Functional Models of Plasticity

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Outline of Lecture

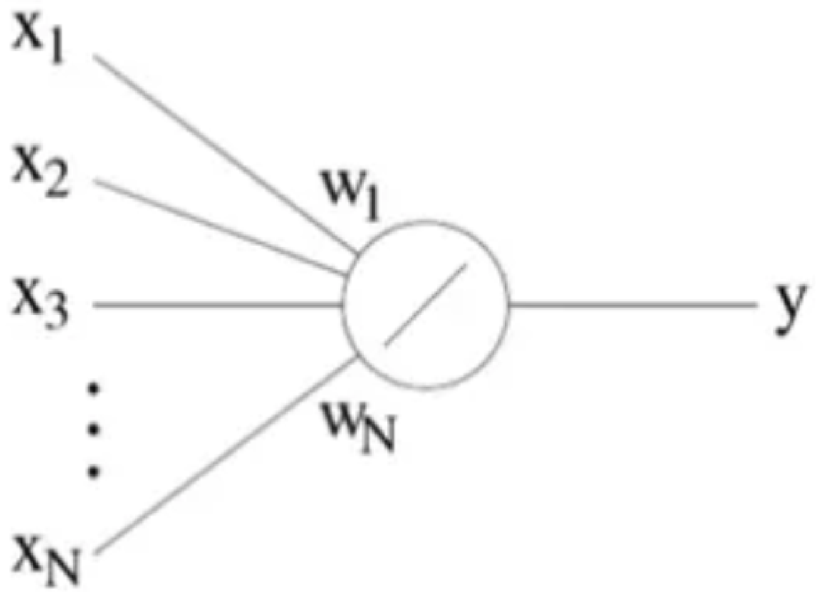
- Hebb’s rule
- The covariance rule
- Oja’s Rule
- Synaptic normalisation
- Learning with multiple neurons

Functional Models of Plasticity

- What does Hebbian learning actually do?
- Can we use Hebbian learning to do something useful?
- What are the challenges/obstacles to implementing Hebb’s rule?
- Are there parallels between unsupervised learning algorithms and learning rules in the brain?
- What are the underlying algorithms/computations that synaptic plasticity implements, and how do they perform learning and memory?

Simplest Case: Linear Feedforward Model

Linear Unit:



$$y = \mathbf{w}^T\mathbf{x}. \quad \text{(linear unit)}$$

- Given a set of input patterns **x**, what weights **w** will be learned?
- First need to specify the mathematical form of the learning rule $\Delta\mathbf{w} = f(\mathbf{x}, y)$

Hebb’s Rule

- How can we operationalise Hebbian learning?
- “Cells that fire together, wire together”, is not a mathematically precise statement - there are many possibilities

- Simplest choice:

- Consider one neuron with firing rate *y* in response to multiple inputs with rates ***x***

Linear model of neural activity

$$y = \sum_{i=1}^{N} w_i x_i = \mathbf{w} \cdot \mathbf{x}$$

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Multiplicative model of Hebb's rule

$$\Delta w_i = \epsilon y x_i$$

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Multiplicative model of Hebb's rule

$$\begin{aligned} \Delta w_i &= \epsilon y x_i \\ &= \epsilon x_i \sum_{j=1}^{N} w_j . x_j \end{aligned}$$

Consequences of Hebb's Rule

- Assume we present *M* input patterns μ once each:

$$\Delta w_i = \epsilon \sum_{\mu=1}^{M} x_i^{\mu} \sum_{j=1}^{N} w_j x_j^{\mu}$$

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- Or we can write in continuous time:

$$\boxed{\tau \frac{d\mathbf{w}}{dt} = Q . \mathbf{w}}$$

Assumptions/Approximations of Hebb's Rule

- We have made several unrealistic assumptions and approximations:

- Linearity of output neuron
- Weights can change sign with learning
- Weight updates are linear/multiplicative
- Can only produce LTP (not LTD) if firing rates are positive
- Weight updates are unbounded/can become arbitrarily large

- These give the plasticity rule undesirable properties, as we will see

Long-Term Behaviour of Hebb's Rule

- Hebb's rule follows the differential equation:

$$\tau \frac{d\mathbf{w}}{dt} = Q.\mathbf{w}$$

- This is a kind of linear dynamical system, which we studied previously. It has solution:

$$\mathbf{w}(t) = \sum_k c_k \mathbf{v}_k e^{\lambda_k t}$$

- Where $\mathbf{v}_k, \lambda_k$ are eigenvectors and eigenvalues of *Q*.

