# THEORETICAL NEUROSCIENCE I

## Lecture 9: Receptive fields and tuning curves

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# Content

1. Frog vision

2. Cat vision

3. Receptive fields, response variability, and tuning curves

4. Reverse correlation methods

## Sensation, perception, and representation

Possible stages of sensory processing (vision, audition, somatosensation, olfaction, gustation):

- **Sensation:** a physical stimulus impinges on receptors cells of a sensory organ. Elementary properties of stimulation are *transduced* into neural activity (e.g., light, sound).
- **Perception (human):** the mental process of becoming aware of, understanding, and recognizing the physical causes of sensory stimulation. Perception produces the insight that guides behaviour.
- **Representation:** As the initial sensory activity propagates from receptors to thalamus, primary sensory cortex, secondary sensory cortex, and associative cortex, its neural representation continues to change. Presumably, this succession of representations contributes to perception.

# 1 Frog vision

From *Lettvin, Maturana, McCulloch, and Pitts (1959)*:

"A Frog hunts on land by vision. He escapes enemies mainly by seeing them. His eyes do not move, as do ours, to follow prey, attend suspicious event, or search for things of interest. If his body changes its position with respect to gravity or the whole visual world is rotated about him, then he shows compensatory eye movements. These movements enter his hunting and evading habits only, e.g. as he sits on a rocking lily pad. Thus, his eyes are actively stabilized. He has no fovea, or region of greatest acuity in vision, upon which he must center a part of the image . . .

From *Lettvin, Maturana, McCulloch, and Pitts (1959)*:

. . . The frog does not seem to see or, at any rate, is not concerned with the detail of stationary parts of the world around him. He will starve to death surrounded by food, if it is not moving. His choice of food is determined only by size and movement. He will leap to capture any object the size of an insect or worm, providing it moves like one. He can be fooled easily not only by a piece of dangled meat but by any moving small object. His sex life is conducted by sound and touch. His choice of paths in escaping enemies does not seem to be governed by anything more devious than leaping to where it is darker. Since he is equally at home in water and on land, why should it matter where he lights after jumping or what particular direction he takes? He does remember a moving thing provided it stays within his field of vision and he is not distracted."

## Frog Eye Characteristics

The thick lens gives the animal a large field of view. The frog is naturally nearsighted (-6 diopters) giving it a focus of approximately 6 inches. Frogs and toads can change their focus by moving the lens out towards the cornea. The advantage of nearsightedness is that it blurs the background clutter making foreground object characterization much easier.

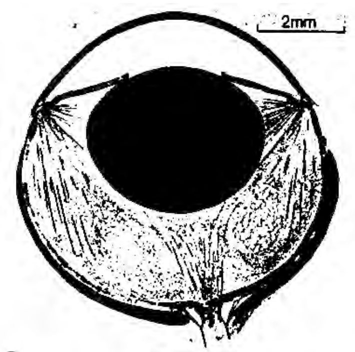


Figure 1
Top View of the Frog Eye (originally from Szent-Gyorgyi - 1914 but scanned from Grusser and Grusser-Cornehls - 1976)

Figure 1: [1]

## Response Classes of the Ganglion Cells

Class 1 and class 2 ganglion cells project to the brain via unmyelinated fibers having conduction velocities of 20 to 50 centimeters per second. They make up 97 percent of the optic nerve (Maturana - 1959).

- Class 1 neurons (edge detectors): These neurons have oval receptive fields from 1.5 to 4 degrees in size. They detect the completeness and sharpness of both light and dark edges. They respond to stationary edges, but more vigorously to edge movement.
- Class 2 neurons (convexity detectors): These neurons have oval receptive fields ranging in size from 2.5 to 5 degrees. They seem to detect the dark leading edge (head) of any worm or bug. If the stimulus stops beforer eaching the RF center, the response slowly

decays. A brief darkness or shadow will permanently stop the response until the object moves again.

## Class 1 and class 2 receptive fields

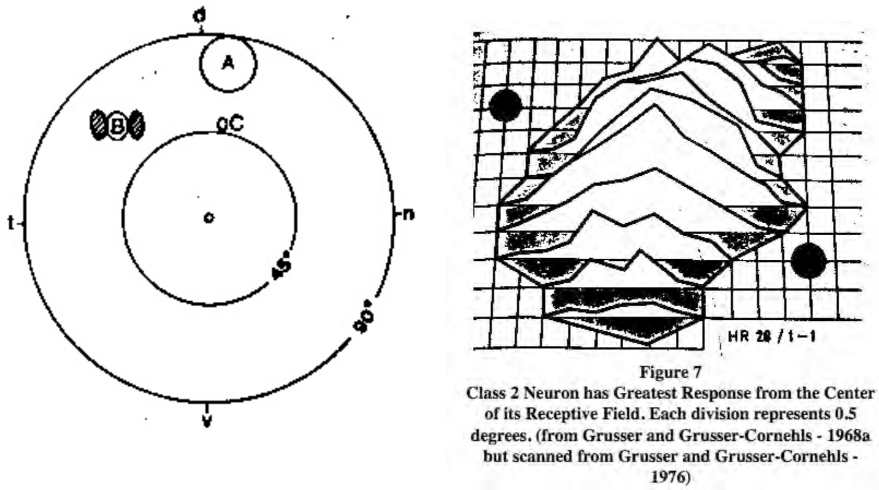


Figure 2: Receptive fields. [2]

