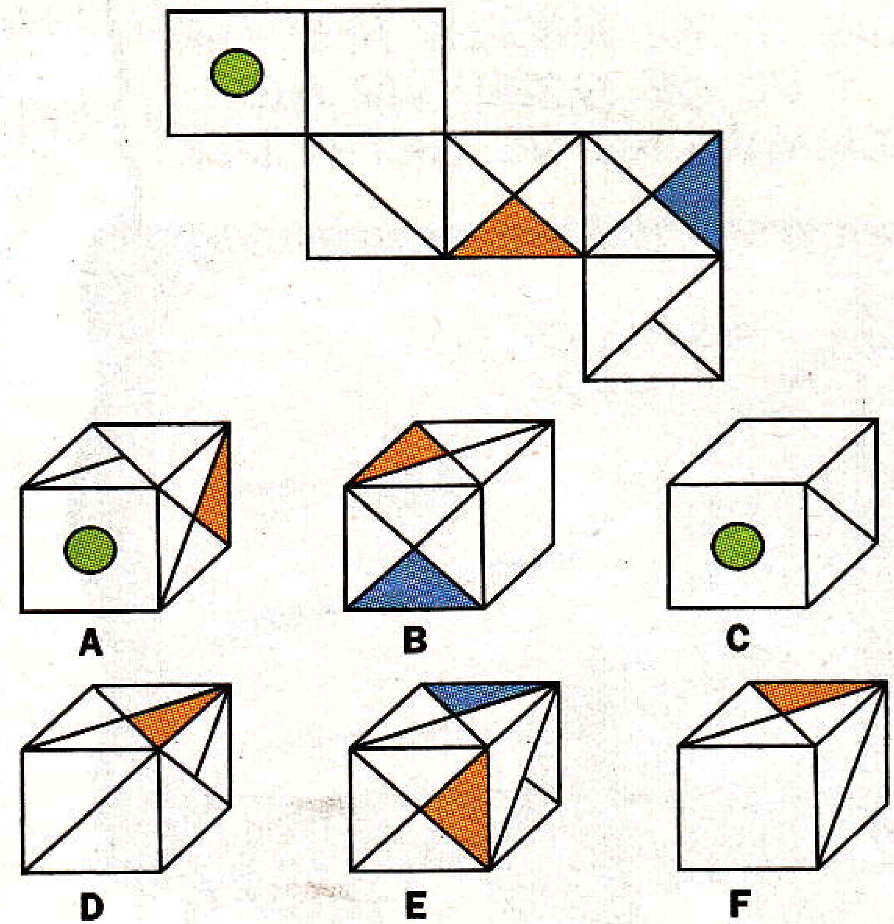
Which of the six boxes below cannot be made from this unfolded box? (There may be more than one.)



BIOPHYSICS @ YORK

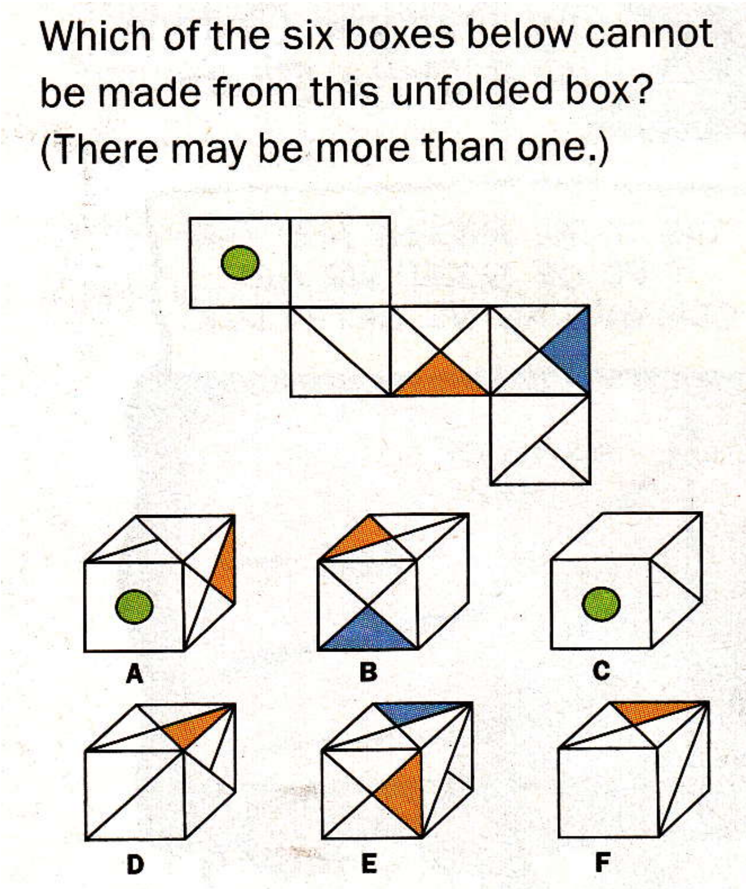
redefine THE POSSIBLE.

UNIVERSITÉ
UNIVERSITY

Peripheral sensory transduction

Christopher Bergevin (York University, Dept. of Physics & Astronomy)

CVR Summer School (2016)



Question:
Physiologically, how did you (try to) solve this puzzle?

→ We'll come back to the basic "units" of this thing in a bit

National Geographic

Question:
How do our sensory systems encode “information” about the world around us?

Consider how you “process” this picture....

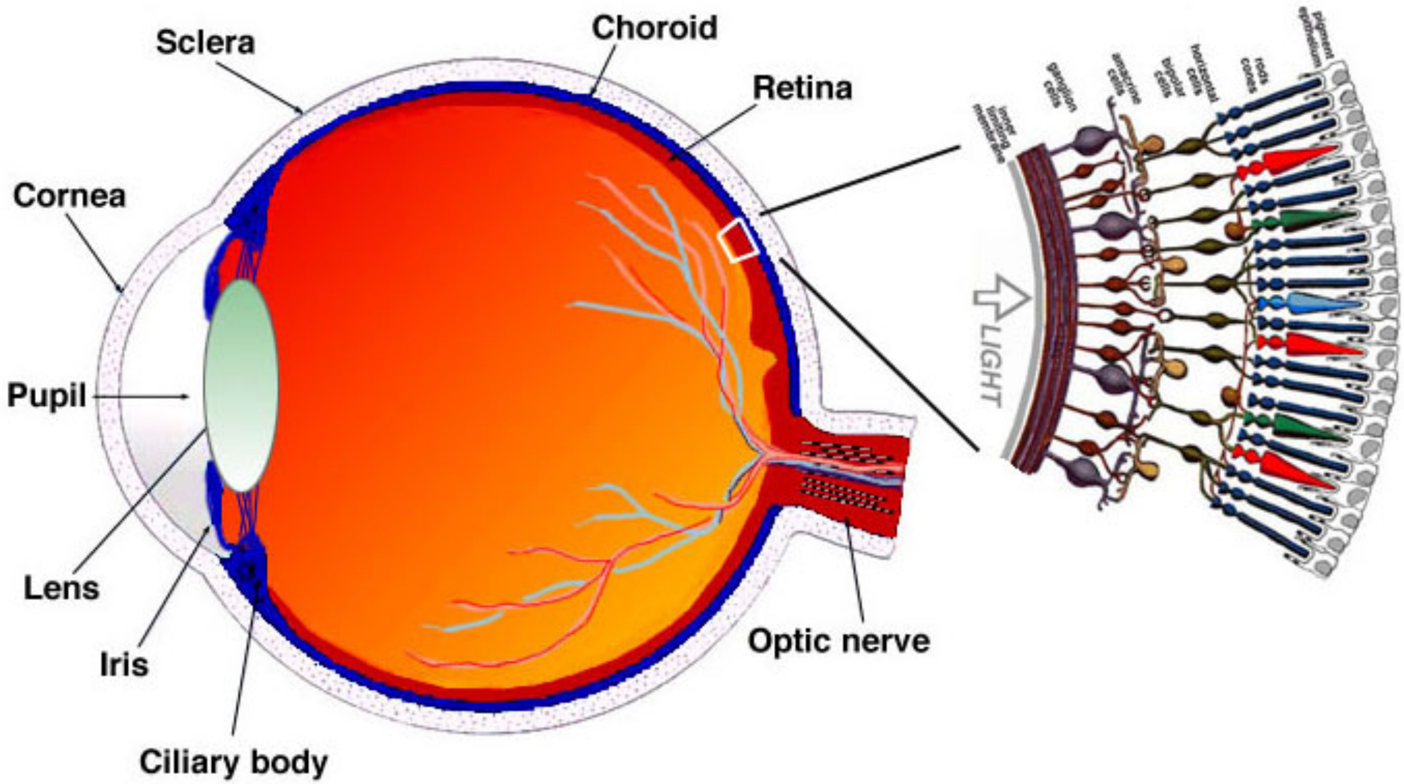
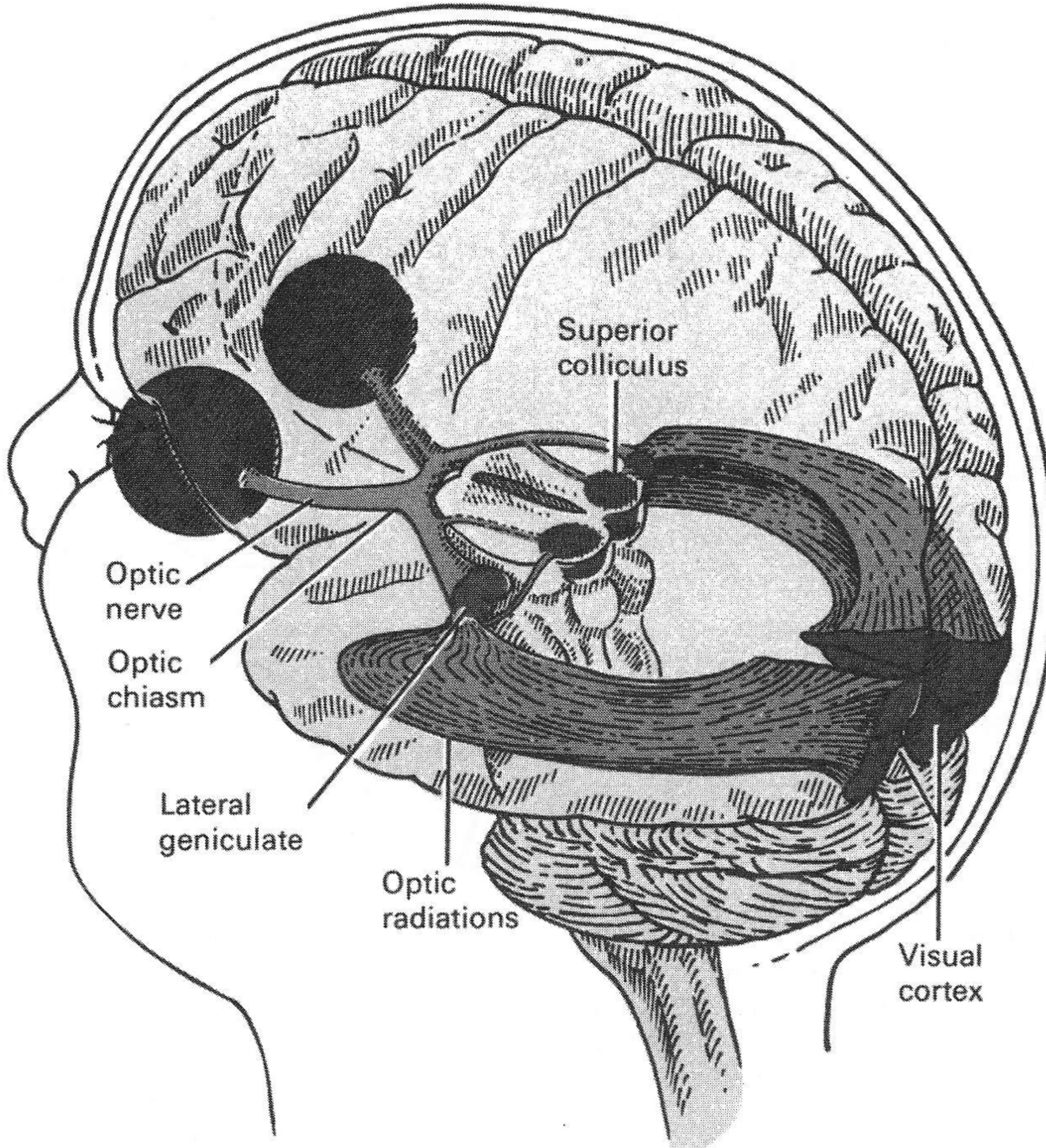


