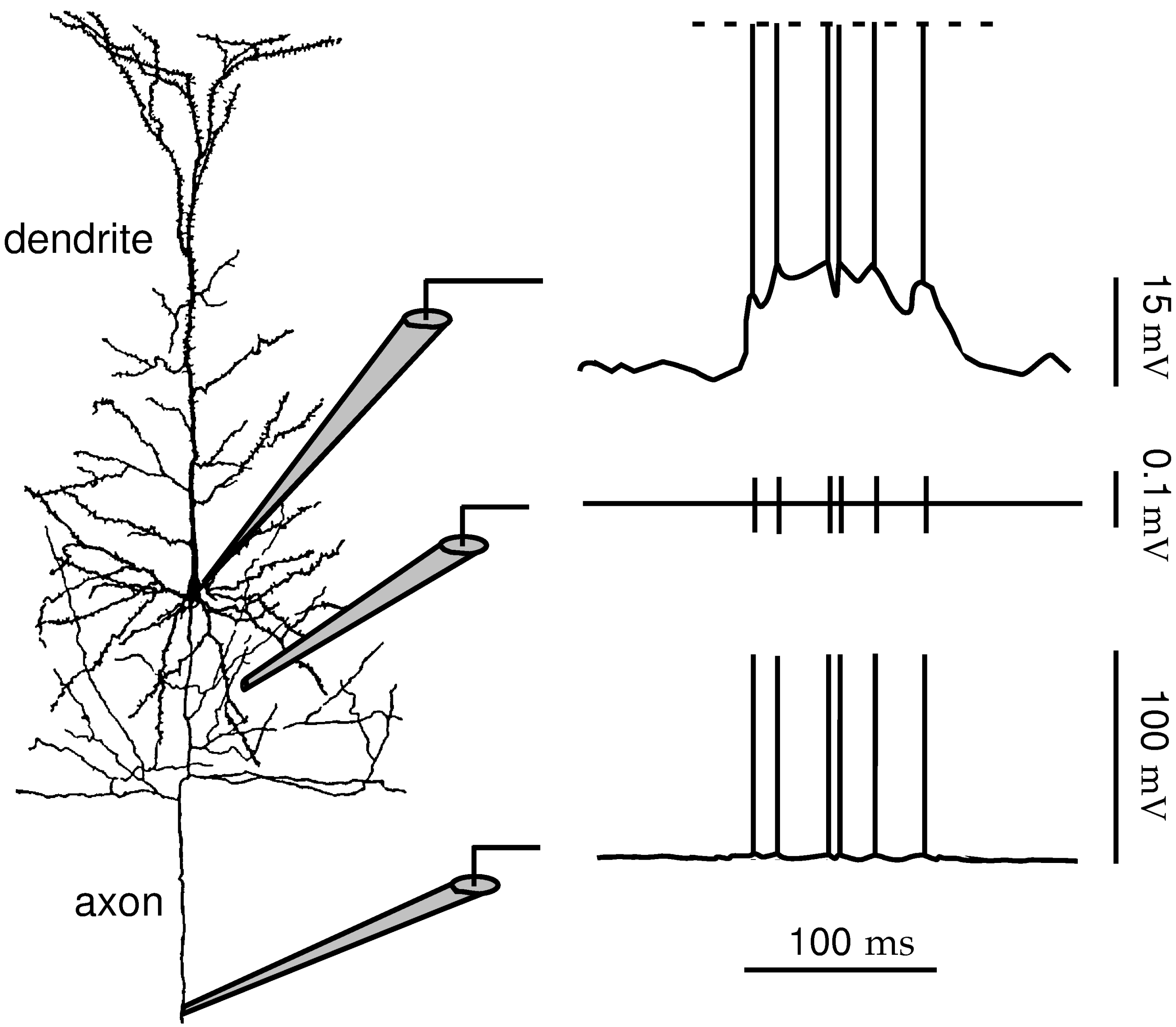
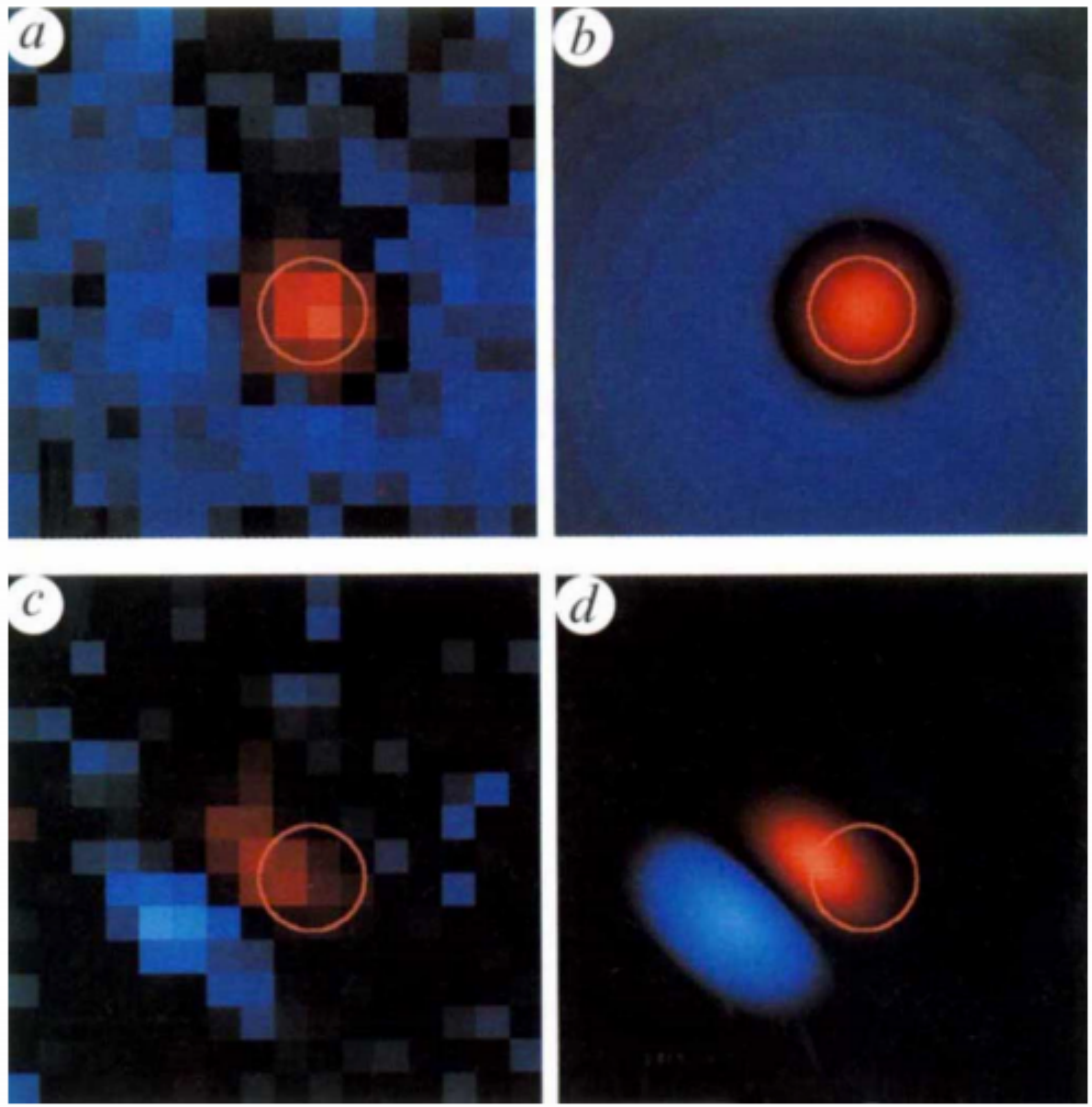
Lecture 5: *Stimulus encoding by single neurons*



$$\mathcal{S} = \{t_1, t_2, \dots t_N\}$$

The basic learning problem: what about the stimulus do neurons respond to?



