

A Brief Overview of Neural Coding

Lecture to Cognitive Neuroscience class

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The Problem

Context of brain science:

- ▶ What principles may be used to describe mental processes?
- ▶ What principles may be used to describe the brain?
- ▶ How does neuronal activity produce behavior?

Perkel and Bullock (1968): The problem of neural coding is to elucidate “the representation and transformation of information in the nervous system.”

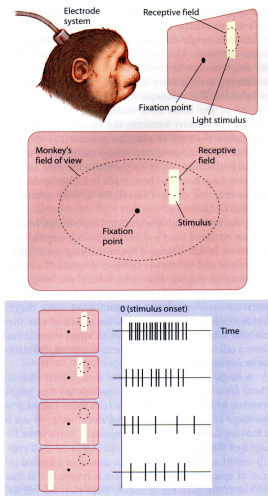
The Starting Point

The simplest (“textbook”) answer to the question “How do neurons carry information?” is that a neuron responds to a relevant stimulus, or contributes to the production of an action, by increasing its firing rate.

Usually attributed to Adrian (e.g., Adrian, 1928).

May be illustrated by receptive field of a neuron in visual cortex (next fig).

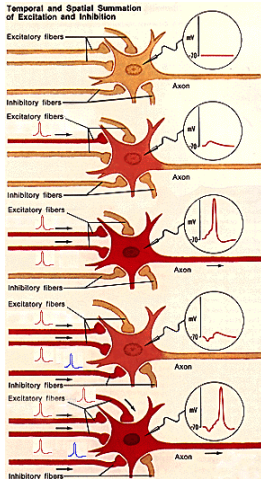
Firing rate increases when stimulus is in receptive field.

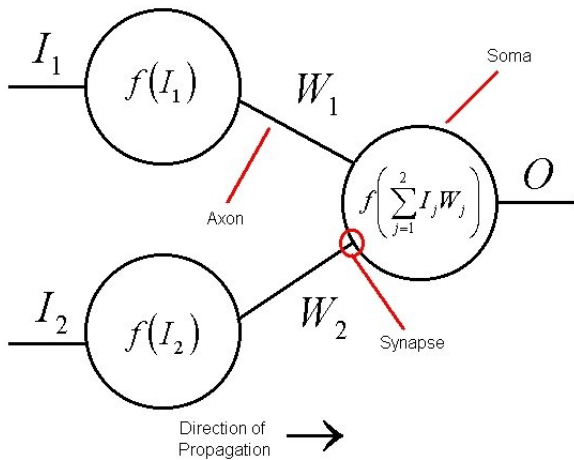


Some Immediate Questions

- ▶ To what extent do simple qualitative descriptions adequately capture the response characteristics of individual neurons?
- ▶ To what extent can results from individual neurons be informative about the extremely complicated network in even a small part of the brain?

Consider a standard conception of the way neural inputs lead to action potentials.

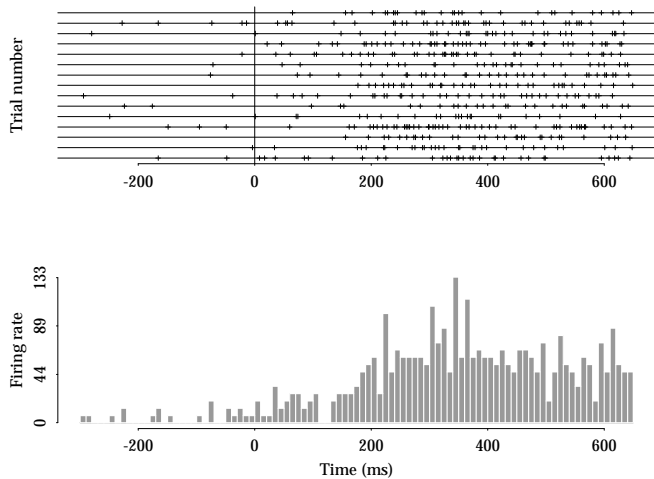




Some Immediate Questions

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- ▶ To what extent can results from individual neurons be informative about the extremely complicated network in even a small part of the brain?

It may help to be reminded of the way spike trains are usually displayed.



Some General Questions

- ▶ Which features of spike trains are “signal” and which are “noise?”