## Response depends on visual movement

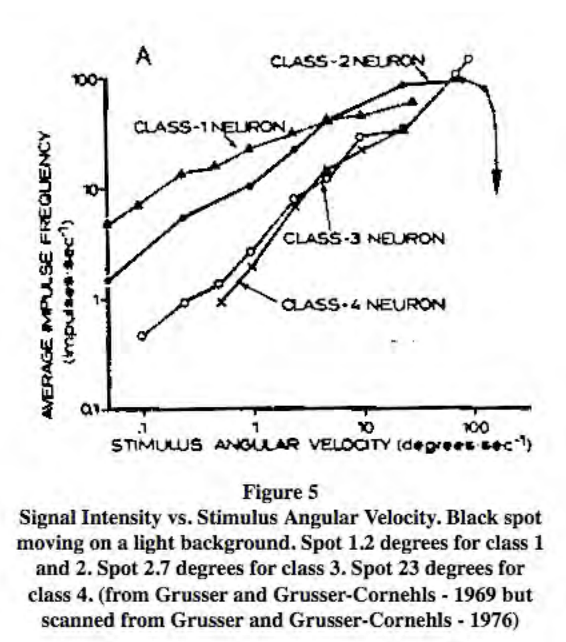


Figure 3: [3]

## What the frog's eyes tell the frog's brain (Lettvin, Maturana, McCulloch, Pitts, 1968)

The output of the retina is a set of four distributed operations on the visual image. 1) local sharp edges and contrasts, 2) curvature of edge of a dark object, 3) movement of edges, 4) local dimmings by movement or darkening. Each operation maps the retina continuously on a single sheet in the frog's brain. There are four such sheets, and their maps are in registration.

We have described each operation in terms of its common factors. So what does a particular fibre measure? The degree to which a particular quality is present (the quality that excites the fibre maximally).

The operations have much more a flavor of *perception* than of *sensation*, if that distinction has any meaning now (1968!).

## Summary frog vision

- "The eye speaks to the brain in a language already highly organized and interpreted, instead of transmitting an accurate copy of light on receptors. ...Since the purpose of a frog's vision is to get him food and allow him to evade predators, it is not enough to know the reaction of his visual system to points of light."

- Sensory systems (e.g., vision) are optimized for a specific ecological niche and behavior.

- Sensory neurons are particularly sensitive to behaviorally relevant stimuli (e.g., edible prey).

- Presumed ('putative') neural correlates of perception already in retinal ganglion cell responses.

## 2 Cat vision

Cat vision had been investigated since the 1940s, culminating in the work of David Hubel and Torsten Wiesel in the 1960s and 1970s.

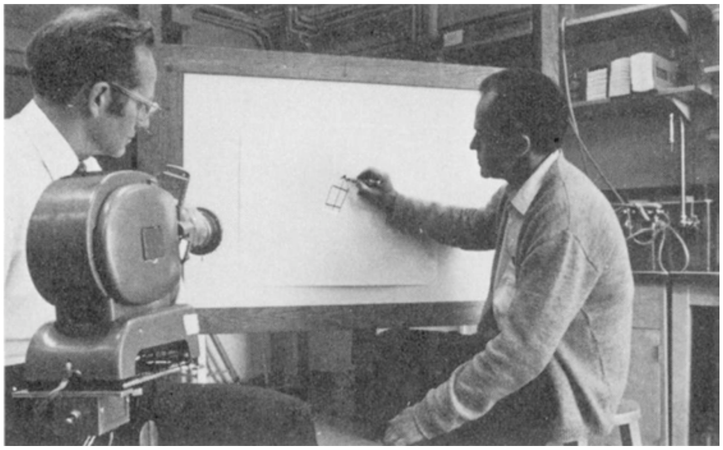

Figure 4: David Hubel and Torsten Wiesel. [4]

### Microelectrode recording

With tungsten microelectrodes, action potential of individual neurons can be recorded in the living animal (either anestethised or awake).

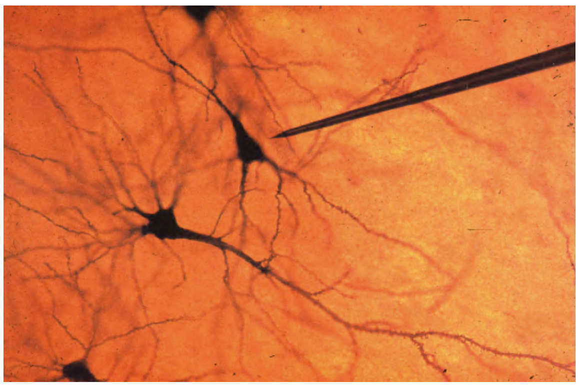

Figure 5: Microelectrode recording. [5]

Visually responsive neurons can be recorded in retina, lateral geniculate nucleus, and visual cortex.

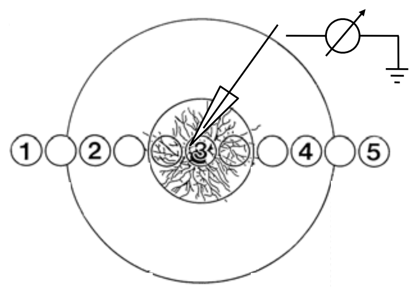


Figure 6: ON/OFF and center/surround structure. [6]