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- But *Q is* symmetric and therefore has positive real eigenvalues, so all terms must grow exponentially
- Hebb's rule is therefore unstable, and always leads to exponentially growing weights

The Covariance Rule

- If firing rates are positive, Hebb's rule can only generate LTP, not LTD…
- Perhaps synapses only update when activity is above a certain threshold:

$$\Delta w_i = \epsilon(x_i - \langle x_i \rangle)(y - \langle y \rangle)$$

$$\langle x_i \rangle = \frac{1}{M} \sum_\mu x_i^\mu$$

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- Averaging over patterns, this gives the same rule as before but with *Q* now the *covariance* matrix of input patterns:

$$\boxed{\tau \frac{d\mathbf{w}}{dt} = Q.\mathbf{w}} \qquad Q_{ij} = \sum_\mu (x_i^\mu - \langle x \rangle)(x_j^\mu - \langle x \rangle)$$

What does Hebb's/Covariance Rule Learn?

- In the long run limit, all terms in the sum grow to infinity, but the term with largest eigenvalue dominates:

$$\mathbf{w}(t) = \sum_k c_k \mathbf{v}_k e^{\lambda_k t} \xrightarrow{t \to \infty} c_1 \mathbf{v}_1 e^{\lambda_1 t}$$

- In other words, this learning rule picks out the eigenvector of the matrix *Q* with largest eigenvalue

- The interpretation depends on the matrix *Q* (different for Hebb vs covariance rule)