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- ▶ Does the PSTH from a single neuron represent well the signal from a population (an “ensemble”) of similar neurons? (Cf. Shadlen and Newsome, 1998)

Or, are there signals carried by populations (“ensembles”) of neurons that are not apparent from individual spike trains?

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- ▶ What time scales are relevant to neural coding?

Some Possibilities, with Terminology

- ▶ Rate coding
- ▶ Temporal coding
- ▶ Population coding
- ▶ Sparse coding

Rate Coding and Temporal Coding

Rate coding refers to information being carried by the firing rate. It is often argued, or assumed, that firing rate captures essentially all relevant information.

Temporal coding may refer to several quite different ideas: (i) Much of the information may be transmitted by a neuron during certain small intervals of time, (ii) synchronous, or what I would call *quasi-synchronous*, firing of neurons within and across ensembles may carry important information, (iii) the precise timing, or pattern, of spikes may carry information.

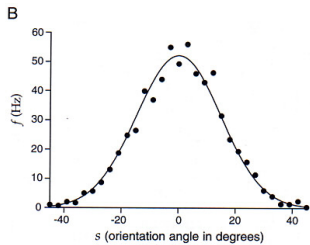
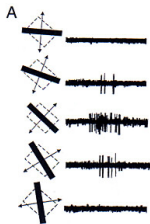
Idea (ii) has received much attention due to its potential for solving the “binding problem.” The arguments in its favor, however, are rather intricate.

Population coding refers to information available from ensembles that goes beyond simple summation of individual signals. It is often associated with the method of Georgopoulos, et al. (1986), but many analysts have also asked what an “ideal observer” could learn from a population of neurons.

Quite different ideas also may be included under the general notion that disparate neural responses may be combined, according to some simple principles, to produce a characterization of a complicated phenomenon.

Sparse coding refers to strong selectivity (narrow *tuning curves*), so that relatively small numbers of neurons would be involved in carrying the signal.

Note that the notion of “tuning” is widely used; the intuition comes mainly from 1-dimensional tuning curves, but is applied in much more complicated situations.



Sparse coding refers to strong selectivity (narrow *tuning curves*), so that relatively small numbers of neurons would be involved in carrying the signal.

Sparseness of individual neuronal responses comes into play in some notions of population coding.

A Fundamental Observation

Perhaps the most important conclusion of the workshop discussions reported by Perkel and Bullock (1968) was that the information represented by a neuronal spike train necessarily depends on the neuron's inputs and outputs, so that one should not expect universally-applicable principles of neural coding (Gerstein, personal communication).

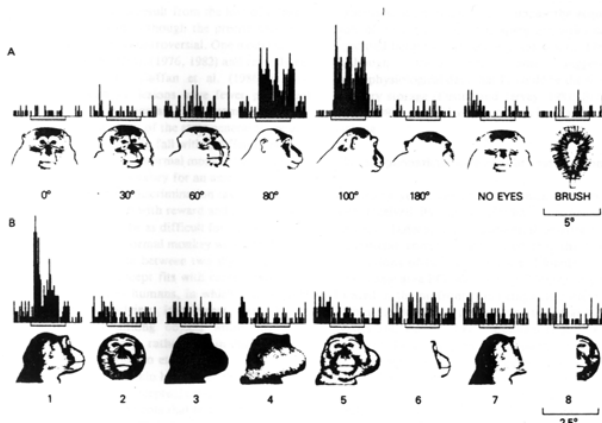
Put differently, the circumstances matter: distinct mechanisms may apply to differing systems, and to differing organisms, stimuli, and collections of neurons within systems.

Single Cells

- ▶ It is universally acknowledged that firing rates carry information. The various possibilities listed speak about elaborations, or additional mechanisms.
- ▶ Barlow (1972) argued in favor of the completeness of single-cell information, in the sense that the firing rate of a single cell could carry all relevant information and populations would add little else. He replaced what William James had called “pontifical cells” with “cardinal cells, ... each [of which] makes a complicated statement [in order to] express the whole perception.” See the discussion of *grandmother cells* by Gross (2002).

There are two aspects to this: (i) sharp selectivity of neuronal response and (ii) relevance to behavior of responses of only a few cells.

Face recognition would apparently be an example of sparse coding, and it may elucidate Barlow's "cardinal cell" remark.



Source: Desimone, R., Ungerlieder, L.G., Handbook of Neurophysiology, page 287, Elsevier Science Publishers, 1989.

