Information coding by spikes

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Plan

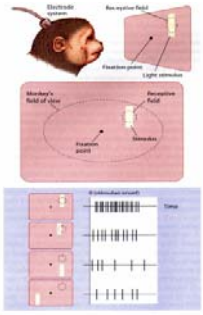
- Models of how spikes transmit information
  - Keeping it simple: Rate coding
  - Thorpe and Time of Onset coding
  - Optican and Richmond and the proposed importance of temporal structure
  - Singer and phase locking for feature binding (and consciousness)
  - The importance of the single spike (Bialek and others)

What are we trying to model?

- Cue the video

Decoding neurons

- One of the main ways that neurons communicate to each other is through spikes
- What is the code used by these neurons?



Rate codes (averaging over time)

- Simplest and oldest hypothesis (Adrian 1926,1928)
- The timing of the individual spikes is irrelevant, what matters is the average rate. The **rate** hypothesis has underpinned the vast majority of work
- Simple: we can
  - record neuron
  - present stimulus
  - Record the number of spikes in a certain period (100-400 msecs)

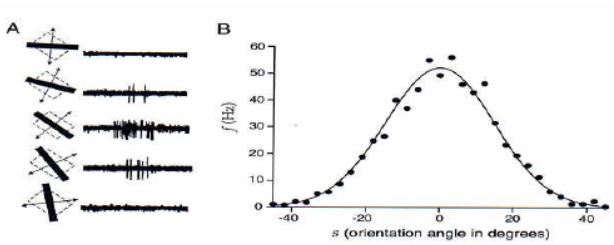
Rate coding continued

- Almost everyone believes the weak rate code hypothesis: there is information present in the firing rate
- More controversial is the strong rate code hypothesis: Knowing the firing rate of a cell tells us all the important signalling characteristics of the cell.

Evidence for the strong rate hypothesis

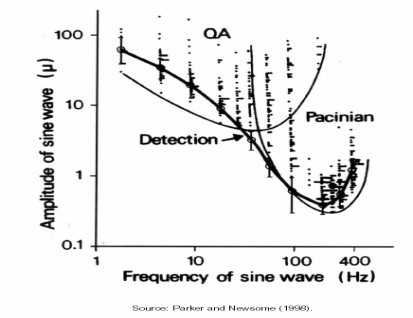
- Strategy: show that if we decode neurons using only the rate information, we get estimates of the system performance that are similar to the animals. For instance:
- For a motion detection experiment: “For half of the neurons in our study, the neurometric function derived from single-unit data was statisticially indistinguishable from the psychometric function measured on the same set of trials.” Britten et al (1992)
- Similar results for contrast detection (Hawken and Parker 1990)
- Excellent review: Parker and Newsome (1998) Sense and the single neuron Annual Review of Neurosicience 21:227-77

Example: orientation



Spike rate is a simple lawful function of orientation

Example: touch



Source: Parker and Newsome (1998).

Alternatives to the rate hypothesis

- Temporal modulation of the spike train conveys information
- Time of Onset matters
- The exact time of each spike relative to the others is informative
- Every spike counts (help)

Optican and Richmond’s Experiment

- Showed a large number of simple stimuli to a primate
- Looked at the firing rate patterns of the cells when the stimuli were shown
- Characterised these responses using principal components analysis
- Tried to see how much structure in the spike trains was useful in guessing which stimulus was shown

Stimuli

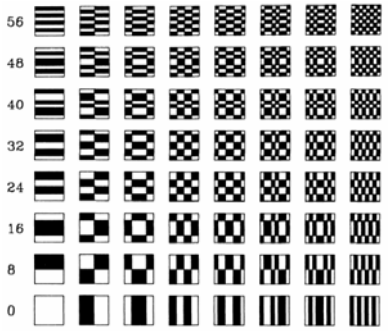
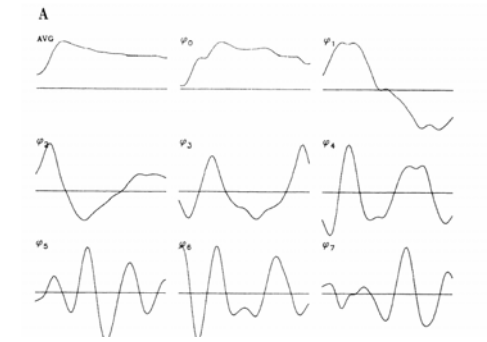


FIG. 2. Two-dimensional Walsh stimuli. These 64 Walsh patterns can represent any black and white picture with a resolution of 1 part in 8. They are numbered sequentially beginning in the *lower left* at 0 and ending in the *upper right* at 63. The numbers of the patterns along the *left edge* are indicated. Many neurons were also tested with the contrast reversed patterns, making a combined stimulus set of 128 patterns.