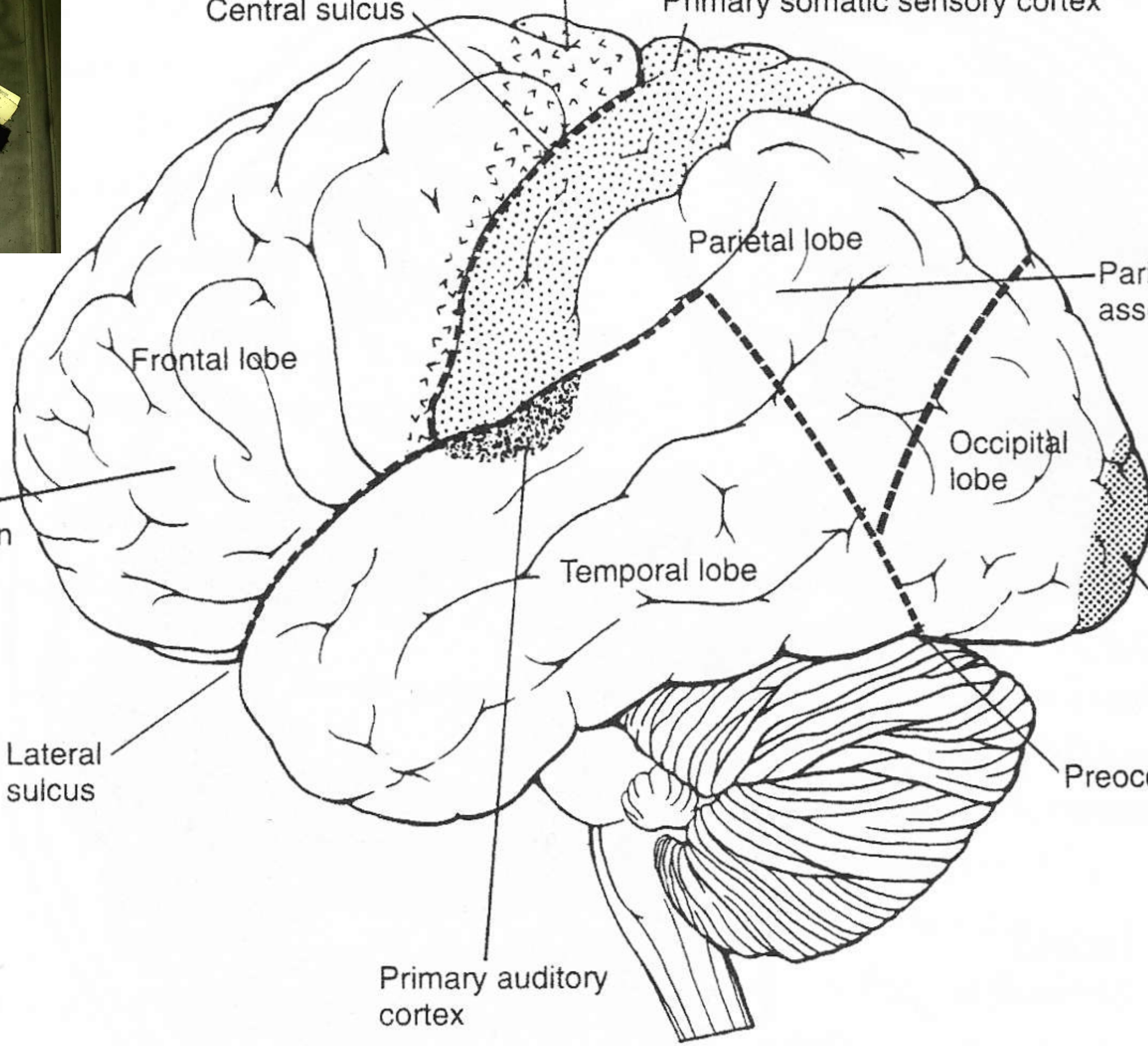
Fig. 1.1. A drawing of a section through the human eye with a schematic enlargement of the retina.

<u>Question</u>: How is information being “transduced” here?

WebVision (Utah)


Superior
colliculus
Optic
nerve
Optic
chiasm
Lateral
geniculate
Optic
radiations
Visual
cortex

Palmer (1999)


Primary motor cortex
Central sulcus
Primary somatic sensory cortex
Parietal lobe
Parietal-temporal-occipital association cortex
Frontal lobe
Rostral
Caudal
Occipital lobe
Prefrontal association cortex
Temporal lobe
Primary visual cortex
Lateral sulcus
Preoccipital notch
Primary auditory cortex

Palmer (1999)

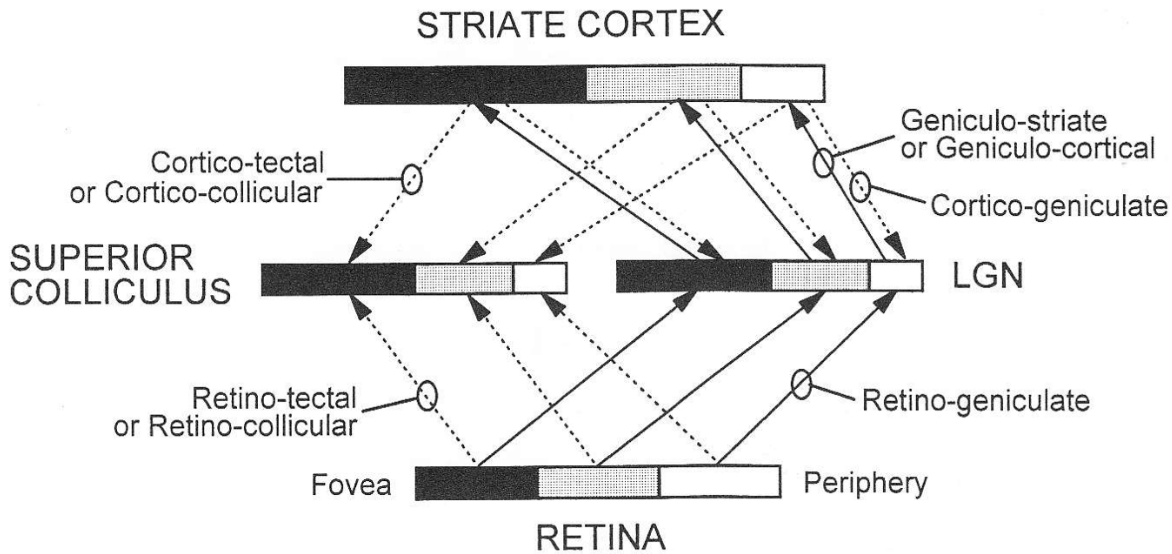
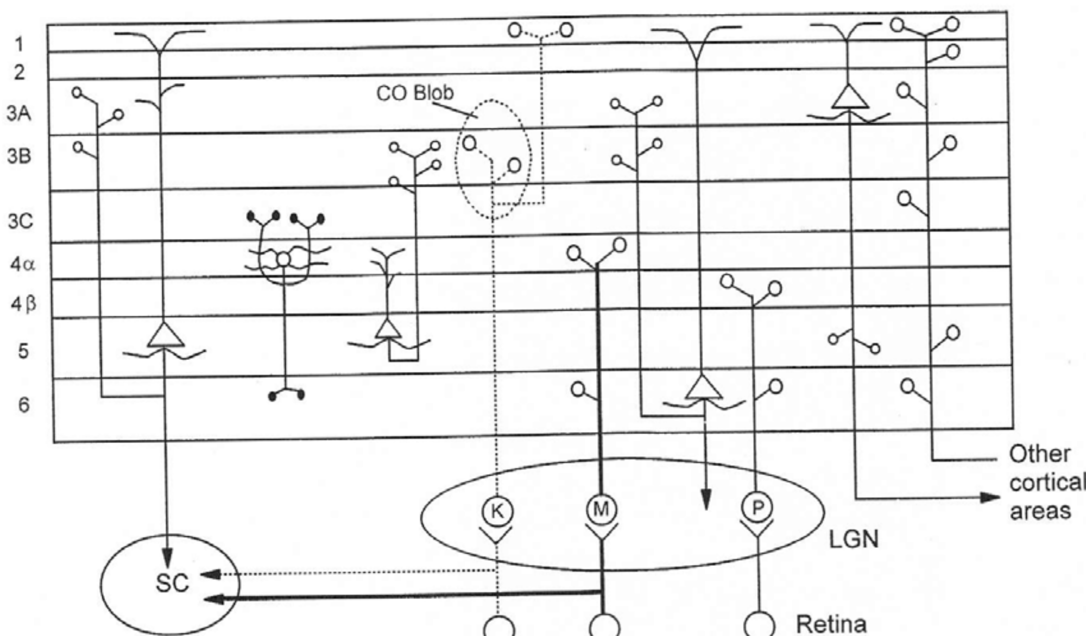