- ▶ A very different case comes from a tantalizing report that there exist motor cortical cells that, after training, respond during an arm movement up and then left (with a sharp left turn) but *not* when the arm movement is straight-line unidirectional (Ashe *et al.*, 1993).

Top: response to sharp left turn (two cells); Bottom: response to straight movements.

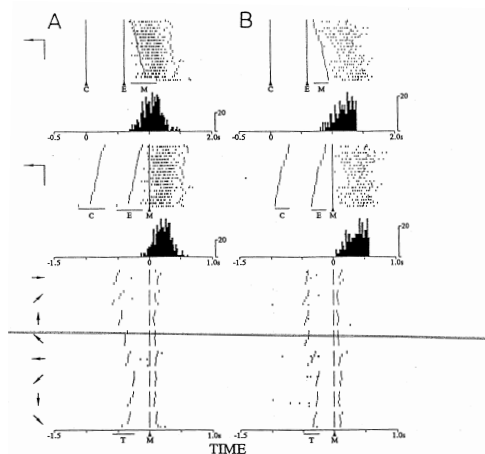
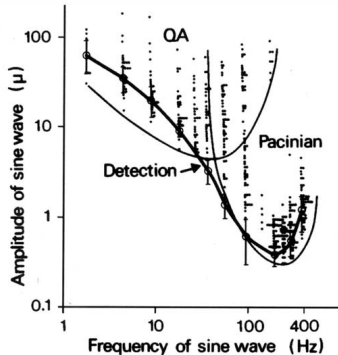


Fig. 5A,B. Changes in cell activity only during the memorized movement task. A Cell P1054q/6; B cell P1062q/4. Conventions as in Fig. 2

Single Cells (Continued)

- ▶ Part of Barlow's argument involved the ability of individual cells to predict psychophysical measurements (absorption of only a few photons in the retina leads to sensation of light). See Fig from Parker and Newsome (1998), involving response to vibration applied to skin at various frequencies and amplitudes.

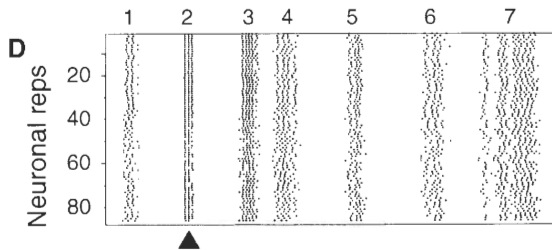
Amplitude required to elicit response among humans (“detection”) is close to the minimal amplitude required for response among two types of sensory neurons in monkeys.



Source: Parker and Newsome (1998).

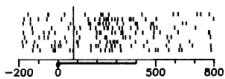
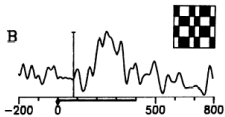
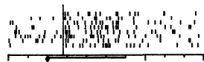
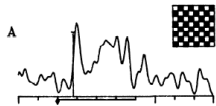
- ▶ Britten, Shadlen, Newsome, and Movshon (1992) considered the ability of single MT neurons to predict eye saccades in response to stochastic dot motion. “For half of the neurons in our study, the neurometric function derived from single-unit data was statistically indistinguishable from the psychometric function measured on the same set of trials.”

- ▶ In early segments of sensory systems very sharp modulations in spiking activity have been observed. Similar effects appear in bird song production (Chi and Margoliash, 2001).



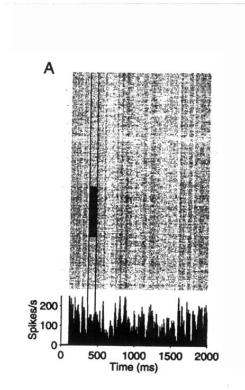
Rate Modulation (Continued)

Optican and Richmond (1987) recorded from IT during presentation of Walsh functions and considered the temporal structure of the spike trains. They concluded that “[their] methods have shown that neurons in [IT] convey messages by temporal modulation of their firing rates.”



