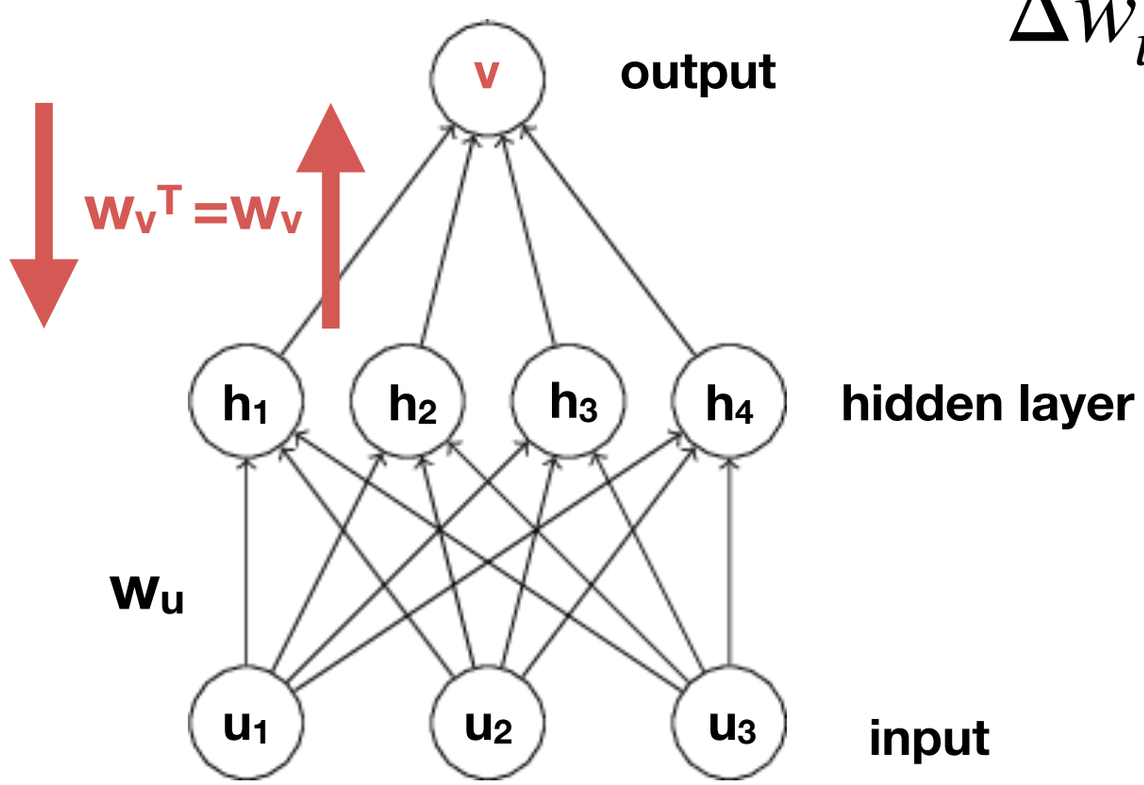
1. **Weight transport problem**: Suggests that feedback weights = feedforward weights
2. **Derivative of activation functions**: Relies on calculating derivatives of the activation functions
3. **Two phase learning**: (1) feedforward propagation of activity and (2) error backpropagation
4. **Separate 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
1. Weight transport problem

Backprop: The chain rule predicts feedback weights that are equal to feedforward weights: $W_v^T = W_v$

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



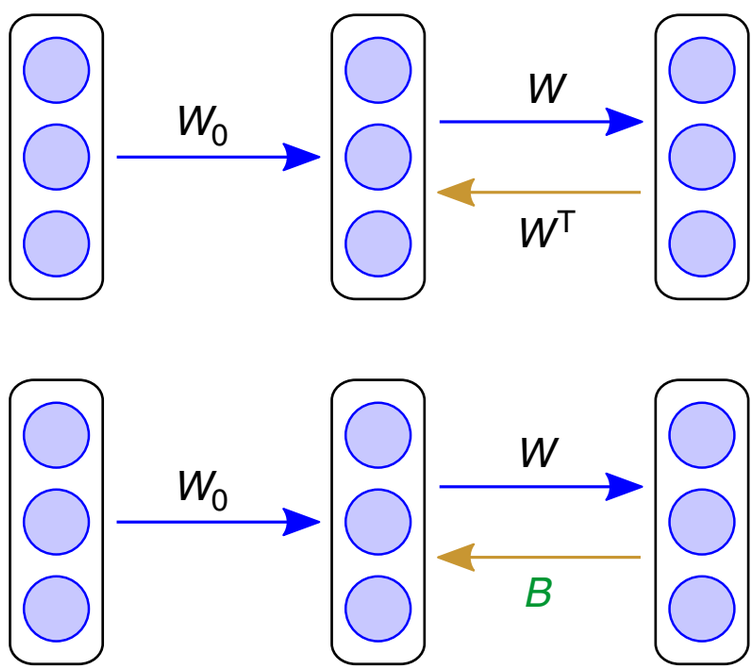
$$\Delta w_u = -\eta \underbrace{(\mathrm{v} - \mathrm{target})}_{\text{error}} \; w_v^T f_h' u$$

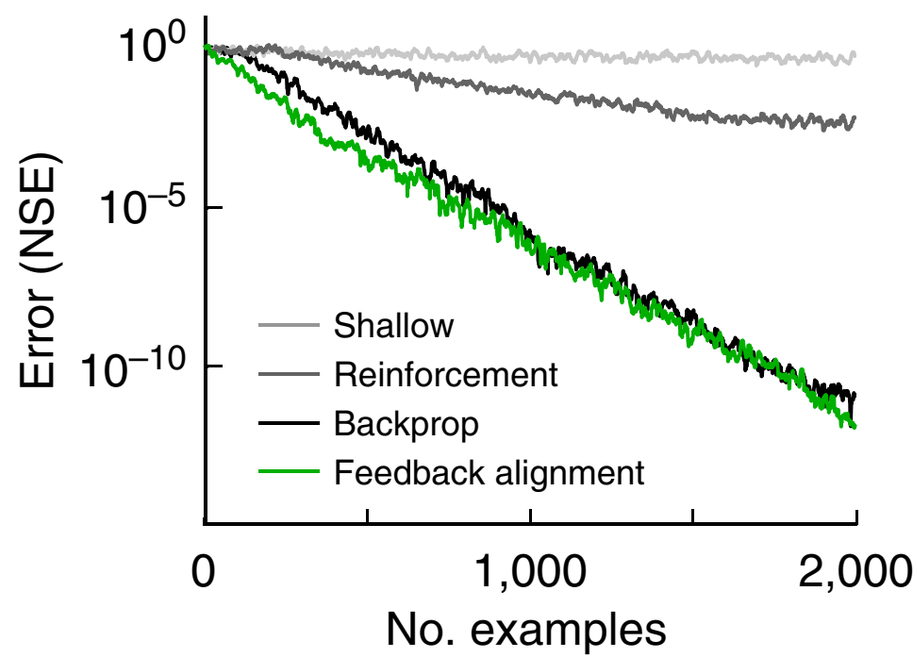
Feedback weights
=
Feedforward weights

$$v = W_v h$$

The backpropagation algorithm
and why it is at odds with biology
1. 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

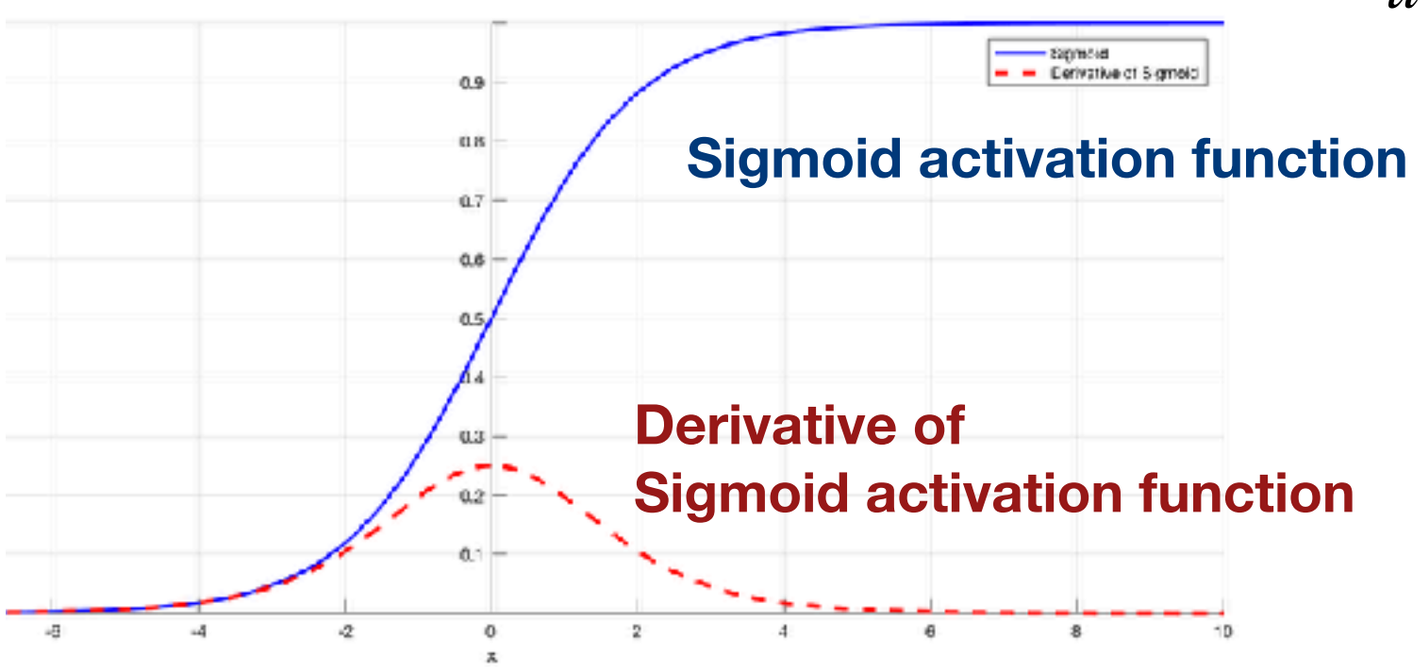
Lillicrap et al., Nature Comms (2016)

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).

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



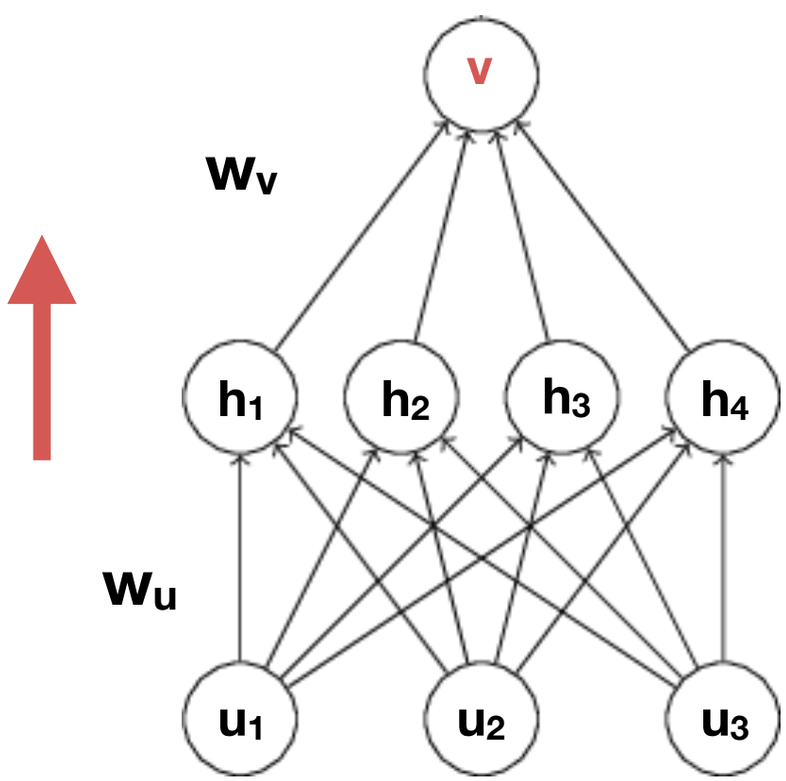
Derivative of activation function

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.

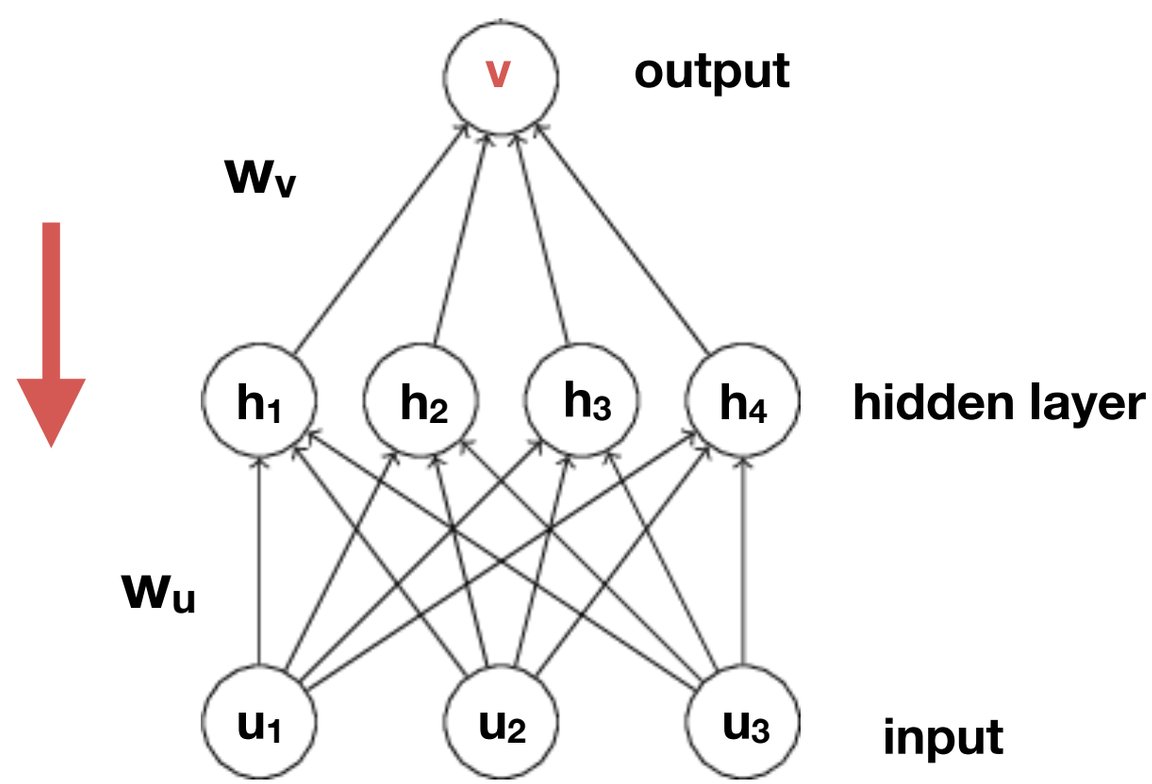
Biology: In the brain there is no clear separation between perception and learning.

