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

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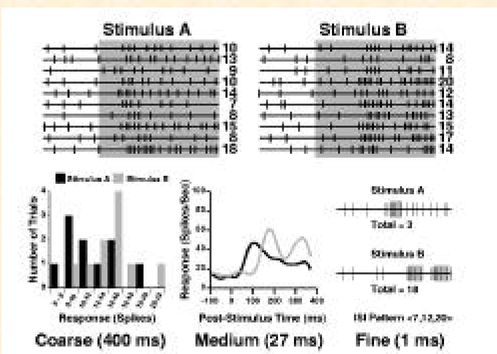
Interest in neural codes

- 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

Muliplexing neural signals

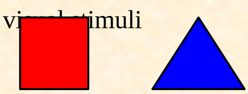


Why complex coding?

- 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 vi[illegible]imuli

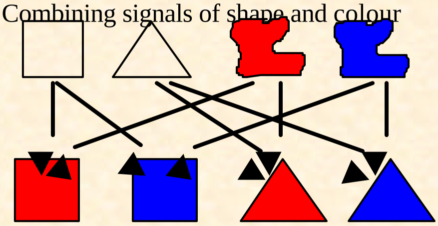


- give rise to neural signals of

Shape and colour

Red square and blue triangle

- Combining signals of shape and colour

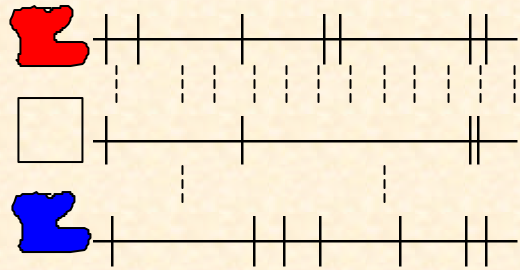


- Binding problem: What’s present?

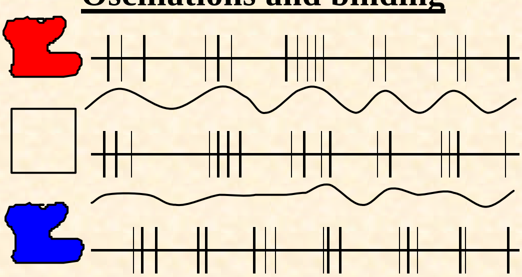
Proposed solution to binding problem

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

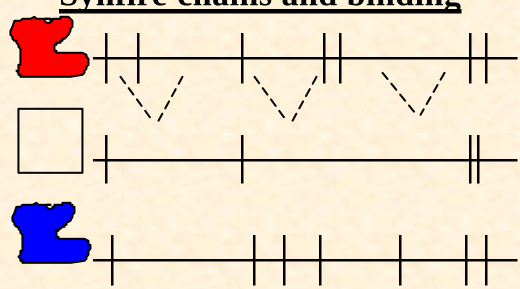
Synchrony and binding



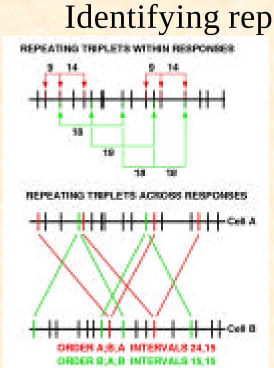
Oscillations and binding



Synfire chains and binding

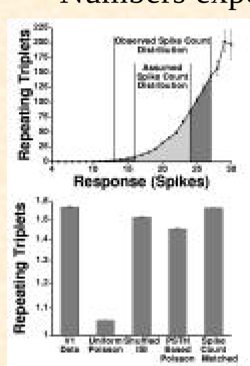


Identifying repeating triplets



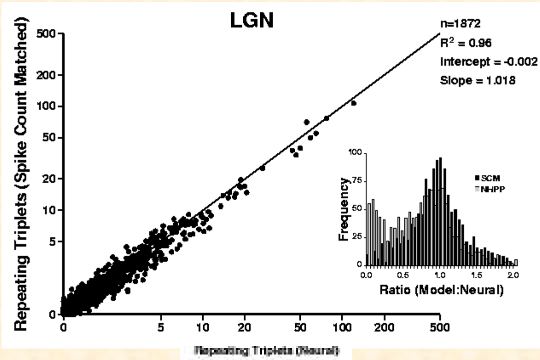
- Synchrony
  - Intervals of 0
- Oscillations
  - Equal intervals
- "Synfire chains"
  - Variable intervals
- Exist in responses of single neurones