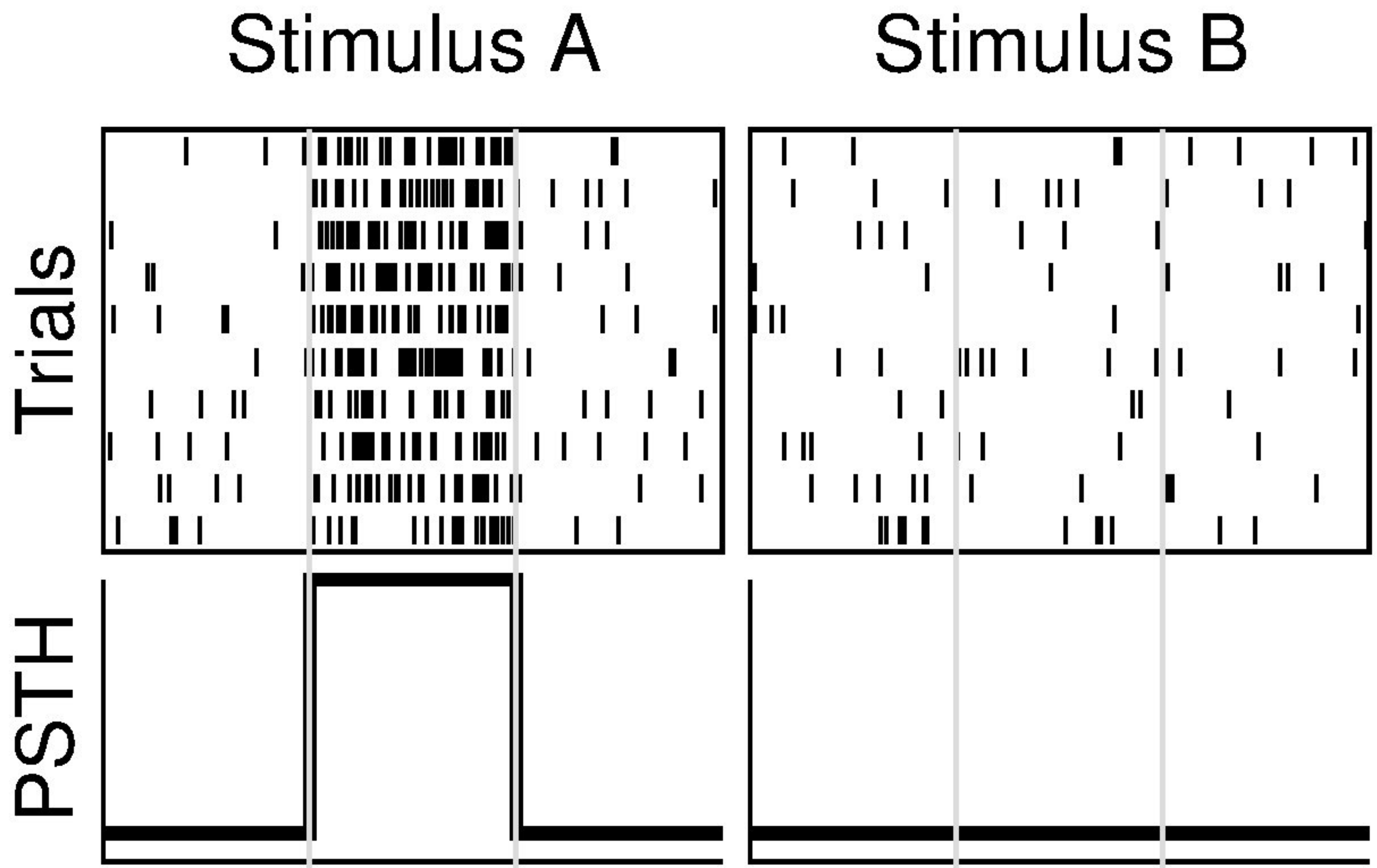
How are external stimuli encoded?

How can we tell which stimulus was shown from the neuronal response?

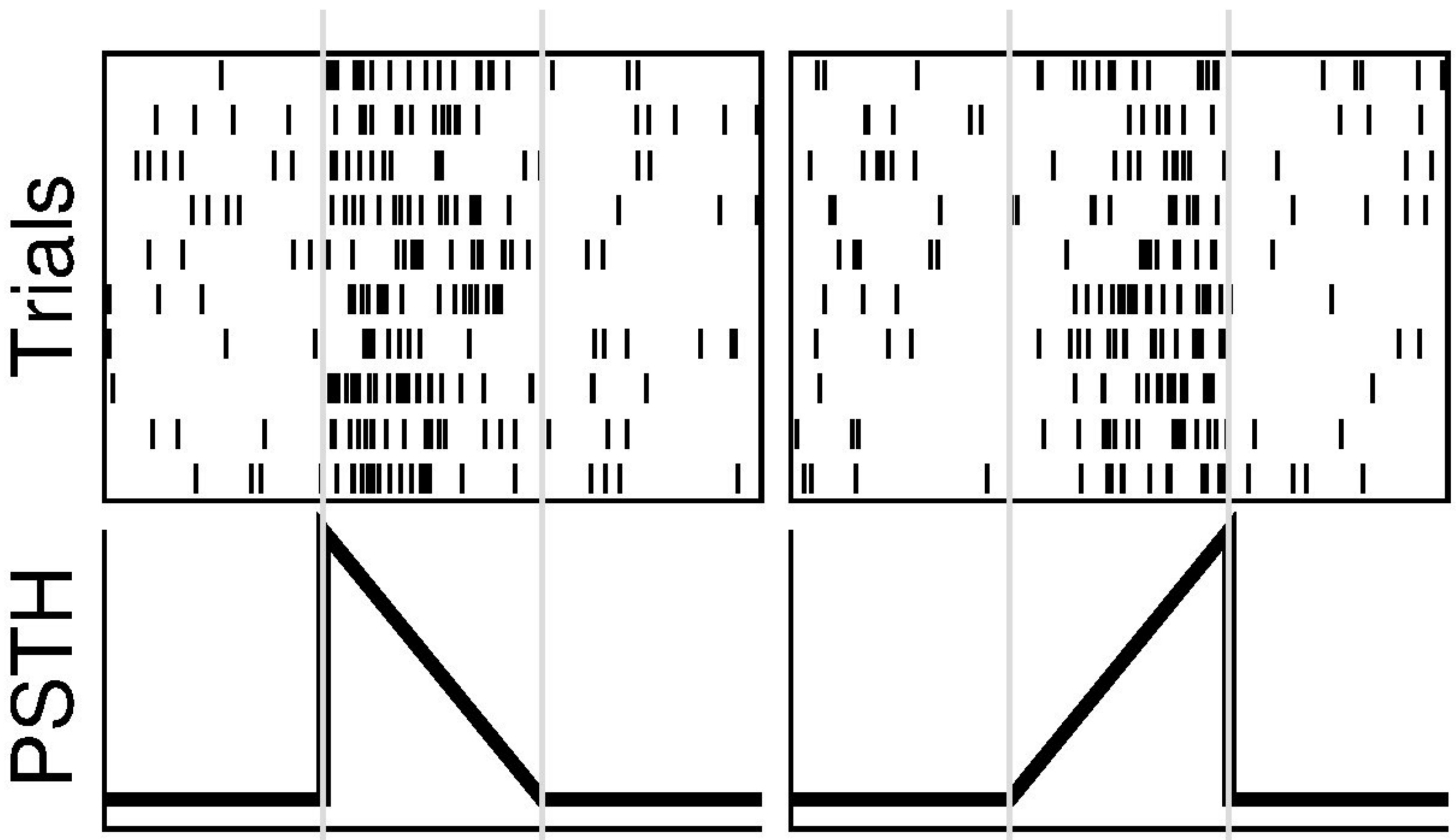
In other words, which features of the neuronal response vary from stimulus to stimulus?

- Spike counts: static rate (spike count) code
- Temporal dynamics of the instantaneous firing rate: instantaneous rate (spike timing) code
- Higher-order correlations: temporal correlation code
- Timing of spikes with respect to a reference signal: phase-of-firing code