Forward phase
(perception)



Backward phase (learning)

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



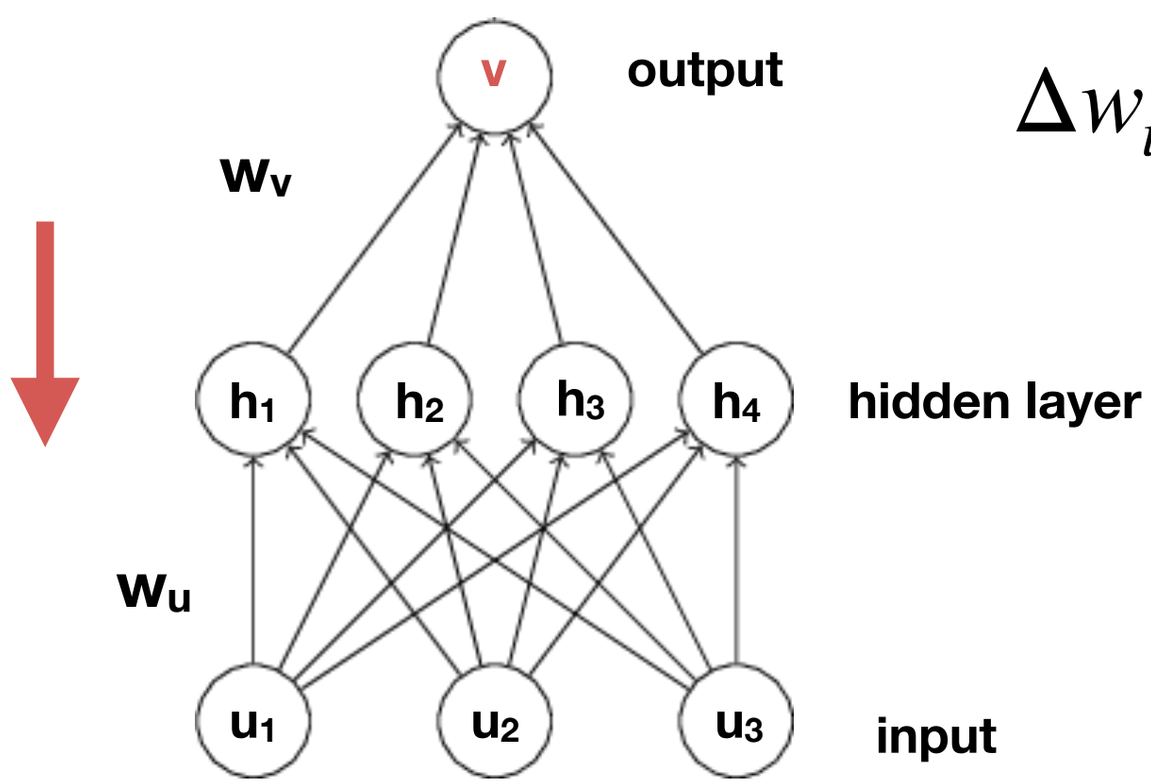
The backpropagation algorithm
and why it is at odds with biology
4. Separate error network

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)

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



EN weights

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

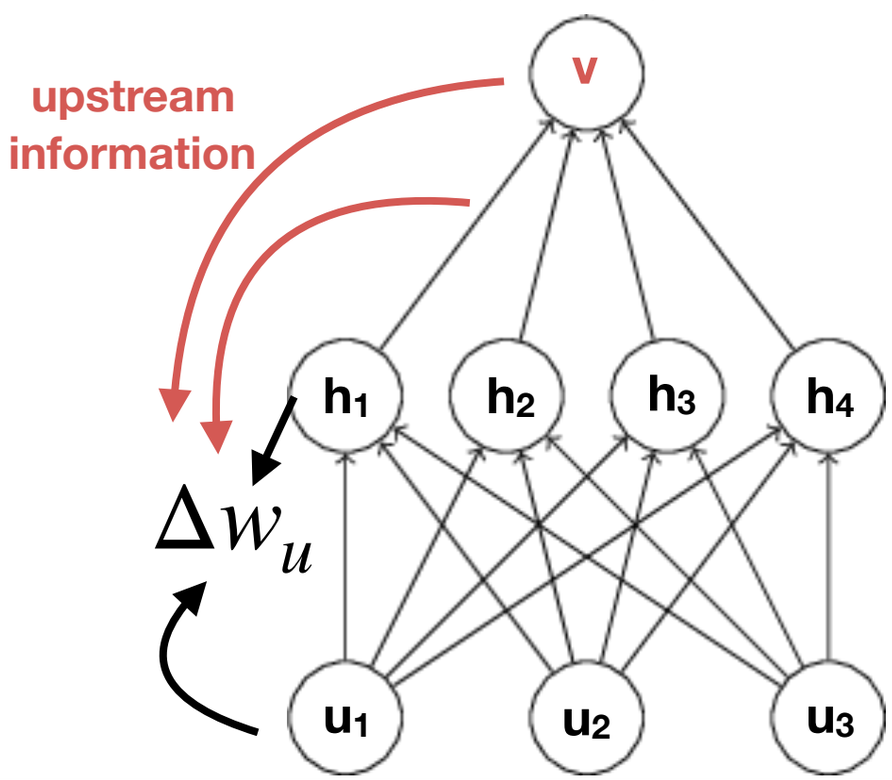
EN activation function

The backpropagation algorithm
and why it is at odds with biology
5. Non-local learning rules

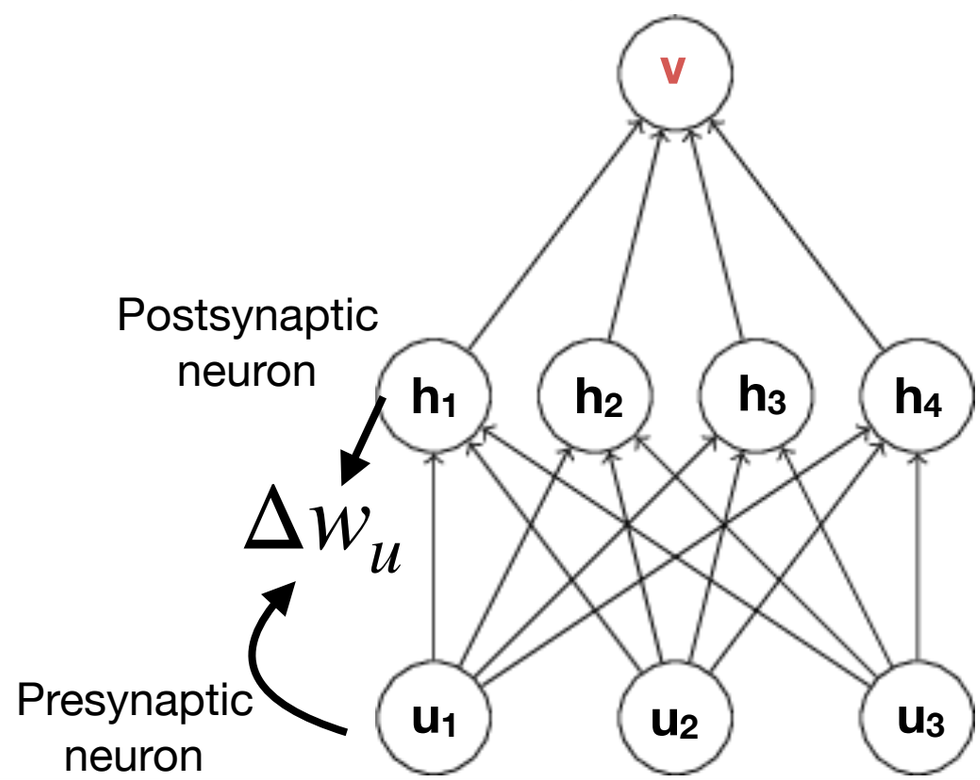
Backprop: Relies on non-local learning rules (i.e. a given neuron needs information about other neurons and layers).

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).

Non-local learning rule
(backprop)



Local learning rule
(biology)



Poll & discussion

groups of 2-3 (5min)

Go to menti.com
Code: 81 30 6

Order the following issues by
least biologically plausible?

Key issues:

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

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

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
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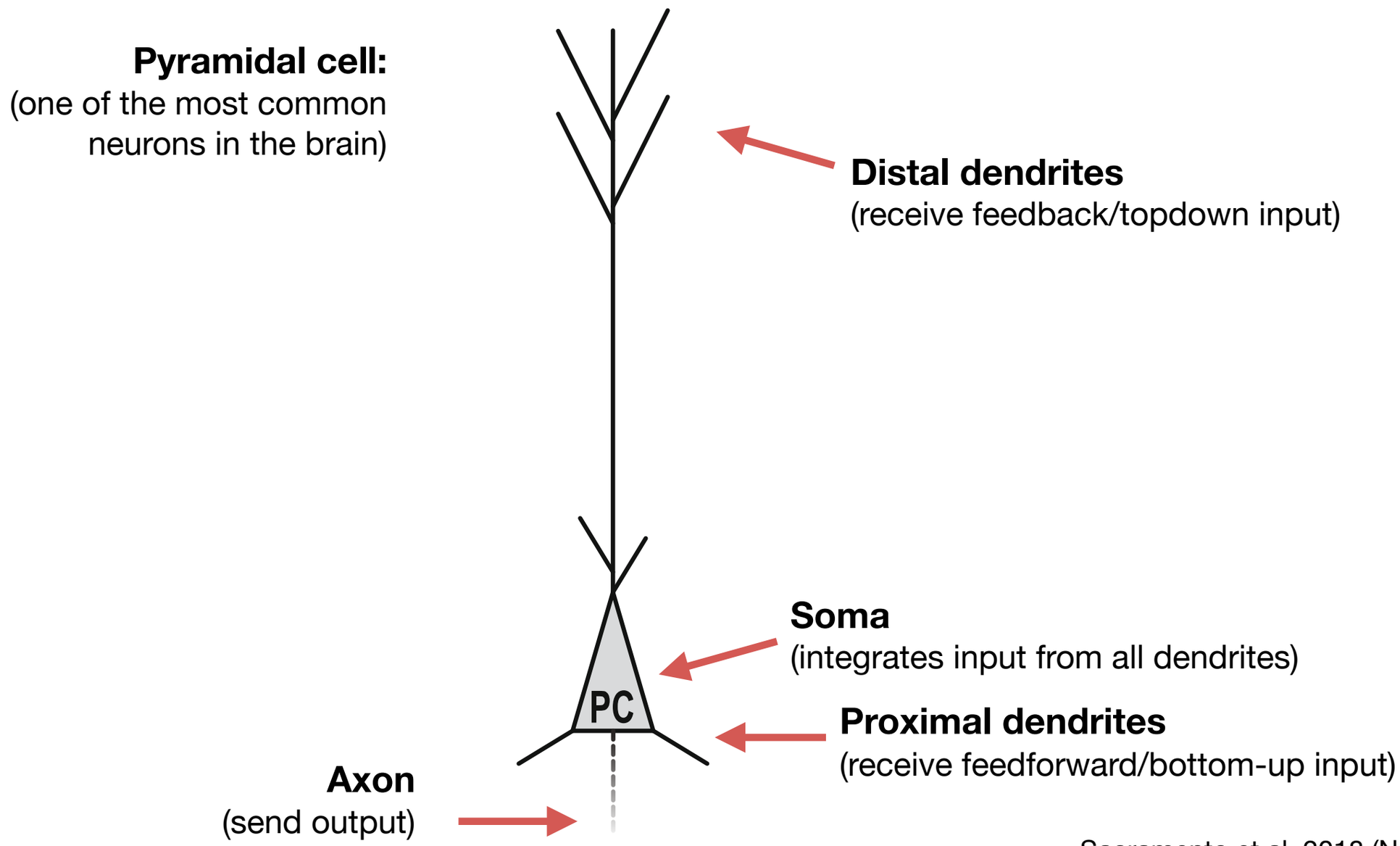
The backpropagation algorithm in the brain

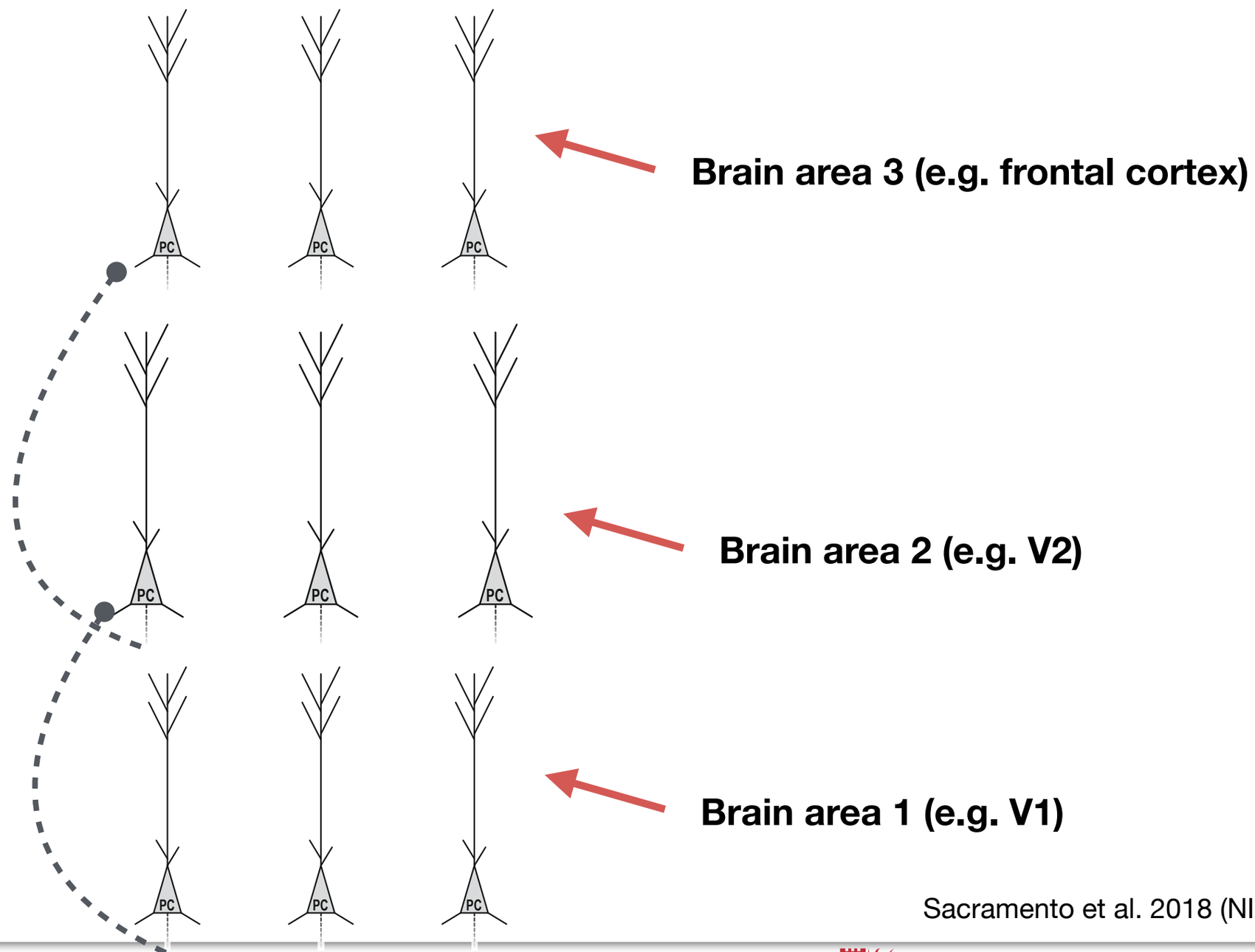
Inspiration from real neurons: pyramidal cells



Sacramento et al. 2018 (NIPS)

