Marr's Theory of the Hippocampus
Part II: Effect of Recurrent Collaterals

Computational Models of Neural Systems
Lecture 3.4

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September, 2013
Two Layer Model Insufficient?

• Marr claimed the two layer model could not satisfy all the constraints he had established concerning:
  - number of stored memories $n$
  - number of cells
  - sparse activity: $n \alpha_i \alpha_{i-1} \leq 1$
  - but patterns not too sparse for effective retrieval
  - number of synapses per cell: $S_i \alpha_i N_i \geq 20 N_{i-1}$

• He switched to a three layer model, with evidence cells, codon cells (“hidden units”), and output cells.

• The output cells had recurrent collaterals.
The Three-Layer Model

$P_1$: $1.25 \times 10^6$ Evidence Cells

$P_2$: 500,000 Codon Cells

$P_3$: 100,000 Output Cells

Representation of event $E_0$

Noisy cue $X$

Pattern $C$ induced by collaterals
The Collateral Effect

- Let $P_i$ be a population of cells forming a simple representation.
- Each cell can learn about 100 input events.
- Population as a whole learns $n = 10^5$ events.
- Hence $\alpha_i$ must be around $10^{-3}$.
- We require $n \alpha_i \alpha_{i-1}$ to be at most 1.
  Estimated value based on the above is 0.1.
- Hence we can let $P_{i-1} = P_i$ and use recurrent collaterals to help clean up the simple representation.
- Result: external input to $P_i$ need not be sufficient by itself to reproduce the entire simple representation.
Parameters of the Three-Layer Model

- $P_1$ has $1.25 \times 10^6$ cells divided into 25 blocks of 50,000.
- $P_2$ has 500,000 cells divided into 25 blocks of 20,000.
- $P_3$ has a single block of 100,000 cells.
- Let number of synapses/cell $S_3 = 50,000$.
- Let $x_i$ be number of active synapses on a cell, i.e., the number used to store one event.
- $n\alpha_i$ is the number of events a cell encodes.
- Probability of a synapse being potentiated is:

$$\Pi_i = 1 - (1 - x_i/S_i)^{n\alpha_i}$$
Parameters of the Three-Layer Model

\[ \Pi_i = 1 - \left(1 - \frac{x_i}{S_i}\right)^{n\alpha_i} \]

\[ x_i = \sum_{r \geq R_i} P_i(r) \cdot r \]

- \( P_i(r) \) is the probability that a cell in layer \( i \) has exactly \( r \) active afferent synapses.
- From the above, we have \( L_3 = \alpha_3 N_3 = 217 \), and \( \alpha_3 = 0.002 \).
- If we want useful collateral synapses in \( P_3 \), must have \( n(\alpha_3)^2 \leq 1 \).
- So with \( n = 10^5 \) events, we have \( \alpha_3 = \) at most 0.003.
Retrieval With Partial/Noisy Cues

- Let $P_{30}$ be the simple representation of $E_0$ in $P_3$.
- Let $P_{31}$ be the remaining cells in $P_3$.
- Let $C_0$ be the active cells in $P_{30}$ representing subevent $X$.
- Let $C_1$ be the active cells in $P_{31}$ (noise).
- Note that $C_0 + C_1 = \text{pattern size } L_3$. 

![Diagram of retrieval with partial/noisy cues](image-url)
Collateral Connections

- The **statistical threshold** is the ratio $C_0:C_1$ such that the effect of collaterals is zero: $C_0:C_1 = C_0':C_1'$.
- Collaterals help when statistical threshold is exceeded.
- Calculating $C_0':C_1'$ is a bit tricky because there is both a subtractive and a divisive threshold; see Marr §3.1.2.
Collateral Effect in $P_{3'}$

- Let $b$ be an arbitrary cell in $P_{3'}$.
- $Z_{3'}$ is probability of a recurrent synapse onto $b$.
- Number of active recurrent synapses onto $b$ is distributed as $\text{Binomial}(L_3; Z_{3'})$ with expected value $L_3 Z_{3'}$.
- Probability that $b$ has exactly $x$ active synapses onto it:
  $$P_{3'}(x) = \binom{L_3}{x} \cdot Z_3^x \cdot (1 - Z_3)^{L_3 - x}$$

- $b$ is either in $P_{30}$ or not. We'll consider each case:
• Suppose $b$ is in $P_{31}$, so not in $P_{30}$.