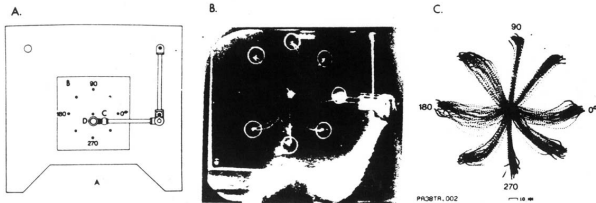
Heller, Hertz, Kjaer, and Richmond (1995) analyzed neurons in V1 and IT and found “all measurable information is carried in an effective time-varying rate, obtained by averaging the neuronal response with a resolution no finer than about 25 ms in [V1] and twice that in [IT].... Most of the information tends to be concentrated in one or, more often, two brief packets, one at the very beginning of the response and the other typically 100 ms later. The first packet is the most informative part of the message....”

Bair and Koch (1996) reported that in MT neurons firing rate could be modulated in a range of about 10 ms (see figure from Shadlen and Newsome, 1998). Rieke, et al. (1996) give similar results in frog auditory and fly visual areas.

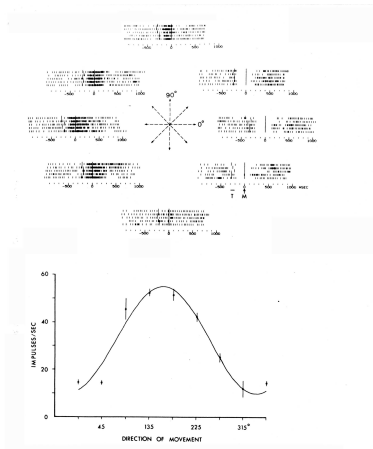


Source: Shadlen and Newsome (1998).

- ▶ Georgopolous, Schwartz and colleagues: Motor cortex neurons are directionally “tuned.”



Source: Georgopoulos et al.



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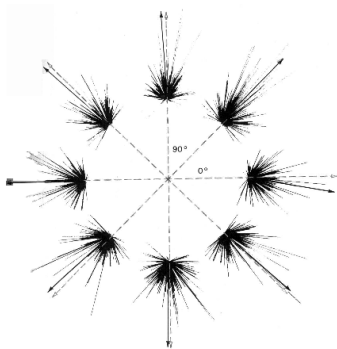
- ▶ Furthermore, Georgopoulos, Schwartz, and colleagues observed that directional tuning could be used for prediction.
- ▶ For movement M

$$\vec{P}(M) = \sum w_i(M) \vec{D}_i$$

\vec{D}_i is direction of maximal firing (“preferred direction”) for i^{th} neuron

$w_i(M)$ is a weight based on firing rate

“Population vector” $\vec{P}(M)$ predicts M .



Source: Kandel, Schwartz, and Jessell

Comments on Population Coding

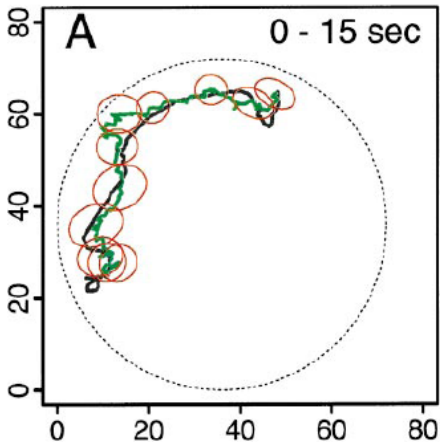
- ▶ Broad tuning and prediction based on populations of neurons are ideas that may be widely applied (e.g., Lewis and Kristan, 1998; Petersen, Panzeri, and Diamond, 2001).
- ▶ But do M1 neurons code for movement direction (velocity)? Note that muscle activity for reaching will also show directional preference. Kakei, Hoffman, and Strick (1999) considered M1 and muscle activity in a wrist movement task. They found some “muscle-like” neurons and some (more) “extrinsic” neurons.

The Ideal Observer

- ▶ Sanger (1994, 1996) noted that the prediction of M by $\vec{P}(M)$ is a mathematical consequence of directional tuning when the preferred directions \vec{D}_i are uniformly distributed.
- ▶ Other statistical prediction methods are possible and can, in fact, be much more efficient. (Nor does one need a uniform distribution of preferred directions.) *Maximum likelihood* and *Bayesian* approaches are fully efficient, in a statistical sense.

Brown et al. (1998) used data from hippocampus “place cells” to reconstruct movement of a rat via Bayes’ Theorem.

Black is rat's path; green is "ideal observer" reconstruction from small number of cells.



But does the nervous system equal or approximate an ideal observer?