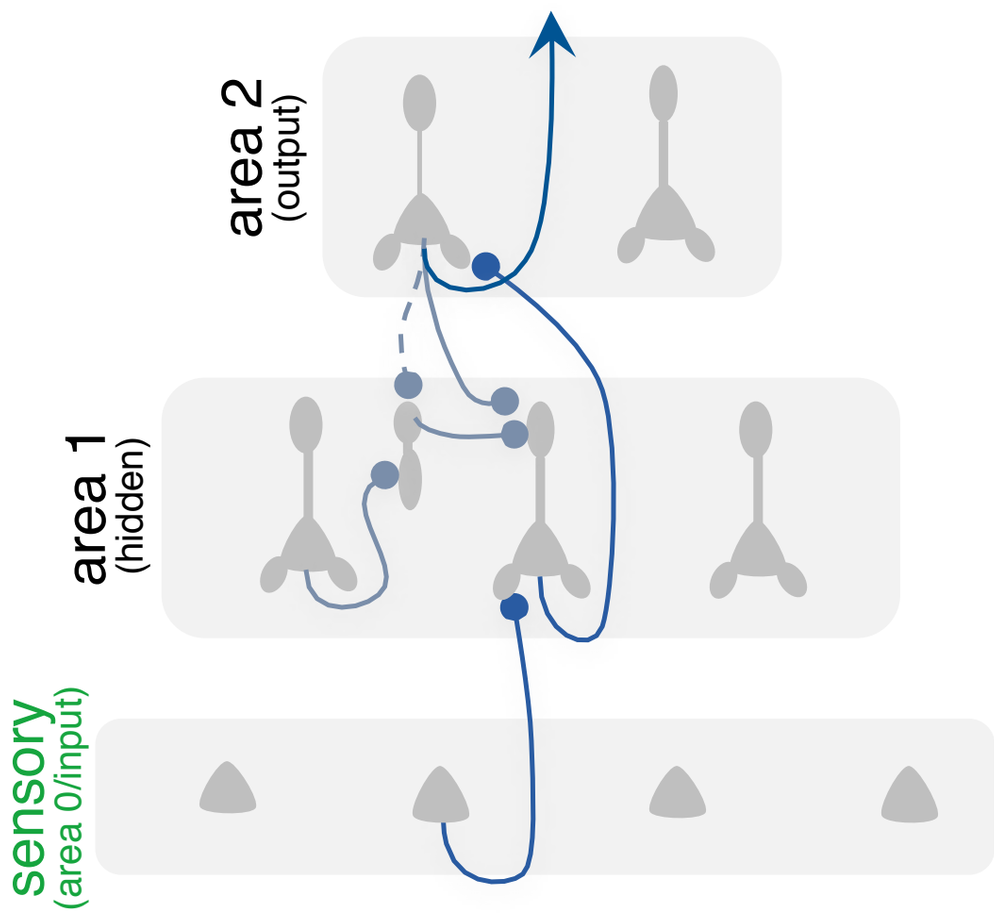
The backpropagation algorithm in the brain

Inspiration from real neurons: pyramidal cells



Sacramento et al. 2018 (NIPS)

Dendritic microcircuits approximate backprop



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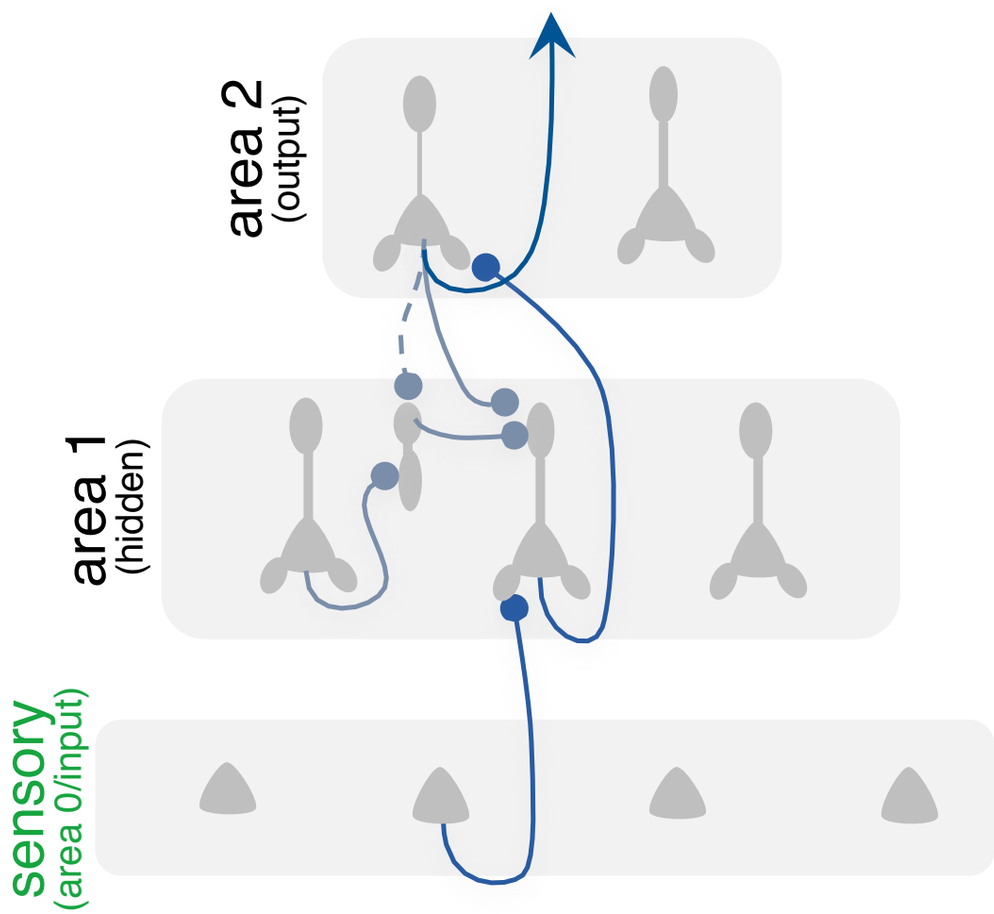
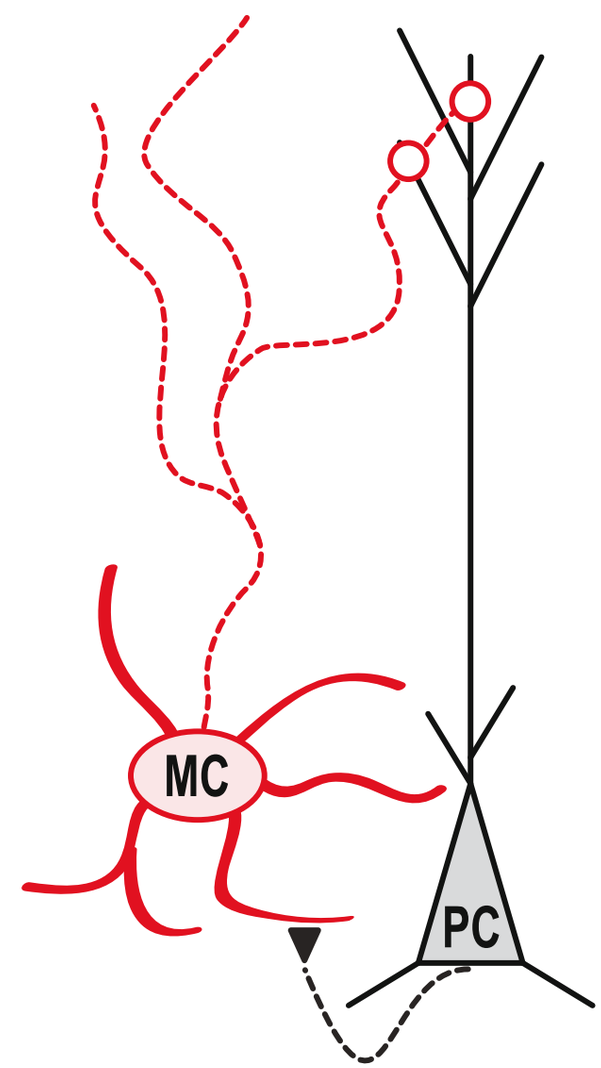


Inspired by two key cell types in the cortex:

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



Sacramento et al. 2018 (NeurIPS)

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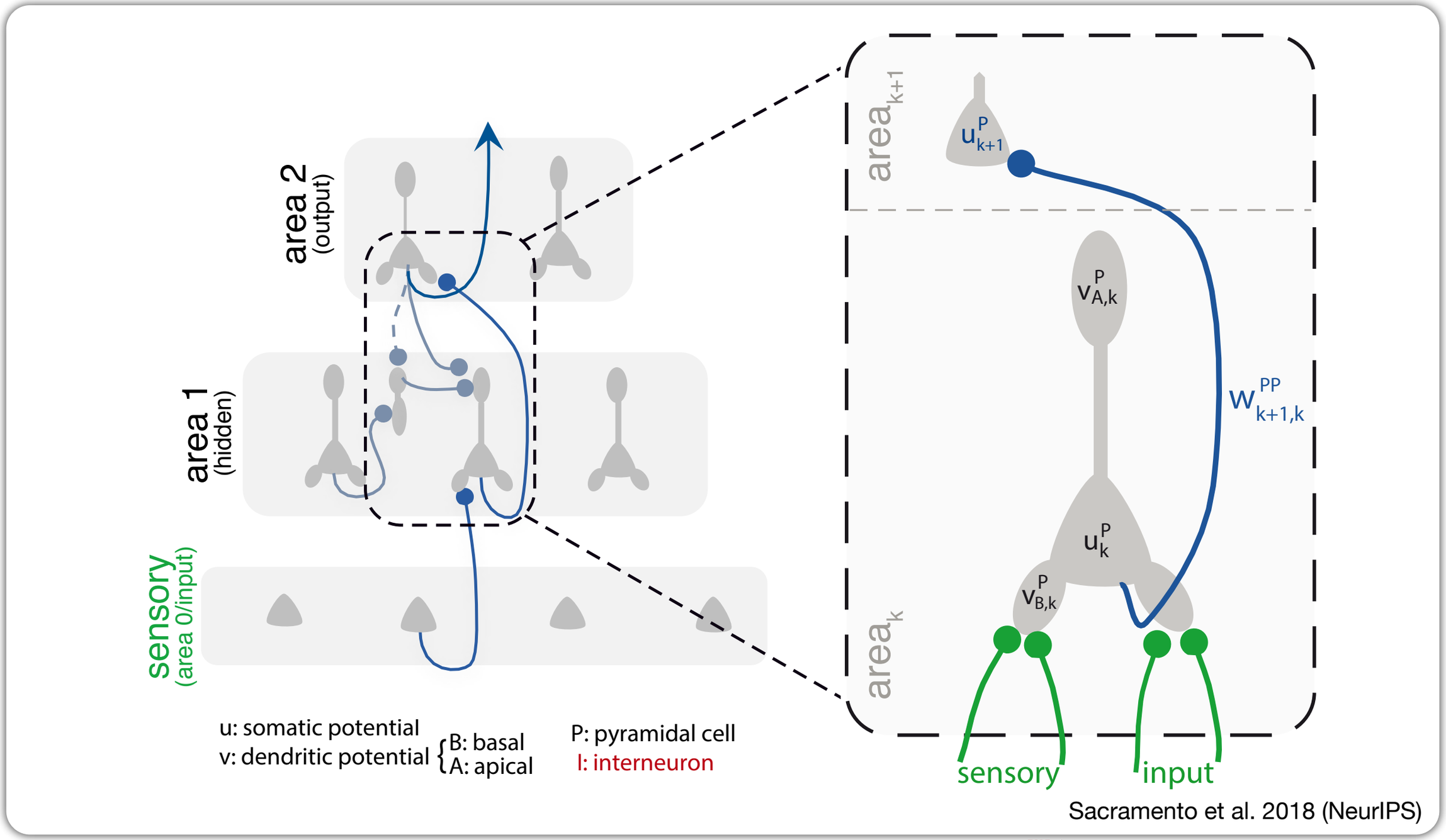

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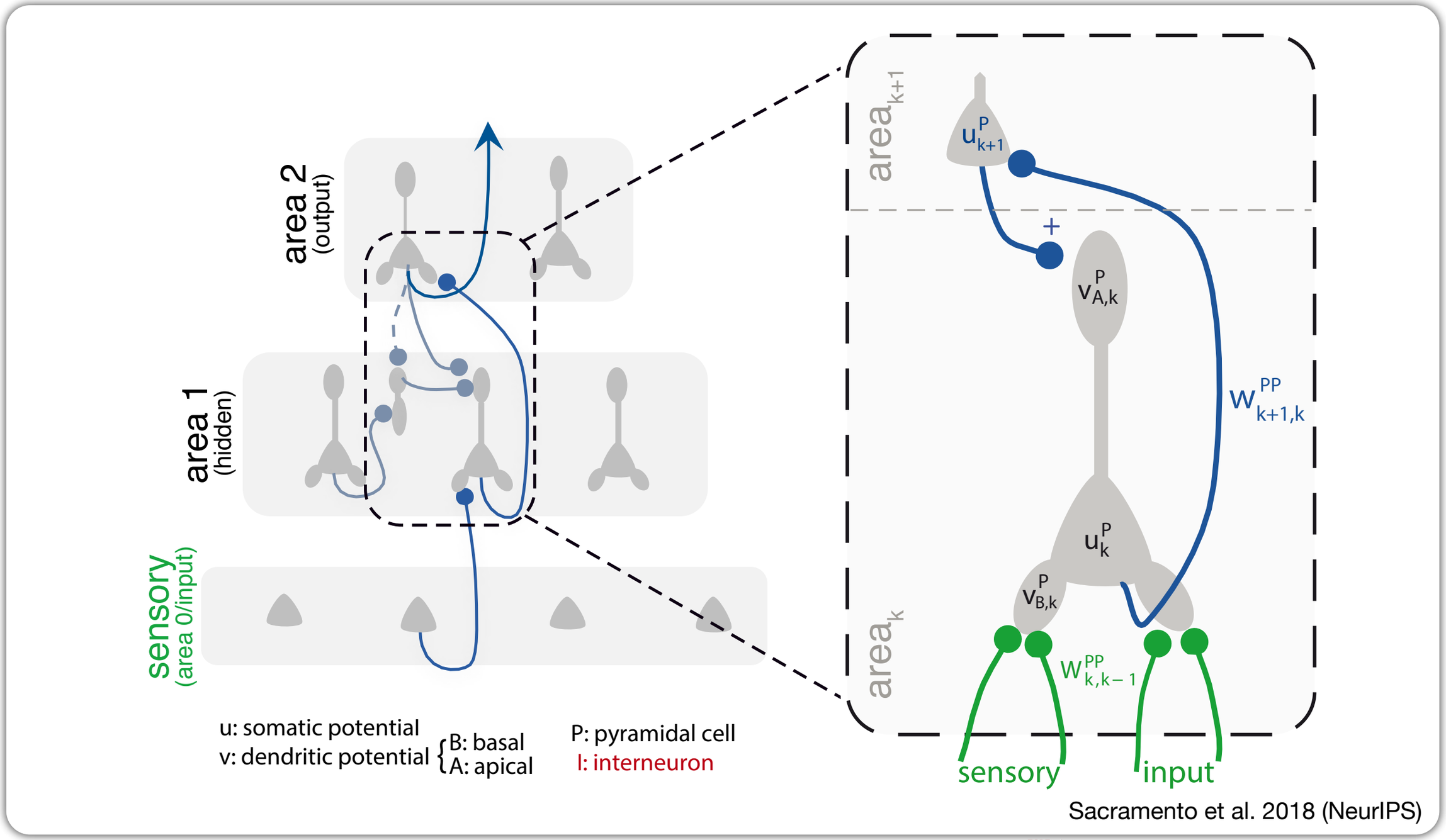