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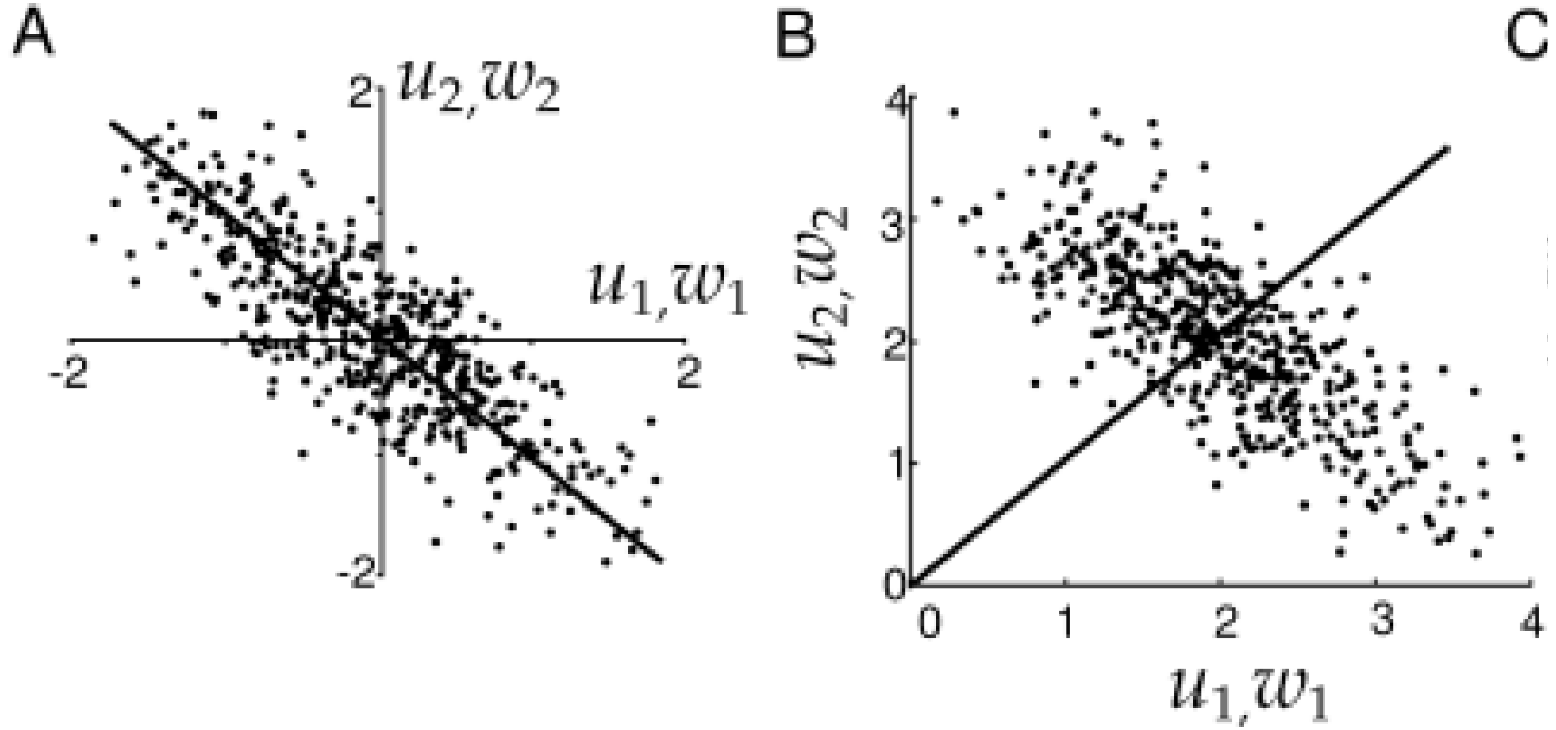