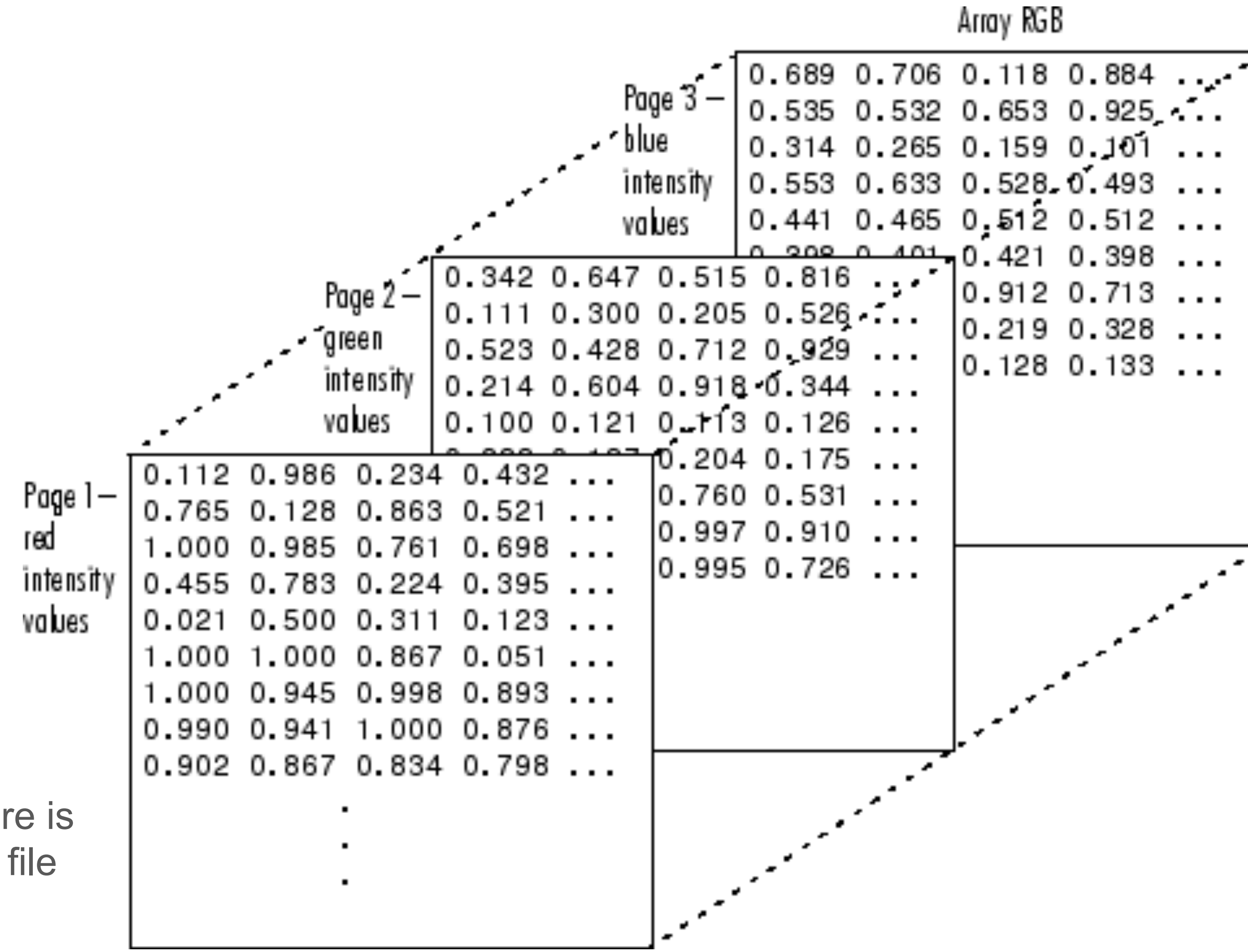
Figure 4.9. Schematic representation of the retino-geniculo-striate and retino-tectal projections and the return projections from the visual cortex.



Question: What are the basic building blocks that make up these "circuits"?

McIlwain (1996)

Aside: Images as numbers (i.e., a “bitmap”)



Note
Even this basic picture is too simple for a jpeg file

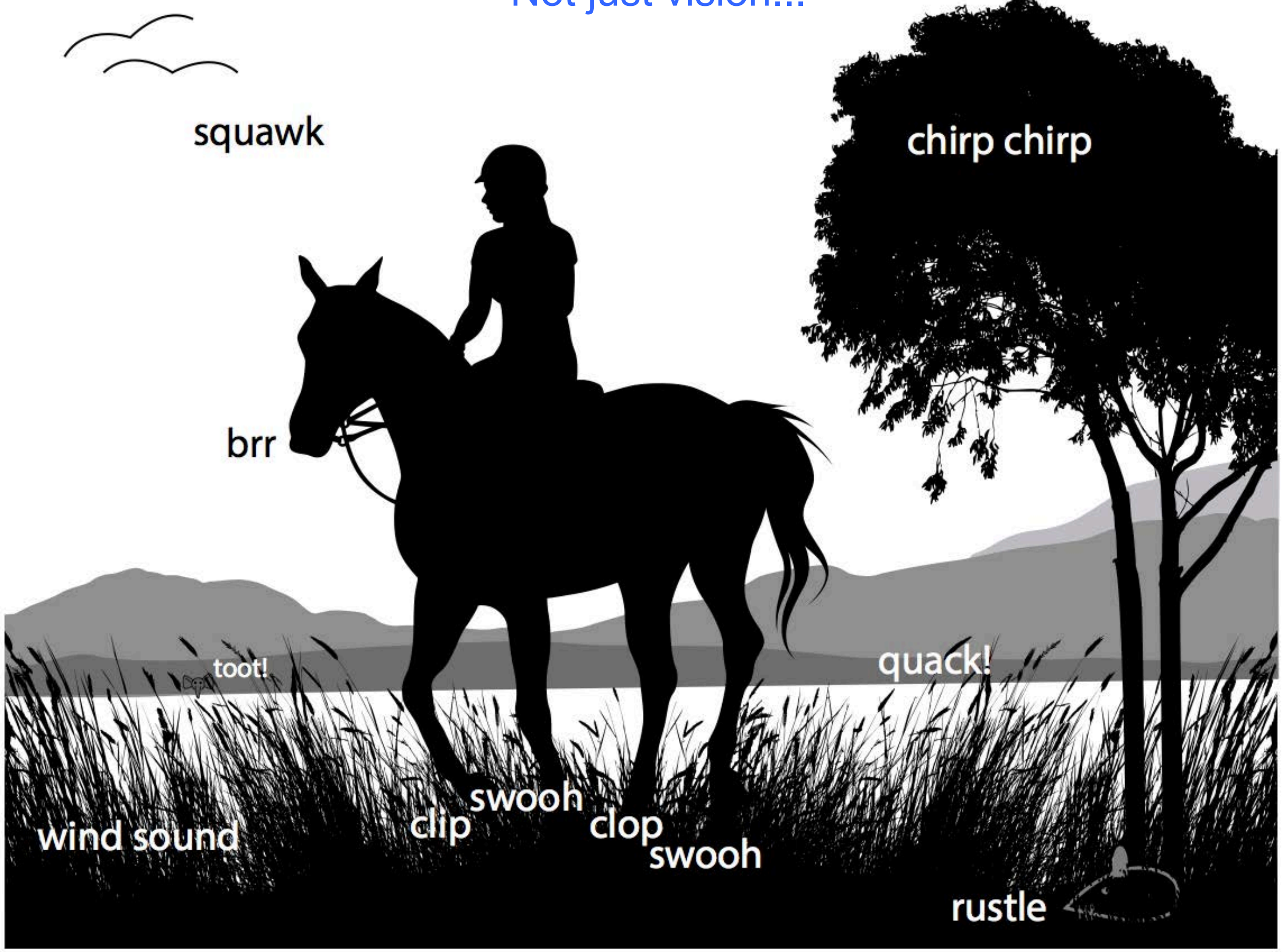
Question: Does your eye/nervous system process and store this image like a computer does?

http://i.stack.imgur.com/kI65e.gif

Big Picture Theme

How do our sensory systems encode "information" about the world around us?

Not just vision...

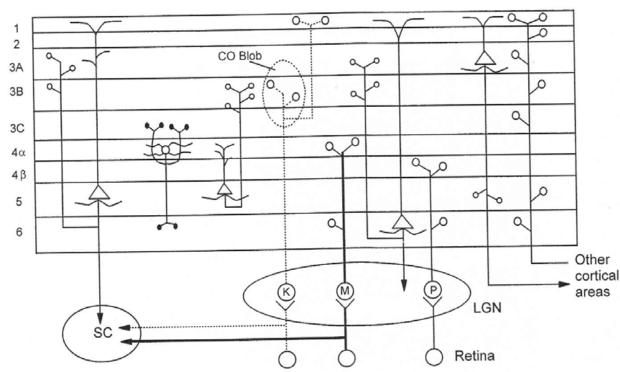


Pulkki & Karjalainen (2015)

Big Picture Theme

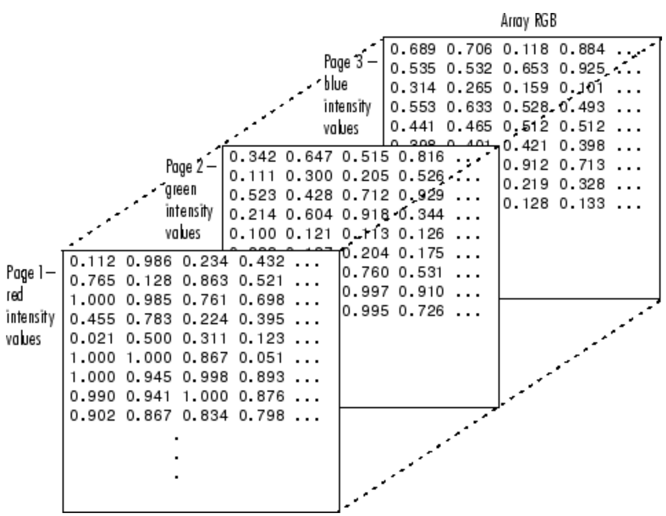
How do our sensory systems encode "information" about the world around us?