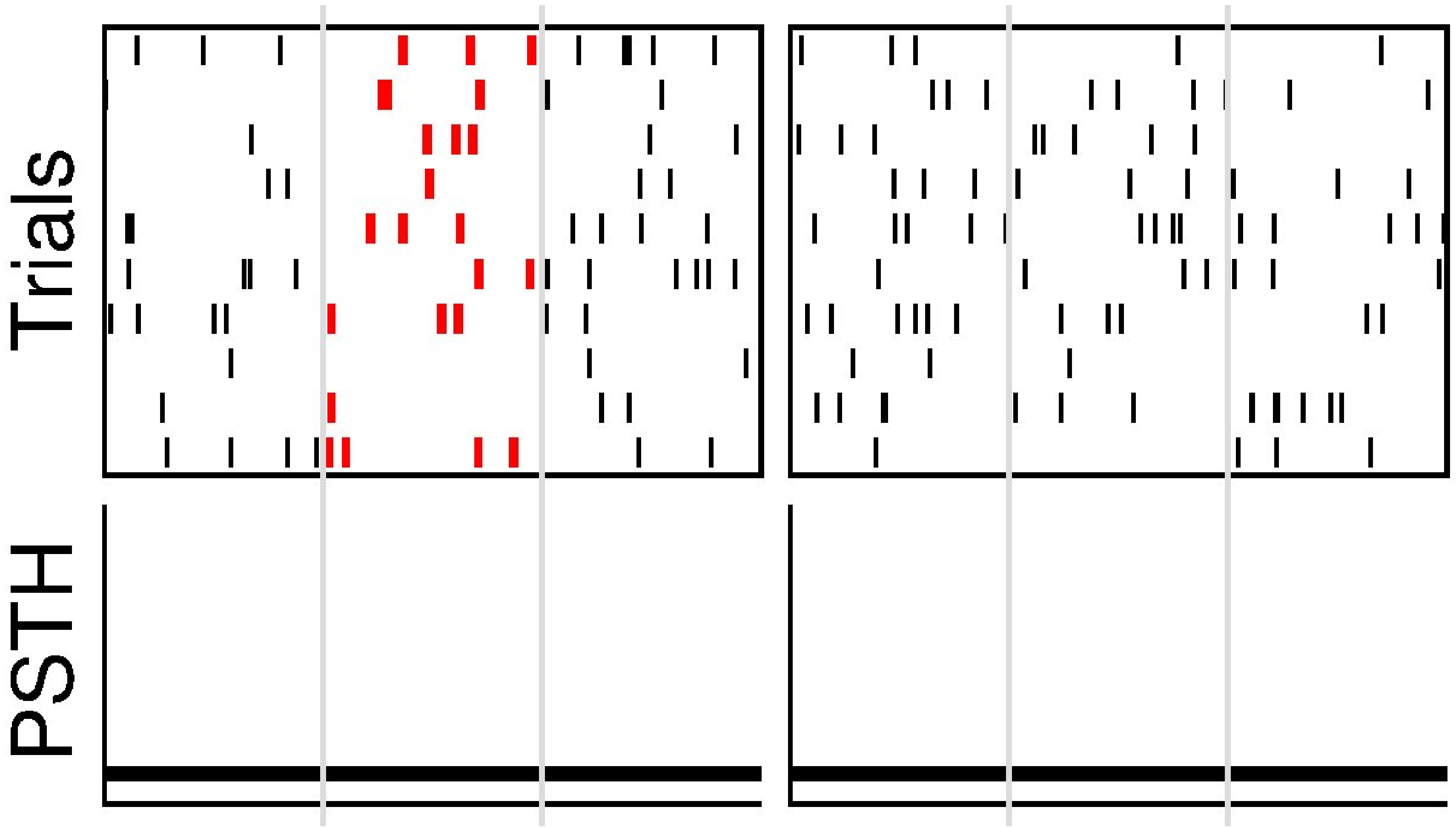
Static rate (spike count) code



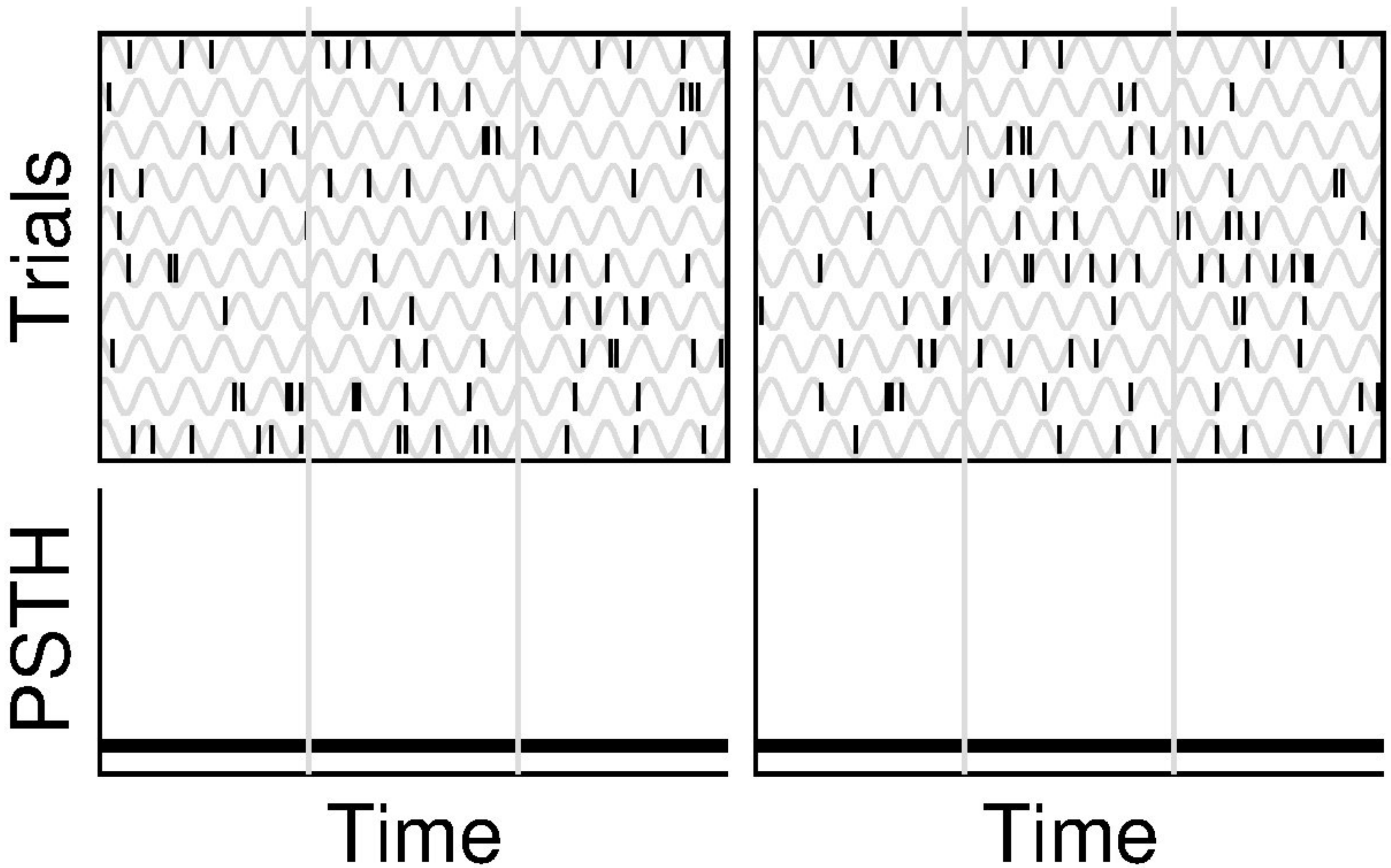
Time-varying rate code



Correlation (spike pattern) code



Phase of firing code



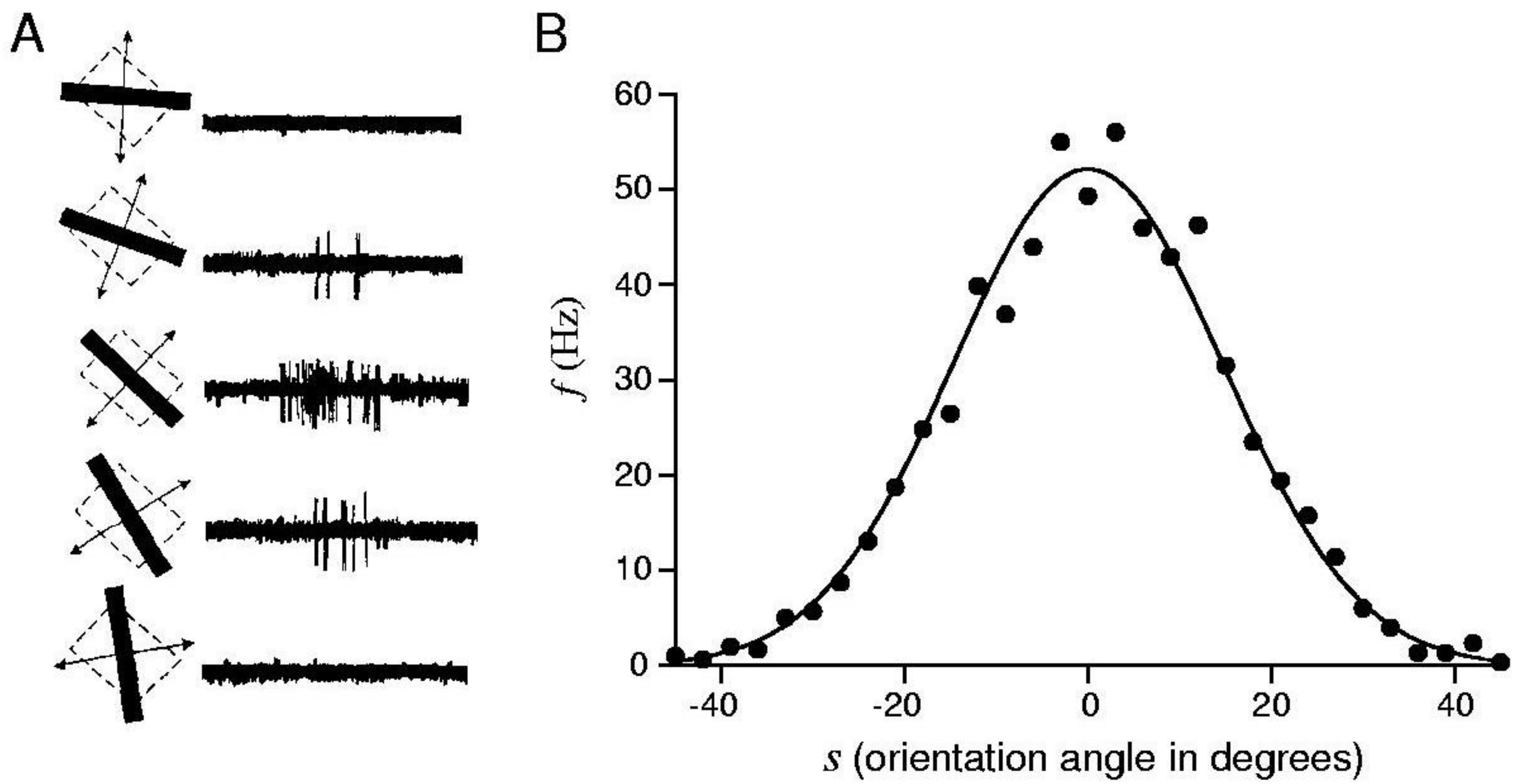
Which coding strategies are used by the brain?

