The temporal resolution of neural codes: A unique role for latency?

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Interest in neural codes

• Simple coding: each neurone conveys single message at a time
  – Easy to decode
  – Limited capacity
• Complex code: each neurone conveys multiple messages simultaneously
  – Hard to decode
  – Enhanced capacity

Multiplexing neural signals

Why complex coding?

• Early visual system
  – Neurones selectively responsive to colour
  – Other neurones selectively responsive to shape
  – Neurones not responsive to both shape and colour (although see Johnson et al. 2001)
• How can we see multiple objects and their colour?
  – The binding problem

Red square and blue triangle

• Two visual stimuli
  • give rise to neural signals of shape and colour

Red square and blue triangle

• Combining signals of shape and colour
  • Binding problem: What’s present?
Proposed solution to binding problem

- Role of precisely timed spikes
  - Proposed by von der Malsburg
  - Many groups studying precisely timed spikes
  - Singer, Abeles, Aertsen, Vaark, Konig, Gray……
  - Different “forms” of precise timing
    - Synchrony, Oscillations, “Synfire chains”.

Synchrony and binding

- Identifying repeating triplets
  - Synchrony
    - Intervals of 0
  - Oscillations
    - Equal intervals
  - “Synfire chains”
    - Variable intervals
  - Exist in responses of single neurones

Oscillations and binding

- Numbers expected by chance
  - Depends on model used
    - Dealing with tail of distribution
  - Spike count distribution and PSTH critical
  - Small effect of ISI’s

Synfire chains and binding
Repeating triplets in early vision

**LGN**

![Graph showing repeated triplets in LGN](image1.png)

**Primary Visual Cortex**

![Graph showing repeated triplets in Primary Visual Cortex](image2.png)

Repeated comparisons

**Graph showing repeated triplets**

Information & repeating triplets

- If multiple signals
  - Information from one signal unavailable from another
- SCM model
  - Predicts number of precisely timed spike patterns
- Information theory
  - Signals are not separable
- NO MULTIPLEXING

Synchrony in motor cortex

- As in other cortical areas, responses are correlated
- This effects synchrony

Excess synchrony in motor cortex

- Synchrony is above chance levels
  - Slope ~ 0.8
- Excess varies with direction of arm movement
  - But only by scaling
- Most of variability explained
  - Expect no additional information
Attention and neural codes
• Attention improves performance
  – reduces false conjunctions
• Attention enhances neural responses
  – Selective for neurones with relevant selectivity
  – Acts as a "gain", multiplying spike count
• Precisely timed spikes
  – Associated with binding
• Does attention influence precisely timed spike patterns?

Delayed match to sample
• Present a sample stimulus
• Sequence of stimuli
• Respond when the sample re-appears

Attention & spike count in TE
• Response to effective stimuli enhanced
• Response to ineffective stimuli unchanged
• Variability to effective stimuli also effected

Attention & triplets in TE

Predicting triplets in TE

Importance of analysis method
Information in triplets

Spike times relative to other spikes
- Spike count matched model
  - Need to match coarse temporal statistics
  - Spike count distribution, PSTH
  - Can predict number & types of precisely timed spike patterns
  - Variable excess does not imply a separate code
  - Excess synchrony was a scaling factor
- Information theoretical analysis
  - No extra information carried by precisely timed spike patterns (Confirms SCM model results)

Attention related information

Ambiguous coding with attention
- Attention modulates only firing rate

Modelling attention

Decoding the neural population
- “Ideal observer” decoding of spike count
  - Require p(r|s), p(s), p(s) set to be equal
  - p(r|s) described by multi-dimensional Gaussian
  \[
  p(r|s) = \frac{1}{\sqrt{(2\pi)^{d}|\Sigma|}} e^{-\frac{1}{2} (r-c)^T \Sigma^{-1} (r-c)}
  \]
- When all p(s) equal, p(s|r) = p(r|s) / \sum p(r|s)
- Two measures from p(s|r)
  - Estimate information
  - max p(s|r) and calculate error
Attention and decoding