Characterising the responses using principle components analysis



There is more information than that in the firing rate

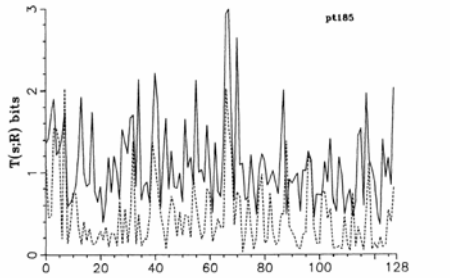


FIG. 2. Transmitted information per stimulus, T(s; R), based on 3 principal components (*solid line*) and on the spike count (*dashed line*). Stimulus number corresponds to the serial ordering of the two-dimensional Walsh stimuli. *Stimuli 0* through *63* have positive contrast, and *64* through *127* have negative contrast.

But not as much as originally claimed

- In the original papers Optican and Richmond's calculation of information was biased.
- Subsequent analysis showed that there was information about the stimulus that was not contained in the firing rate
- This information arrived quickly

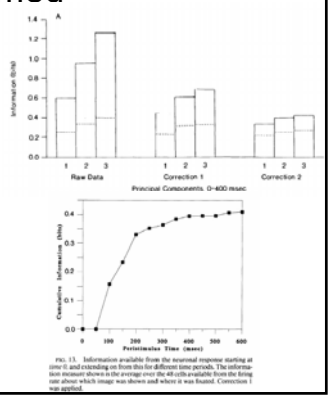
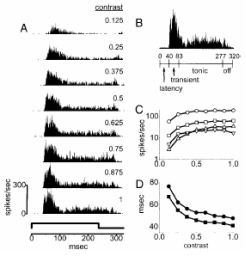


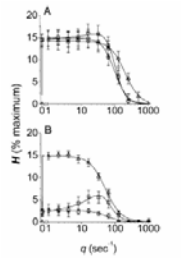
FIG. 13. Information available from the neuronal response starting at *time* t_1 and extending on from this for different time periods. The information measure shown is the average over the 48 cells available from the firing rate about which image was shown and where it was fixated. Correction 1 was applied.

Summary of Optican and Richmond's study

- Displayed simple grid like patterns to primates and recorded IT cells responses
- Worked out the principal components of the firing rate: a set of descriptors for describing firing patterns: only the first is highly related to firing rate
- Found information was present in at least three components
- Conclusion: information about visual stimulation is present in the pattern of firing in the spike trains, not just the raw firing rate

Time of onset





•For cells in V1, the time that firing starts is highly related to the stimulus

•In fact, for simple cells, you can often extract nearly as much information from the (time of the) first spike as from all the spike together (see for instance Reich et al 2001)

Thorpe's rank order coding proposal

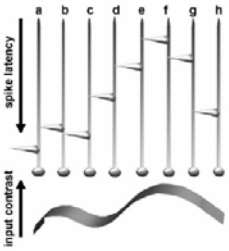


Fig. 1. When a given input pattern is presented to a neural population, the early part of the population response can be described as a spatio-temporal wave of spikes. Within such a wave, a simple consequence of the basic properties of integrate-and-fire neurons is that the most activated cells will have the shortest latencies. Input contrast thus translates into temporal asynchrony. The specific order in which different cells fire can also be used as a code. With 8 input neurons, 8! (more than 40,000) different input patterns can be distinguished.