Numbers expected by chance

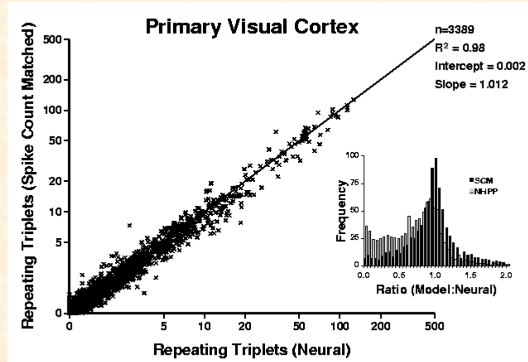


- Depends on model used
  - Dealing with tail of distribution
- Spike count distribution and PSTH critical
- Small effect of ISI's

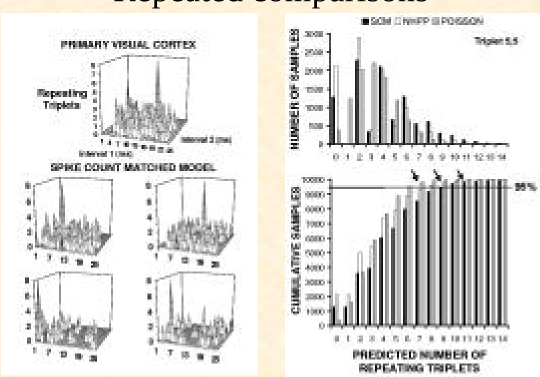
Repeating triplets in early vision



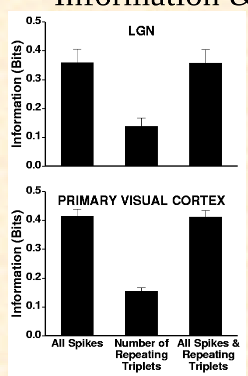
Repeating triplets in early vision



Repeated comparisons

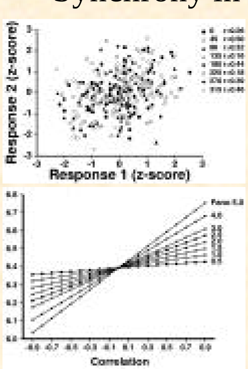


Information & repeating triplets



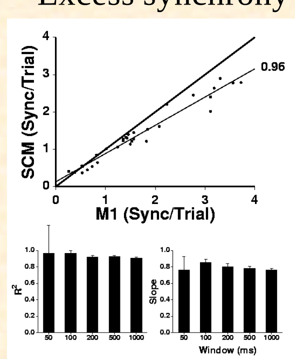
- If multiple signals
  - Information from one signal unavailable from another
- SCM model
  - Predicts number of precisely timed spike patterns
- Information theory
  - Signals are not separable
- NO MULTIPLEXING

Synchrony in motor cortex



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

Excess synchrony in motor cortex



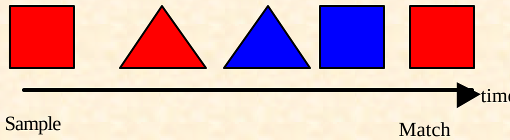
- Synchrony is above chance levels
  - Slope ~ 0.8
- Excess varies with direction of arm movement
  - But only by scaling
- Most of variability explained
  - Expect no additional information

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?

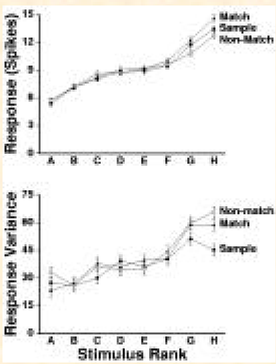
Delayed match to sample

- Present a sample stimulus
- Sequence of stimuli
- Respond when the sample re-appears



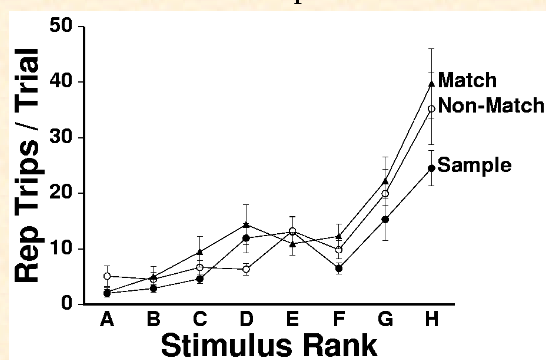
- Involves
  - Short term memory
  - Attention