- Decoding depends on how select $p(r|s)$
- Ideal = “know” $p_{\text{ignore}}(r|s)$ & $p_{\text{attend}}(r|s)$
- Choose constant distribution (e.g. $p_{\text{ignore}}(r|s)$)
- Assume learning of combination of both distributions

Benefit of increasing attention is limited

V1 Response latency

V1 Response latency & magnitude

V1 Information

Temporal precision of latency
**Stimulus contrast and STS responses**

**Contrast-latency relationship**

Increases through the visual system

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**Latency is a multiplexed code**

- Latency varies with stimulus contrast
  - Carries all available information about contrast
  - Does not depend on spike count
  - Has a temporal precision < 10ms
  - Should be considered a multiplexed signal

**Predicting behaviour from the neural code**

- Make “decision” when available information reaches threshold
  - Information rises with spike count in early part of the response
- The nature of the neural representation determines the behavioural results
  - What about response latency?
    - Ignore the trivial “low contrast stimuli take longer to recognise”

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**Behaviour from the neural code**

- Take response profiles
  - Stimuli that change in perspective view
- Convert to cumulative
  - When reach threshold?
- What happens if there is a delay in starting the accumulation?

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**Behaviour from the neural code**

- Take response profiles
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- Convert to cumulative
  - When reach threshold?
- What happens if there is a delay in starting the accumulation?

**Executive & slave processes**

- Use dual task paradigm to distinguish
  - Doing one task when a second task starts
- If executive process
  - Can’t start 2nd task until 1st task is complete
  - Speed of processing unaffected by 1st task
- If slave process
  - 2nd task can start (slave) while 1st task finished
  - Speed of processing influenced by 1st task

**Testing the prediction**

- Use dual task paradigm to distinguish
  - Doing one task when a second task starts
- 1st Task: Counting task
  - Odd or even number (1-4 pips)
- 2nd Task: Mental rotation task
  - Is a letter (R or G) a normal or mirror image
  - Presented at different orientations
  - Presented at 2 contrast levels (High & low)

**Testing the prediction**

- 2 delays between last pip and presentation of the visual image
  - No delay
    - Assume subjects doing the counting task
    - 1 second delay
    - Assume the subjects have decided odd or even
- Subjects respond in reverse
  - Odd or even number of pips then
    - Normal / mirror image
    - Avoids interference from response preparation

**From neural codes to executive function**

- Central executive as a serial processor
  - Can only perform one process at a time
  - Performs decision making
- Slave systems
  - Can run in parallel with each other
  - Includes the “visual-spatial sketchpad”
Predicted pattern of results

Predicted pattern of results

Neural code explanation

• Executive functioning
  – Makes “decision”
• Slave system functioning
  – The neural coding determines the results
• Less total activation
  – Rate of accumulation of evidence slower
  – Occurs for orientation, perspective view, size
  – An “executive process”
• Response latency changes
  – Occurs for contrast
  – A “slave process”

Summary

• Precisely timed spike patterns relative to other spike times
  – Critical to incorporate all coarse & medium resolution statistics (LGN, V1, TE)
  – An excess over chance levels does not imply multiplexing (Motor cortex)
  – Attention does not influence fine temporal structure
    • No latency change, attention is not like contrast
• Implications for cognitive processes
  – Benefits of attention limited by the mechanism
  – Decreased accuracy for unattended stimuli consistent with psychological studies

Summary

• Precisely timed spike patterns relative to stimulus onset
  – Response latency varies with stimulus contrast
  – Resolution < 10ms
  – Evidence for multiplexing - a unique role?
• Implications for cognitive processes
  – Variable activation of representations can predict mental rotation (Perrett et al. 1998)
  – Variable response latency can predict dual task performance
  – Distinction of executive & slave systems needs to take neural code and neural representation into account