- In the vast majority of brain areas investigated so far, spike counts carry information about external stimuli;
- In many cases, temporal structure of instantaneous firing rate carry additional significant information;
- In some cases, higher order correlations and/or phase of firing carry additional significant information;
- How much information is carried by these different variables? Can be quantified using tools from information theory (see next week)

How firing rates depend on external stimuli: the tuning curve

- **Tuning curve**: how firing rate depends on a (typically continuous) parameter characterizing the stimulus.
- **Bell-shaped** tuning curves are widespread
  - Orientation selectivity in V1;
  - Direction selectivity in MT;
  - Spatial location of the animal in HPC of the rat;
  - Spatial location of stimulus: PPC, PFC
  - Location of a saccade: FEF
  - Direction of the arm: M1
  - Head direction: DTN, thalamus, subiculum;
- **Monotonic** tuning curves are also widespread
  - Eye position in oculomotor nuclei
  - Angular velocity of the head in vestibular nuclei
  - Frequency of vibration in S1, S2, PFC
  - Retinal disparity in V1

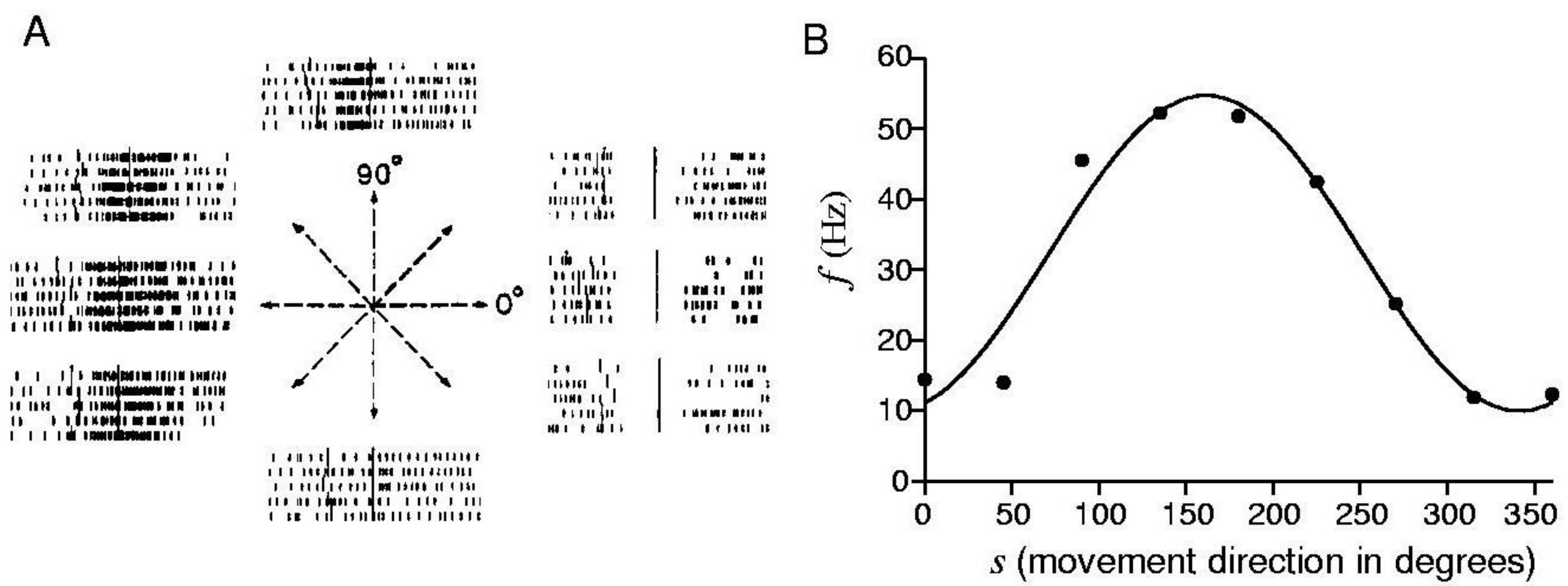
V1: orientation



$$r = r_0 + (r_{max} - r_0)\exp\left(-\frac{1}{2}\left(\frac{s - s_{max}}{\sigma}\right)^2\right)$$