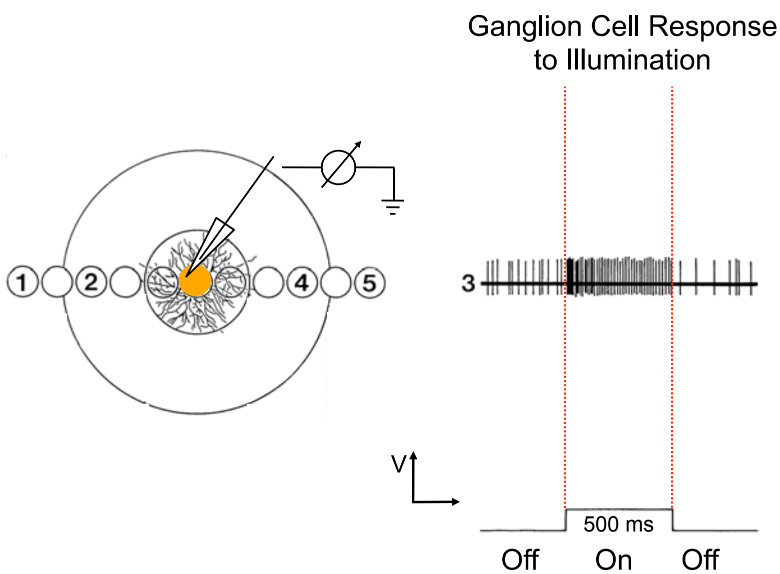


Figure 7: ON/OFF and center/surround structure. [7]

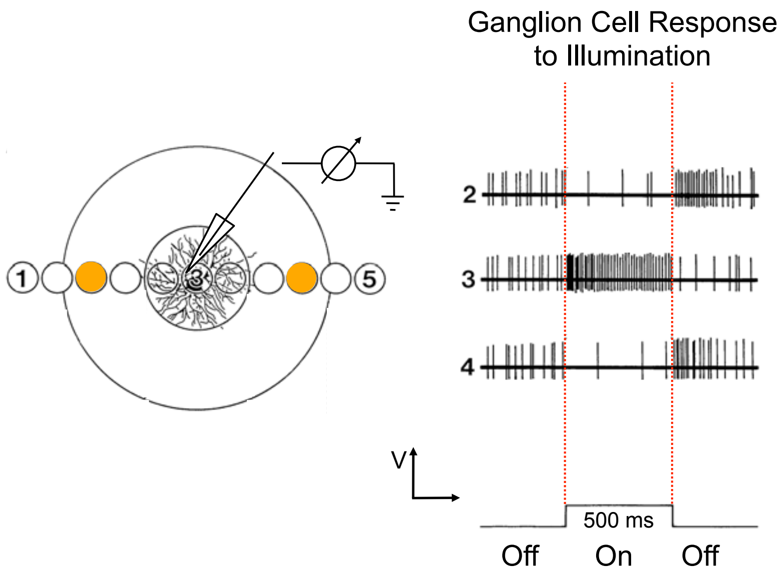


Figure 8: ON/OFF and center/surround structure. [8]

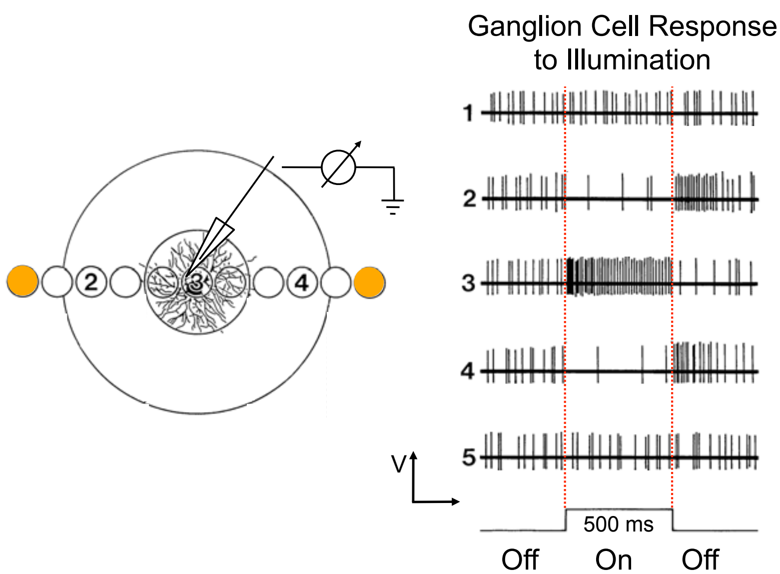


Figure 9: ON/OFF and center/surround structure. [9]

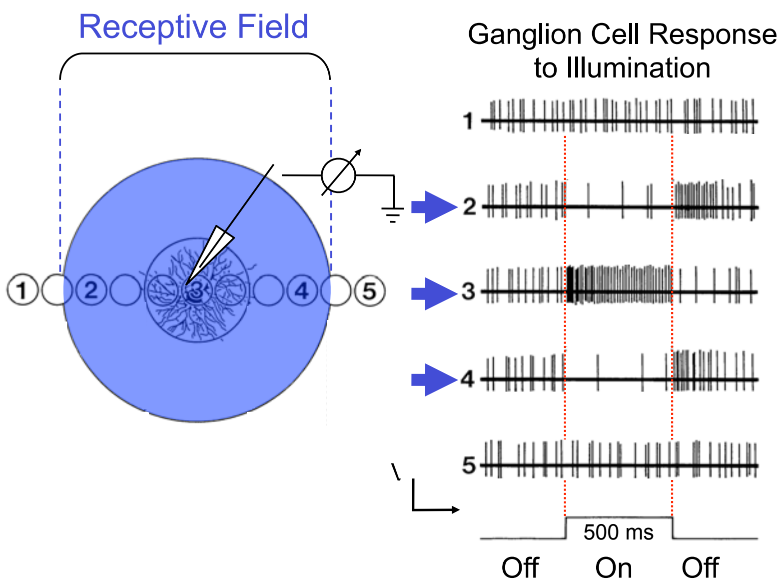


Figure 10: ON/OFF and center/surround structure. [10]