• Of the $x$ active synapses onto $b$, the number of facilitated synapses $r$ is distributed as $\text{Binomial}(x; \Pi_{31})$.

• Probability that exactly $r$ of the $x$ active synapses onto $b$ have been modified when $b$ is in $P_{31}$ is:

$$Q_{31}(r) = \binom{x}{r} \cdot \Pi_{31}^r \cdot (1-\Pi_{31})^{x-r}$$
• Suppose \( b \) is in \( P_{30} \).

• All afferent synapses from other cells in \( P_{30} \) onto \( b \) will have been modified.

• Active synapses onto \( b \) are drawn from two distributions:
  
  – Binomial\( (C_0; Z_{3'}) \) for cells in \( P_{30} \) – modified with probability 1
  
  – Binomial\( (C_1; Z_{3'}) \) for cells in \( P_{31} \) – modified with probability \( \Pi_{3'} \)

• Approximate this mixture with a single distribution for the number of modified active synapses:
  
  – Binomial\( (x; (C_0+C_1 \Pi_{3'})/(C_0+C_1)) \)
Let $C$ be the expected fraction of synapses onto $b$ in the subevent $X$ that have been modified:

$$ C = \frac{C_0 + C_1 \Pi_3'}{C_0 + C_1} $$

Probability that $r$ of $x$ active synapses have been modified when $b$ is in $P_{30}$ is:

$$ Q_{3.0}(r) = \binom{x}{r} \cdot C^r \cdot (1-C)^{x-r} $$

Note: this differs from Marr's formula 3.3.
If all cells in $P_{3'}$ have threshold $R$, then:

- Size of the simple representation $P_{30}$
  \[ C_{0'} = L_3 \cdot \sum_{r \geq R} \sum_{x=r}^{L_3} P_{3'}(x) Q_{3', 0}(r) \]

- Number of potential $P_{31}$ noise cells
  \[ C_{1'} = (N_3 - L_3) \cdot \sum_{r \geq R} \sum_{x=r}^{L_3} P_{3'}(x) Q_{3', 1}(r) \]

- Statistical threshold is the ratio where
  \[ C_0 : C_1 = C_{0'} : C_{1'} \]

subject to

\[ C_0 + C_1 = C_{0'} + C_{1'} \approx L_3 \]
Dealing With Variable Thresholds

- In reality, cells in $P_3$ do not have fixed thresholds $R$. They have:
  - A subtractive threshold $T$
  - A divisive threshold $f$

- Combined threshold:
  \[ R(b) = \max(T, fx) \]

- Can calculate $C_0^*$ and $C_1^*$ using $R(b)$ instead of $R$.

- Details are in Marr §3.1.2.
Results

• More synapses help: $Z_{3^*} = 0.2$ gives a statistical threshold twice as good as $Z_{3^*} = 0.1$.

• Good performance depends on adjusting $T$ and $f$. ($f$ should start out low and increase; $T$ should decrease to compensate.)

• Collaterals can have a big effect.

• Recovery of $E_0$ is almost certain for inputs that are more than $0.1 \, L_3$ above the statistical threshold.

• Example: Marr table 7: $L_3 = 200$, threshold is 60:140.

• In general: collaterals help whenever $n\alpha^2 \leq 1$.
  (Sparse patterns; not too many stored memories.)
Marr's Performance Estimate

- Input patterns: $L_1 = 2500$ units (25 blocks; 100 active units in each block)

- Output patterns: $L_3 = 217$ units out of 100,000.