Two broad topics to cover

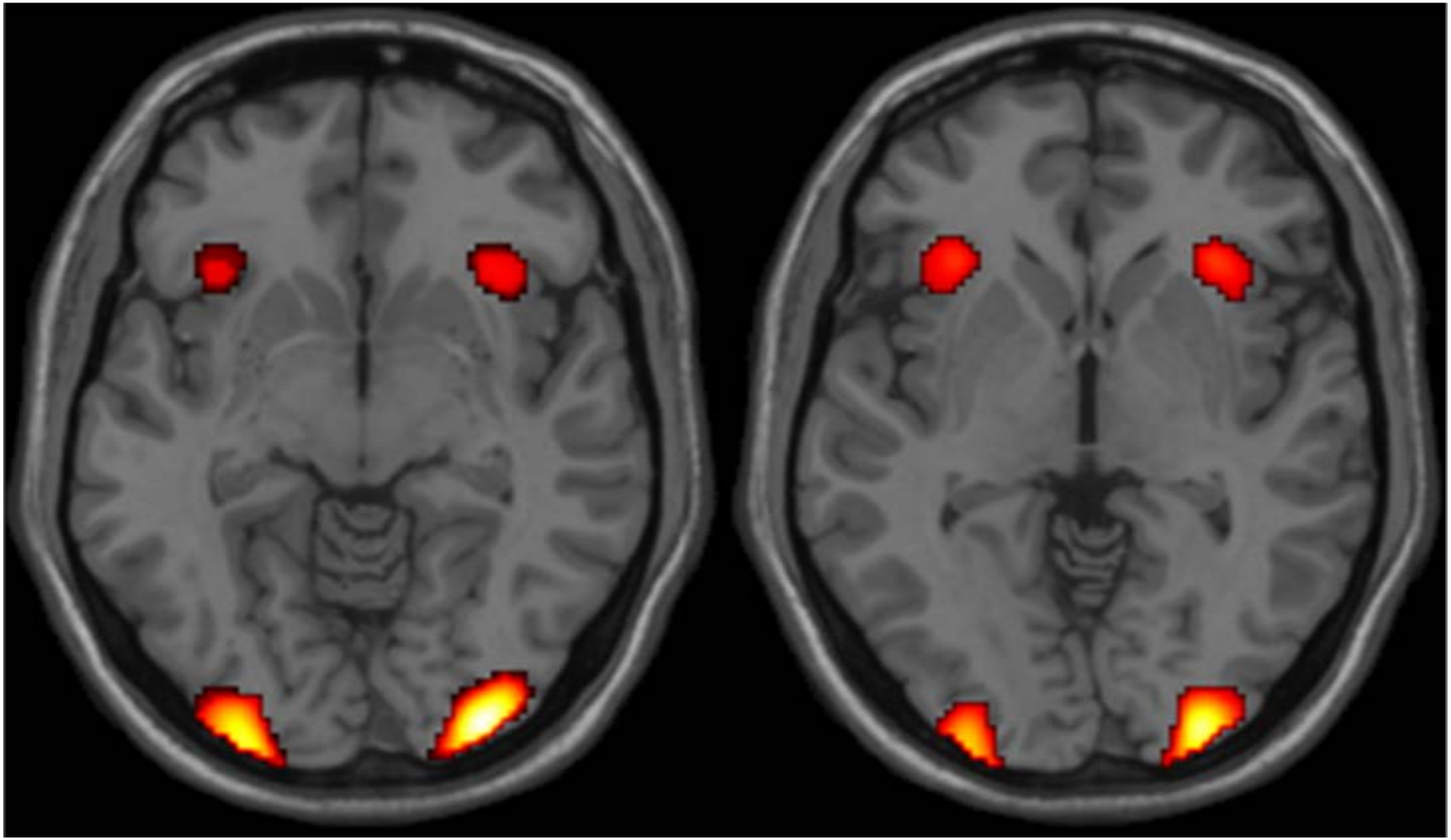


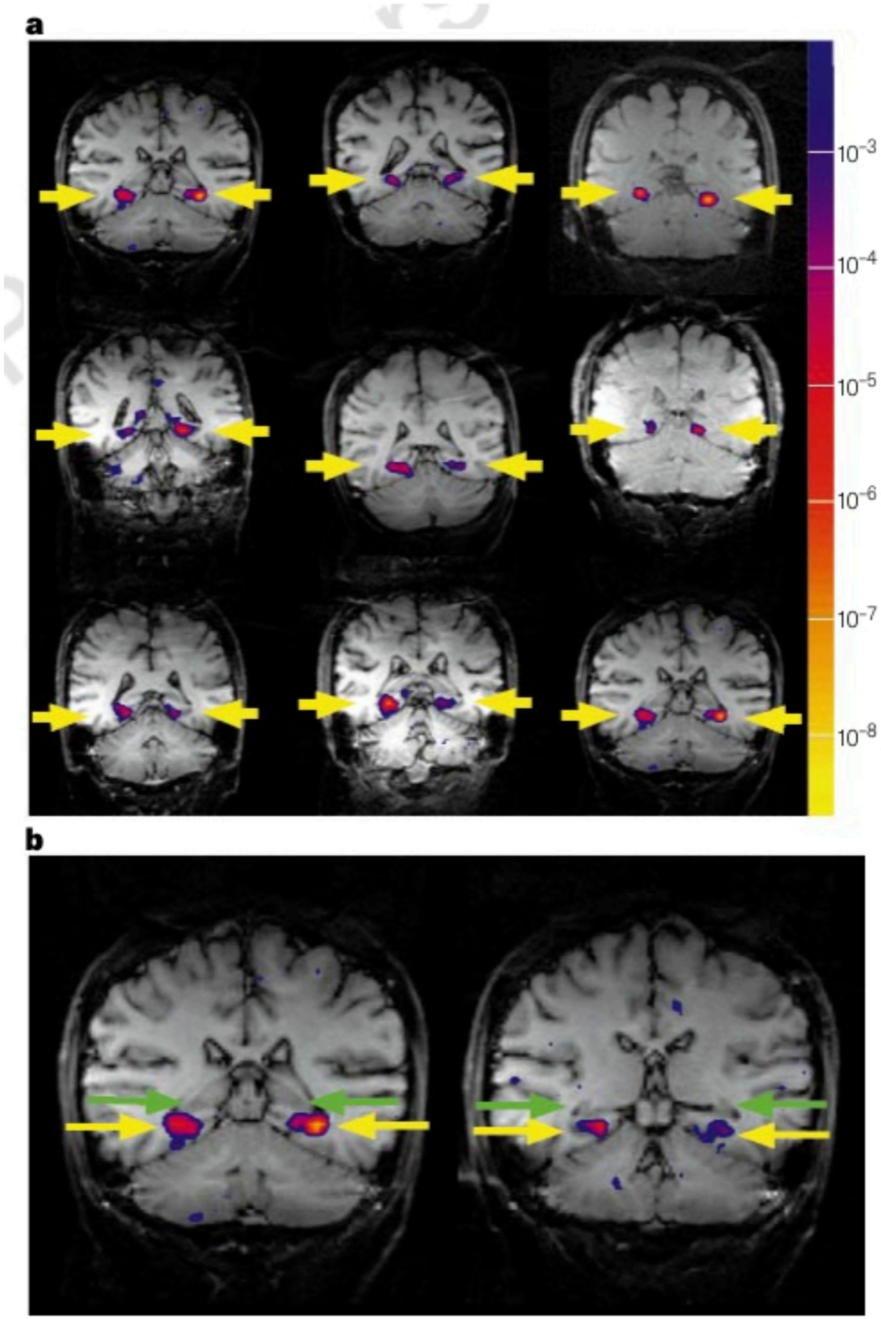
What are the basic building blocks that make up these "circuits"?

What are some basic (signal processing) considerations about "transforming" information?



→ How might you go about measuring “brain activity”?





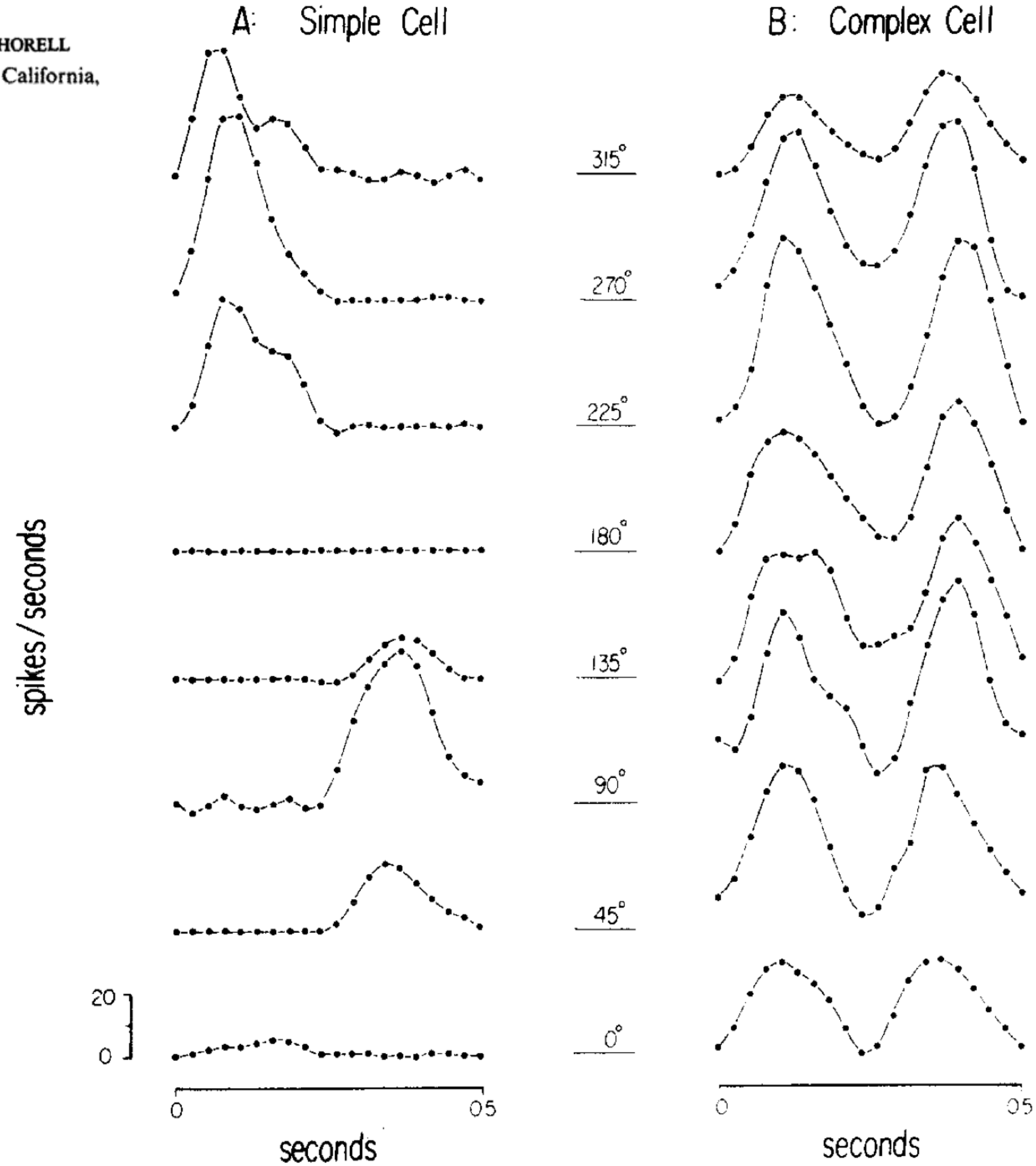
Epstein & Kanwisher (1998)

What are these methods used to “measure neural activity” actually telling us?

SPATIAL FREQUENCY SELECTIVITY OF CELLS IN MACAQUE VISUAL CORTEX

RUSSELL L. DE VALOIS, DUANE G. ALBRECHT* and LISA G. THORELL
Primate Vision Laboratory, Department of Psychology, University of California, Berkeley, CA 94720, U.S.A.

Vision Res. Vol. 22, pp. 545 to 559, 1982



Why/how are “direct” neurophysiological responses commonly measured as “*spike rates*”?

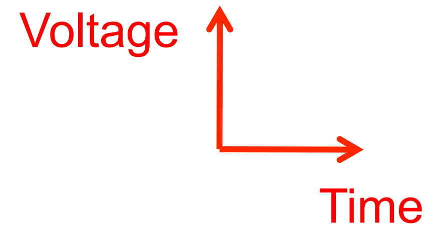
106

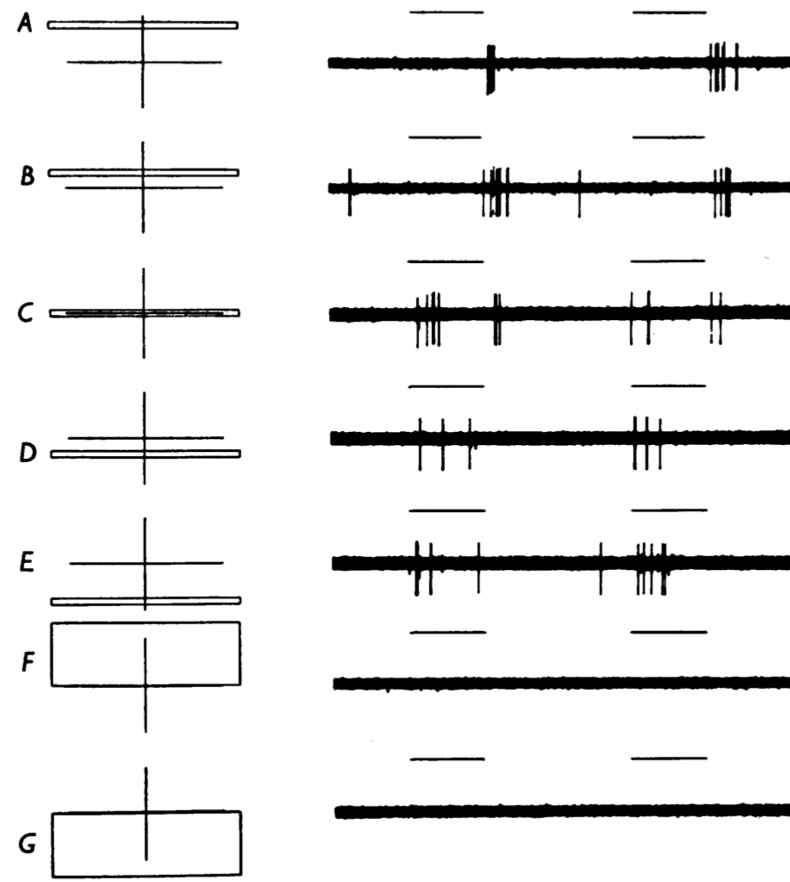
J. Physiol. (1962), **160**, *pp.* 106–154
With 2 plates and 20 text-figures
Printed in Great Britain

RECEPTIVE FIELDS, BINOCULAR INTERACTION AND FUNCTIONAL ARCHITECTURE IN THE CAT'S VISUAL CORTEX

By D. H. HUBEL and T. N. WIESEL

From the Neurophysiology Laboratory, Department of Pharmacology Harvard Medical School, Boston, Massachusetts, U.S.A.