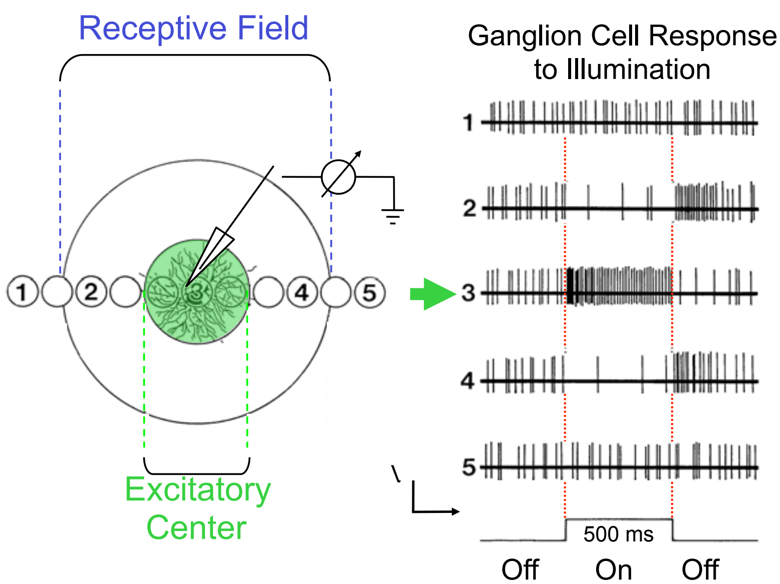


Figure 11: ON/OFF and center/surround structure. [11]

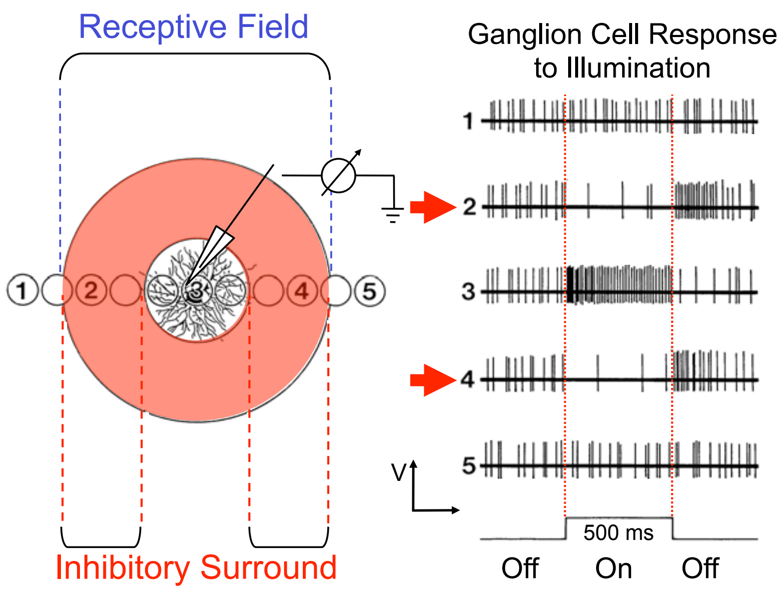


Figure 12: ON/OFF and center/surround structure. [12]

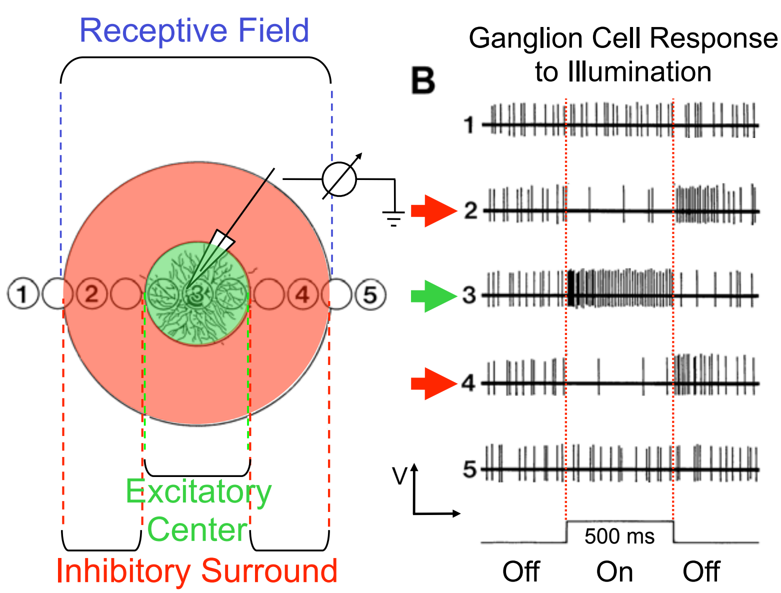


Figure 13: ON/OFF and center/surround structure. [13]

# Summary ON/OFF and center/surround

Visually response neurons in the cat retina and in the lateral geniculate nucleus of the thalamus show a particular receptive field structure:

- Small size ($\sim 0.1^\circ$ in fovea).
- Separate ON and OFF regions.
- ON regions respond to *onset of light* or *offset of dark.*
- OFF regions respond to *onset of dark* or *offset of light.*
- Small center with larger (concentric) surround.
- ON-center, OFF-surround (or vice versa).

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CATS SEE SUBJECTIVE CONTOURS

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**Abstract**—Behavioural techniques were used to determine whether cats are able to see subjective contours. Through several stages of testing with increasingly complex displays, cats continued to respond to a figure defined by subjective contours. This result provides the first direct evidence that a nonhuman perceives subjective contours.