Conceivably, systems like the local bend network in the leech might be a starting point for research in this direction (Lewis and Kristan, 1998).

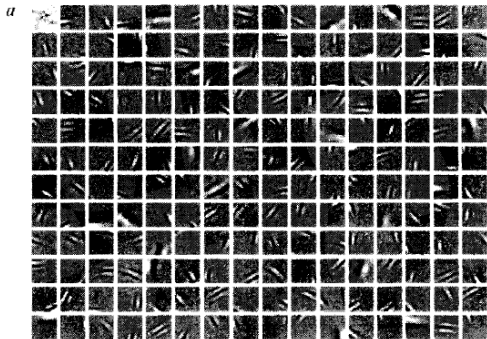
Sparse Population Coding: Visual System

Olshausen and Field (1996)

- ▶ Found basis set for a sample of 2D images that maximized

$$\text{fit} + \lambda \cdot \text{sparseness}$$

- ▶ Produced basis functions that are localized, oriented, and narrow in spatial frequency, like V1 simple cells.

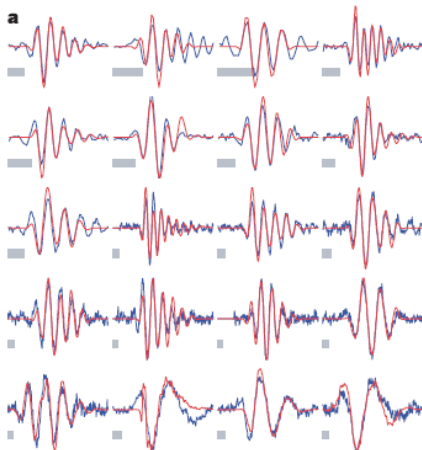


Sparse Population Coding: Auditory System

Smith and Lewicki (2006)

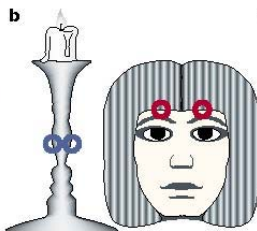
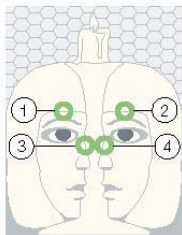
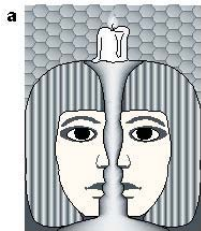
- ▶ Found basis set for a sample of acoustic signals to maximize fidelity of fit, subject to being sparse.
- ▶ Produced basis functions that are asymmetric sinusoids, with sharp attack and gradual decay, like auditory neuronal signals.

Red theoretical functions match blue signals from cat auditory nerves.



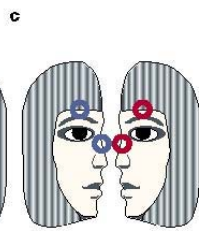
Oscillations and “synchrony” may bind disparate components of perception and awareness (Singer and Gray, 1995; Engel and Singer, 2001; Engel, Fries, and Singer, 2001). The argument has several steps:

1. Quasi-synchronous firing could, in principle, contribute the kind of boost in information that seems essential for solving the binding problem.



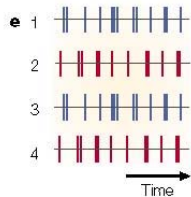
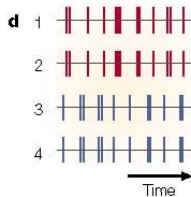
Object 1

Object 2



Object 1

Object 2



Timing in ensembles

The argument has several steps:

1. Quasi-synchronous firing could, in principle, contribute the kind of boost in information that seems essential for solving the binding problem.
2. Oscillations can produce quasi-synchronous firing.
3. Oscillations have been observed, and vary with cognitive state.

Awake



Beta waves
(fast, messy)

Stage 0



Alpha waves
(rhythmic, fast)

Stage 1



Theta (less rhythmic)

Stage 2



Theta, some sleep
spindles

Stage 3



Spindles

Stage 4



Delta, slow waves,
some spindles

Stage I-Rem



Theta + REM

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1. Quasi-synchronous firing could, in principle, contribute the kind of boost in information that seems essential for solving the binding problem.
2. Oscillations can produce quasi-synchronous firing.
3. Oscillations have been observed, and vary with cognitive state.
4. Quasi-synchronous firing has been observed in a variety of studies (see Engel and Singer, 2001).
5. There are mechanisms that may enable neuronal coincidence detection. (Dendritic time constants appear to be about right; see London and Häusser, 2005.)