Hubel and Wiesel 1968

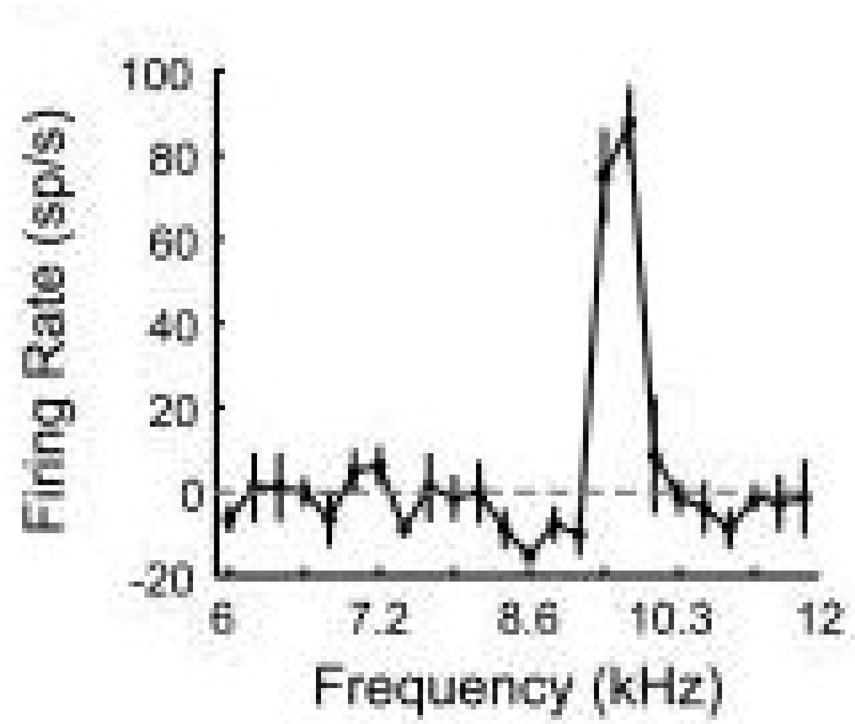
M1: arm direction



$$r = r_0 + (r_{max} - r_0)\cos(s - s_{max})$$

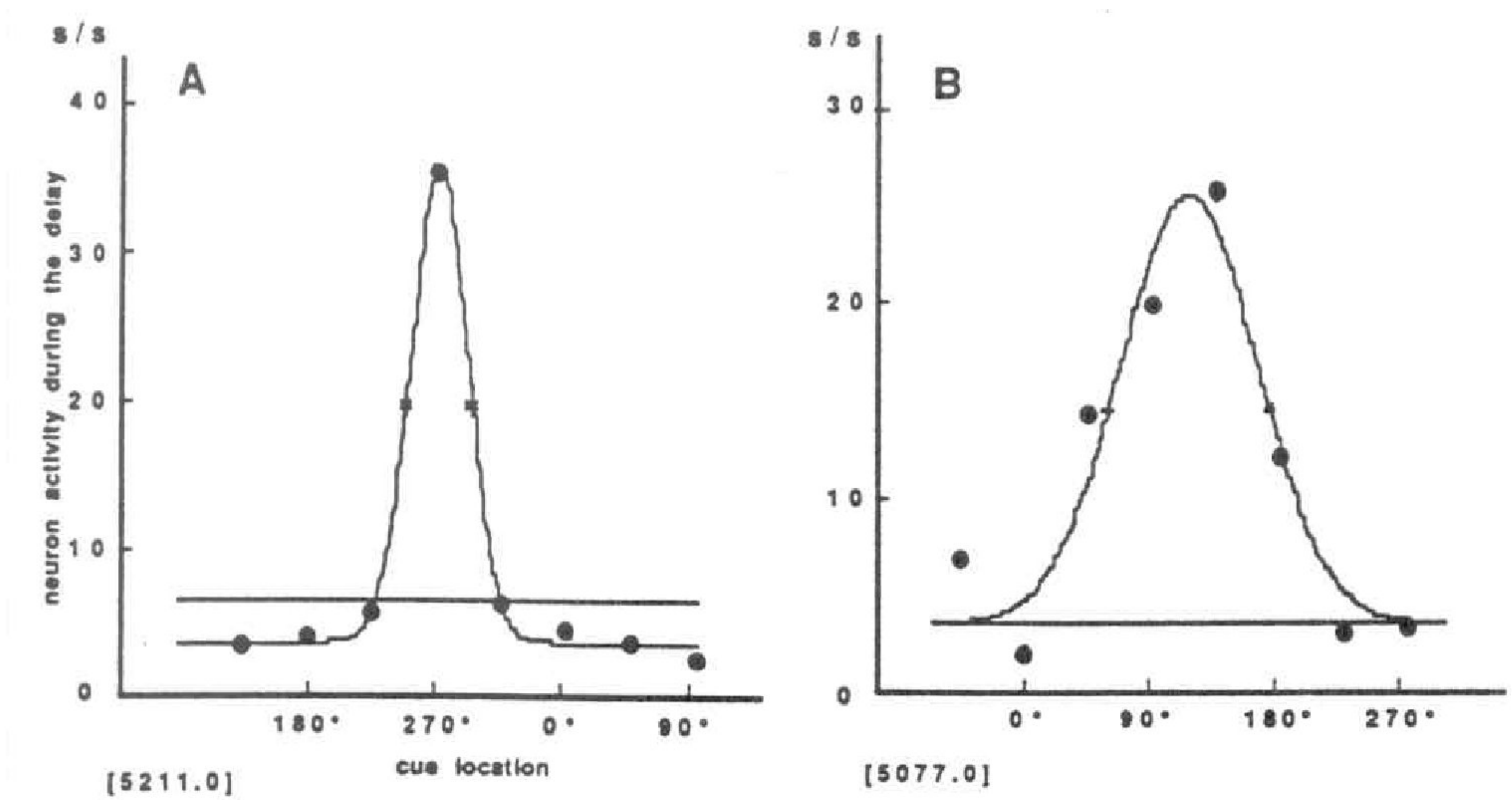
Georgopoulos et al 1982

Auditory system: frequency



Bartlett et al 2011

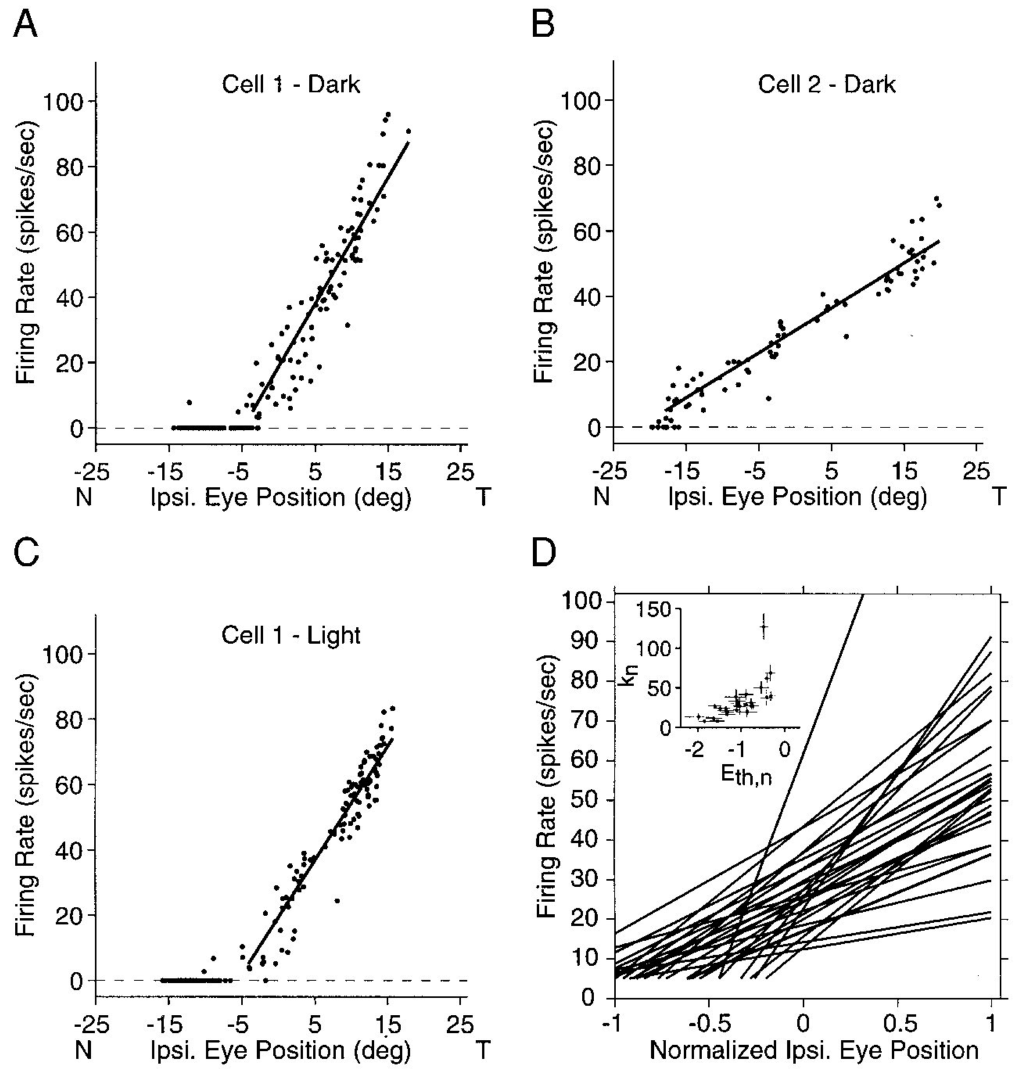
Prefrontal cortex



$$r = r_0 + (r_{max} - r_0)\exp\left(-\frac{1}{2}\left(\frac{s - s_{max}}{\sigma}\right)^2\right)$$

Funahashi et al 1989

Oculomotor nuclei: eye position



Aksay et al 2000

What's the mapping between the stimulus and the firing rate? (without having to guess what matters to the neuron)

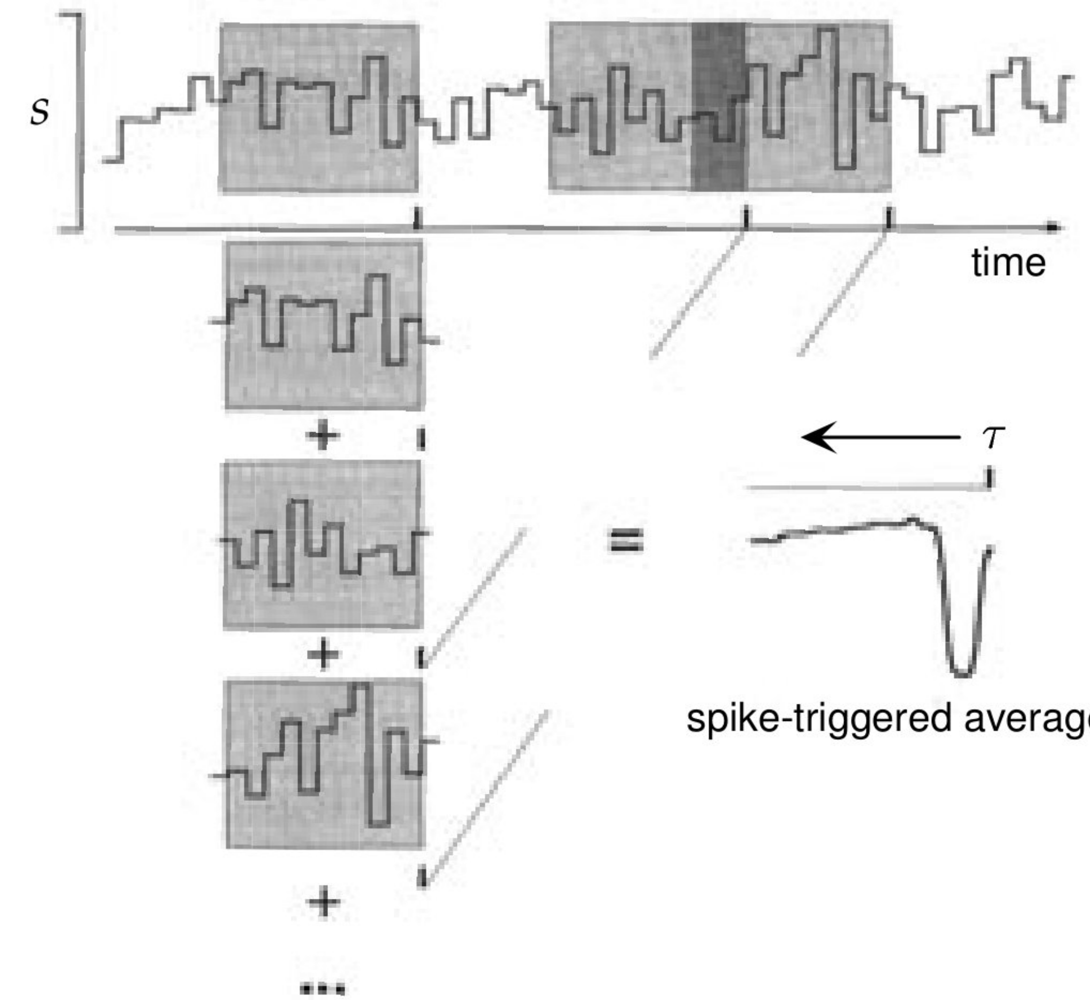
The spike-triggered average (STA)