Figure 14: Cats see subjective contours paper. [14]

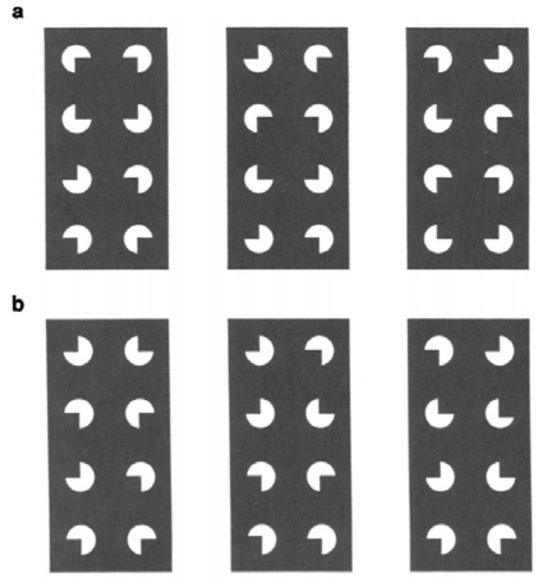


Fig. 2. (a) Three frames from a movie of a subjective square undergoing apparent motion. The perception of the square is vivid over a range of frame durations. (b) Three frames from the control movie in which a given configuration of sectored disks is displaced over frames. This configuration occupies the same position as that occupied by the subjective square in a. With the configuration illustrated in b, neither apparent motion, a subjective figure nor the configuration itself is seen at any movie speed.

Figure 15: Perception of squares. [15]

## General-purpose vision

- No ‘putative’ correlates of ‘perception’ in retinal ganglion cells (RGC) of cat: no evident relation to behaviorally relevant stimuli.

- Instead, RGC reflect the statistics of the natural visual environment.

- Light/dark contrasts two nearby points are common (due to solid surfaces and sharp boundaries).

- Cat RGC constitute first step of mammalian *general purpose* vision, which seems specialized for distinguishing and recognizing all (natural) visual objects.

# 3 Receptive fields, response variability, and tuning curves

Neuroscientists describe the responses of sensory neurons and formulate hypotheses as to their contribution to behaviour.

Several heuristic concepts have proven extremely useful.

We now introduce three of these concepts.

Adopting this descriptive approach, we do not take any position on the issue of 'perception' versus 'sensation'. The neural responses we describe will gradually become less 'sensation-like' and more 'perception-like'.

**Definition:**
**A "receptive field" is the area in sensory space where stimulation is required to drive a neuron.**

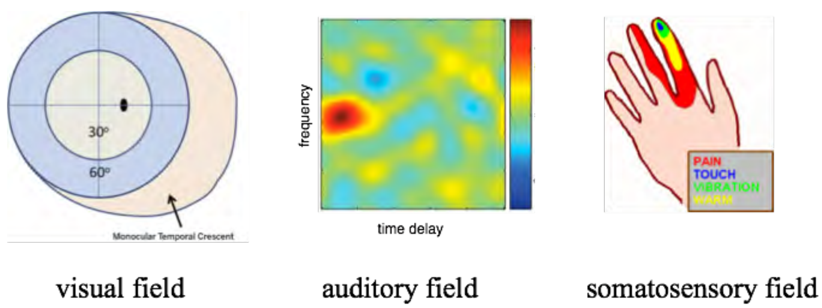


Figure 16: Receptive fields. [16]

**Definition:**
**"Response variability" is the variability of a neuron's response to repeated presentation of identical stimuli.**

The activity of neurons is variable both in the absence and in the presence of stimuli. Thus, repeated presentation of identical stimuli typically elicits a wide range of responses.

Consequently, the response of a neuron to different stimuli needs to be characterized statistically. Measurements must be performed multiple times to establish response mean and response variance.

Response variability *limits the informativeness* of a neuron's response!

**Definition:**
**A "tuning curve" is the dependence of the average response on one particular stimulus parameter.**

A neuron's response typically depends on many different stimulus parameters. A tuning curve characterizes the response as a function of just one of these parameters. It is measured by repeatedly presenting stimuli with different parameter values.

A neuron has many different tuning curves (one for each parameter affecting its response). A tuning curve characterizes the neuron's response partially, but never completely.

**A tuning curve $r = f(s)$ is the average number of spikes $r$ elicited by presentation of a particular stimulus attribute $s$.**

**Gaussian tuning**

Tuning for stimulus orientation in the primary visual cortex of monkey:

$$r = f(s) = r_{max} \exp\left[-\frac{1}{2}\left(\frac{s - s_{max}}{\sigma_s}\right)^2\right] \qquad \text{Gaussian tuning}$$

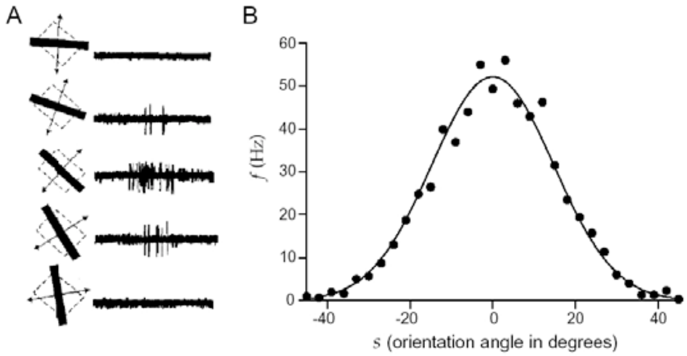


Figure 17: Gaussian tuning. [17]

## Cosine tuning

Tuning for direction of arm movement in the primary motor cortex of monkey:

$$r = f(s) = r_0 + (r_{max} - r_0)\,\cos(s - s_{max}) \qquad \text{Cosine tuning}$$