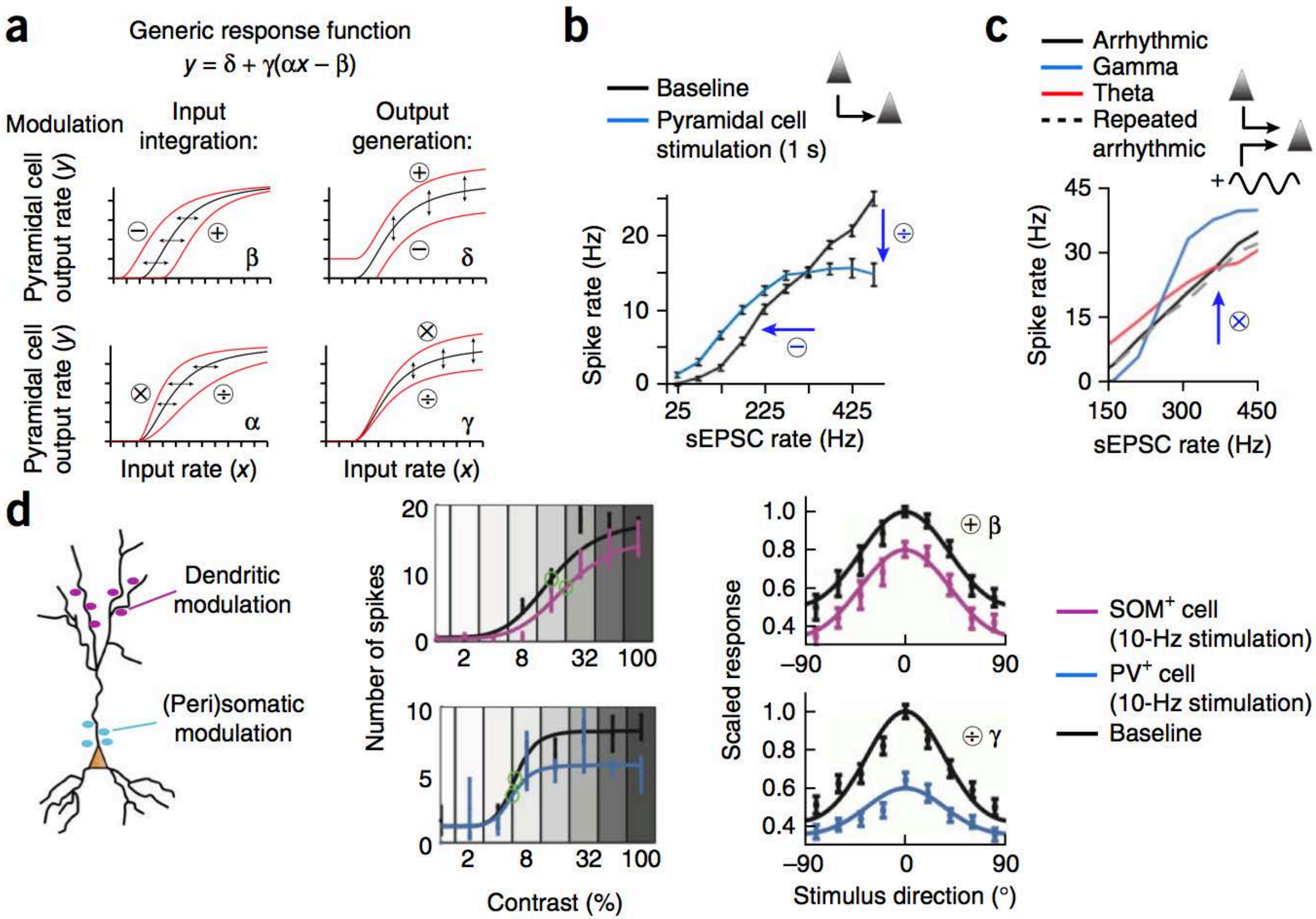
→ Why/how are "responses" commonly measured as "spike" rates?

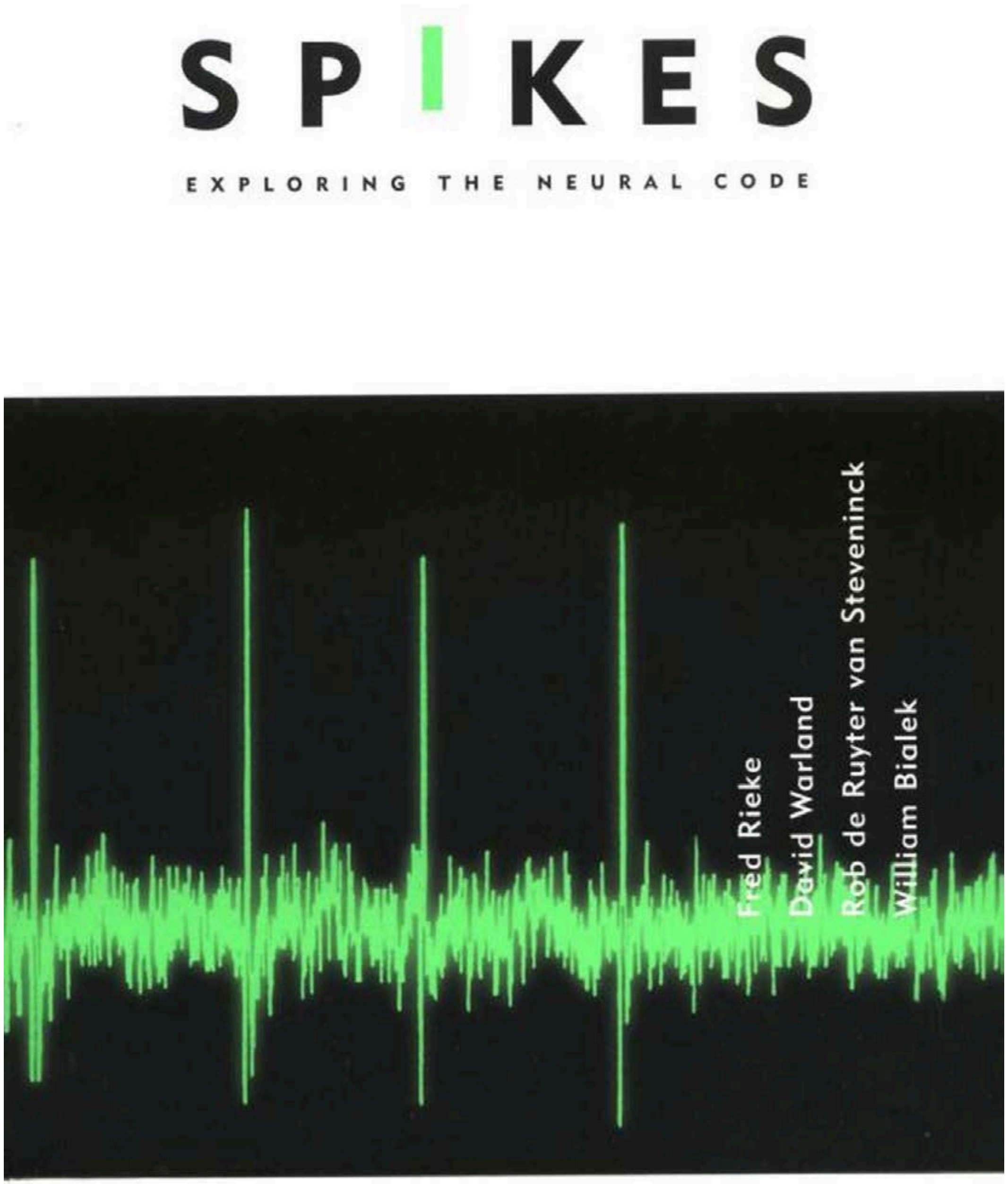
Note: This work led to Hubel & Wiesel winning the 1981 Nobel Prize

Dynamic circuit motifs underlying rhythmic gain control, gating and integration

Thilo Womelsdorf[1,2], Taufik A Valiante[3,4], Ned T Sahin[5,6], Kai J Miller[7,8] & Paul Tiesinga[9]

NATURE NEUROSCIENCE VOLUME 17 | NUMBER 8 | AUGUST 2014





“Neural code”

Aside

Is our central nervous system essentially “digitized”?

- What is a “spike”?
- What is being measured”
- How is such measured?

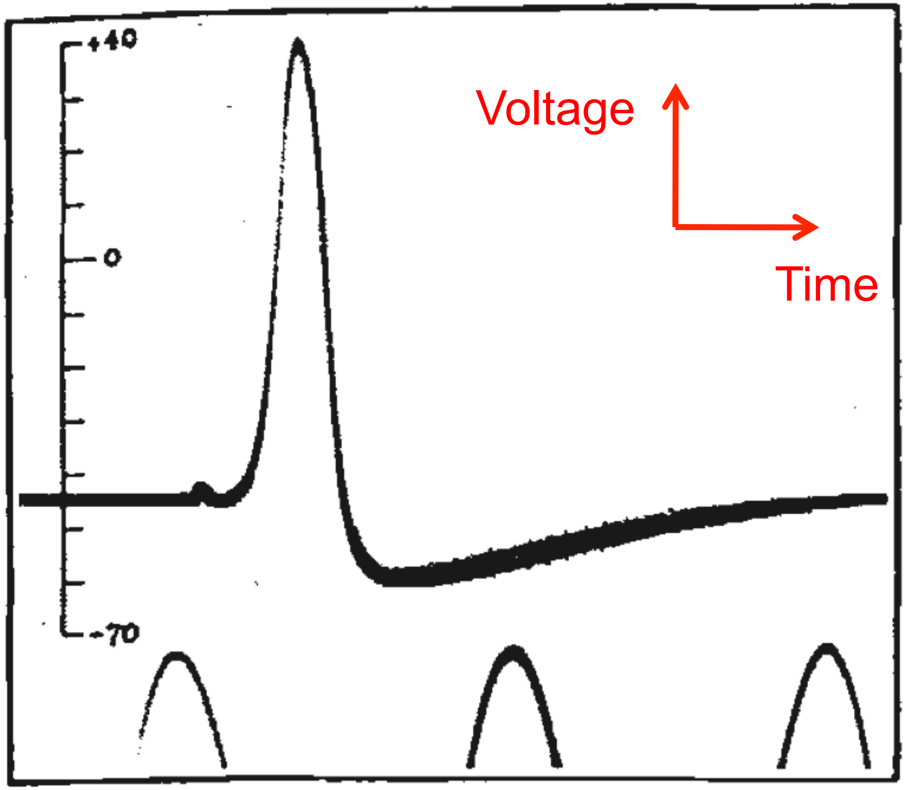


Fig. 2.