Attention & spike count in TE

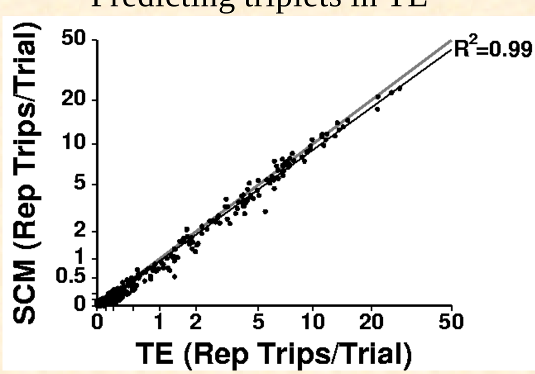


- Response to effective stimuli enhanced
- Response to ineffective stimuli unchanged
- Variability to effective stimuli also effected

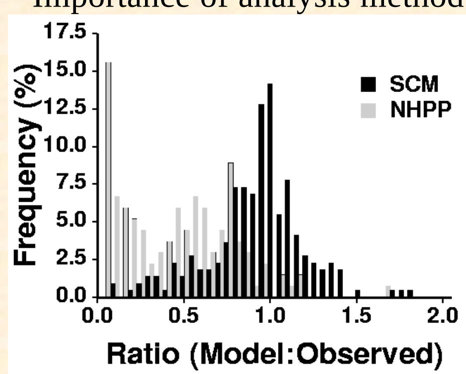
Attention & triplets in TE



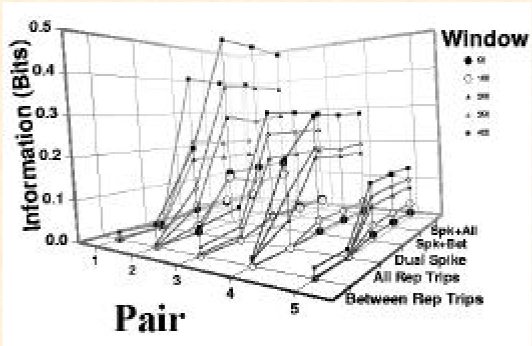
Predicting triplets in TE



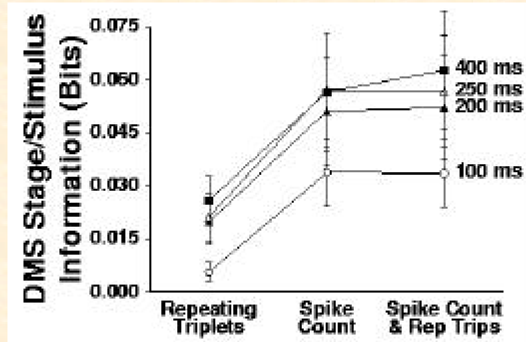
Importance of analysis method



Information in triplets



Attention related information

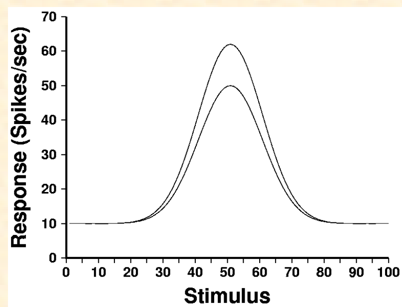


Spike times relative to other spikes

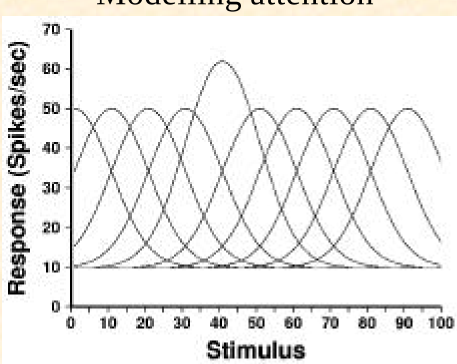
- Spike count matched model
  - Need to match coarse temporal statistics
    - Spike count distribution, PSTH
  - Can predict number & types of precisely timed spike patterns
  - Variable excess does not imply a separate code
    - Excess synchrony was a scaling factor
- Information theoretical analysis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