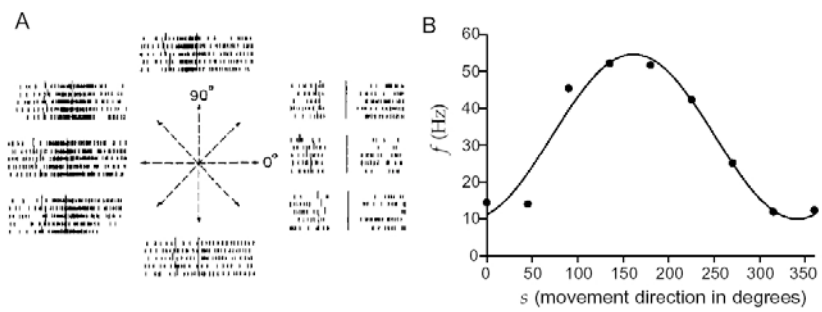


Figure 18: Cosine tuning. [18]

## Sigmoidal tuning

Tuning for binocular disparity in the primary visual cortex of monkey (approximated by logistic function):

$$r = f(s) = \frac{r_{max}}{1 + \exp\left(-\frac{s - s_{1/2}}{\Delta_s}\right)} \qquad \text{Sigmoidal tuning}$$

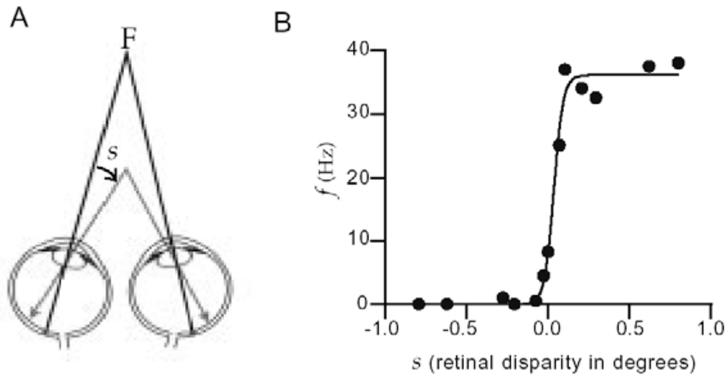


Figure 19: Sigmoidal tuning. [19]

## Summary receptive fields ...

- The following heuristic concepts are useful in describing the responses and the function of sensory neurons.
- A "receptive field" is the area in sensory space (visual, auditory, somatosensory, ...) in which stimulation drives a neuron.
- "Response variability" refers to the variability of a neuron's response to repeated presentation of identical stimuli.
- A "tuning curve" is average response as a function of one particular stimulus parameters.
- Typically, there are many relevant stimulus parameters and, thus, many different "tuning curves".
- Tuning curves show many different shapes, which may be approximated by various functions (including Gaussian distribution, cosine function, and logistic function).

# 4 Reverse correlation methods

We seek more systematic and objective ways of describing neuronal responses.

To this end, we bombard a neuron with a rapid sequence of stimuli, drawn randomly from a large ensemble.

We average all stimulus-sequences leading up to responses to form a "preferred" stimulus.

Several methods may be used, including *spike-triggered averaging (STA)* and *response-weighted averaging (RWA)*.

Mathematically, these methods are equivalent to computing a 'reverse correlation'.

**Spike-triggered average**

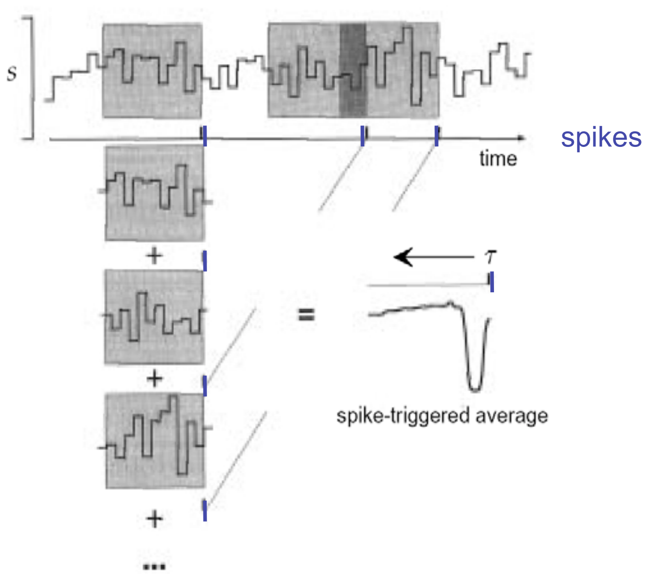


Figure 20: Spike triggered average. [20]

**Definition:**

**The spike-triggered average stimulus $\langle s(-\tau) \rangle$ is the average value of the stimulus at some time $\tau$ before a spike is fired.**

$$\textit{Spike times} \qquad t_i$$

$$\textit{Stimulus function} \qquad s(t)$$

$$\textit{Reversed and shifted} \qquad s(t_i - \tau)$$

Note that $s(t_i - \tau)$ is the stimulus stretching backwards in time from $t_i$, as $\tau$ grows from 0 to $\infty$

To compute the spike-triggered average stimulus, we average over the stimulus functions which stretch back in time from each spike $t_i$:

$$\langle s(-\tau) \rangle = \frac{1}{n} \sum_{i=1}^{n} s(t_i - \tau)$$

where $n$ is the number of spikes per trial.