ACTION POTENTIAL RECORDED BETWEEN INSIDE AND OUTSIDE OF AXON. TIME MARKER, 500 CYCLES/SEC. THE VERTICAL SCALE INDICATES THE POTENTIAL OF THE INTERNAL ELECTRODE IN MILLIVOLTS, THE SEA WATER OUTSIDE BEING TAKEN AT ZERO POTENTIAL.

Hodgkin & Huxley (1939)

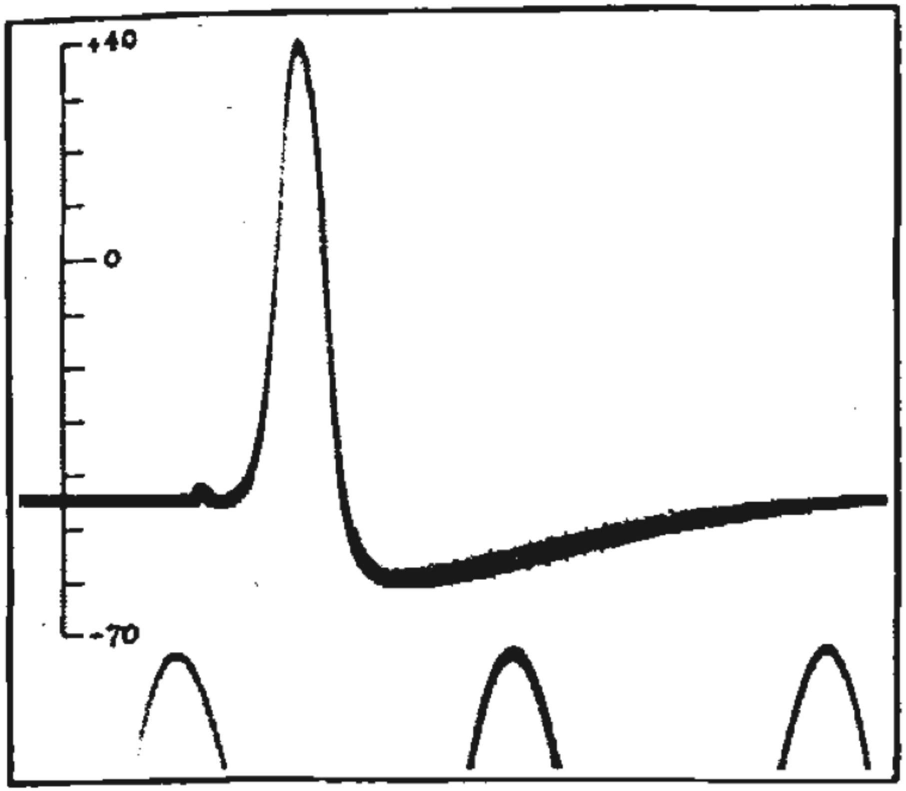


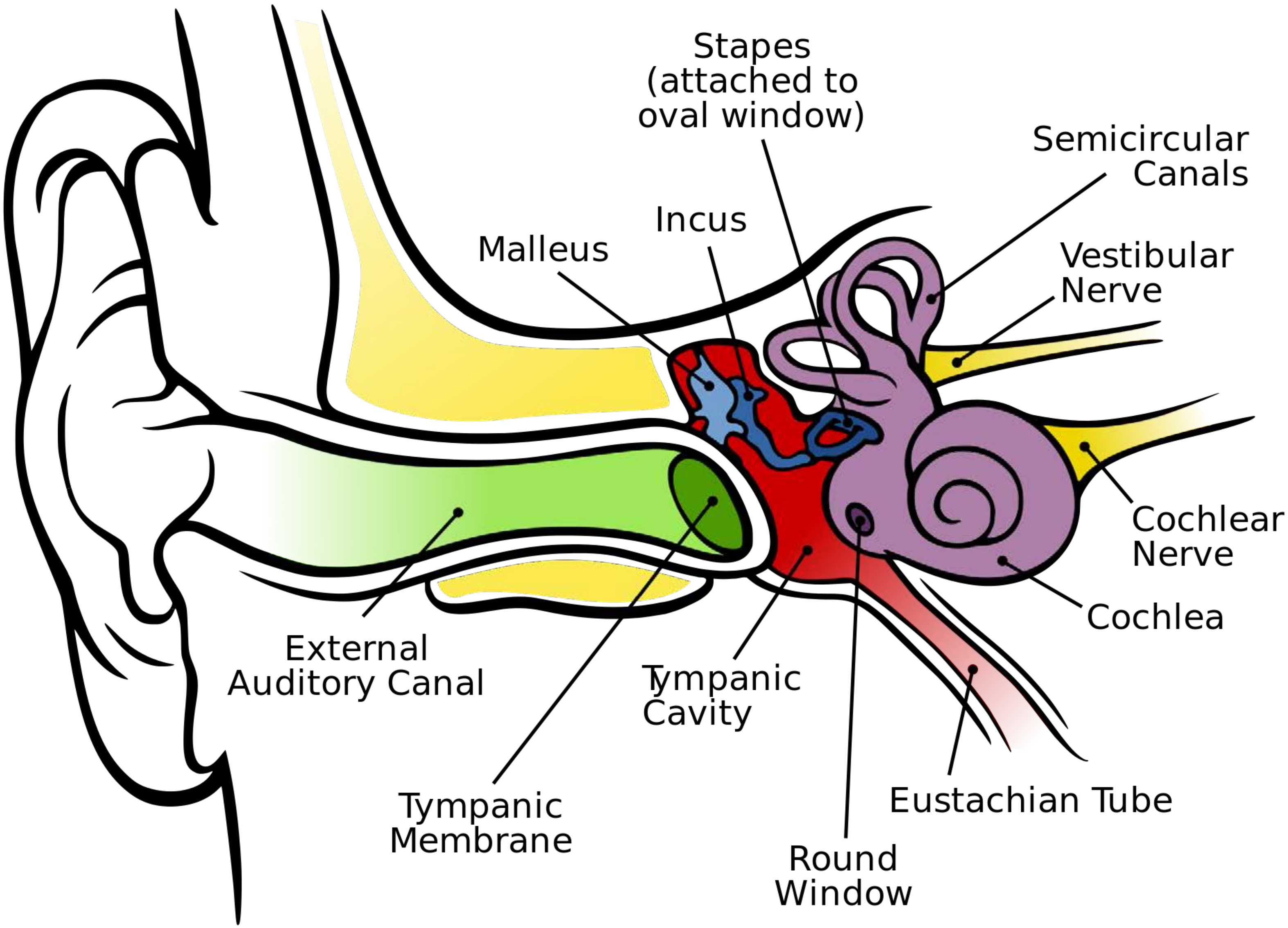
Fig. 1.

PHOTOMICROGRAPH OF ELECTRODE INSIDE GIANT AXON. 1 SCALE DIVISION = 33 μ.

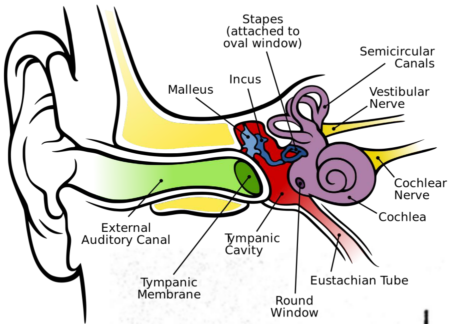
Hodgkin & Huxley (1939)