- Stimulus $s(t)$
- Measure spike train

$$y(t) = \sum_{i=1}^{n} \delta(t - t_i)$$

- Spike triggered average (STA)

$$\begin{aligned} C(\tau) &= \frac{1}{n}\sum_{i=1}^{n} s(t_i - \tau) \\ &= \frac{\int s(t-\tau)y(t)dt}{\int y(t)dt} \end{aligned}$$



STA and reverse correlation

- Average over trials

$$r(t) = \langle y(t) \rangle$$

- Average over time

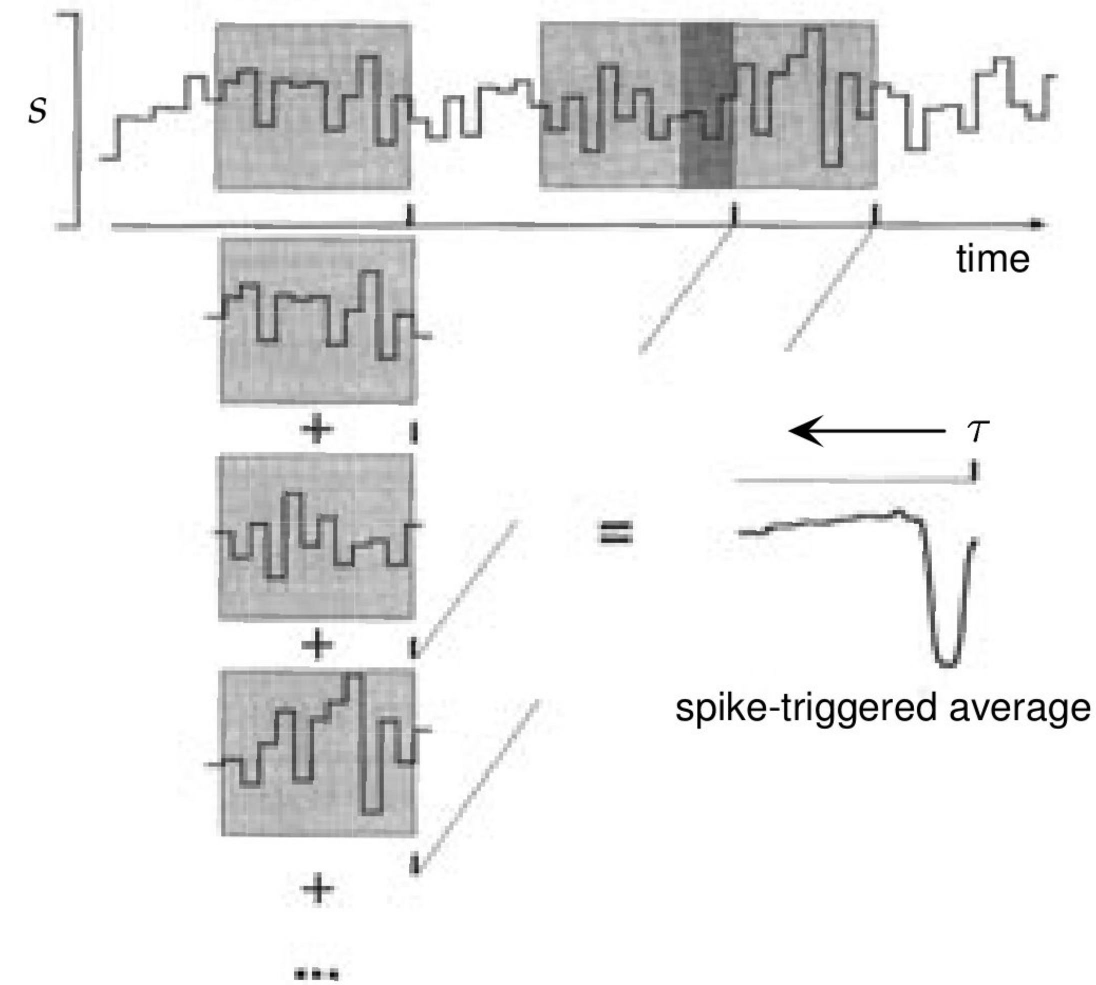
$$R = \frac{1}{T} \int r(t)dt$$

- Spike triggered average (STA)

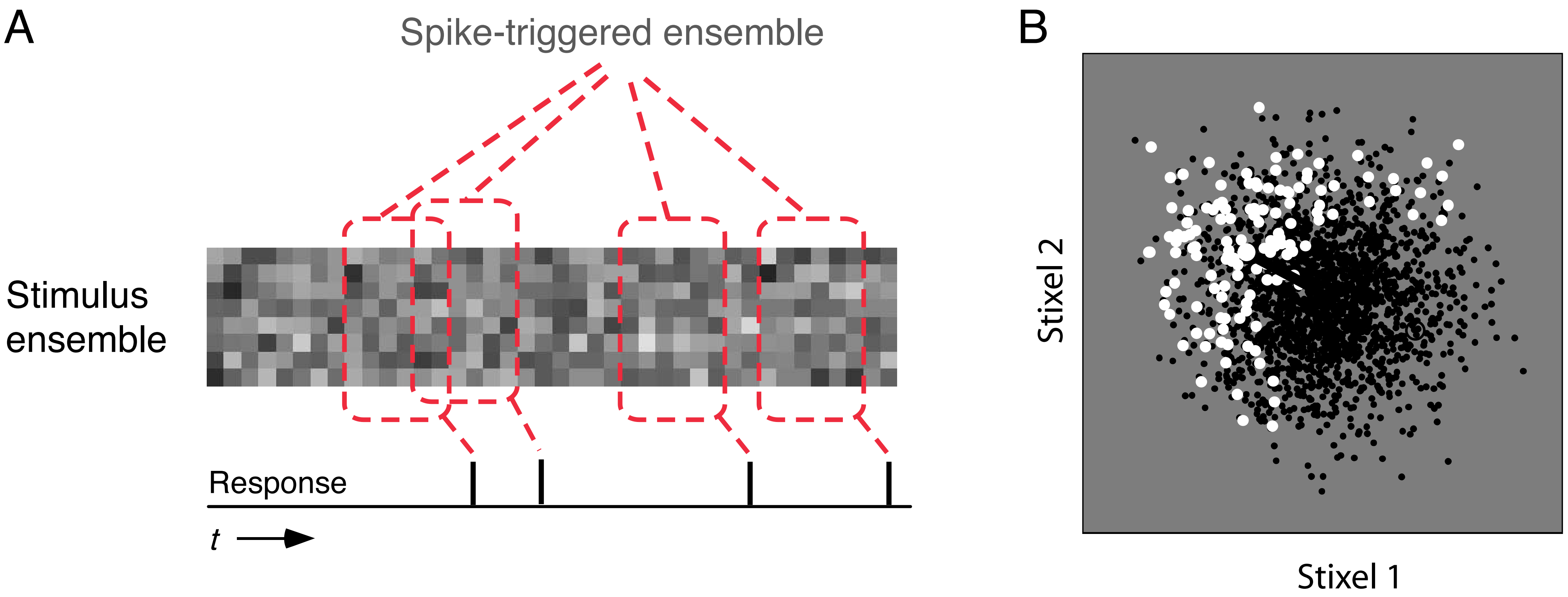
$$\begin{aligned} \langle C(\tau) \rangle &= \frac{1}{RT} \int dt r(t) s(t-\tau) \\ &= \frac{Q(-\tau)}{R} \end{aligned}$$