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

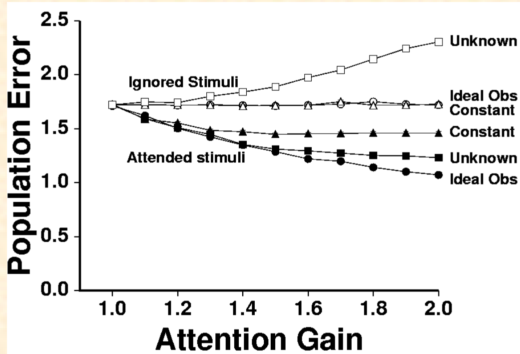
$$p(r \mid s) = \frac{1}{\sqrt{(2p)^n |C|}} e^{-\frac{1}{2}\left((\bar{r}-r)^T C^{-1} (\bar{r}-r)\right)}$$

- When all p(s) equal, $p(s|r) = p(r|s) / \sum_{i=1}^{n} p(r|s_i)$
- Two measures from p(s|r)
  - Estimate information
  - max p(s|r) and calculate error

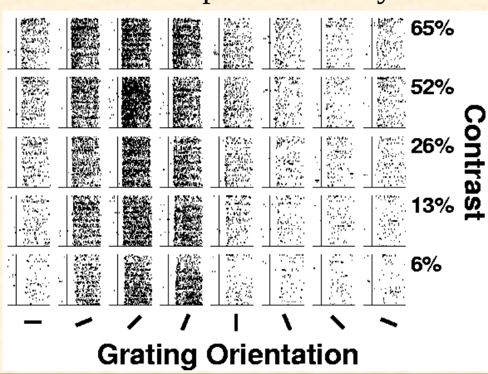
Attention and decoding

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

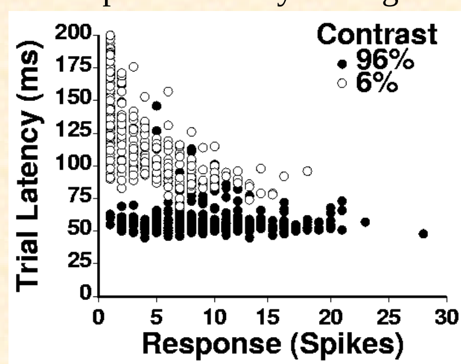
Benefit of increasing attention is limited