Ex. Neural coding of sound

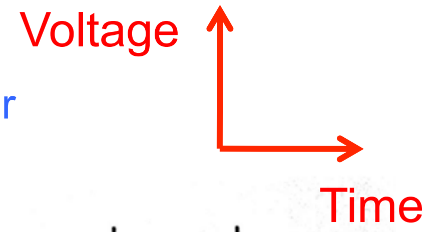
Cochlear nerve contains ~30000 fibers

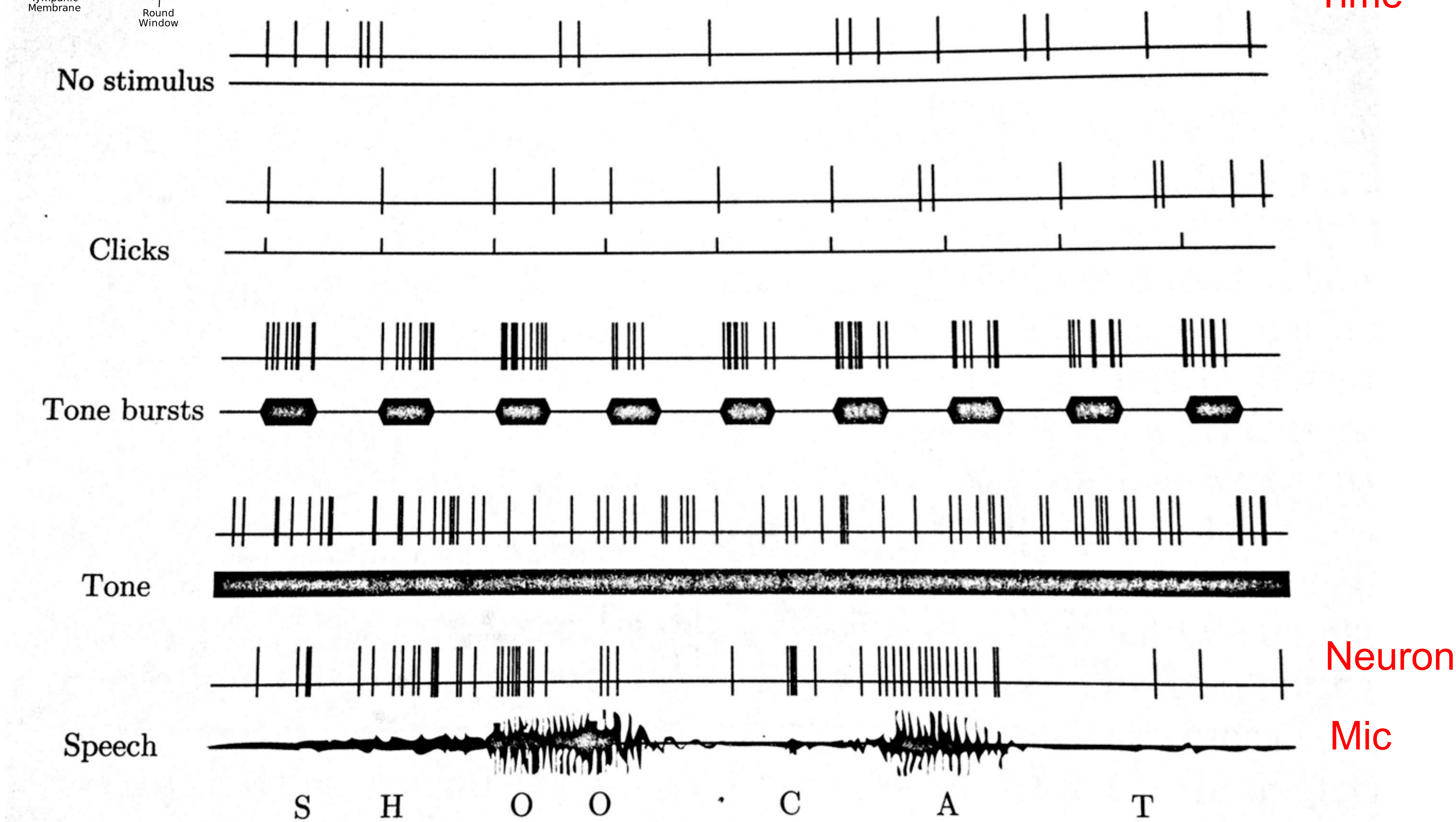


https://en.wikipedia.org/wiki/Auditory_system



Response of a single cochlear nerve fiber





Kiang

Neurons

Neurons ("fibers")
= Information highway

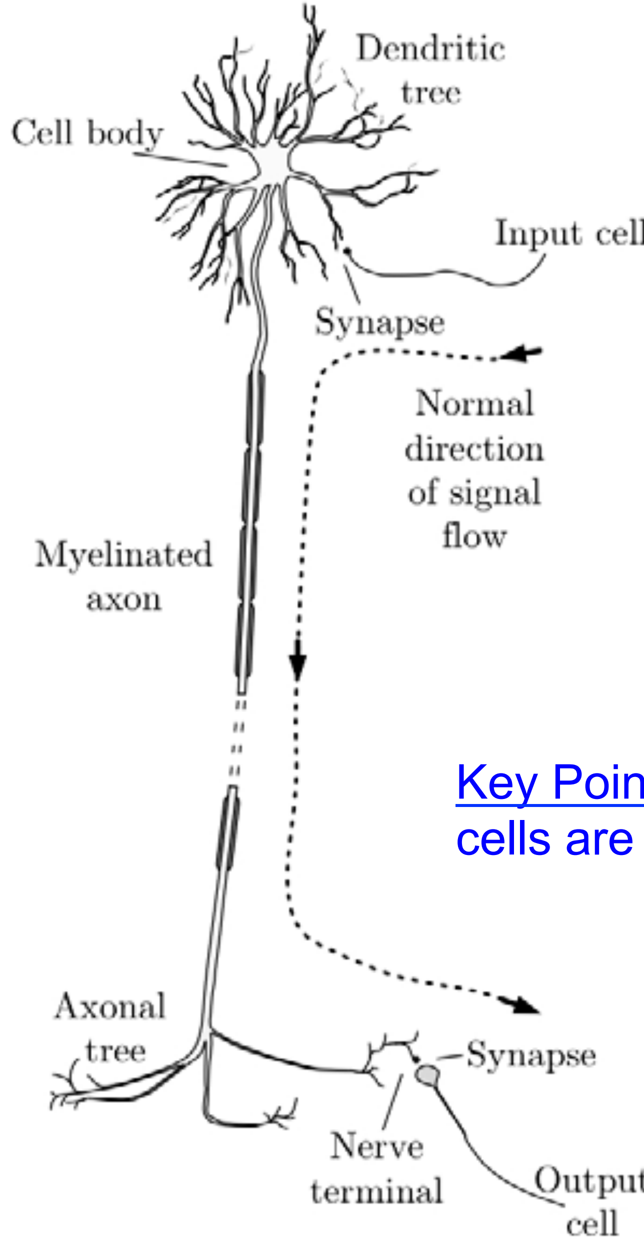


Figure 1.22

Key Point: Electrical properties of cells are important

Weiss (1996)

Action potentials

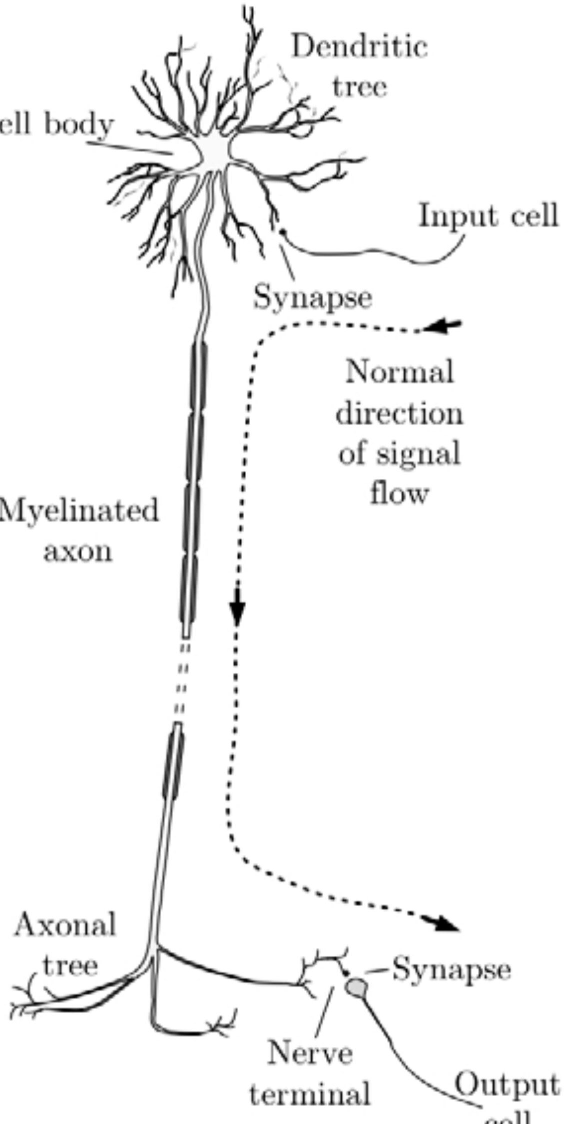
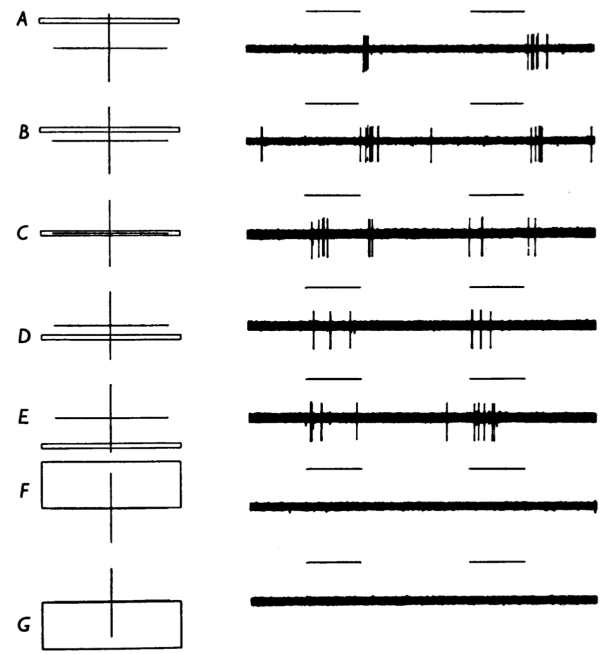
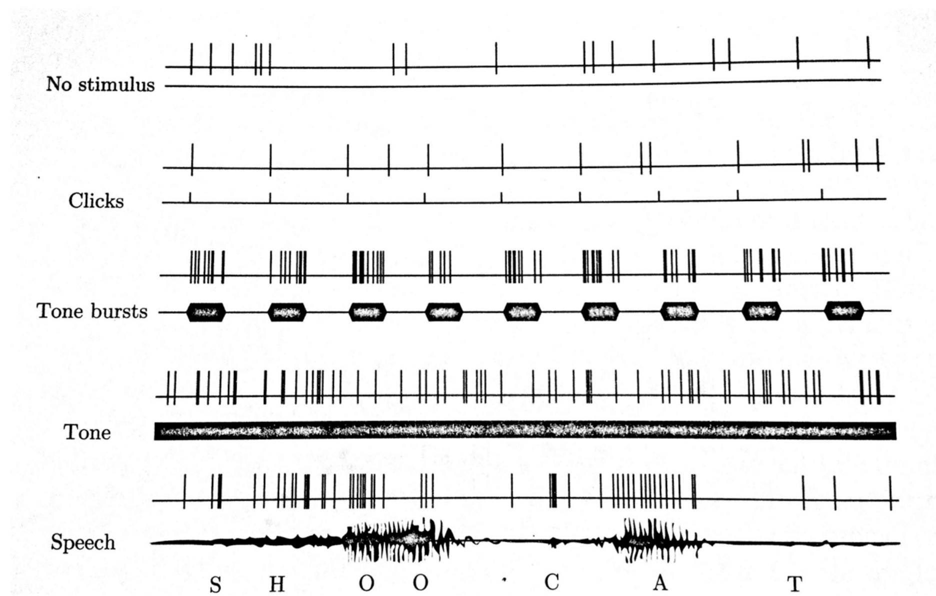


Figure 1.22





)6)