where Q is the correlation of the firing rate and stimulus

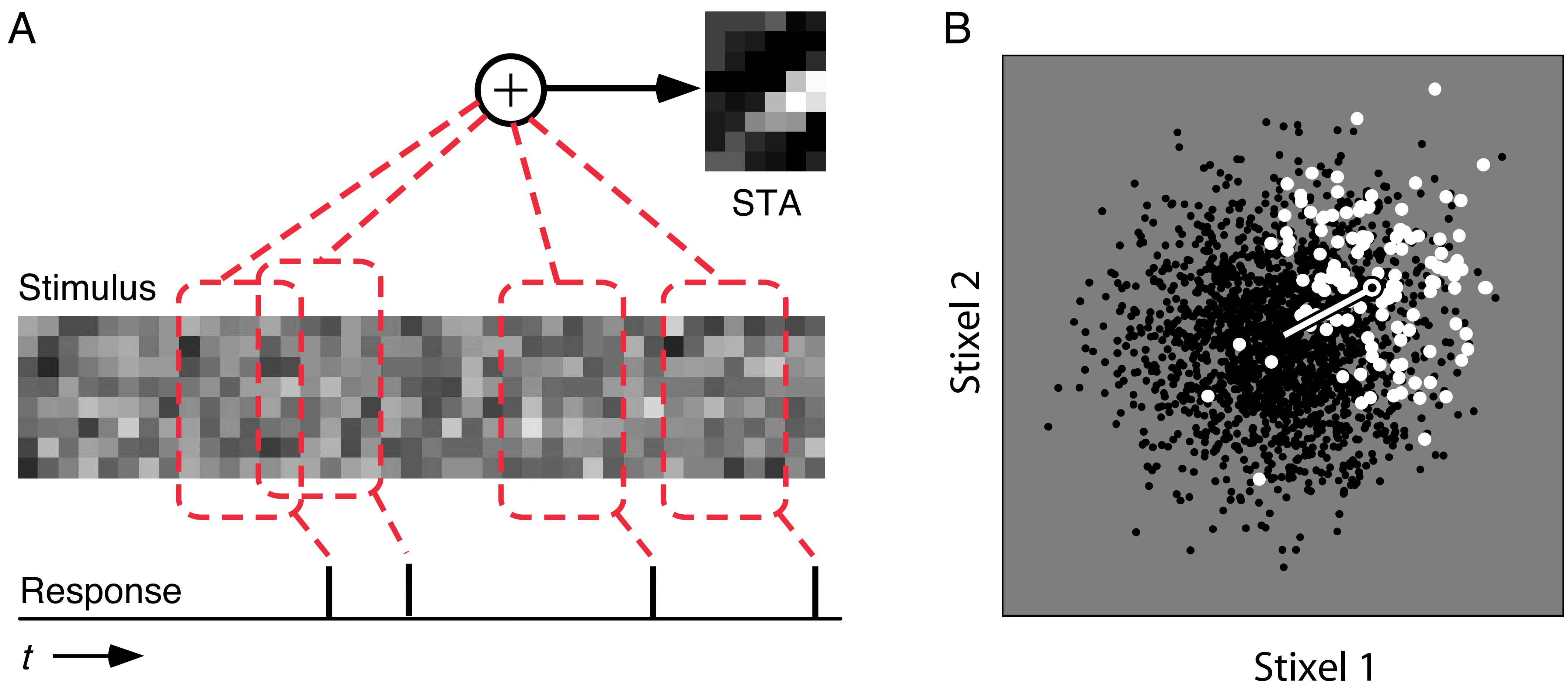
$$Q(\tau) = \frac{1}{T} \int dt r(t) s(t+\tau)$$



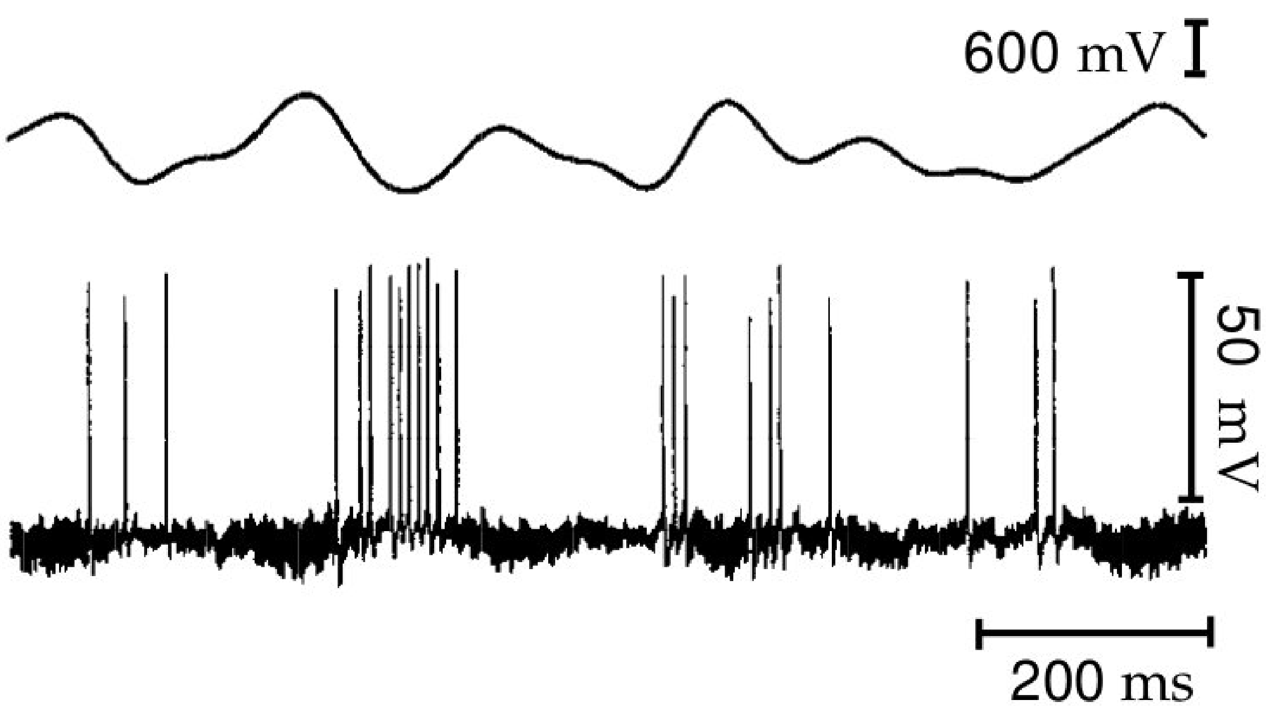
Graphical example:

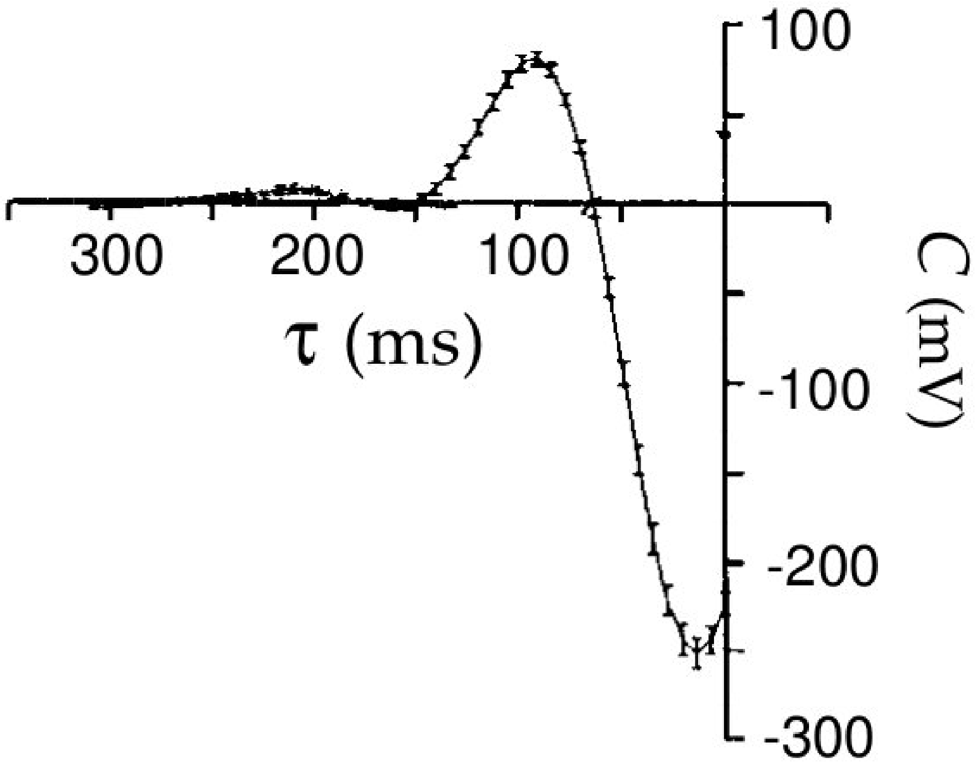


Graphical example:

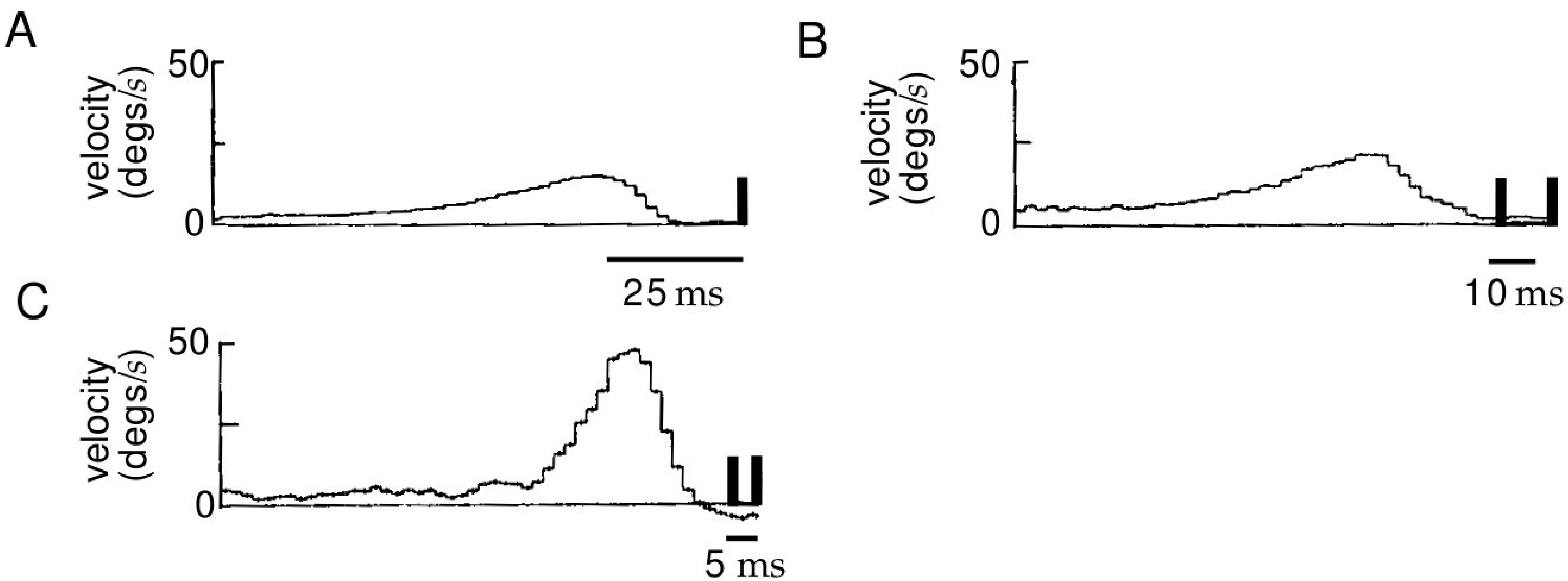


STA example: electrosensory system





Multiple spike triggered average



- H1 neuron in the fly visual system (de Ruyter van Steveninck and Bialek, 1988)

Volterra and Wiener expansions:

$$\mathrm{r}_{\mathrm{est}}(t) = \mathrm{r}_0 + \int_0^{\infty} d\tau\, D(\tau) s(t-\tau)$$

$$\begin{aligned}\mathrm{r}_{\mathrm{est}}(t) \quad &= \quad \mathrm{r}_0 + \int d\tau\, D(\tau) s(t-\tau) + \int d\tau_1 d\tau_2\, D_2(\tau_1, \tau_2) s(t-\tau_1) s(t-\tau_2) + \\ &\quad \int d\tau_1 d\tau_2 d\tau_3\, D_3(\tau_1, \tau_2, \tau_3) s(t-\tau_1) s(t-\tau_2) s(t-\tau_3) + \ldots\end{aligned}$$

Characterizing input/output transformation: Volterra series

- A function of one variable can be expanded in a Taylor series:

$$y = f(x) = f(x_0)+f'(x_0)(x-x_0)+\frac{1}{2}f''(x_0)(x-x_0)^2+\frac{1}{6}f'''(x_0)(x-x_0)^3+\ldots$$

- We are interested in characterizing a functional F that transforms a time-dependent input $s(t)$ into a time-dependent neuronal output $y(t)$.

- Volterra series:

$$\begin{aligned} y(t) = F[s(t)] \quad &= \quad h_0 + \int dt_1 h_1(t_1) s(t-t_1) \\ &+ \int dt_1 dt_2 h_2(t_1,t_2) s(t-t_1) s(t-t_2) \\ &+ \int dt_1 dt_2 dt_3 h_3(t_1,t_2,t_3) s(t-t_1) s(t-t_2) s(t-t_3) \end{aligned}$$

- $h_n =$ **Volterra kernels**

Wiener series

- Wiener approach:
  - $s(t) =$ Stochastic process
  - Rewrite expansion so that individual terms are statistically independent gaussian
- Simplest case: $s(t) =$ white noise,

$$
\begin{aligned}
\langle s(t) \rangle &= 0 \\
\langle s(t_1)s(t_2) \rangle &= S\delta(t_1 - t_2) \\
\langle s(t_1)s(t_2)s(t_3) \rangle &= 0 \\
\langle s(t_1)s(t_2)s(t_3)s(t_4) \rangle &= S^2\delta(t_1 - t_2)\delta(t_3 - t_4) \\
&\quad +S^2\delta(t_1 - t_3)\delta(t_2 - t_4) \\
&\quad +S^2\delta(t_1 - t_4)\delta(t_2 - t_3)
\end{aligned}
$$

Wiener series

$$
\begin{aligned}
y(t) &= G_0 + G_1 + G_2 + G_3 \dots \\
G_0 &= g_0 \\
G_1 &= \int_0^\infty dt_1 g_1(t_1) s(t-t_1) \\
G_2 &= \int_0^\infty dt_1 \int_0^\infty dt_2 g_2(t_1,t_2) s(t-t_1) s(t-t_2) \\
&\quad -S \int_0^\infty dt g_2(t,t) \\
G_3 &= \int_0^\infty dt_1 \int_0^\infty dt_2 \int_0^\infty dt_3 h_3(t_1,t_2,t_3) s(t-t_1) s(t-t_2) s(t-t_3) \\
&\quad -3S \int_0^\infty dt_1 dt_2 g_3(t_1,t_1,t_2) s(t-t_2)
\end{aligned}
$$

- $g_n =$ Wiener kernels
- Different terms are statistically independent!

Computing Wiener kernels

- Correlate output with powers of white noise input:

$$
\begin{aligned}
g_0 &= \langle y(t) \rangle \\
g_1(\tau) &= \frac{1}{S} \langle y(t) s(t-\tau) \rangle \\
g_2(\tau_1, \tau_2) &= \frac{1}{2S^2} \langle y(t) s(t-\tau_1) s(t-\tau_2) \rangle \\
&\cdots
\end{aligned}
$$

- $g_0 =$ mean firing rate
- $g_1(\tau) = \frac{g_0}{S} C(\tau)$ where C is the STA
- ...

Why do we call this ‘reverse-correlation’?

$$C(\tau) = \frac{1}{\langle r \rangle} Q_{\mathrm{r}s}(-\tau)$$

The STA as the optimal kernel for estimating r(t) (for white noise stimuli!):

$$E = \frac{1}{T}\int_0^T dt\ \left(\mathrm{r}_{\mathrm{est}}(t) - \mathrm{r}(t)\right)^2$$

chalkboard interlude

The STA as the optimal kernel (for white noise

$$E = \frac{1}{T}\int_0^T dt\ (\mathrm{r}_{\mathrm{est}}(t) - \mathrm{r}(t))^2$$

$$\int_0^\infty d\tau'\, Q_{ss}(\tau - \tau')D(\tau') = Q_{\mathrm{r}s}(-\tau)$$

$$Q_{ss}(\tau) = \sigma_s^2 \delta(\tau)$$

$$\sigma_s^2 \int_0^\infty d\tau'\, \delta(\tau - \tau')D(\tau') = \sigma_s^2 D(\tau)$$

$$D(\tau) = \frac{Q_{\mathrm{r}s}(-\tau)}{\sigma_s^2} = \frac{\langle r\rangle C(\tau)}{\sigma_s^2}$$