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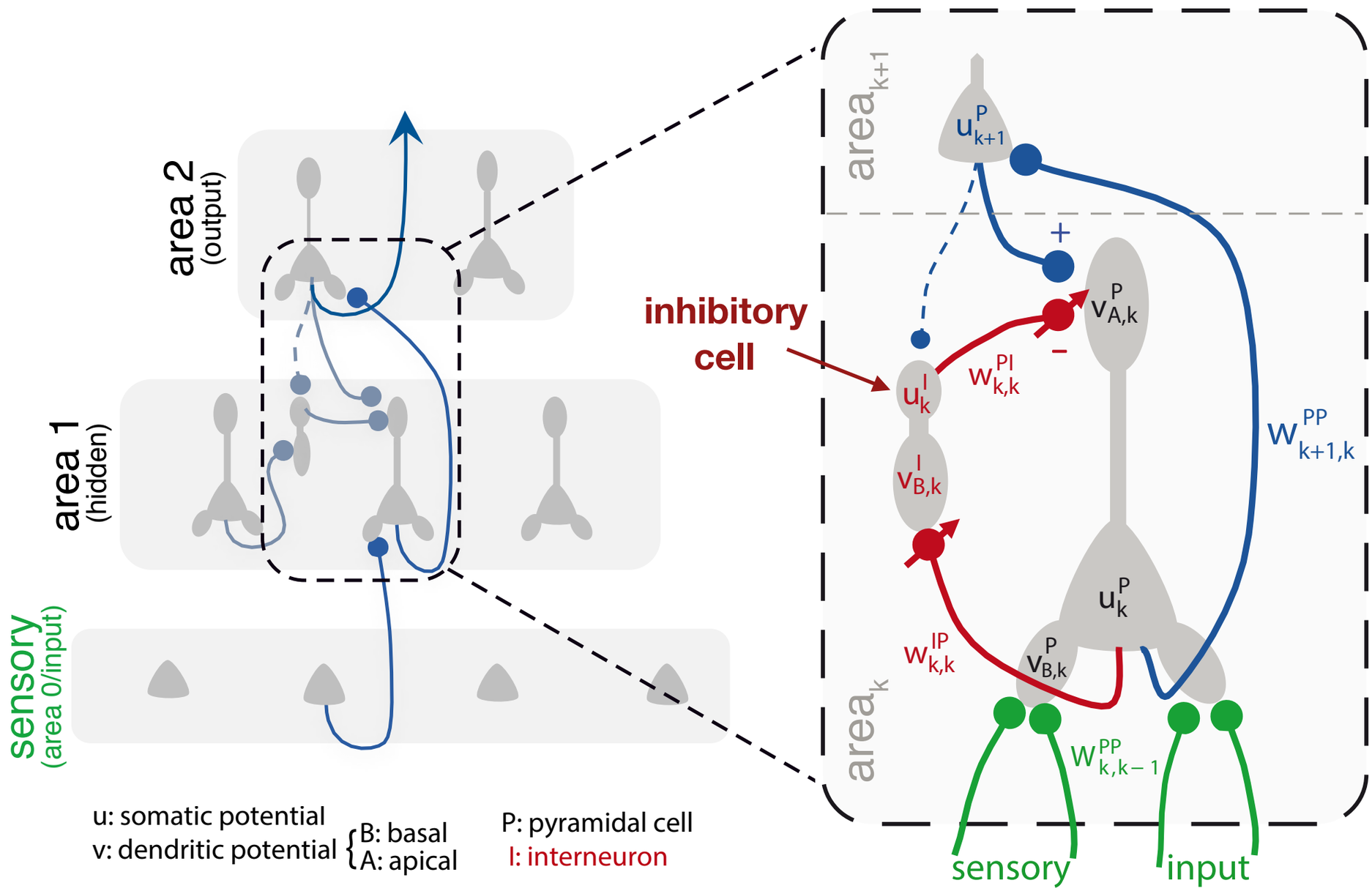

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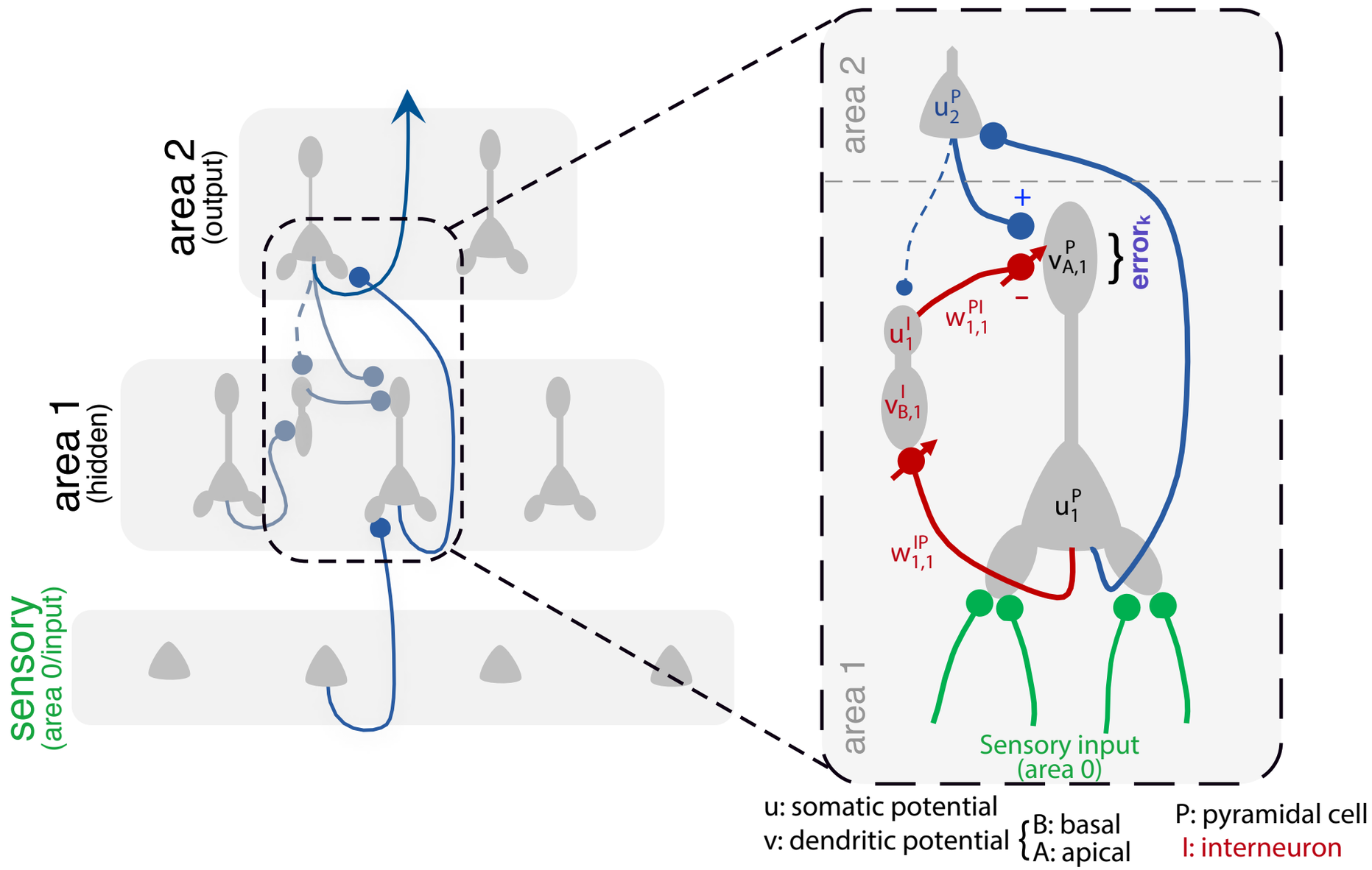
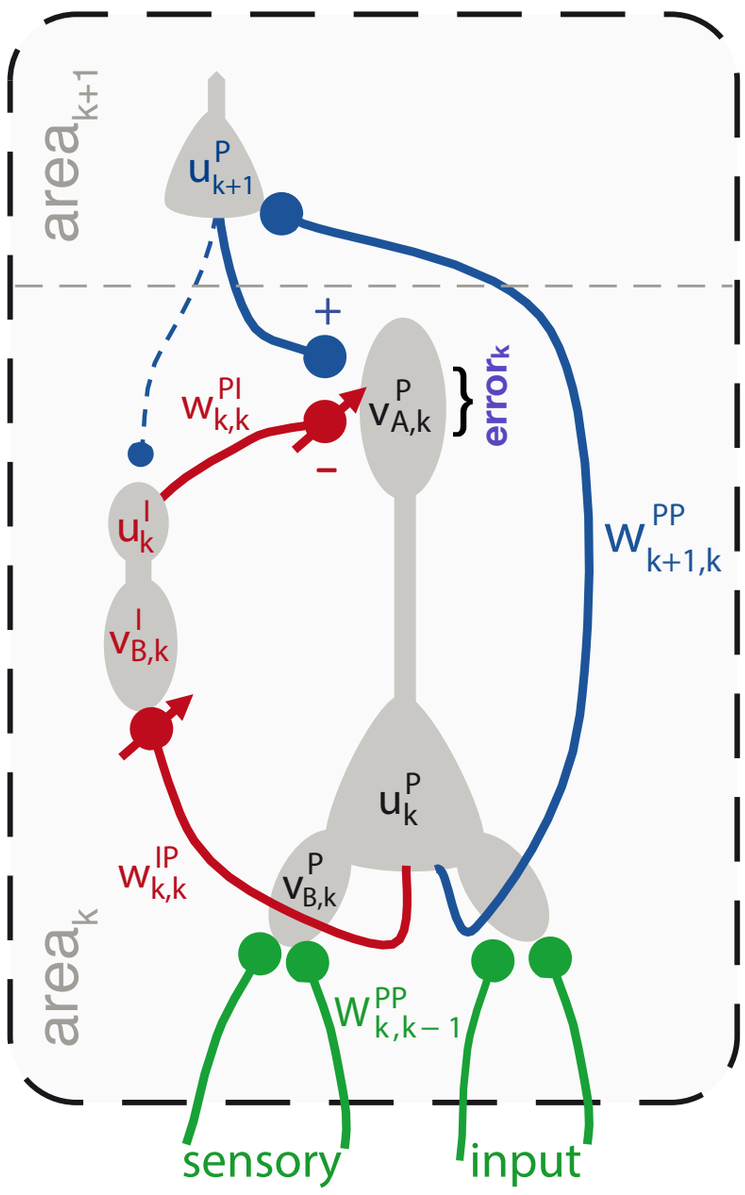


Sacramento et al. 2018 (NIPS)

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^P_{k+1} and lateral inhibition u^I_k generates an **error** signal:

$$v^P_{A,k} \sim u^P_{k+1} - u^I_k$$

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

$$w^{PP}_{k,k-1}$$

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.:

$$u^I_k \sim u^P_{k+1}$$

Sacramento et al. 2018 (NIPS)

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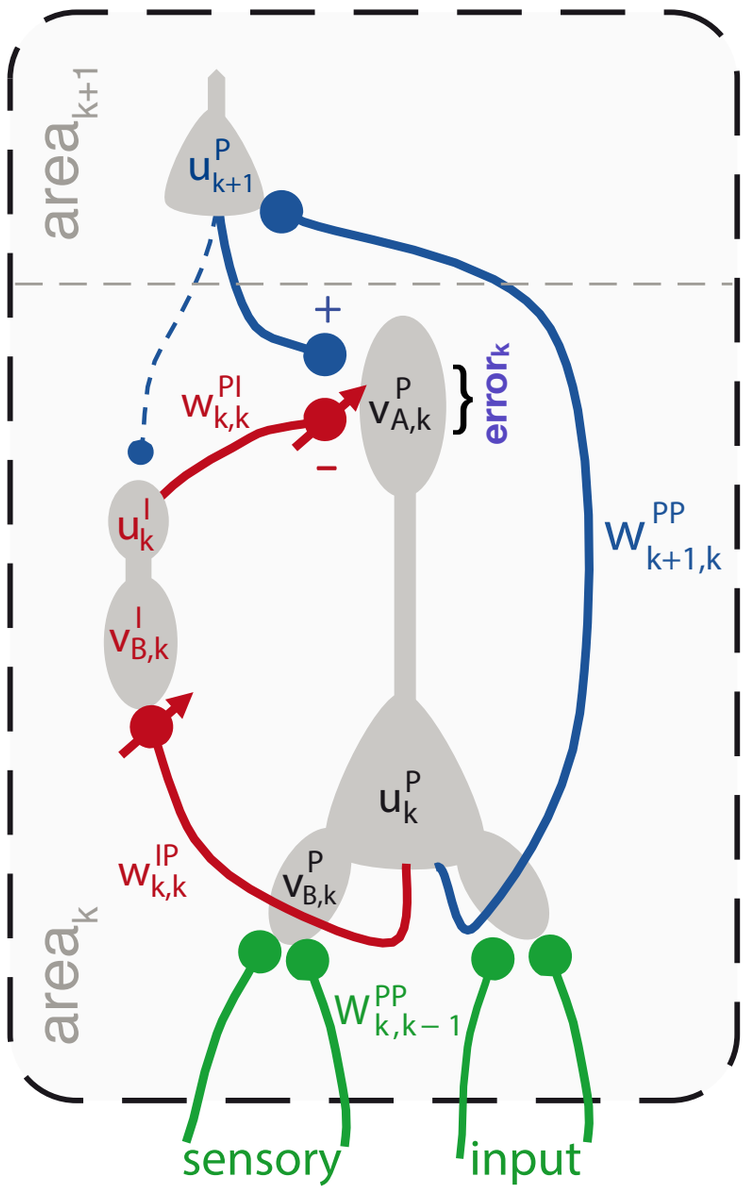

General form of the (local) learning rule:

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

Sacramento et al. 2018 (NIPS)

Dendritic error microcircuits

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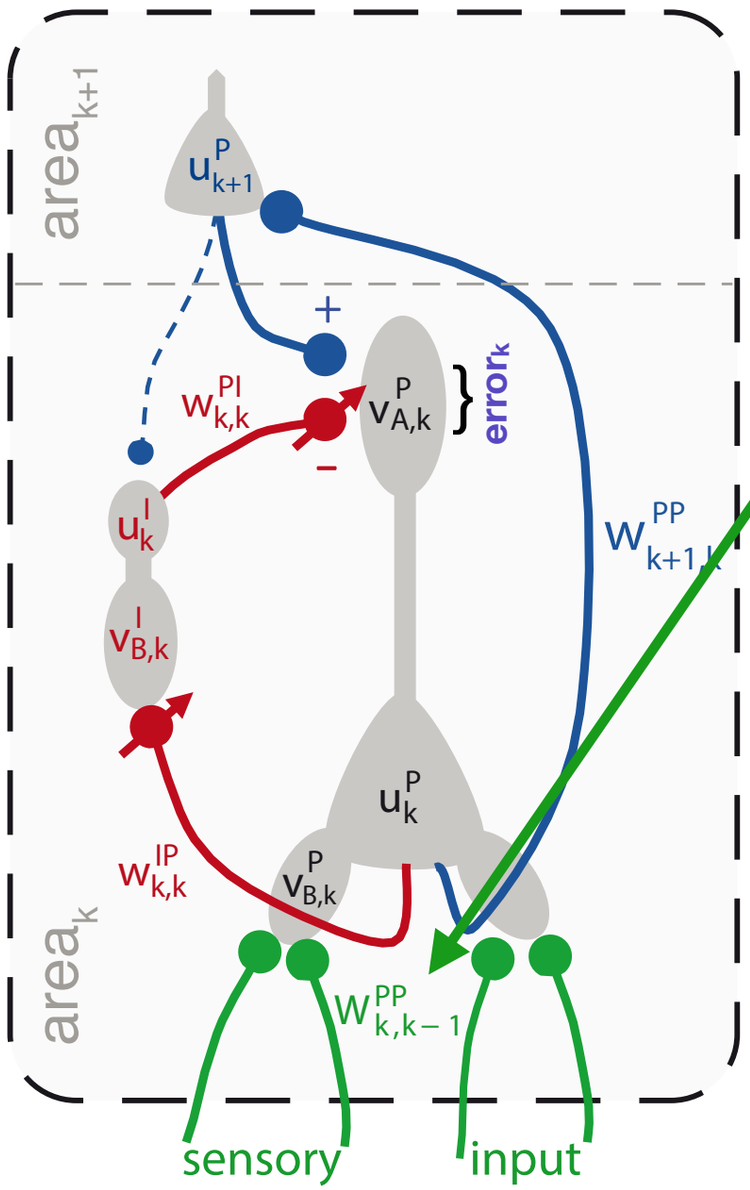


