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coincidence detection. So now the output neuron will only fire for this pattern of input. If there is a different pattern, the conduction delays will not fit and the firing will not summate.

The network looks like a perceptron, but the firing rate is substitute for timing of spikes and the connection weights are substituted by conduction delays.

The Hopfield's network poses a problem as there is no biologically plausible way of implementing different conduction delay lines in the brain.

Standard neural networks have to normalise inputs to do scale-invariant recognition, normalisation could be achieved by feedback inhibition, but this still poses a problem. Standard neural networks are strength dependent rather than pattern dependent. A strong input neuron would usually have a strong connection and a weak input neuron would have a weak connection and make less of a difference to the final output. This weak input is not fundamental in deciding what the outcome is. However, if the network is pattern based, then the weak input would be crucial in identifying the overall input.

This means standard neural networks cannot do scale-invariant recognition. Linear pattern separation, e.g. perceptrons, are not suitable; head direction and place cells, the network that tunes to respond at a given absolute value also cannot compute scale-invariant recognition.

2. Describe the main features of Hebbian learning rules, and their use in competitive learning and the learning of topographic maps (6 marks).

Hebb's law states the connection between neurons that are active at the same tend to be strengthened- cells that fire together, wire together. This is a form of long-term potentiation. When the cells don't fire together, long-term depression occurs. Hebbian learning is a form of unsupervised learning meaning that there is no transfer or feedback about right or wrong inputs.

Competitive learning is another form of unsupervised learning. There are recurrent inhibition weights to start with, then input pattern is presented. This makes an output news neire. There are recurrent inhibition between output neurons so there is only one 'winner'. Then the connection weights between neuron and the input neuron that fires are increased. Hot han learning. Normalisation of connection weights then occurs and the next pattern is presented.

In the learning of topographic maps, e.g. in the retina, the same ideas apply except that there is not only one winner. In Wilshaw and Von der Malsburg's model (1976), the connections between nearby output neurons are excitatory, but the connections between far apart output neurons are inhibitory. This means nearby neurons to the winner neuron learn to respond to similar input patterns. In Kohonen's feature map (1982), the Hebbian learning rule is modified so that weights to outputs neighbouring the winner are also modified using a 'neighbourhood function'.

Wij \rightarrow Wij + ϵ F (i,k) (Xjn – Wij)

Describe the delta rule and its use in the perceptron learning algorithm (5 marks).

The delta rule changes the connection weights according to:

$W_{ij} \rightarrow W_{ij} + \epsilon X_j^n (t_i^n - o_i^n)$

 $(t_i^n - o_i^n)$ is known as delta, it is the error made by output i for the input pattern n. The delta rule changes weights to reduce this error. So basically, the delta rule changes connections weights to make a specific input pattern lead into a specific output pattern.

The perceptron learning algorithm teaches the output neuron to recognise a particular pattern of activity from the input neurons. You can present patterns to the perceptron, the patterns that are meant to be detected will have target output value 1, and the other foil patterns will have target value 0. For each pattern, apply the delta rule. So that if the target value is bigger than the actual output value, then the connection weight increases, if target value is smaller than the actual output value the connection weight decreases. After many presentations of the whole training set, the best linear discrimination of targets from foils can be found.

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BVCs for shorter distances, more broad tuning for longer distances. BVCs receives some cues from the environment about distances of the boundaries. Place fields are modelled as the threshold sum of 2 or more BVC firing fields. Because BVCs don't care about the actual orientation of the rat, place cells don't either. Place cell firing in new environmental layouts can be predicted using BVCs. BVCs subsequently found in the subiculum of the hippocampal formation (Lever et al. 2009).

Sharp's model takes learning aspects, but not sensory aspects. The BVCs model is good at capturing sensory aspects, but it doesn't take learning into account.

Biologically speaking, synaptic modification is required to explain place cell firing. Place field stability in a novel environment depends on NMDA receptors in CA3 (Kentros et al. 2000) and robustness to cue-removal (Nakazawa et al. 2002). Also slow experience-dependent 'remapping' of the place cell representation occurs (Lever et al. 2002) and place cells distinguish locations with experiences (Barry et al, 2006). They both show synaptic plasticity which is not taken into account in Sharp's or the BVCs model.

Head direction cells: Ranck (1984) first discovered them in the dorsal presubiculum. The cell fires whenever the rat's head points in a specific direction relative to the environment, irrespective of its location or whether it is moving or still. The primary correlate is the azimuthal orientation of the head in the horizontal plane.

Grid cells: found in layer 2/3 of medial entorhinal cortex, discovered by Hafting et al. (2005). They are similar to place cells in that they have localised regions in which they fire, but grid cells fire in a hexagonally symmetric pattern, which tessellates the environment in which the rat is placed. Nearby gird cells have grids of similar orientation and scale, but they are shifted to tile the environment. Grid scale increases as the cell move from dorsal to ventral medial entorhinal cortex.

Describe how these cells could be used to provide a spatial navigation system enabling the rate return to a previously visited location (8 marks).

Path integration is used to enable the rat to return to a previous viewed location.

Zhang (1996) and McNaughton et al. (1996) are cred that the patterns on activity shown by the place cells formed a continuous attractor. Imagine an environment bound by the t-al (1)-axis with a rat running around in it. Take every place cell in CA3 and mactiver position onto this grad that environment. Each cell's location reflects the location of its firing field in the environment (note that mit can be how it is arranged in the brain). As rats runs around this environment, the place cells that have place fields next to each other will be wired together due to Hebbian learning, as those two cells are likely to fire together when a rat is in/near that particular place field location. So a map is formed where each cell in this network is strongly connected to those next to it and weakly connected to those far away. Then the firing rate can be plotted on the z-axis, then the network encodes the position of the animal. The bump (z-axis plot) indicates the rat's location and moves as the rat moves. The bump is a Gaussian shape. If the connections between all the cells solely reflect the cells separation, so that nearby cells have stronger connections than far apart ones, the set of 'bumps' of activation form a continuous attractor. This continuous attractor network ensures that only a single location is represented. The cells at the current location excite the cells near it, but inhibit the cells far away to ensure that there is only one 'bump', i.e. one location represented in the brain.

To do path integration, the bump just have to be moved along according to self-movements, which gives the internal code for one's location.

The bumps can be moved by adding asymmetric connections in a particular direction. This makes the activity bump shift in that direction, with a speed proportional to the strength of the asymmetric connections. Shifter cells have been proposed (Burgess and Barry 2014). There are two types of shifter cells. The first one bases firing rate on direction and speed. These shifter cells gives input to the synapses between the place cells- multiplicative synapses. The multiplicative synapses introduces asymmetrical connections to make the bump of activity shift along that direction. It does this by increasing the synaptic strength of one place cell with another place cell. However, multiplicative cells do not exist in the brain.