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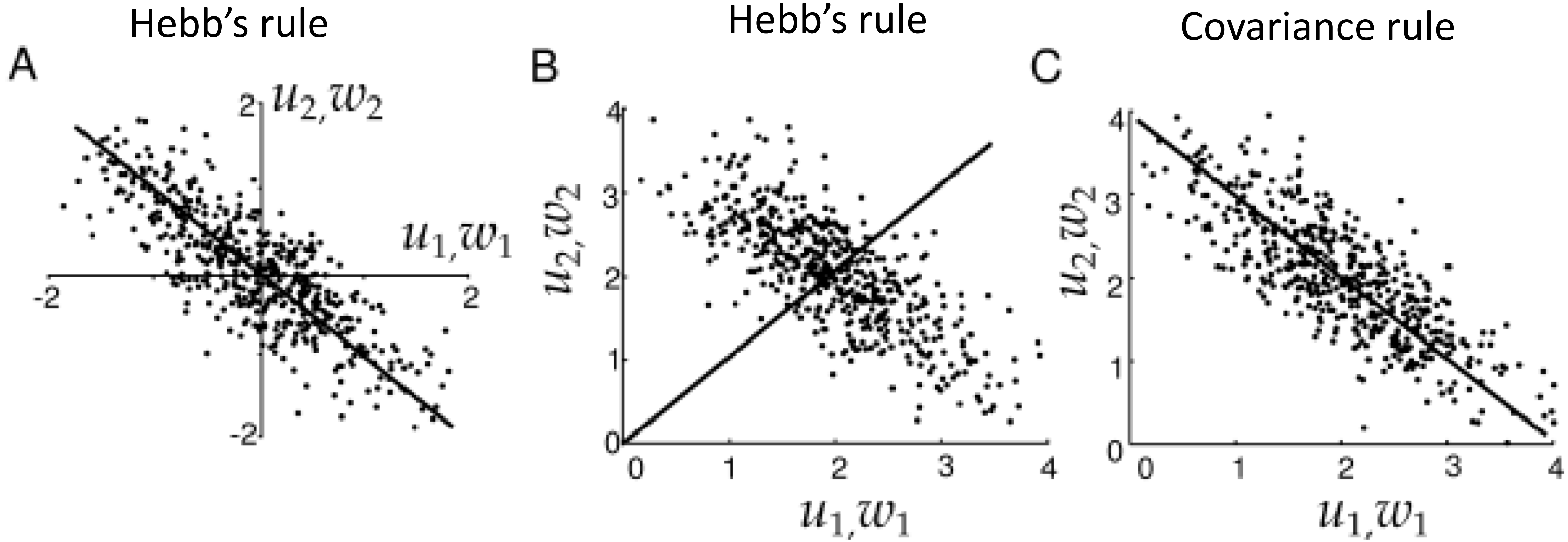
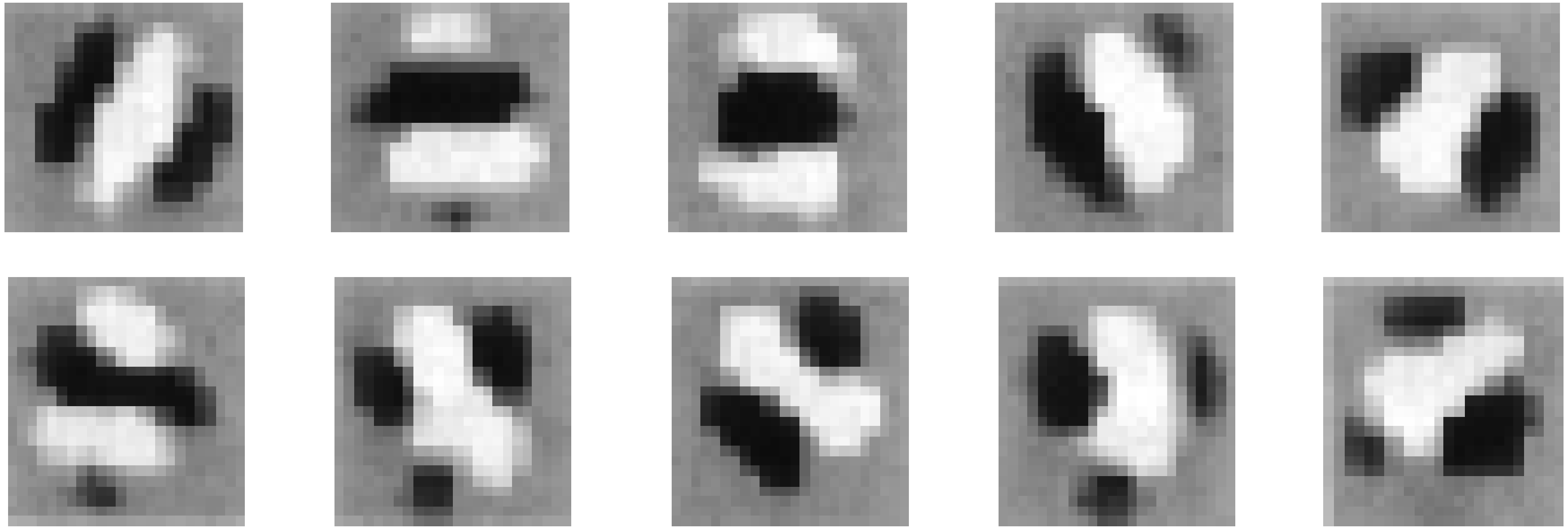


- If data aren't zero mean, Hebb's rule is sensitive to the mean
- Covariance rule picks out largest eigenvector of input covariance matrix
- This is just principal component analysis (but with only one PC)

Hebbian Learning of Orientation Tuning

- Hebbian learning in a neuron receiving multiple LGN ON-OFF receptive field inputs
- Requires some special constraints and assumptions, but can learn Gabor receptive fields

Receptive fields learned via Hebbian plasticity



Miller, 1994 (see Dayan and Abbott Ch. 8)