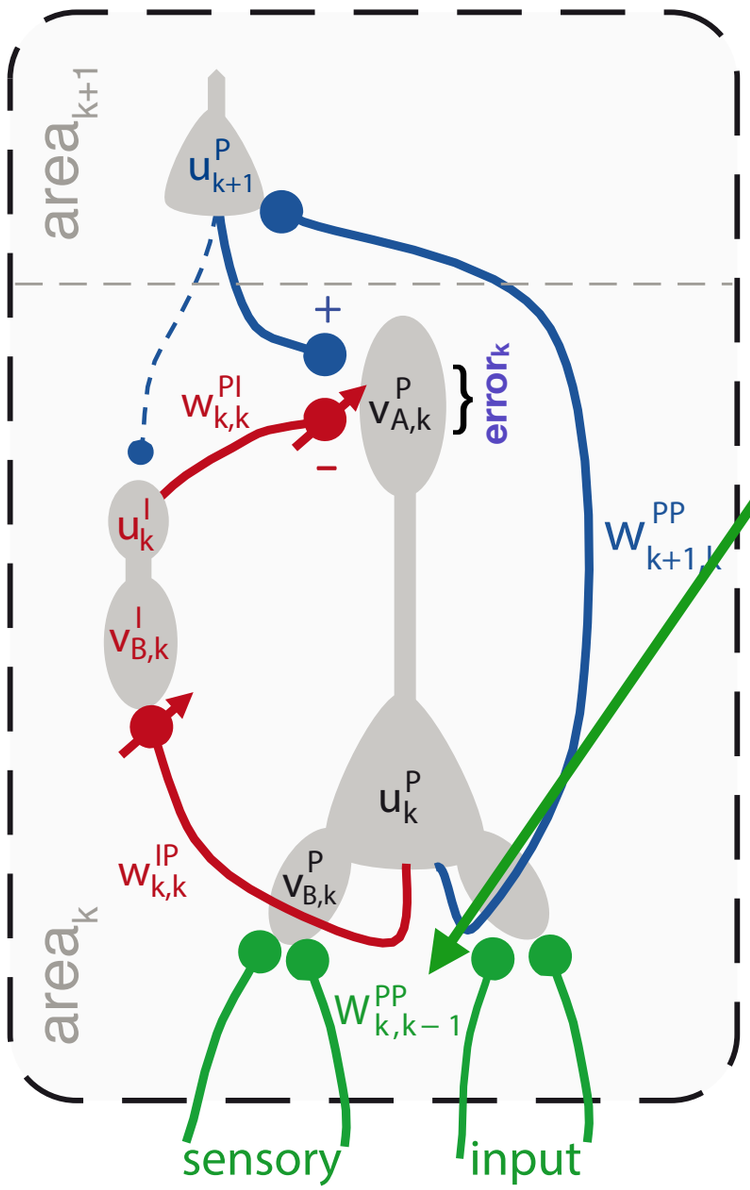
Learning rule for bottom-up synapses:

$$\frac{d}{dt} w^{PP}_{k,k-1} \sim \eta (u^P_k - v^P_{B,k}) r^P_{k-1}$$

Sacramento et al. 2018 (NIPS)

Dendritic error microcircuits

local error-correcting learning rules



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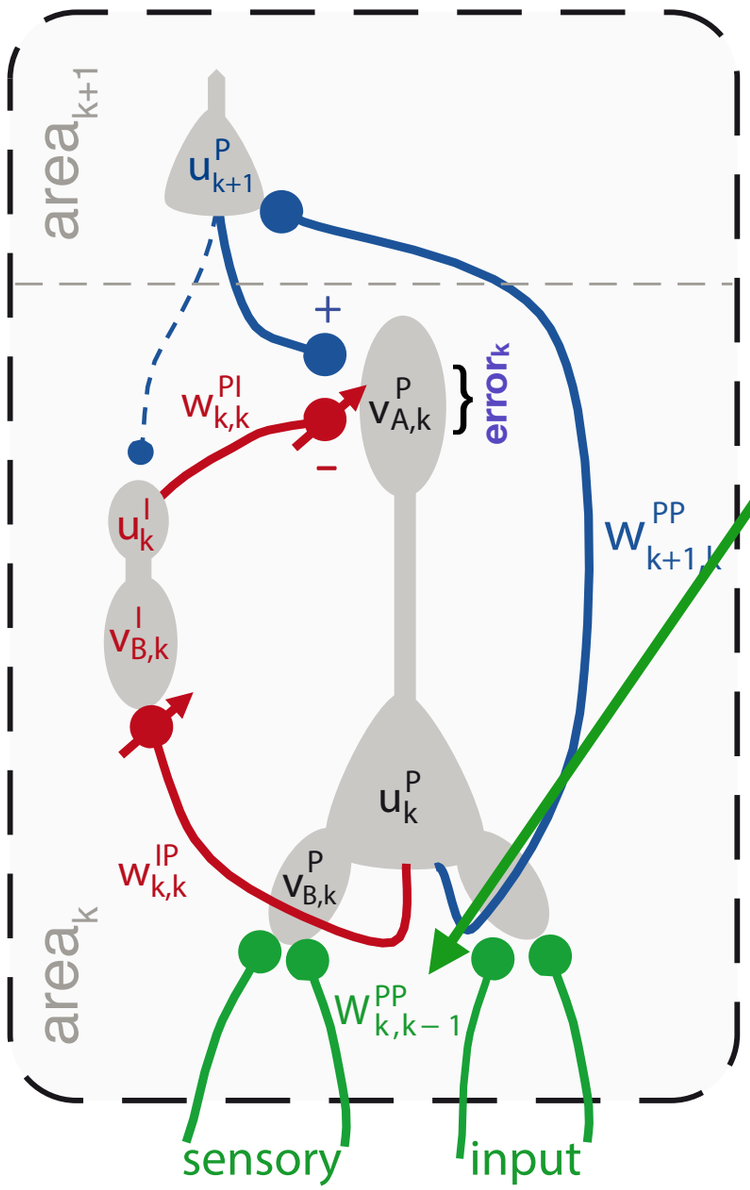
$$u^P_k \sim \underbrace{(u^P_{k+1} - u^I_k)}_{v^P_{A,k} \sim \text{error}} + v^P_{B,k})$$

Sacramento et al. 2018 (NIPS)

Dendritic error microcircuits

local error-correcting learning rules



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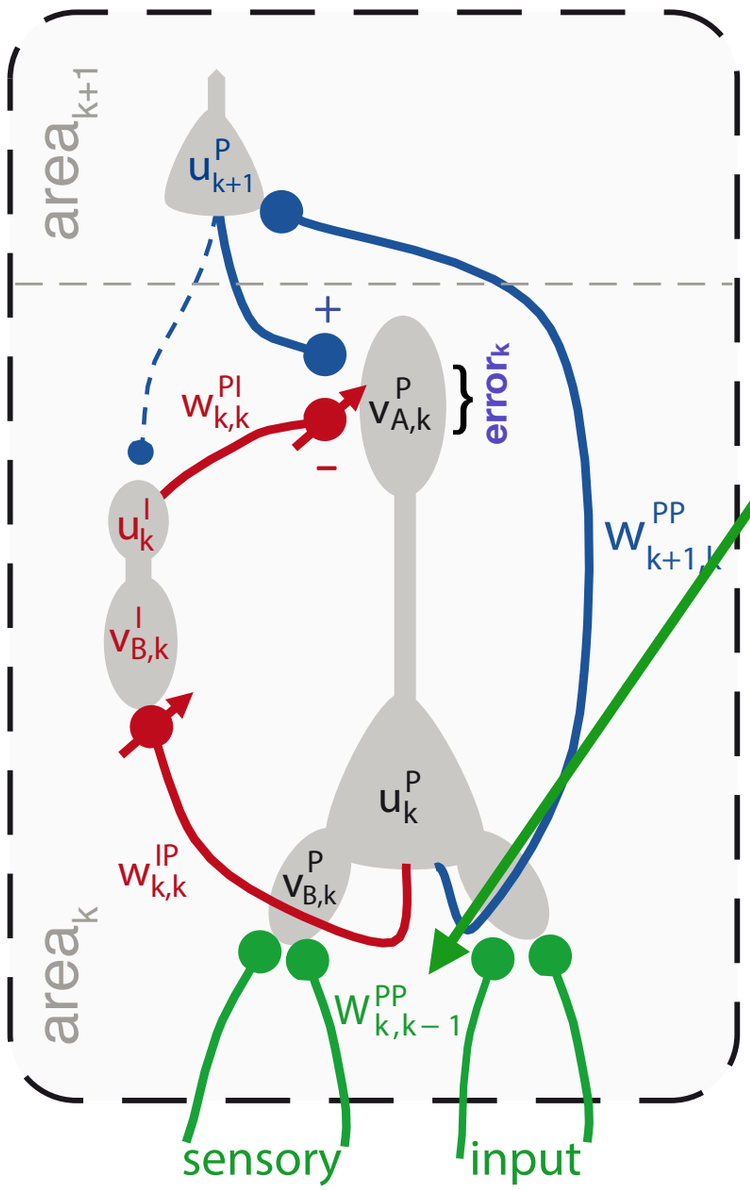
$$\frac{d}{dt} w^{PP}_{k,k-1} \sim \eta \underbrace{(u^P_{k+1} - u^I_k)}_{v^P_{A,k} \sim \text{error}} r^P_{k-1}$$

Note: To a first approximation the model dynamics and learning rules are equal to backprop (see details in paper).

Sacramento et al. 2018 (NIPS)

Dendritic error microcircuits

local error-correcting learning rules



Learning rule for bottom-up synapses:

$$\frac{d}{dt} w^{PP}_{k,k-1} \sim \eta \underbrace{(u^P_{k+1} - u^I_k)}_{v^P_{A,k} \sim \text{error}_k} r^P_{k-1}$$

Similar to **backprop learning rule**:

$$\Delta w^{PP} \sim \eta \, \text{error}_k \, r^P_{k-1}$$

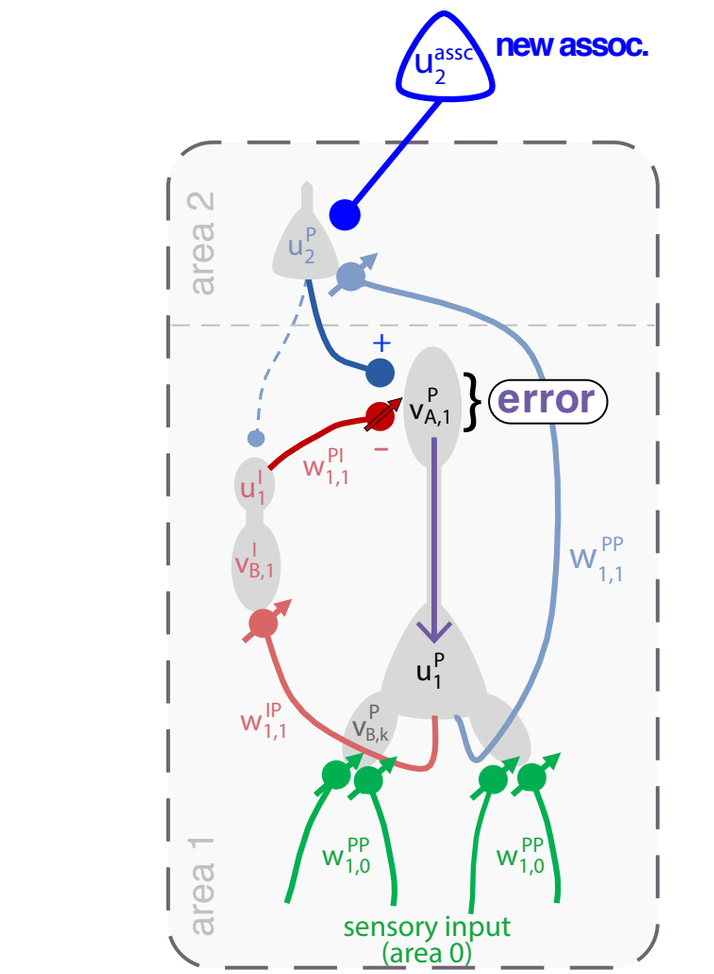
$$r^P_{k-1} \sim u^P_{k,k-1}$$

error_k : Error (or gradient) for area *k* backpropagated through all the areas above it

To a first approximation the model dynamics and learning rules give backprop. see details in paper:

Sacramento et al. 2018 (NIPS)