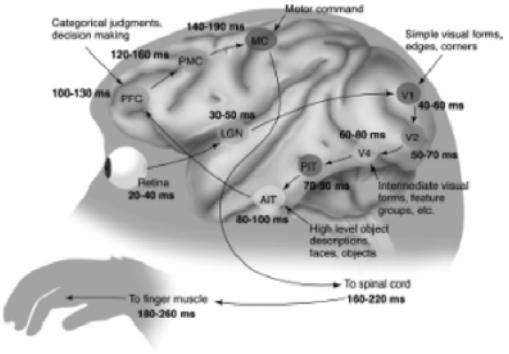
In words

- The important signal for coding is the relative time of the spikes arriving at later levels
- The first spike is from the most important feature, the second from the next and so on.
- Specifically, the cells output is coded by the rank of the spike timing relative to all other cells

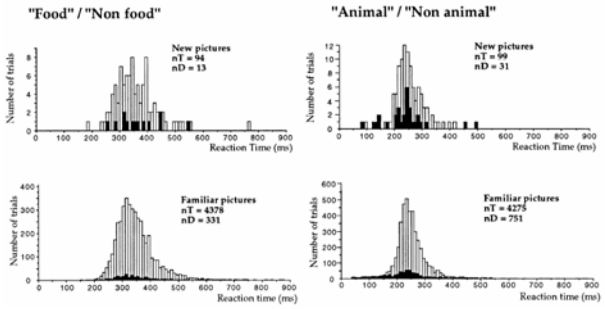
Advantages of Thorpe's proposal

- Very high information capacity
- Invariant to illumination change: changing the contrast may change
- Fast!!!!!!!!!
  - To calculate a rate, we need to wait until a fair number of spike have been sent
  - To calculate the time to the first spike, we only need to wait for the first spike
- Are we this fast?

Constraints on speed of response



Are we very fast?



Yes!

Summary of Thorpe's model

- We can respond very fast to visual stimuli (animal non-animal distinctions can be made in photographs presented for only 80ms)
- Rate codes will have trouble at these speeds
- But some latency based code will be fast enough
- Latency seems important, jury still out on rank order hypothesis

Singer et al an synchronous firing

- Often we want know not only which features are present in the world, but which features belong together (the feature binding problem)
- One attractive proposal that has had a huge impact is that cells that correspond to the same object fire together
- This firing together can be of two related types:
  - Synchronous an oscillating (50 hertz)
  - Simply synchronous
- This was originally proposed to be happening by von de Malsburg
- Experimental evidence for this was provided by Wolf Singer and colleagues

Typical Experiment Results

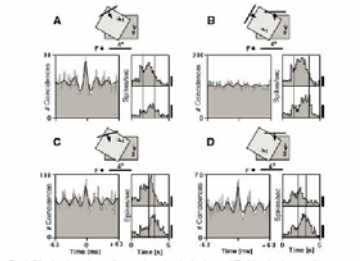


Fig. 1. Stimulus-dependence of neuronal synchronization in area MT of the visual cortex of a macaque monkey carrying out a fixation task. Neuronal responses were obtained from two cell groups with different directional preferences. The figure shows cross-correlograms and peri-stimulus-time histograms for four different stimulation conditions. The small insets indicate the receptive field locations (1,2) with respect to the fixation point (F) and the directional preference of the neurons (small arrows). (A) A single moving stimulus bar, whose direction of motion was intermediate between the neurons' preferences, led to a pronounced synchronization of the two cell groups, as indicated by the central maximum in the cross-correlogram. (B) Presentation of two stimuli moving in the respective preferred directions of cell group 1 and 2 abolishes synchronization. (C, D) The synchronization observed with a single stimulus does not depend on its particular orientation. (C) Changing orientation and direction of motion by 15° or (D) using one of the bars from the configuration in (B) had little influence on synchronization. Scale bars for the peri-stimulus-time-histograms correspond to 40 spikes/sec. The continuous line superimposed on the correlograms represents a damped cosine function that was fitted to the data to assess the significance of the correlogram modulation. (Modified from Kreiter and Singer 28)

Biased Summary of work

- Oscillations seem to be a bit of a red herring: they are mainly due to very strong stimuli being used
- Many groups do not find this kind of effects
- Synchrony between cells is more plausible (current position of Singer and colleagues) but many neuroscientists do not believe this is happening

Summary

- Rate code: basis for almost all neuro physiological work: the signal is simply read from the rate of firing, the fine pattern of responding does not matter
- Optican and Richmond (1987) showed you could get more information about the stimulus that was presented by looking at the pattern of firing later work showed that the most important aspect of this pattern was the latency or time of first firing
- Thorpe and colleagues emphasised the importance of the time of first spike. Also showed we can extract information very quickly from images
- Singer emphasised the importance in considering more than one neuron at a time. In particular synchronous firing between neurons tuned to the same object could be used to signal binding

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Best of all references

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