Summary of Hebb/Covariance Rule

- Both Hebb's rule and covariance rule are unstable, leading to exponentially growing weights

- Hebb's rule can only produce LTP, but covariance rule can produce both LTP and LTD

- Both rules cause the neuron to learn the dominant eigenvector of Q (but Q is slightly different for the two rules)

- A major limitation of both rules is the lack of stability/competition between synapses (all synapses update independently and grow to infinity)

Normalisation

- We saw that Hebb/covariance rule leads to infinite weights
- In reality, weights must saturate/be regulated somehow
- Simplest choice: impose a hard limit

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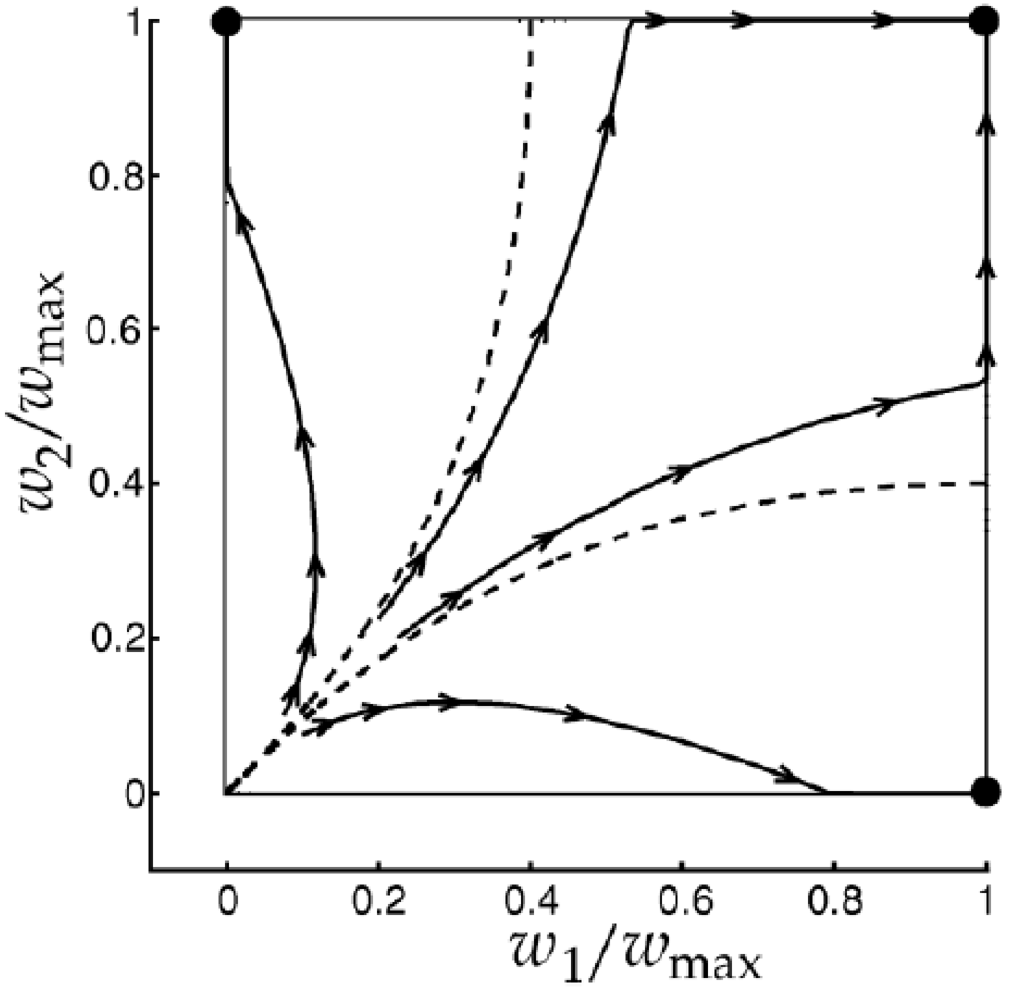