Dendritic error microcircuits approximate backprop: toy task

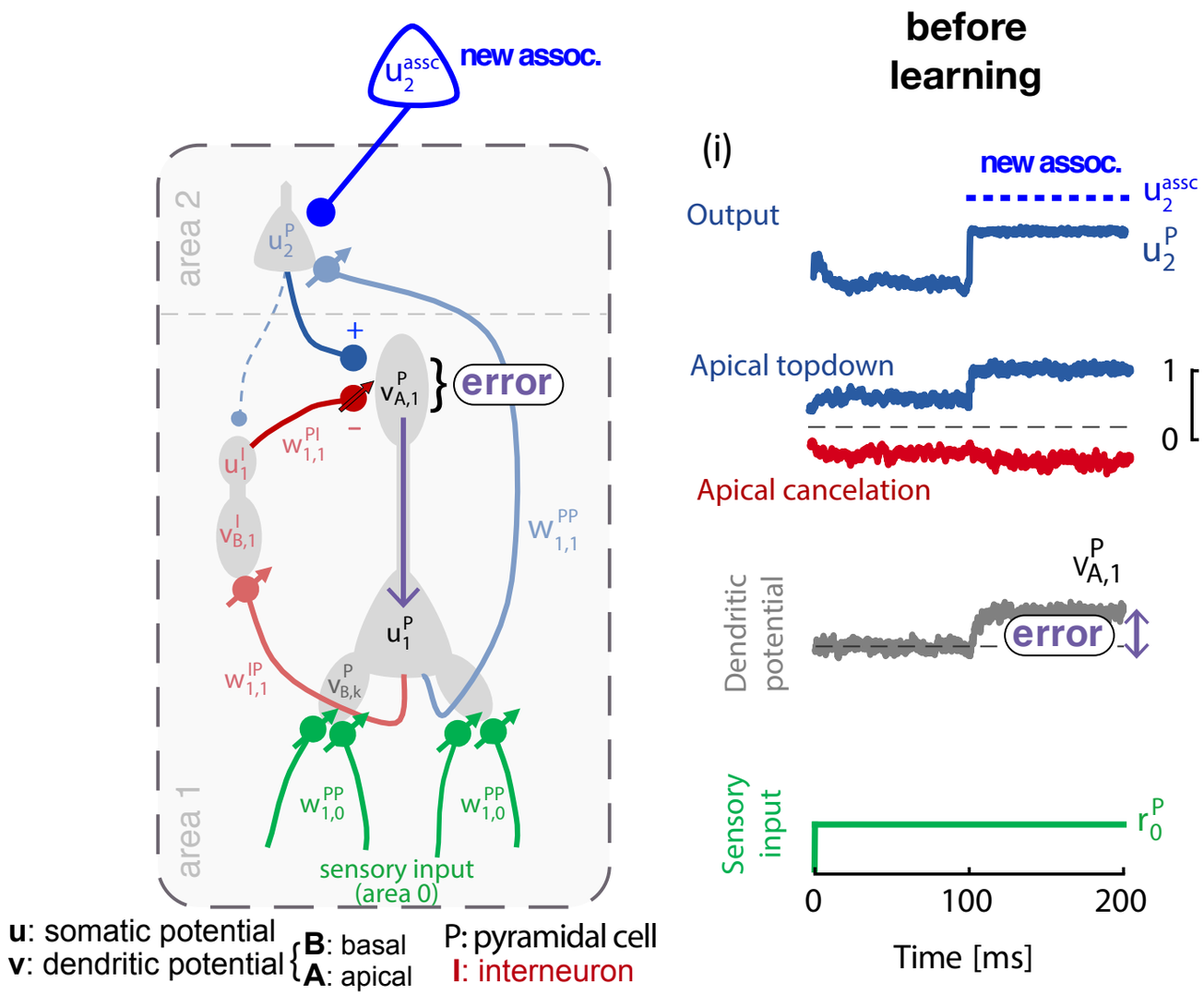


u: somatic potential
v: dendritic potential { **B**: basal, **A**: apical

P: pyramidal cell
I: interneuron

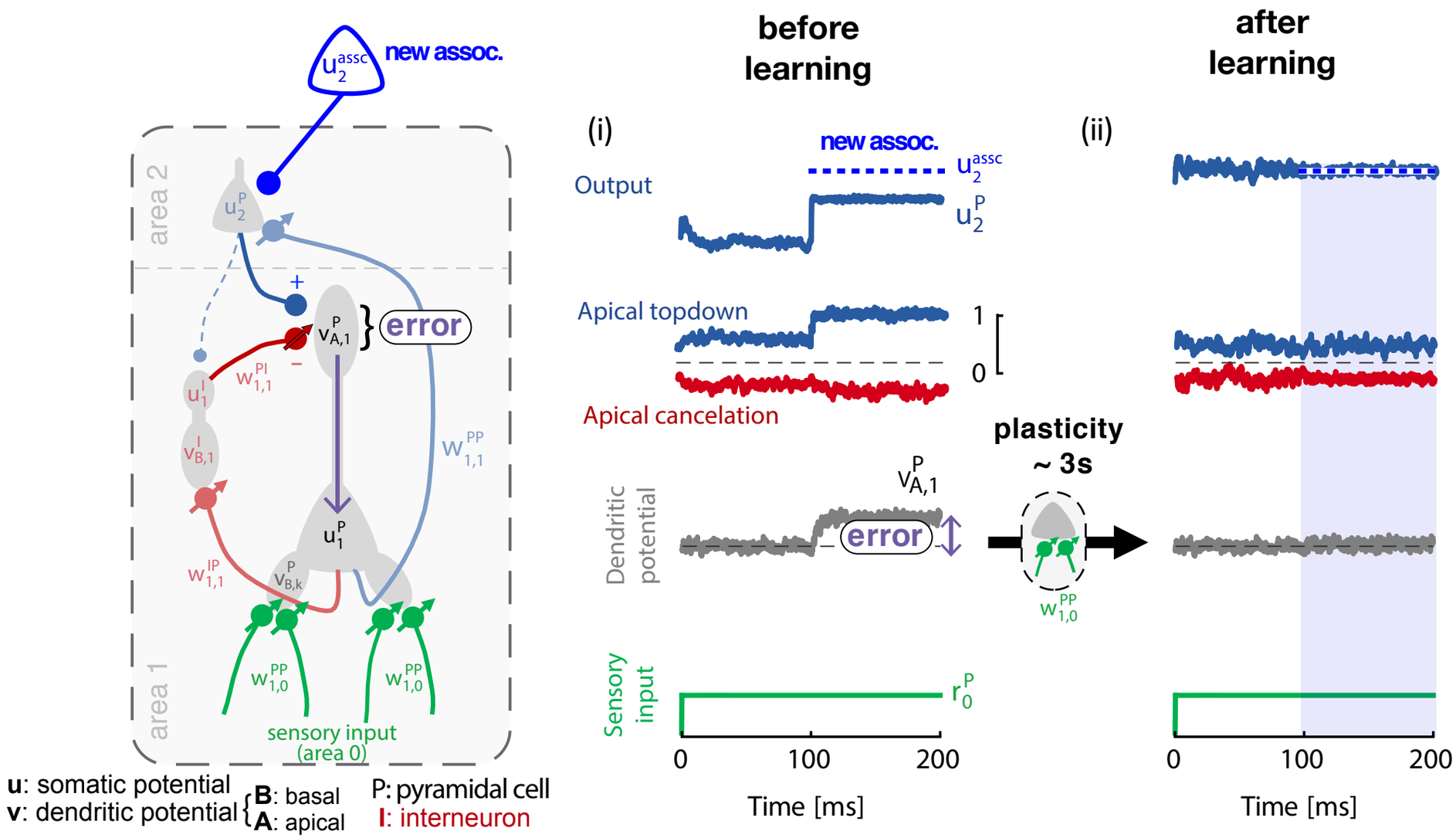
Sacramento et al. 2018 (NIPS)

Dendritic error microcircuits approximate backprop: toy task



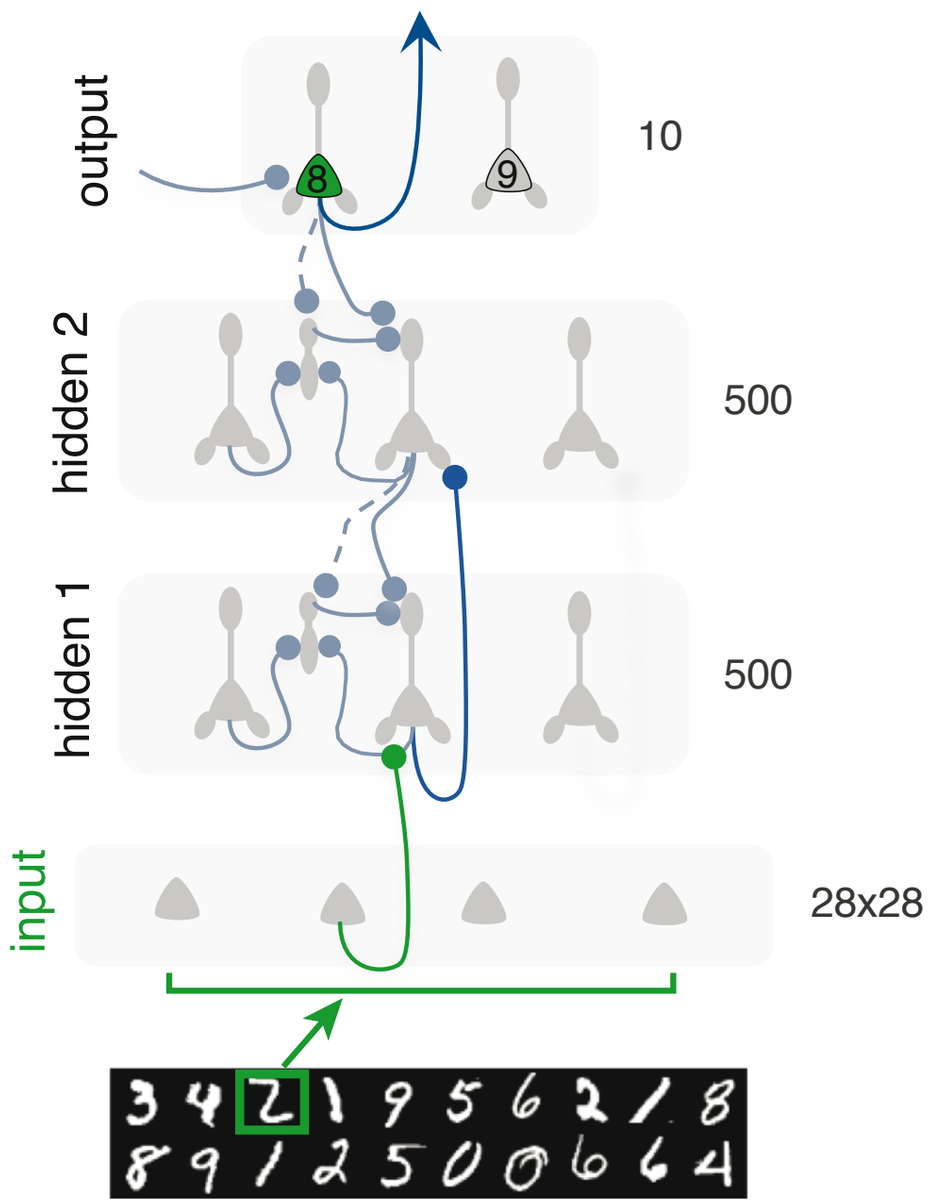
Sacramento et al. 2018 (NIPS)

Dendritic error microcircuits approximate backprop: toy task



Sacramento et al. 2018 (NeurIPS)

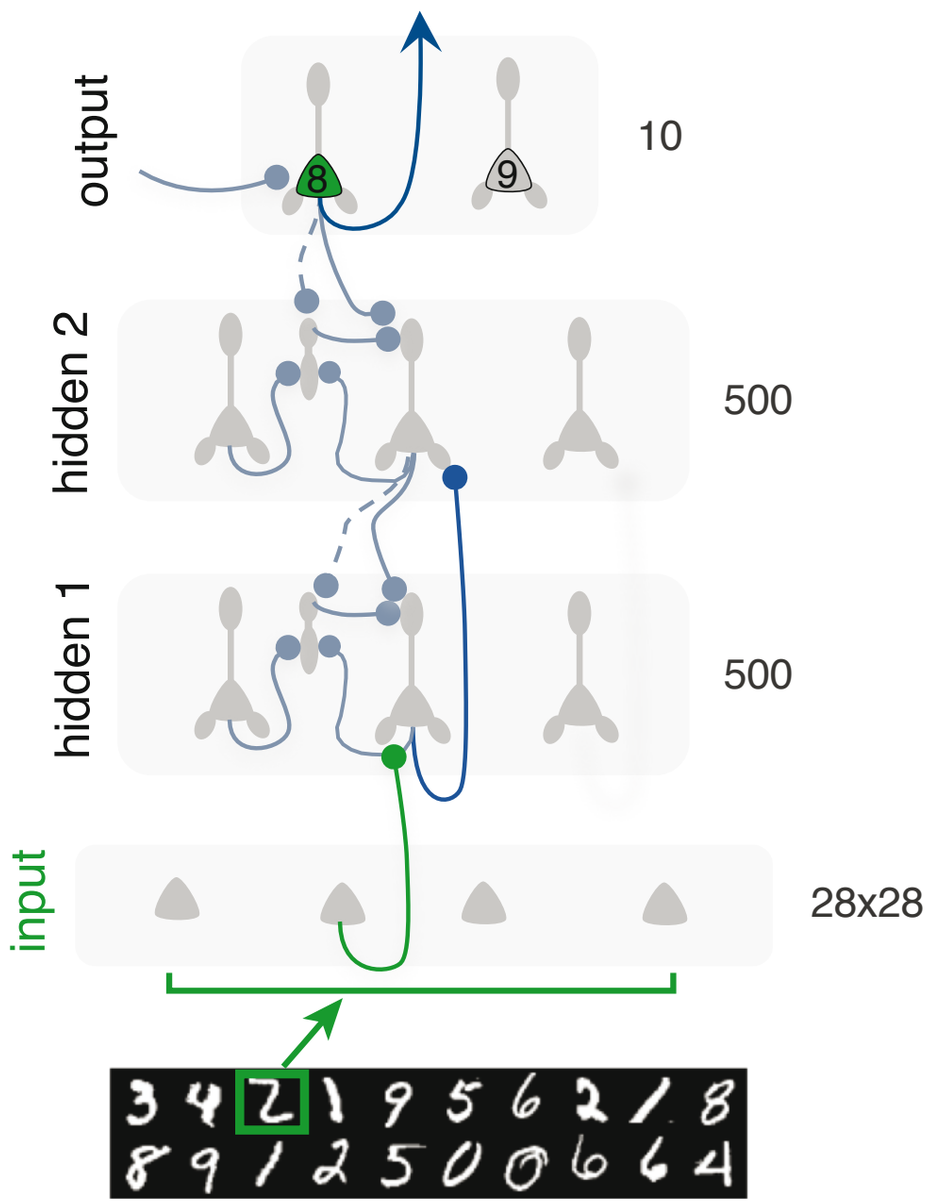
Dendritic error microcircuits learn to classify hand-written digits



MNIST handwritten digit images

Sacramento et al. 2018 (NIPS)