Timing in ensembles

Time scale is crucial: What would be the effect of jittering spike times by $\Delta t = 1, 5, 10, 50$ ms.?

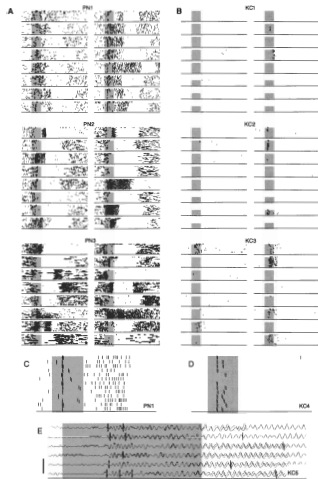
Correlation (of spikes, or spike counts) across neurons again depends on time scale.

Timing in ensembles: Example 1

- ▶ Locust antennal lobe: transformation from widely responsive Projection Neurons (PN) to sparsely responsive Kenyon Cells (KC) (Perez-Orive *et al.*, 2002).

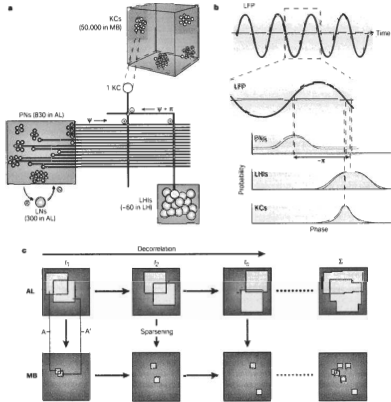
Note: approximately 830 PNs and 50,000 KCs; each PN contacts approximately 600 KCs; each KC gets input from approximately 10-20 PNs.

(Figure shows responses to 16 odors in 3 PNs (A) and 3 KCs (B).)



Transformation in Antennal Lobe

Laurent (2002), and colleagues, argue that KCs are coincidence detectors, and that differing temporal responses among PNs enable sparsening—if a particular combination of PNs fire synchronously then a KC will fire.



Transformation in Antennal Lobe

1. KCs get input from few PNs and PN inputs vary across time.
2. Lateral Horn Interneurons (LHIs) deliver inhibitory input to KCs, roughly in phase opposite to KC local field potential oscillations (Perez-Orive *et al.*, 2002).
3. KC EPSPs are narrowed during excitation (Perez-Orive *et al.*, 2002).
4. There is compelling evidence that oscillations exist and are behaviorally relevant (Stopfer, Bhagavan, Smith, and Laurent, 1997).

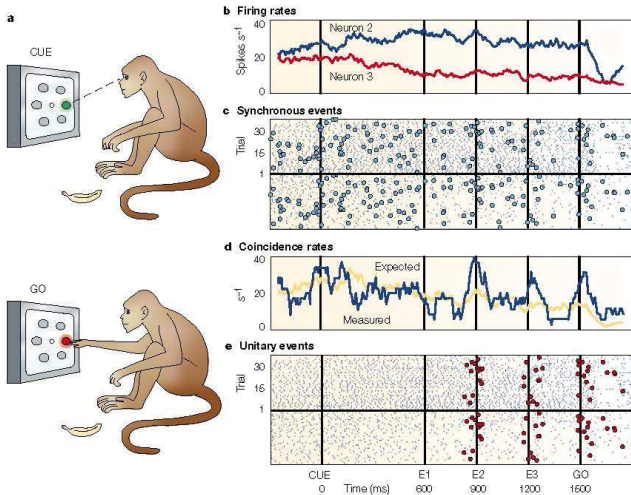
Items 1-3 create conditions for rare KC firing. Item 4 seems to indicate that some mechanism of this sort is likely to explain sparsening and its importance.

Transformation in Antennal Lobe

Note: Here, the “synchrony” corresponding to reported 20-30 Hz oscillations is at a time scale of roughly 10 ms (i.e., relevant spikes occur within, very roughly, about 5-10 ms of each other).

Timing in ensembles: Example 2

Riehle, Grün, Diesmann, and Aertsen (1997) examined neurons in motor cortex during a delayed-response hand-reaching task and found occasional synchronous firing, within 5 ms window, at times of anticipation of the signal to move.



