From neural codes to cognitive processes and perception: What we need to model and why

Mike Oram
School of Psychology
University of St Andrews

Overview

• Why is attention limited?
  – Need to do more “realistic” modelling work
• How does stimulus contrast influence neuronal activity?
  – Need to understand the processing
• Why should we care?
  – Predicting visual search with stimulus inversion
    • Can this be related to “optimal” attention?
  – Predicting visual search with contrast
    • Oh my £U&K*NG G&D – what is going on?

Framework of research

Neural codes and attention

• Fixating monkey doing sequential DMS task

Sample  Non-match  Non-match  Match

Attention and neuronal codes

Spike count  Time of spike count effect

Fine temporal response measures

Identifying repeating triplets  Behavioural relevance
Neural codes in visual system

- Coarse/medium (20-500ms resolution)
  - Plenty of evidence for spike count
  - Evidence of medium (Richmond)
- Fine temporal measures (1-2ms resolution)
  - “Synfire chains” (includes synchrony)
    - We find no evidence (LGN, V1, Motor)
    - Even with behavioural relevance (Oram, Lui, Richmond, in prep)
  - Synchrony
    - No evidence (TE/STS, Rolls et al. 2003, 2004)

Why is attention limited?

- Doesn’t seem to be a “I’m attending” signal
- Response magnitude to attended stimuli boosted
  - Inhibitory interactions between neurones biased
- Examine decoding of signals to answer?

Decoding

- Model response distributions
  - Mean ~ Variance relationship
  - Non-Gaussian, Non-Poissonian spike count distributions
  - Use Fano factor (Variance/mean) 1.5
  - Truncate the Gaussian
- Apply Bayesian decoding
  - Get $p(s)$ for each stimulus: Use MAP = ML in these simulations
  - Estimate error & information
Model different decoding

- "Ideal observer" decoding
  - Assumes that system "knows" which response distribution the signal came from (stimulus ignored or stimulus attended)
- Constant decoding
  - Decode assuming responses generated from distributions when stimuli attended
  - Decode assuming responses generated from distributions when stimuli ignored
  - Decode assuming responses generated from mixture of distributions (ignored/attended)
Decode as unattended when the stimulus is attended?

- **Attended and Ignored populations**

  - **Response (Spikes/sec)**
  - **Stimulus Class**

  ![Graph of attended and ignored populations](image1)

Decode as attended when the stimulus is unattended?

- **Attended and Ignored populations**

  - **Response (Spikes/sec)**
  - **Stimulus Class**

  ![Graph of attended and ignored populations](image2)

Why is attention limited?

- **Simulations**
  - Optimal decoding does not give highest information!
    - Does about stimulus/attention combination
  - Decoding assuming ignored “better”
    - Information to attended stimuli rises faster than ideal observer
    - Error has local minimum

- **Anyone want to find out what’s going on?**
  - Do we still see this with more “accurate” model of attention (biases in inhibitory interactions)?
  - How does this local minimum vary?
Stimulus contrast and neuronal response latency

- Latency increases and response magnitude decreases as stimulus contrast is decreased
- Carrandini & Heeger model “explains” this
  - Pooled activity across neurones gives shunting (divisive) inhibitory input
  - Changes the membrane time constant (RC circuit)
  - Gives results from V1
  - But NOT STS

Stimulus contrast and response latency in TE/STS

Latency change and specificity

- Why should effect of contrast vary with degree of response selectivity?
  - Latency to high contrast stimuli the same
  - Increase in latency with decreasing contrast higher for neurones showing higher response selectivity
  - Not effect of changes in response magnitude
  - Not effect of “type” of effective stimulus
  - Possible effect of “contrast” (difference) in inputs

Neural codes in late visual system

- Evidence for spike count and response latency
  - Information encoded by spike count, latency when
- Do these codes “mean” anything?
  - Spike counts
    - Micro-stimulation studies (e.g. Newsome, Parker)
  - Latency
    - How to test?
    - Can’t stimulate to change latency
    - Want to relate to behaviour

Models of decisions

- Information acquisition hypothesis
  - Decisions when information reaches threshold
    - Ratcliff 1978
    - McClelland 1979
    - Carpenter & Williams, Nature 1995
    - Gold & Shadlen, TICS, 2001
    - Carpenter & Williams, Nature, 1995
Modeling a decision

Create 2nd “distracter” response (0.8 * Target)

Threshold the difference to get RT

0 500
Time (ms)

What do neural codes predict for RT?
– Latency (change contrast)
– Magnitude (change orientation)

What happens experimentally?
– Are the codes reflected in behaviour (i.e. “mean” anything)?