Dendritic error microcircuits learn to classify hand-written digits



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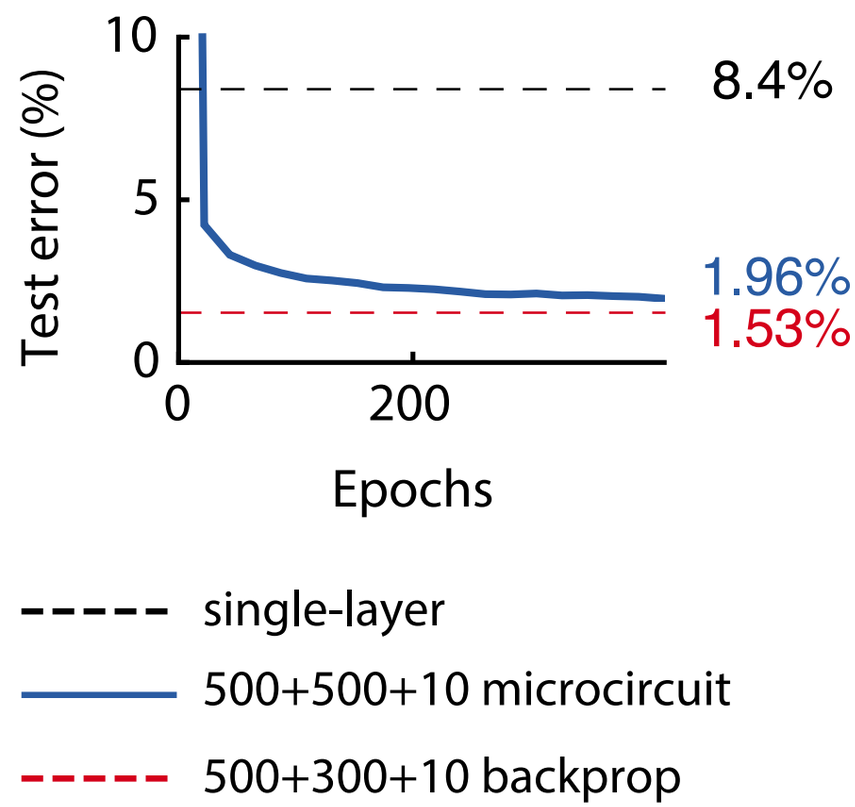
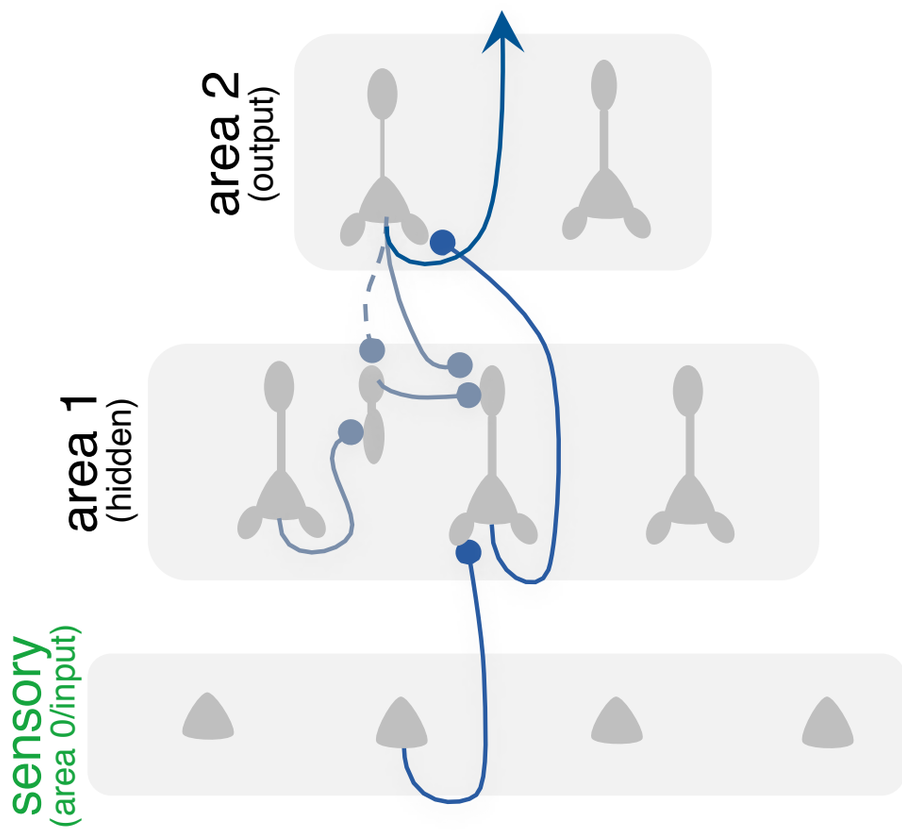


Sacramento et al. 2018 (NIPS)

Dendritic error microcircuits approximate backprop



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 Guerguiev et al. eLife 2017

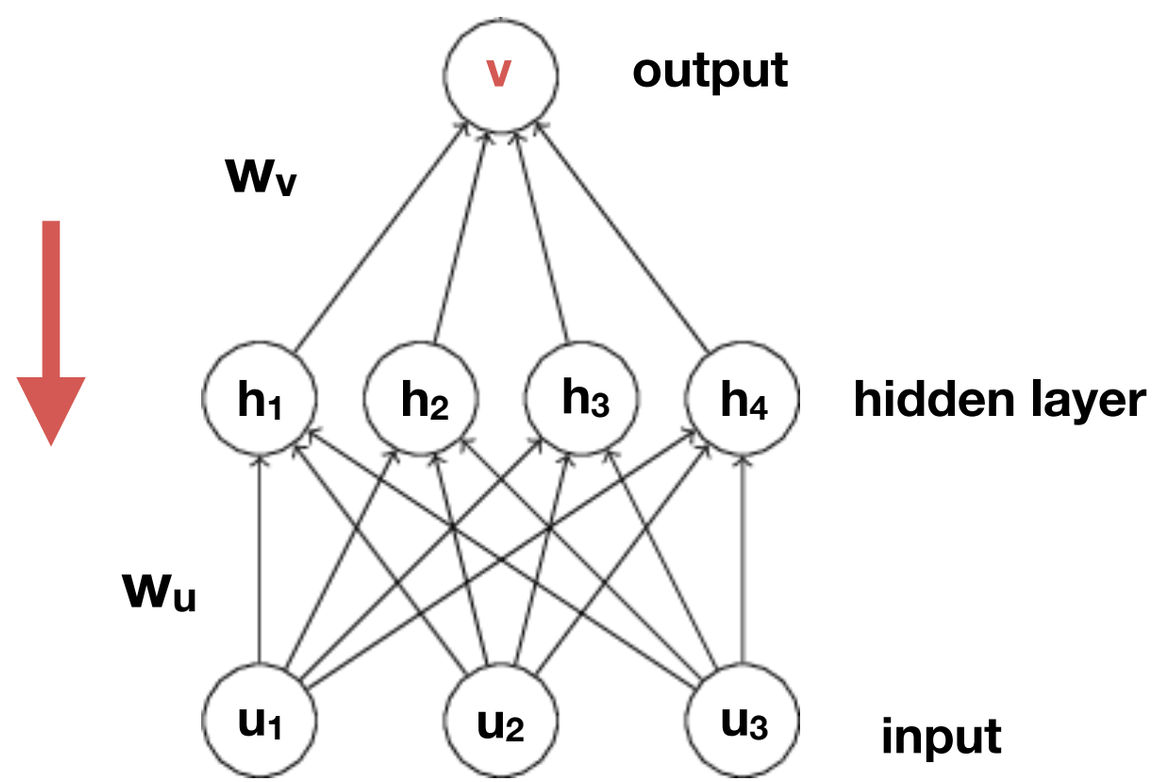
Sacramento et al. 2018 (NIPS)

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.

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



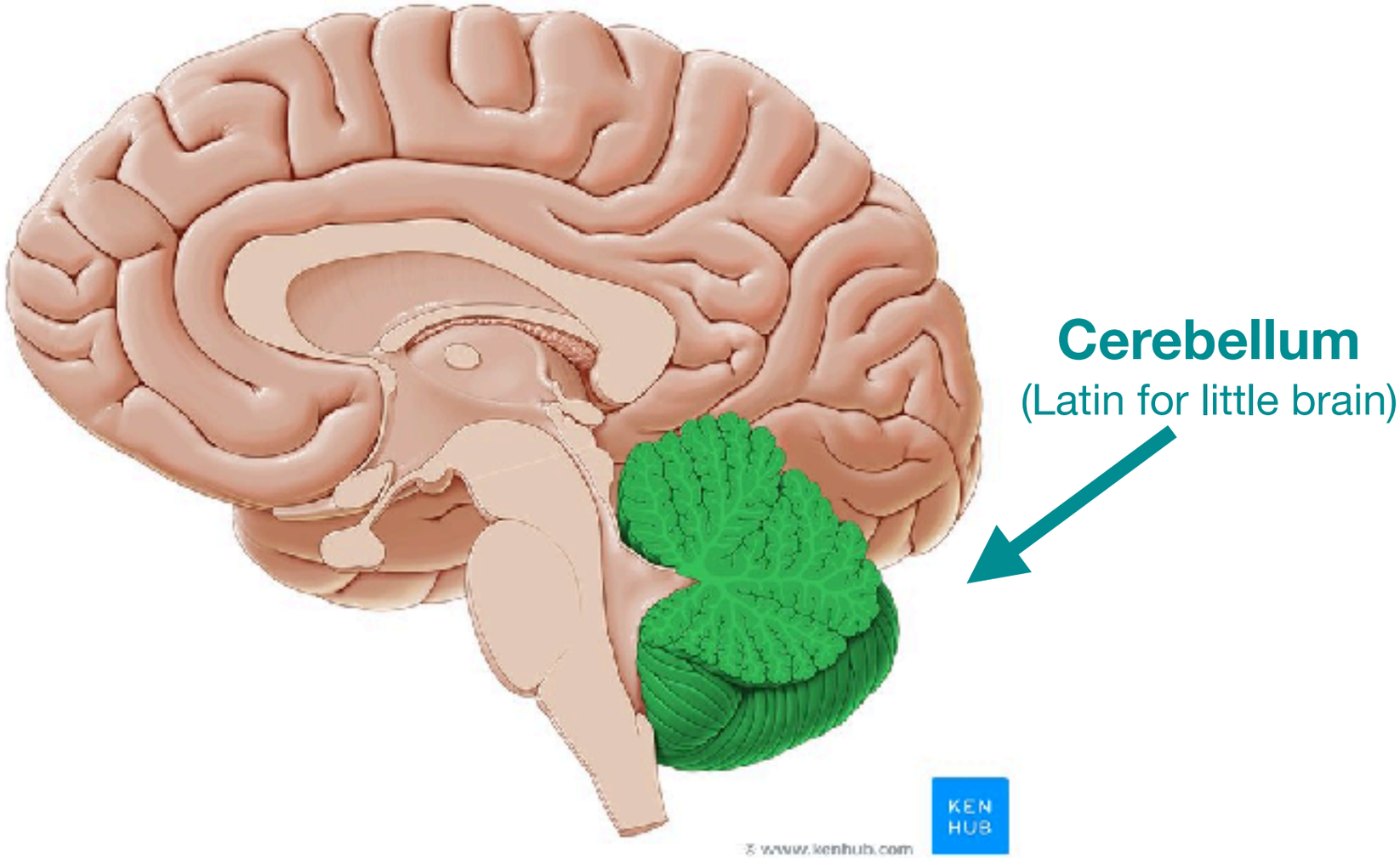
The backpropagation algorithm
and why it is at odds with biology
6. Target

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).

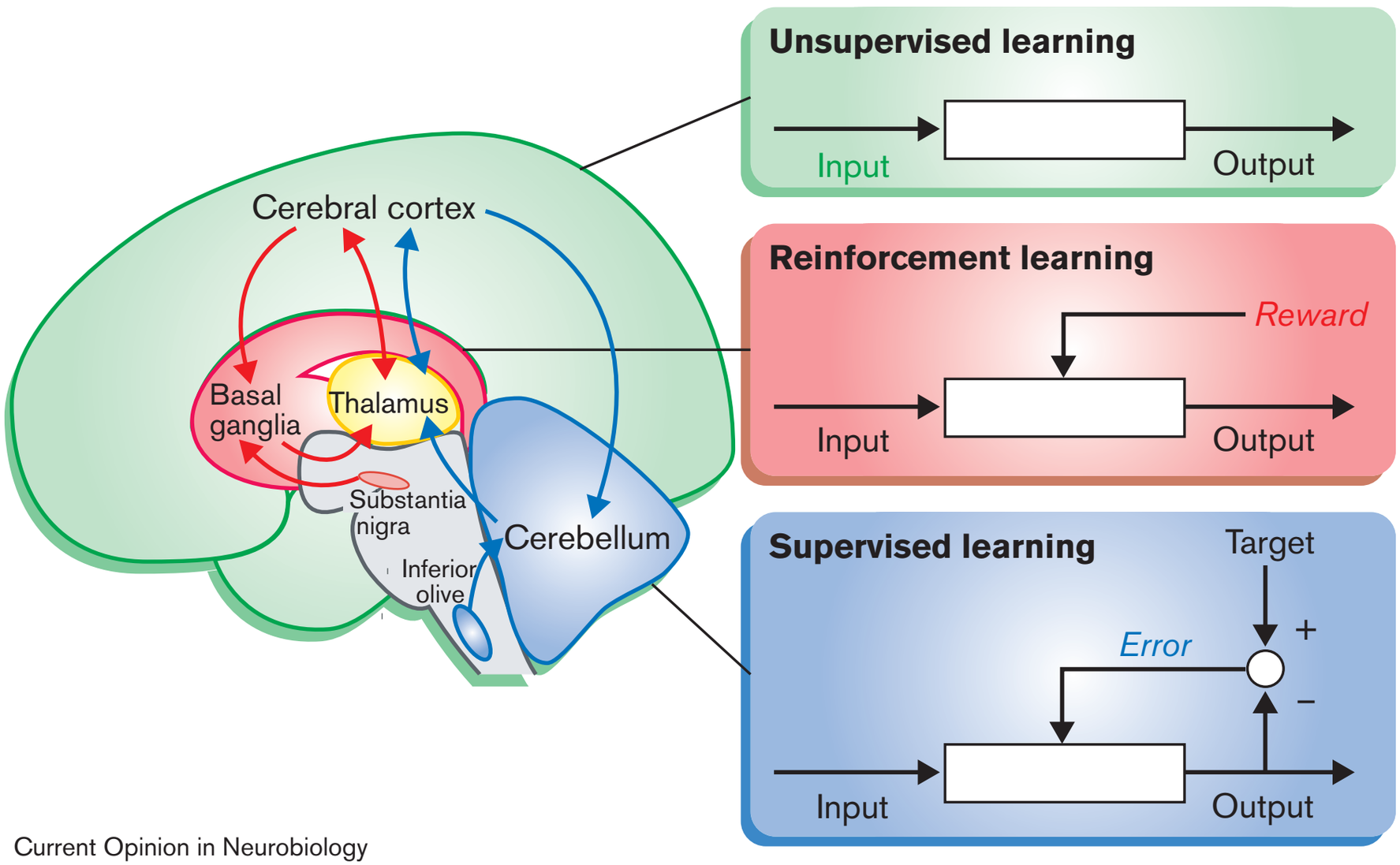
Cerebellum, the brain supervisor?

The **cerebellum** (small brain in Latin) has a stereotypical structure, and the most numerous neuron in the brain (Purkinje cells). It is classically involved in motor error correction, but growing evidence suggests to be also involved in regulating many other aspects of behaviour.



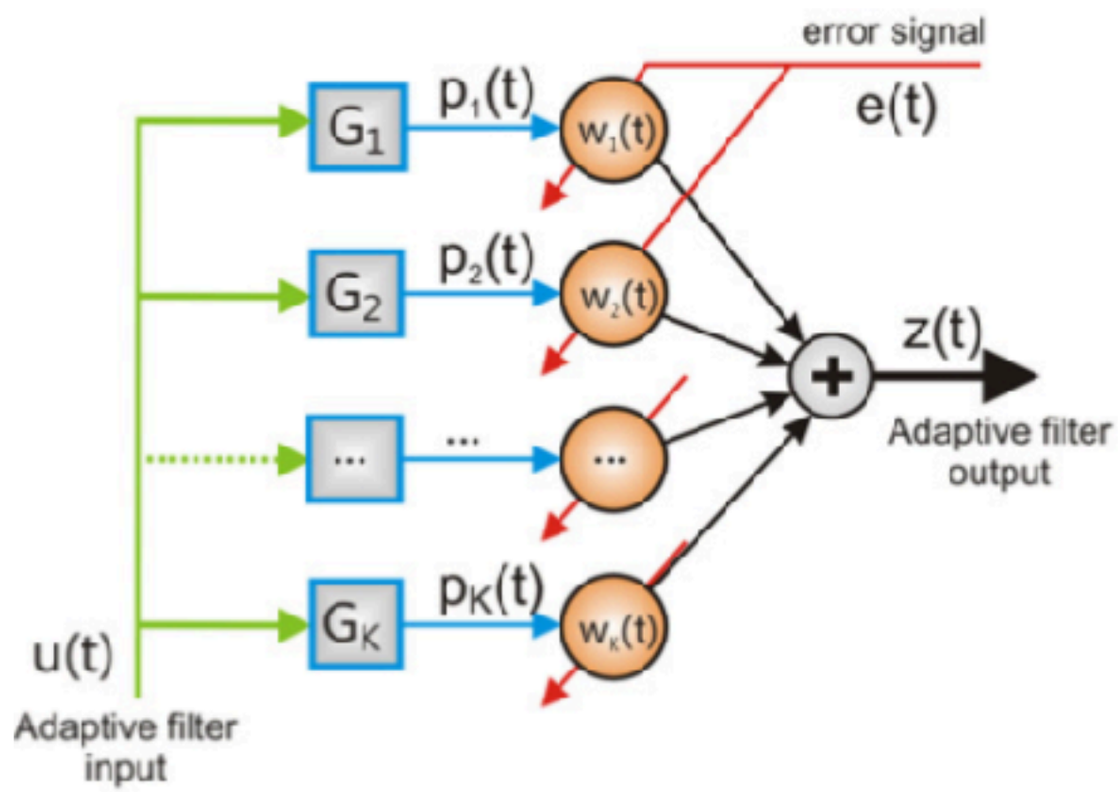
Cerebellum, the brain supervisor?