**STA example**

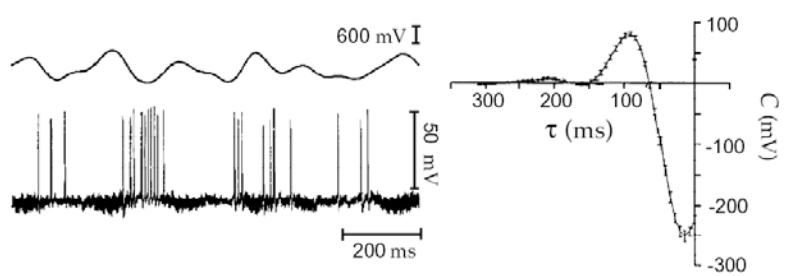


Figure 1.9: The spike-triggered average stimulus for a neuron of the electrosensory lateral-line lobe of the weakly electric fish *Eigenmania*. The upper left trace is the potential used to generate the electric field to which this neuron is sensitive. The evoked spike train is plotted below the stimulus potential. The plot on the right is the spike-triggered average stimulus. (Adapted from Gabbiani *et al*, 1996.)

Figure 21: STA example. [21]

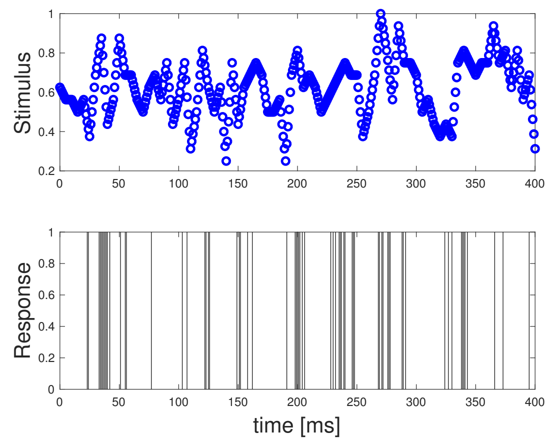


Figure 22: Example stimulus and response.

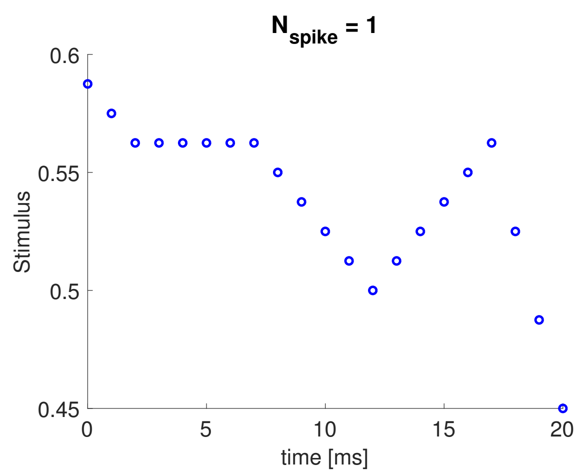


Figure 23: Spike-triggered average.

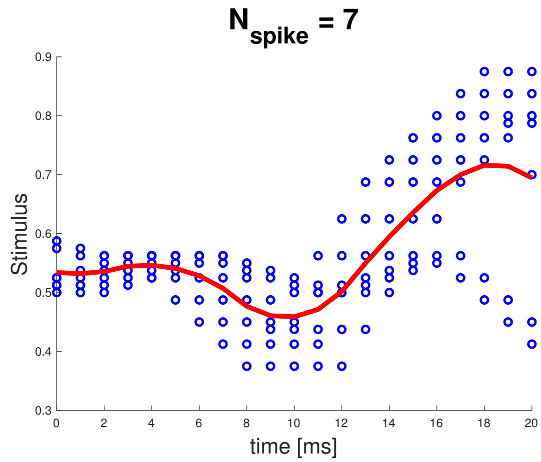


Figure 24: Spike-triggered average.

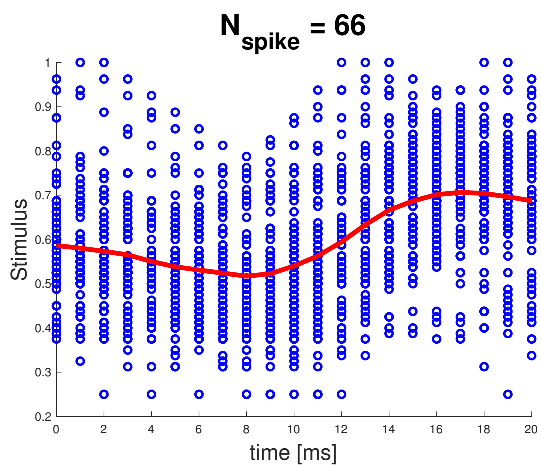


Figure 25: Spike-triggered average.

## Response-weighted average, discrete time-samples

When measuring firing rates rather than individual spikes, one may compute the **response-weighted average stimulus**. For a time-dependent stimulus $s(t)$ and responses $r(t)$ recorded at discrete times $t_i$

$$\langle s(-\tau) \rangle = \frac{1}{T} \sum_i \frac{r(t_i)}{\langle r \rangle} s(t_i - \tau), \qquad \langle r \rangle = \frac{1}{T} \sum_i r(t_i)$$

where $s(t_i - \tau)$ is the stimulus prior to $t_i$.

## Response-weighted average, continuous time-samples

For continuously recorded responses $r(t)$ we may similarly compute

$$\langle s(-\tau) \rangle = \frac{1}{T} \int_0^T \frac{r(t')}{\langle r \rangle} \, s(t' - \tau) \, dt', \qquad \langle r \rangle = \frac{1}{T} \int_0^T r(t') \, dt'$$

where $s(t' - \tau)$ is stimulus prior to $t'$ and $\langle r \rangle$ is average response.

The convolution integral is called a 'reverse correlation', because it 'correlates' two functions, of which one has been 'reversed'.

Convolution integrals will star in the next lecture!