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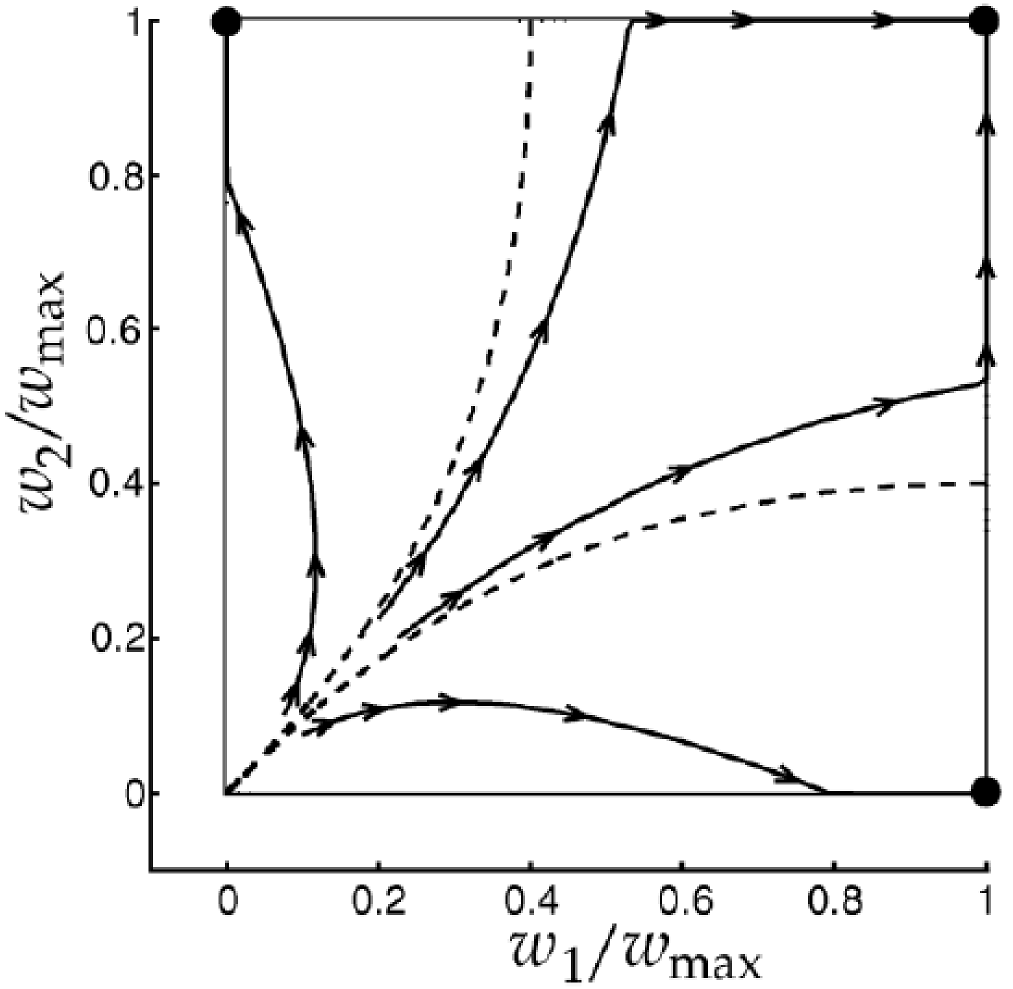

- For two inputs with anticorrelated *Q,* can produce 3 stable weight configurations depending on initial conditions
- For positively correlated input *Q*, both weights must saturate (not shown)