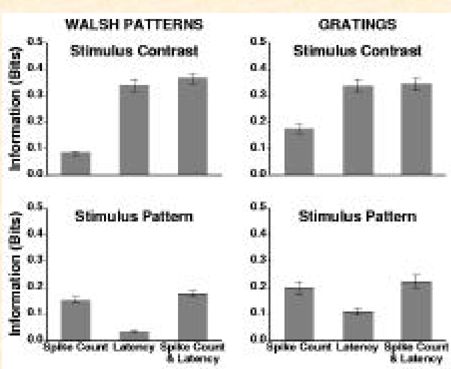
V1 Response latency



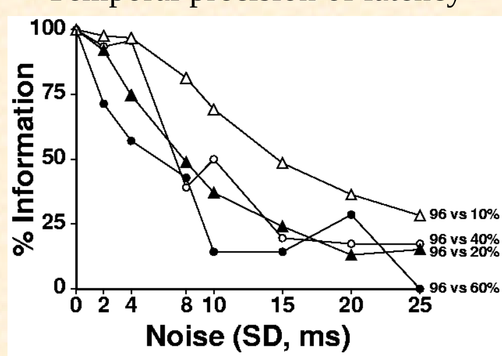
V1 Response latency & magnitude



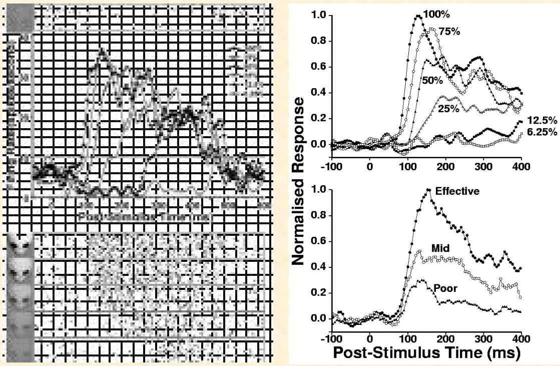
V1 Information



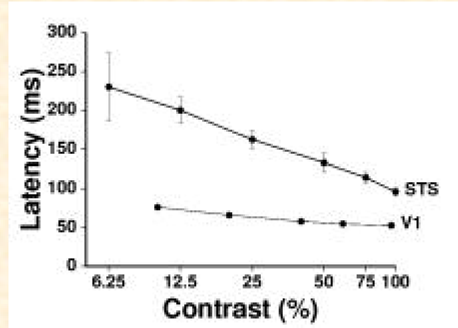
Temporal precision of latency



Stimulus contrast and STS responses



Contrast~latency relationship increases through the visual system



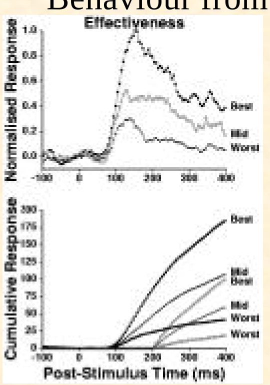
Latency is a multiplexed code

- 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

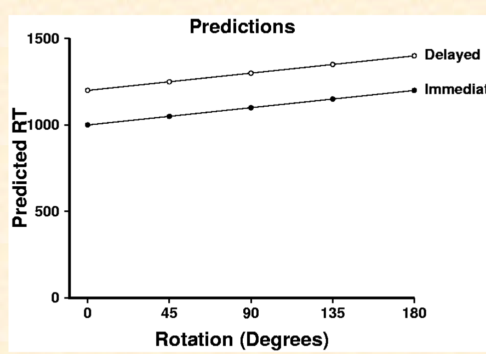
- Make “decision” when available information reaches threshold
  - Information rises with spike count in early part of the response
- The nature of the neural representation determines the behavioural results
  - What about response latency?
    - Ignore the trivial “low contrast stimuli take longer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

Behaviour from the neural code

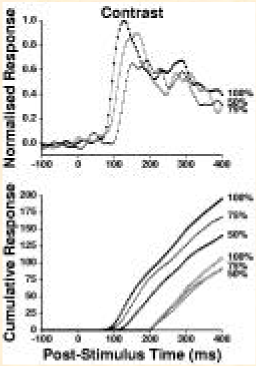


- Take response profiles
  - Stimuli that change in perspective view
- Convert to cumulative
  - When reach threshold?
- What happens if there is a delay in starting the accumulation?

Behaviour from the neural code



Behaviour from the neural code



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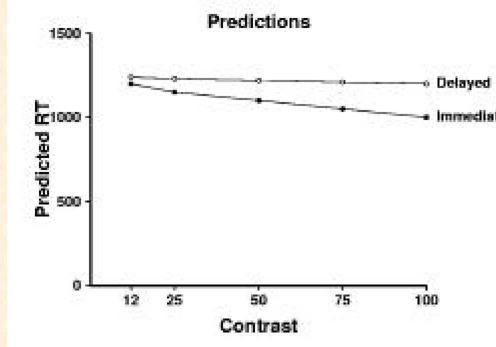


From neural codes to executive function

- 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”

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

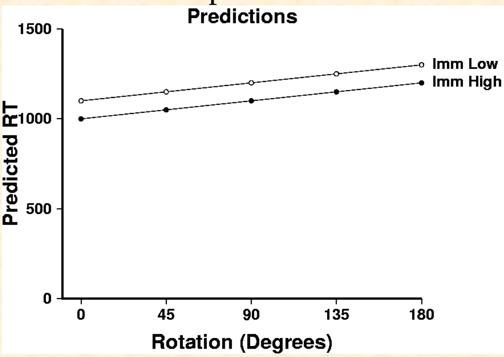
Testing the prediction

- 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

Predicted pattern of results



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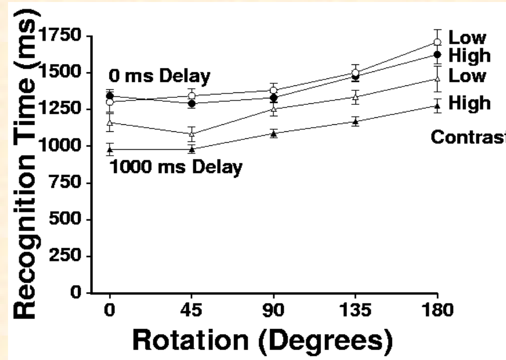

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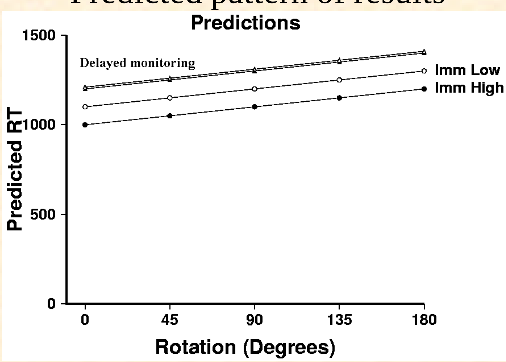

Neural code explanation

- 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