## Response-weighted average, stimulus patterns

Observing responses $r_i$ to stimulus patterns $s_i(x, y)$ presented in different trials $i$, we may compute a response-weighted pattern

$$\langle s(x, y) \rangle = \frac{1}{N} \sum_i \frac{r_i}{\langle r \rangle} \, s_i(x, y), \qquad \langle r \rangle = \frac{1}{N} \sum_i r_i$$

where $s_i(x, y)$ and $r_i$ are the stimulus and response of trial $i$, respectively, and where $\langle r \rangle$ is the average response.

See exercise "Mysterious neurons"!

## Summary reverse correlation

- Stochastic stimulus sequences (drawn randomly from some ensemble) offer a comparatively unbiased way to probe response properties.
- To apply this method, responses are correlated with reversed stimulus sequences (*i.e.*, sequences leading up to responses).
- A *spike-triggered average* stimulus sequence can be obtained if individual spikes are recorded.

- A *response-weighted average* stimulus sequence can be computed if firing rates are recorded.
- Mathematically, both methods involve the *reverse correlation*, or *convolution*, between response and stimulus sequences.
- A *response-weighted average* can be computed also for distinct stimulus patterns.

# 5 References


1. Neurophysology of the Anuran Visual System*. J. Grsser, et al. Page 298, figure 1A . Ref: https://link.springer.com/chapter/10.1007

2. Heinz Wscle, personal communication.

3. Heinz Wscle, personal communication.

4. Deep Learning Summit (DLS01-1). Slide Share. Anonymous, 2017. Slide 17. Ref: https://www.slideshare.net/AmazonWebServices/deep-learning-summit-dls011

5. Eavesdropping on Neurons. Harvard Brain Tour. Anonymous, 2016. Image 3 Ref: http://braintour.harvard.edu/archives/portfolio-items/eavesdropping-on-neurons

6. Dendritenbaum und konzentrisches rezeptives Feld einer ON-Zentrum-Ganglienzelle. Extrem News. Anonymous. Image 1 Ref: https://www.extremnews.com/berichte/gesundheit/e01c12cc1d3c89f/d02812cc2034dd9/info

7. Dendritenbaum und konzentrisches rezeptives Feld einer ON-Zentrum-Ganglienzelle. Extrem News. Anonymous. Image 1 Ref: https://www.extremnews.com/berichte/gesundheit/e01c12cc1d3c89f/d02812cc2034dd9/info

8. Dendritenbaum und konzentrisches rezeptives Feld einer ON-Zentrum-Ganglienzelle. Extrem News. Anonymous. Image 1 Ref: https://www.extremnews.com/berichte/gesundheit/e01c12cc1d3c89f/d02812cc2034dd9/info

9. Dendritenbaum und konzentrisches rezeptives Feld einer ON-Zentrum-Ganglienzelle. Extrem News. Anonymous. Image 1 Ref: https://www.extremnews.com/berichte/gesundheit/e01c12cc1d3c89f/d02812cc2034dd9/info

10. Dendritenbaum und konzentrisches rezeptives Feld einer ON-Zentrum-Ganglienzelle. Extrem News. Anonymous. Image 1 Ref: https://www.extremnews.com/berichte/gesundheit/e01c12cc1d3c89f/d02812cc2034dd9/info

11. Dendritenbaum und konzentrisches rezeptives Feld einer ON-Zentrum-Ganglienzelle. Extrem News. Anonymous. Image 1 Ref: https://www.extremnews.com/berichte/gesundheit/e01c12cc1d3c89f/d02812cc2034dd9/info

12. Dendritenbaum und konzentrisches rezeptives Feld einer ON-Zentrum-Ganglienzelle. Extrem News. Anonymous. Image 1 Ref: https://www.extremnews.com/berichte/gesundheit/e01c12cc1d3c89f/d02812cc2034dd9/info

13. Dendritenbaum und konzentrisches rezeptives Feld einer ON-Zentrum-Ganglienzelle. Extrem News. Anonymous. Image 1 Ref: https://www.extremnews.com/berichte/gesundheit/e01c12cc1d3c89f/d02812cc2034dd9/info

14. Cats see subjective contours. Cresap Neuroscience Laboratory. 1988. Mary Bravo, et al. Ref: https://www.gwern.net/docs/catnip/1988-bravo.pdf

15. Cats see subjective contours. Cresap Neuroscience Laboratory. 1988. Mary Bravo, et al. Fig. 2 Ref: https://www.extremnews.com/berichte/gesundheit/e01c12cc1d3c89f/d02812cc2034dd9/info

16. Visual fields interpretation in glaucoma: A focus on static automated perimetry. Community eye health / International Centre for Eye Health. 25. 1-8. Yaqub, Moustafa, 2012. Figure 2. `https://www.researchgate.net/figure/Diagram-of-the-visual-fi-eld-for-the-right-eye-The-three-regions-of-the-fi-eld-are-the_fig1_248384750`

17. Motion-based position coding in the visual system: a computational study. A Khoei, Mina, 2014. Figure 1. Ref: https://www.researchgate.net/figure/Seminal-results-of-Hubel-and-Wiesel-figure-adopted-from-Hubel-and-Wiesel-1968_fig1_280736145

18. What is the neural code? Spike coding. Sekuler lab, Brandeis. Slide 11. Ref: https://courses.cs.washington.edu/courses/cse528/09sp/Lect2.pdf

19. What is the neural code? Spike coding. Sekuler lab, Brandeis. Slide 12. Ref: https://courses.cs.washington.edu/courses/cse528/09sp/Lect2.pdf

20. What is the neural code? Spike coding. Sekuler lab, Brandeis. Slide 20. Ref: https://courses.cs.washington.edu/courses/cse528/09sp/Lect2.pdf

21. What is the neural code? Spike coding. Sekuler lab, Brandeis. Slide 21. Ref: https://courses.cs.washington.edu/courses/cse528/09sp/Lect2.pdf