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



Doya, Curr Opin Neurobiol (2000)

Cerebellum as a adaptive filter/controller



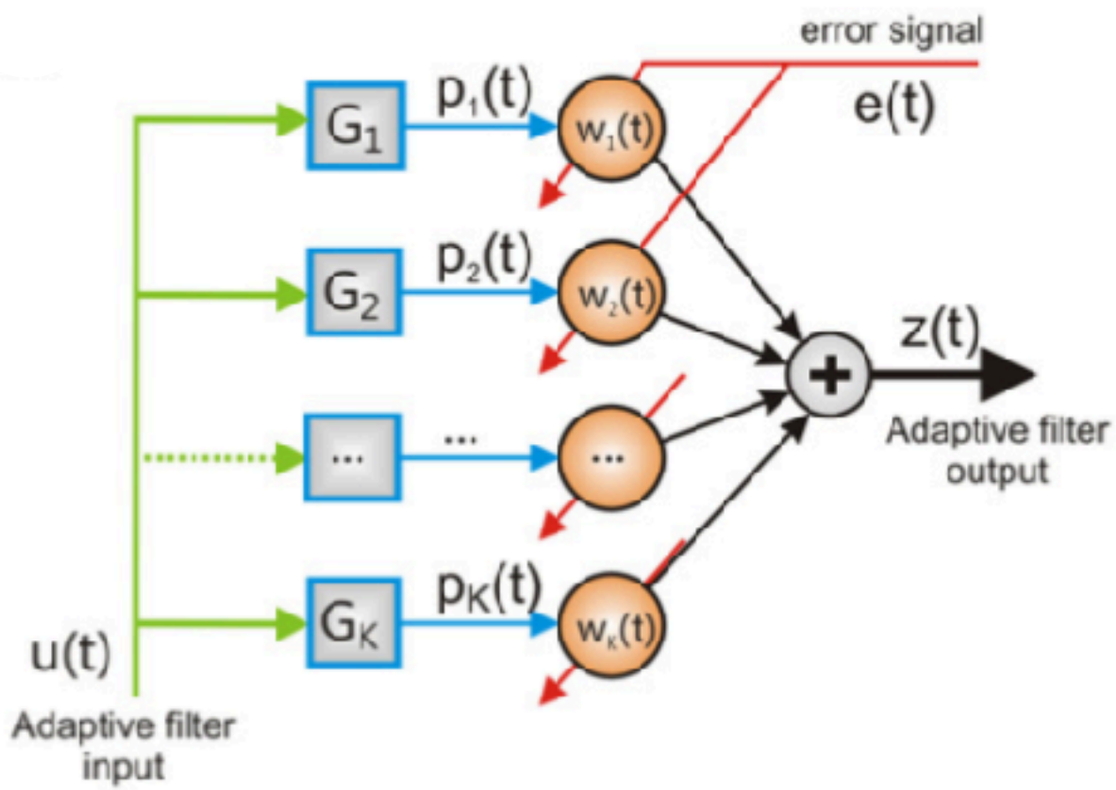
Task: Online control (via z(t)) of movements to achieve a desired outcome (learning occurs via e(t))?

Porrill et al. Neural Networks (2013)

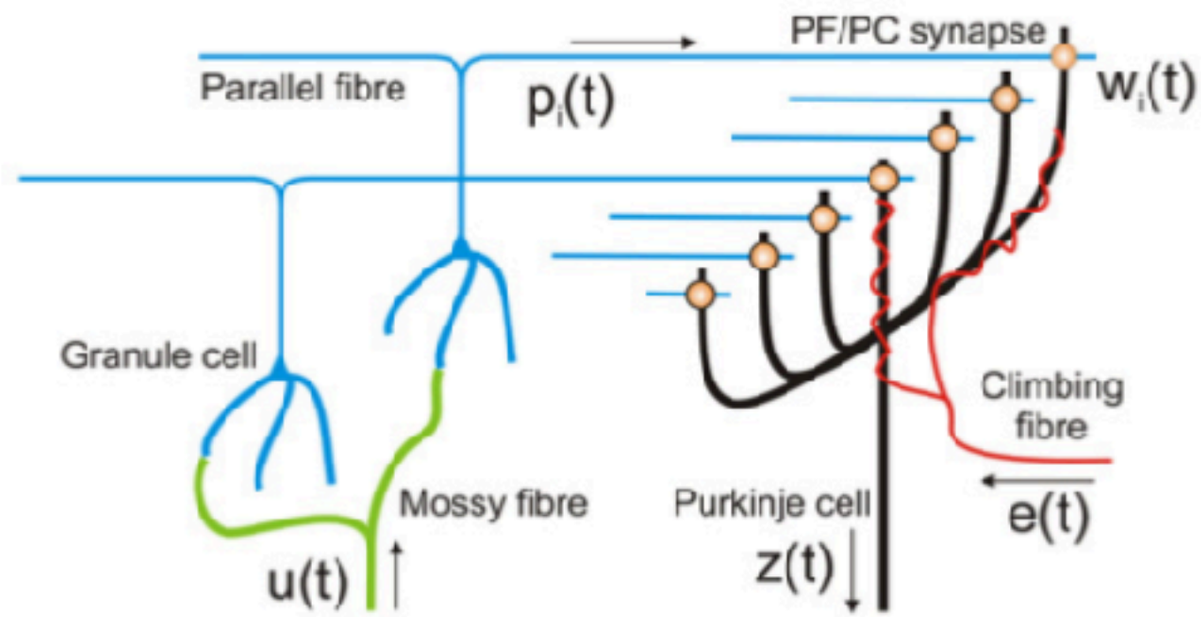
Raymond and Medina, Annual Rev Neurosci (2018)

Cerebellum as a adaptive filter

Controller/filter model



Neurobiology of the cerebellum



Sensory input/ motor copy

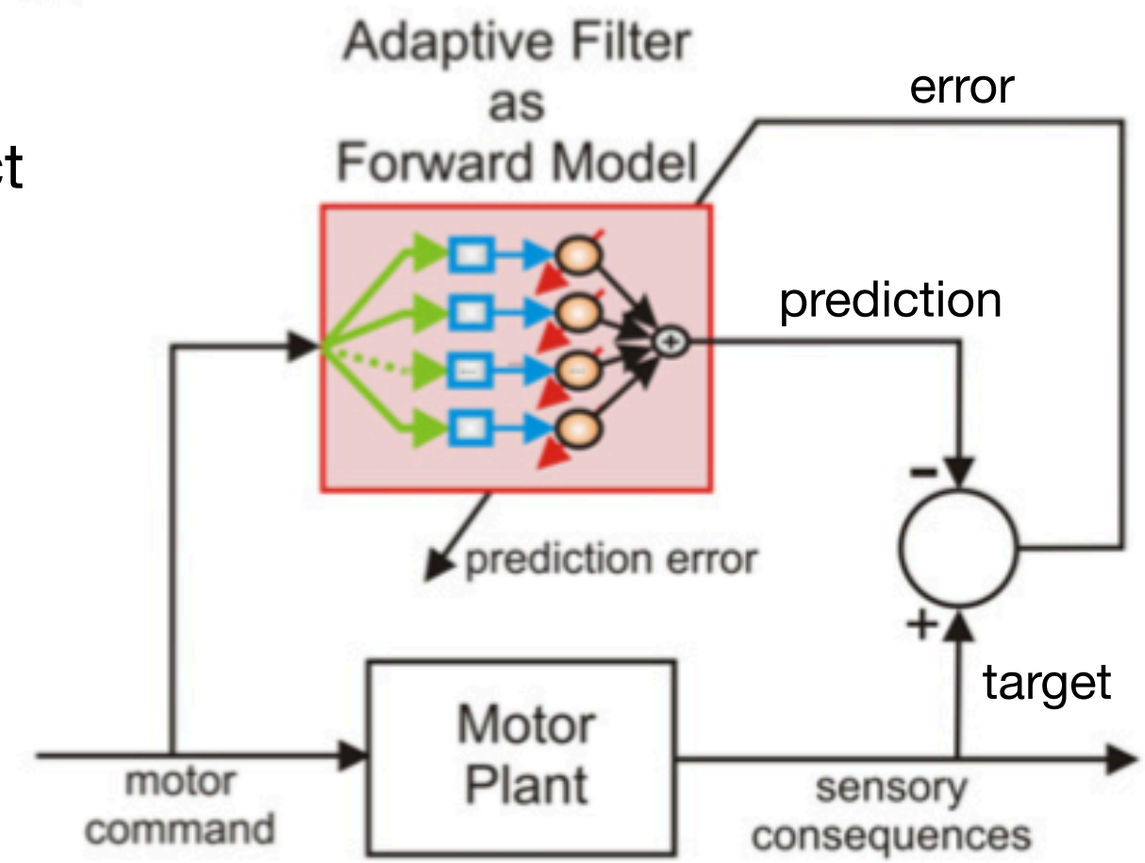
Prediction

Porrill et al. Neural Networks (2013)

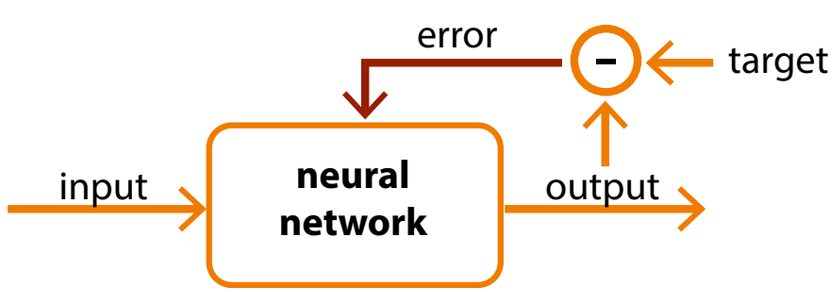
Raymond and Medina, Annual Rev Neurosci (2018)

Forward model of the cerebellum

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



Similar to:

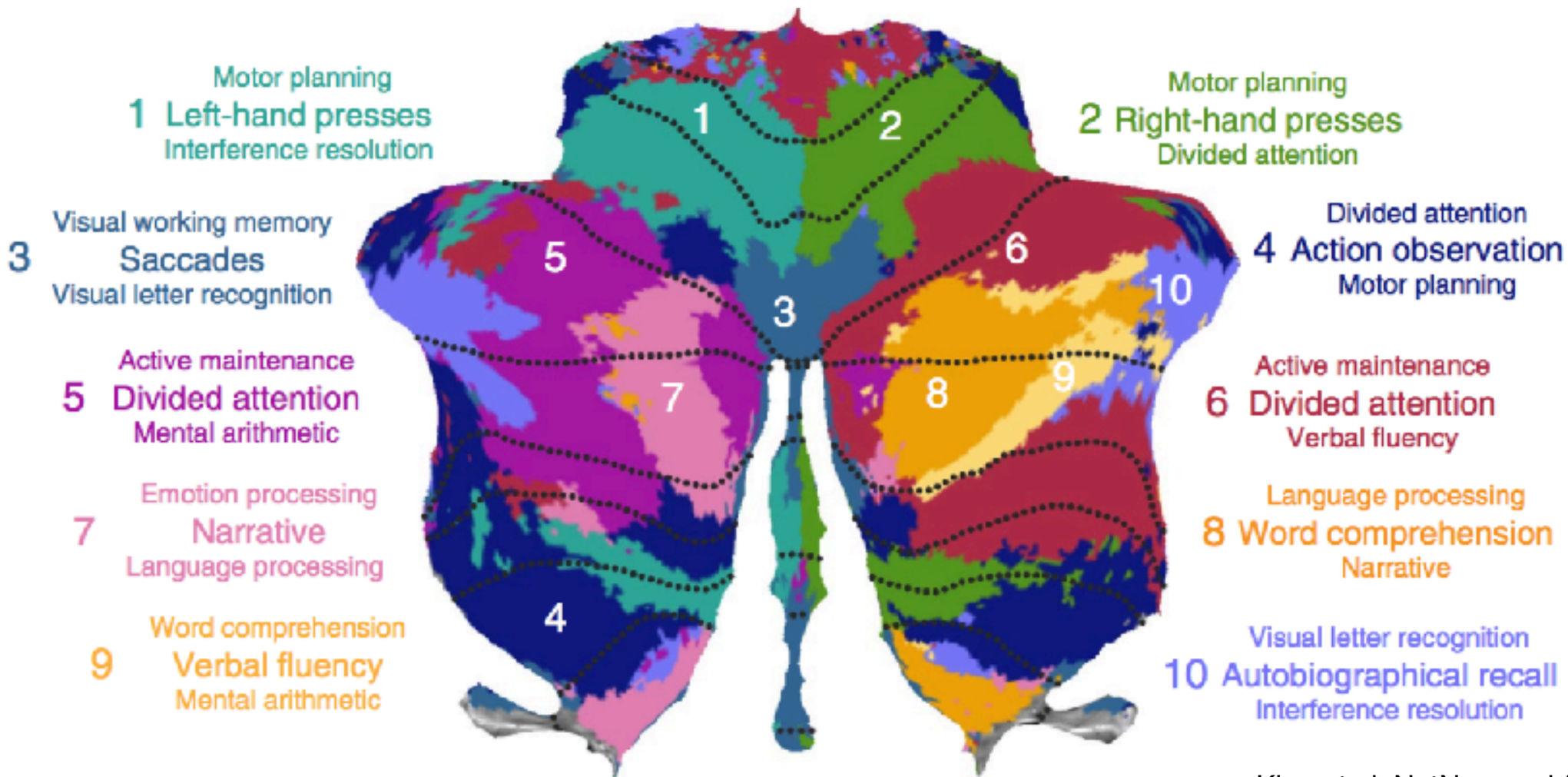


Porrill et al. Neural Networks (2013)

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

1. **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 uses supervised learning**

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

Questions?

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., NIPS (2018) (shows how dendritic microcircuits may approximate backprop)

Upcoming lectures

- L11[6]: Neural circuits and learning: introduction
- L12[6]: Visual system: deep learning?
- **L13[7]: Supervised learning & backprop**
- **L14[7]: Unsupervised learning**
- L15[9]: Reinforcement learning
- L16[9]: Temporal processing & recurrent neural networks
- L17[10]: Recurrent neural networks
- L18[10]: Brain vs machine: meta-learning and inductive bias
- L19-20[11]: Neural data analysis (by Cian)
- L21-22[12]: Revision week