Both predict change in RT

Count from 0 ms
Count from 150 ms

Response Latency
Response Magnitude

Both give RT changes

Unless can delay the start of counting

Predicting mean RT

Time to threshold (ms)

0 1000 ms interval
1000 ms interval
Contrast

0 ms interval
Low (5%)
High (100%)
Low (5%)
High (100%)

Rotation (Degrees)

0 45 90 135 180

Testing mean RT predictions

Recognition Time (ms)

0 1250 1500

0 ms interval
Low
High
Low
High
Contrast

Orientation (Degrees)

0 45 90 135 180

Oram et al. Phil Trans R Soc, 2002
Latency and RT

- Model the latency shifts:
  - Mutually inhibitory populations
  - Integrate & fire neurones in simple network (Mark van Rossum: How’s it going?)
- Model predicted RT distributions:
  - Model RT distributions from
    - diffusion models,
    - accumulator models,
    - leaky accumulator models
  - Compare with experimental data

Visual search as signal processing

- Use the same model and apply to visual search
- Target is attended (looked for)
  - Gives a neural response “gain” of about 1.2 to 1.5
- Inhibitory interactions between neurones
  - Attention biases the interactions (see Reynolds)

Modelling visual search

- As the number of stimuli increase, firing rate decreases ((1/sqrt(N) - Ward & McClelland 1986)
- Attention biases the competition
  - Firing rate of neurones selective for the attended stimulus act as if gain control
- Take the modelled activity levels
  - Use in the accumulator model
  - Do pair-wise comparisons in parallel
Visual search: Accumulator model

- **RT(Y) determined by orientation of target**
  - Last time-to-threshold when target identified
  - With all upright:
    - Target upright vs distracter upright
  - With all inverted:
    - Target inverted vs distracter inverted
  - With half upright, half inverted:
    - **Target upright:** Target upright vs distracter upright
    - **Target inverted:** Target inverted vs distracter inverted
- All upright=Mix upright < All inverted=inverted

- **RT(N) determined by distracter inversion**
  - Last time-to-threshold when identified as non-target
  - With all upright:
    - Non-target upright vs distracter upright
  - With all inverted:
    - Non-target inverted vs distracter inverted
  - With half upright half inverted:
    - **Non-target upright:** some non-target inverted vs distracter inverted (same as all inverted)
    - **Non-target inverted:** Non-target inverted vs distracter inverted (same as all inverted)
- **RT(N) mix inversion = all inverted**

Modelling visual search: Inversion

- **Inversion: STSS like visual search**

Visual search: STSS model

- **RT(Y) ½ way between all upright and all inverted**
  - $RT(Y_{mix}) = 0.5 \cdot N_{items} \cdot (t_{switch} + t_{need_rot} + 0.5 \cdot t_{rotate} + t_{decision} + t_{last}) + t_{resp}$
  - $RT(Y_{up}) = 0.5 \cdot N_{items} \cdot (t_{switch} + t_{need_rot} + 0.5 \cdot t_{rotate} + t_{decision} + t_{last}) + t_{resp}$
  - $RT(Y_{inv}) = 0.5 \cdot N_{items} \cdot (t_{switch} + t_{need_rot} + t_{decision} + t_{last}) + t_{resp}$
  - **Target orientation does not matter**

- **Guided search (Wolfe):**
  - $RT(Y_{mix-up}) < RT(Y_{up})$
  - $RT(Y_{mix-inv}) > RT(Y_{inv})$

Visual search with mixed inversion

- **Self-terminating serial search model**
  - **RT(Y) ½ way between all upright and all inverted**
  - **RT(N) ½ way between all upright and all inverted**
  - **Target orientation does not matter**

- **Accumulator model:**
  - **RT (Y):** All upright=mix upright < All inverted=mix inverted
  - **RT (N):** Half-inverted = All inverted
Visual search: Mixed orientation

Search & inversion

• Is the pattern of results related to “optimal” attention
  – Use a more complete model of neural populations (e.g. I&F, attention bias of inhibitory interactions)
  – What is “optimal” attention modulation as number of stimuli increases?
  – What happens to modelled activity levels as more and more stimuli are processed?
Search and contrast

• Results inconsistent with STSS and guided search
• Accumulator model is underspecified
  – What happens to inhibitory interactions when some signals are delayed?
  – What does this predict for RT?
  – Can we reject the simple accumulator model?
    • If so, any ideas as to what is happening?