Source: Riehle et al.

Correlation and Its Effects

- ▶ There have been many reports of correlation among neurons and discussions of its physiological interpretation. The question is, In what ways is the correlated activity of neurons relevant to their transmission of information? The answers depend, in part, on the way “correlation” and “information” are defined.

Note that correlation could be measured (i) across stimuli, (ii) within trials, or (iii) across trials.

Statistically, in each case, one evaluates whether two neurons appear to be spiking together more frequently than would be predicted under independence.

- ▶ Zohary, Shadlen, and Newsome (1994) found that pairs of simultaneously recorded MT neurons (during stochastic dot motion) exhibited correlation (across trials) of about $r = .12$. This redundancy can limit the signal amplification possible from ensembles: the amplification gain from 100 correlated neurons is roughly equivalent to that obtained from only a few independent neurons. “Our analysis suggests that the covariation of single-neuron responses and psychophysical detections, an observation that strains credulity at first glance, is a logical consequence of weakly correlated noise within the pool of sensory neurons leading to a decision.”
- ▶ Combining this with the psychometric efficiency of single neurons led Shadlen and Newsome (1998) to suggest that “50-100 neurons might constitute a minimal signaling unit.”

- ▶ However, Abbott and Dayan (1999) pointed out that the analysis of Shadlen and Newsome (1998), noting the deleterious effect of neuronal correlation, assumes an output neuron averages its inputs. If, instead, it uses maximum likelihood (or any statistically efficient decoding method) to “estimate the stimulus” then correlation among neurons will not degrade the estimate (unless the pooled neurons have identical tuning curves).
- ▶ In much the same vein, using information theory, Reich *et al.* (2001) found that “keeping track of which neuron fires each spike preserves a considerable amount of information ... and it prevents an even greater information loss [which would be obtained] from summing responses of neurons with different selectivities.”

Further Relevance of Correlated Spiking

- ▶ Hatsopoulos, Ojakangas, Paninski, and Donoghue (1999) found that excess correlated spiking in pairs of M1 neurons carried substantial information about movement direction for a simple movement task. “Information” here refers to information-theoretic calculations. (See Borst and Theunissen, 1999, for a description of information-theoretic methods.)
- ▶ On the other hand, Nirenberg, Carcieri, Jacobs, and Latham (2001) analyzed responses of retinal ganglion cells to natural scenes. Again using information theoretic methods they found that 90% of the information about the scene could be obtained by assuming the neurons fired independently.

Precise Timing: Analytical Caveats

- ▶ Careful investigations of synchrony at short time scales involve quantitative evaluation of rarity among rare events. Here, spike sorting becomes very important. Bar-Gad, Ritov, Vaadia, and Bergman (2001) have shown how errors in spike sorting can lead to spurious indications of near-synchronous firing. Bar-Gad, Ritov, and Bergman (2001) have also shown how failure to take account of the refractory period can produce misleading indications of oscillatory behavior.
- ▶ Abeles (1991) and others have argued that precisely timed spike patterns carry information beyond what is available from firing rates. This is subtle, statistically. (See Oram, Wiener, Lestienne and Richmond, 1999.)

Statistical Problems

- ▶ Describing and analyzing temporal response to stimuli.
- ▶ Describing, and accounting for, variability across repeated trials.
- ▶ Describing tuning curves.
- ▶ Developing “ideal observer” analyses.
- ▶ Analyzing phase in neural response relative to LFP.
- ▶ Analyzing correlation across sets of neurons.
- ▶ Describing precise timing relationships among correlated neurons.

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 - ▶ Analyzing phase in neural response relative to LFP.
 - ▶ Analyzing correlation across sets of neurons.
 - ▶ Describing precise timing relationships among correlated neurons.
- Careful statistical analysis is important in understanding neural coding.

Reprise: How do neurons code information?

- ▶ There remain many possibilities:
 - ▶ Firing rates among pools of similar neurons;
 - ▶ Rates among small numbers of neurons;
 - ▶ Population coding (in some form);
 - ▶ Correlated or synchronous activity, but time scale matters (“quasi-synchronous” might be a better term).
- ▶ What do we mean by “information?”

Apparently, the context matters. Though general principles appear to be emerging, we must remember to specify *which* neurons and *what* information. Also, the data analysis can be delicate.

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