- With $n = 10^5$ stored events, accurate retrieval from:
  - 30 active fibers in one block, all of which are in $E_0$
  - 100 active fibers in one block, of which 70 are in $E_0$ and 30 are noise

- With $n = 10^6$ stored events, accurate retrieval from:
  - 60 active fibers in one block, all of which are in $E_0$
  - 100 active fibers in one block, of which 90 are in $E_0$
Willshaw and Buckingham's Model

• Willshaw and Buckingham implemented a simplified 1/100 scale model of Marr's architecture
• Didn't bother partitioning $P_1$ and $P_2$ into blocks.
• $P_1 = 8000$ cells, $P_2 = 4000$ cells, and $P_3 = 1024$ cells.
• For two-layer version, omit $P_2$.
• Performance was similar for both architectures.
• Memory capacity was roughly 1000 events.
  - Partial cue of 8% gave perfect retrieval 66% of the time.
  - In two-layer net, 16% cue gave perfect retrieval 99% of the time.
  - In three-layer version, 25% cue gave 100% perfect retrieval.
Three-Layer Model Parameters

\[ \alpha_1 = 0.03 \quad \alpha_2 = 0.03 \quad \alpha_3 = 0.03 \]

\[ N_1 = 8000 \quad N_2 = 4000 \quad N_3 = 1024 \]

\[ S_2 = 1333 \quad S_3 = 2666 \]

\text{calc.:}

\[ L_1 = 240 \quad L_2 = 120 \quad L_3 = 30 \]

\[ Z_2 = 0.17 \quad Z_3 = 0.67 \]

\[ \Pi_2 = 0.41 \quad \Pi_3 = 0.41 \]
Two vs. Three Layers

- Dashed line is two layer; solid is three layer.
- Two and three layer models perform similarly.
Effects of Memory Load

Two Layer

Three Layer

50% genuine bits in cue
25% genuine bits in cue
8% genuine bits in cue
Division Threshold

- I cell supplies divisive inhibition based on the number of active input lines that synapse onto the pyramidal cell, independent of whether they've been modified.

- P cell measures number of active synapses that have been modified, S. Has absolute threshold T (not shown).

- Cell should fire if $S > fA$ and $S > T$. 
How to Set the Thresholds?

• Maximal similarity strategy: choose T and f that cause the smallest number of cells to be in the wrong state. (May not be biologically realizable.)

• Staircase strategy: start with small f and high T. Lower T until enough cells become active. Then raise f slightly and lower T to restore the activity level. Repeat until can no longer maintain activity level or f = 1.

• Competitive strategy: set f = 0 and lower T until the required activity level is reached. This is a k-winner-take-all strategy.

• Measure performance as: # of perfectly recalled patterns divided by total # of patterns. Used 1000 patterns in most experiments.
Comparing Threshold Setting Methods

Two Layer

Three Layer

- max similarity
- staircase
- competitive
Effect of Collaterals

- Marr estimates that the collaterals should have made their full contribution to recovering the event in about 3 cycles. Additional cycles would provide no benefit.

- McNaughton's commentary:
  - Oscillating cycle of excitation and inhibition in hippocampus, known as the theta rhythm: around 7 Hz (140 msec cycle).
  - Hippocampal cell output is phase-locked to the theta rhythm.
  - Assume pattern completion takes place in the $\frac{1}{4}$ cycle where excitation is increasing: 35 msec window.
  - Conduction delay and synaptic delay total 6–8 msec.
  - This leaves room for just 4–6 cycles in that 35 msec window: very close to Marr's prediction.
Assessment of Marr's Theory

• Strong points:
  – Sparse connectivity: more biologically realistic.
  – Multiple inhibitory mechanisms: subtraction and division.
  – Predicts when recurrent collaterals will help retrieval.
  – Anticipated many important findings: LTP, division operations, information transfer during sleep.

• Weak points:
  – Ignores the trisynaptic circuit. Vague about the anatomy. It seems like $P_1$ is neocortex, $P_2$ is EC, and $P_3$ is CA3.
  – Says nothing about CA1. Ignores the direct perforant path input to CA3 (and to CA1).
  – Claim that three layers of cells are necessary was unjustified.
  – Unanswered question: how are memories transferred from hippocampus to the neocortex?