Multiplicative and Subtractive Normalisation

- Instead of a hard bound, add a term to the weight update to scale down weights over time

$$\tau \frac{d\mathbf{w}}{dt} = Q.\mathbf{w} - \gamma(w)\mathbf{w}(t)$$

Multiplicative and Subtractive Normalisation

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- Simplest options: multiplicative or subtractive scaling

$$\tau \frac{d\mathbf{w}}{dt} \quad = \quad Q.\mathbf{w} - \gamma(w)\mathbf{w}(t) = Q.\mathbf{w} - [\frac{\mathbf{n}.Q.\mathbf{w}}{\mathbf{n}.\mathbf{w}}]\mathbf{w} \;\; \text{Multiplicative}$$

$$\mathbf{n} = (1, 1, 1, ...)$$

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$$= Q.\mathbf{w} - \epsilon(w)\mathbf{n} = Q.\mathbf{w} - [\frac{\mathbf{n}.Q.\mathbf{w}}{\mathbf{n}.\mathbf{n}}]\mathbf{n} \text{ Subtractive}$$

$$\mathbf{n} = (1, 1, 1, ...) \quad \mathbf{n} \cdot \mathbf{w} = \sum_i w_i \quad \frac{d\mathbf{n} \cdot \mathbf{w}}{dt} = 0 \implies \sum_i w_i = \text{const}$$

Divisive and Subtractive Normalisation

- Both multiplicative and subtractive keep sum of weights constant in time (easy to verify analytically)

- This implicitly sets *competition* between weights – one weight can only increase if others decrease

- Such competition is called *heterosynaptic* plasticity. Heterosynaptic plasticity requires weight changes even when pre-synaptic neuron is inactive; homosynaptic plasticity requires coactivity of pre and post.

- In practice, subtractive normalisation is more strongly competitive than multiplicative normalisation (and unrealistically so)

Oja’s Rule

- Normalisation and synaptic competition can also be implicitly incorporated using other learning rules

- One example is Oja’s rule: $\Delta w_i = \epsilon(x_i y - w_i y^2)$

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$$
\begin{aligned}
\Delta w_i &= \epsilon \sum_{\mu,j} w_j x_i^\mu x_j^\mu - \epsilon \sum_{\mu,j,k} w_i w_j w_k x_j^\mu x_k^\mu \\
0 &= Q.\mathbf{w} - (\mathbf{w}.Q.\mathbf{w})\mathbf{w}
\end{aligned}
$$

(at steady state)

- The quadratic term normalises/stabilises the weights
- The final equation tells us that, at steady state, the weights ***w*** are an eigenvector of *Q*

Oja's Rule

- Oja's rule implements a kind of multiplicative normalisation
- Oja's rule is not biologically motivated – what is the interpretation of the quadratic dependence on y?
- Theoretical motivation: Oja's rule does PCA (finding the first PC) while maintaining stable weights
- This alone is ultimately not very powerful – if we have multiple such neurons, they will all learn the same PC…

Learning with Multiple Neurons

- Oja's rule for one neuron is: $\Delta w_i = \epsilon(x_i y - w_i y^2)$

- Now assume we have *M* neurons. To avoid all neurons learning the same PC, we can add "interactions" between the neurons:

$$\Delta w_{ij} = \epsilon(x_i y_j - y_j \sum_{k=1}^{M} w_{ik} y_k)$$

- We can interpret these interactions as lateral inhibition (sort of…)
- This rule can be shown to learn the first *M* principal components of the input covariance matrix *Q*

Other Learning Rules: Generative Models

- Earlier in the course we looked at sparse coding, ICA, and predictive coding

- Each of these has a learning rule for the weight updates

- However, in those models the learning rules are derived from an underlying generative model of the input data

- There are two approaches to studying plasticity: 1) incorporate detail from biology and study the consequences 2) start from a generative model/objective function and derive a learning rule

Summary

- Hebbian learning picks out the dominant eigenvector of the input
- Hebbian learning is unstable without mechanisms to limit synaptic weights
- Competition between weights can help with stability and learning of interesting patterns
- Competition between neurons can lead to different neurons learning different input patterns
- Synaptic learning rules can be linked to unsupervised algorithms (e.g., PCA)

Bibliography

- Lecture notes Ch. 13

- Dayan and Abbott Ch. 8