Action potentials

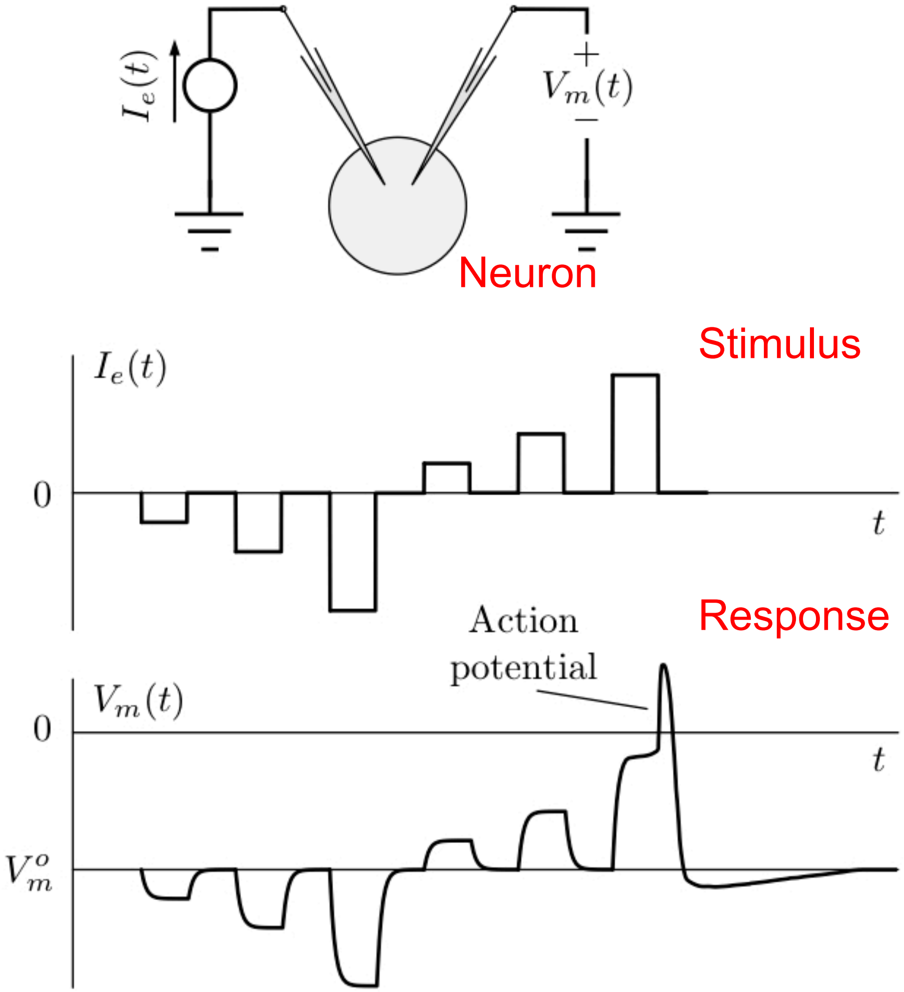


Figure 1.8

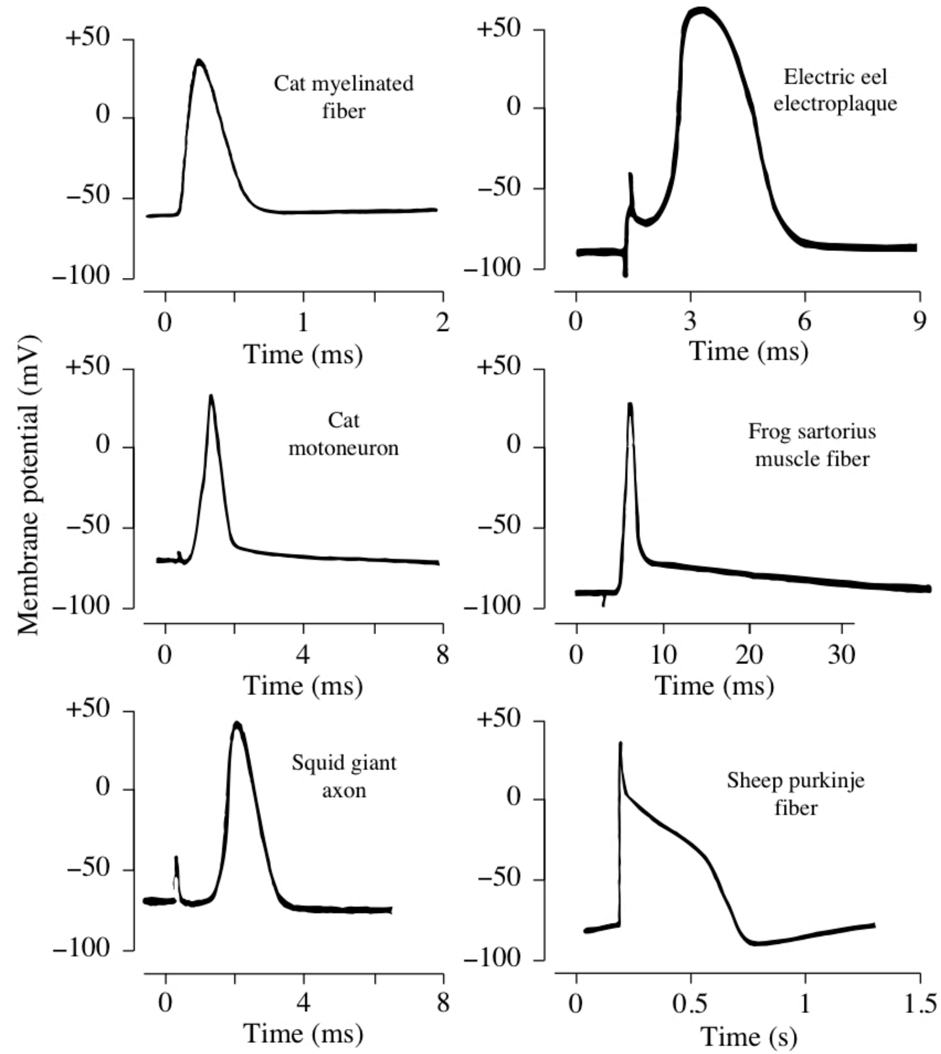


Figure 1.9

→ Neurons send info via electrical pulses (spikes) occurring ***across*** the cell membrane

Weiss (1996)

Cell membrane

- Membrane primarily consists of a "lipid bilayer" (to separate inside from outside)
- All sorts of "stuff" embedded inside, to allow for "communication" across membrane

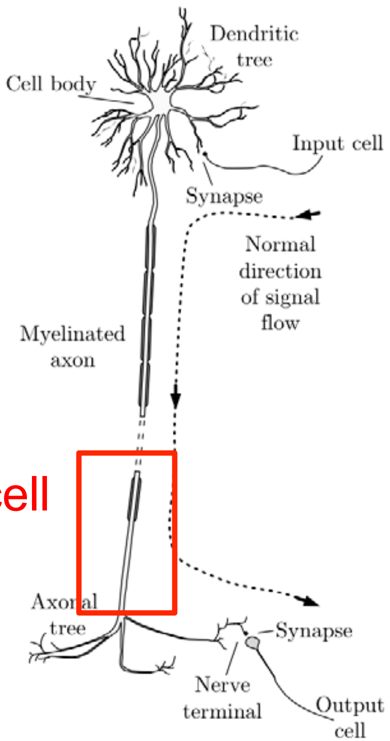


Figure 1.22

zoom in on cell membrane

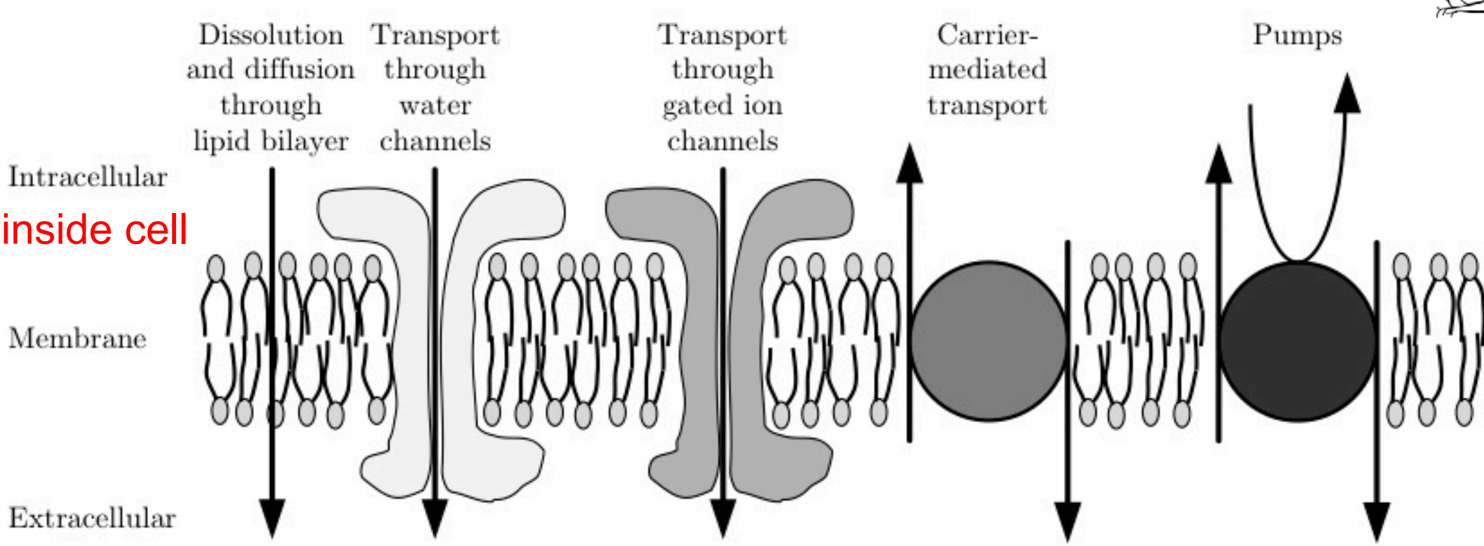
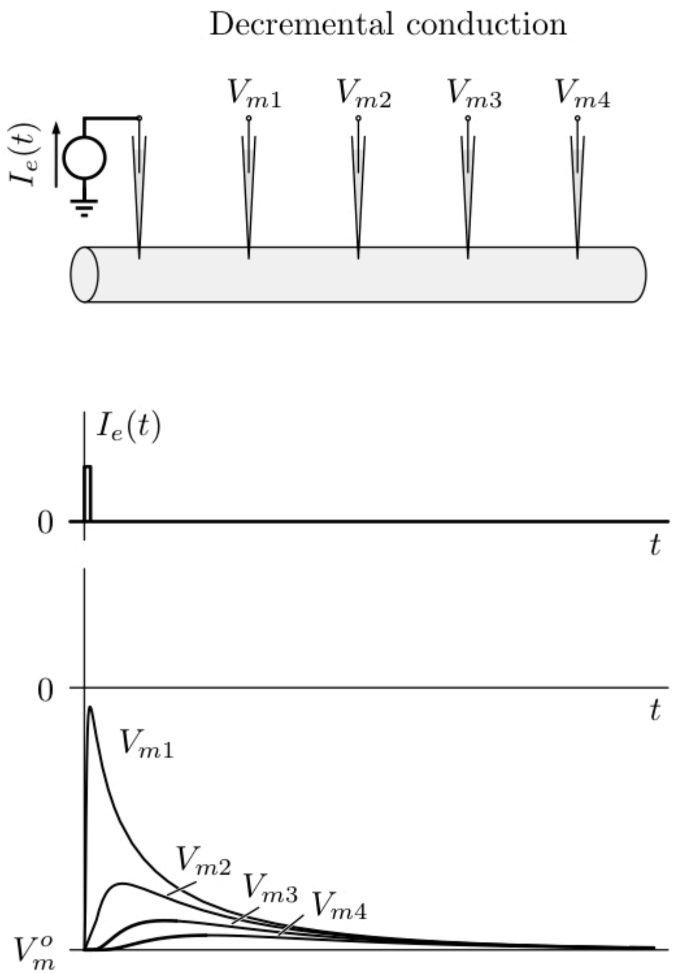


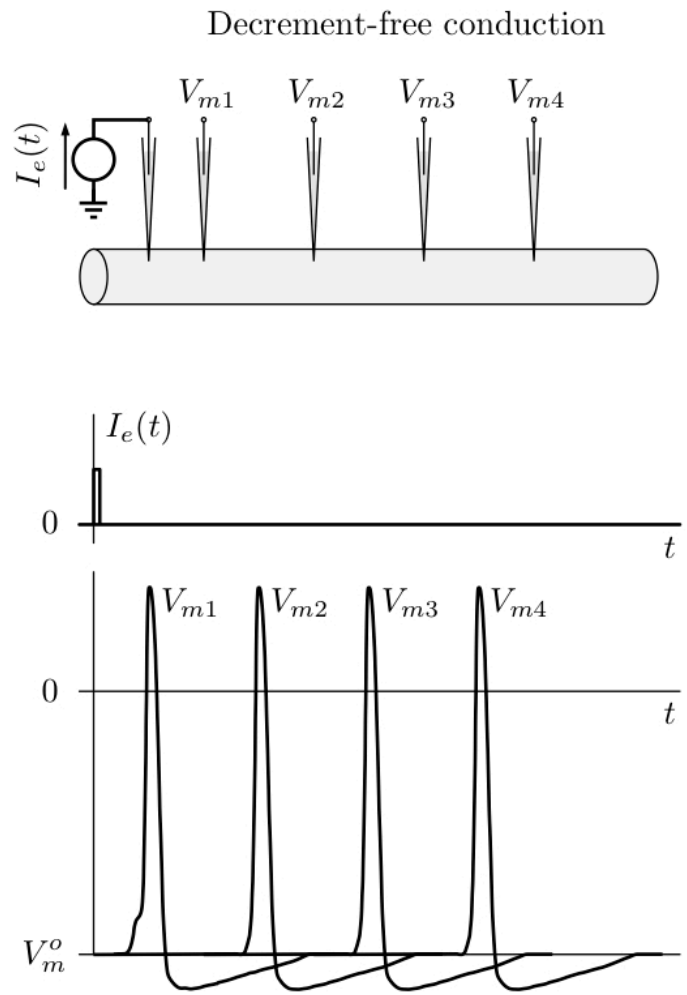
Figure 2.19

Weiss (1996)

Electrical excitability



electrically inexcitable cell



electrically excitable cell

Weiss (1996)

Electrical Responses in Sensory Systems

Photoreceptors

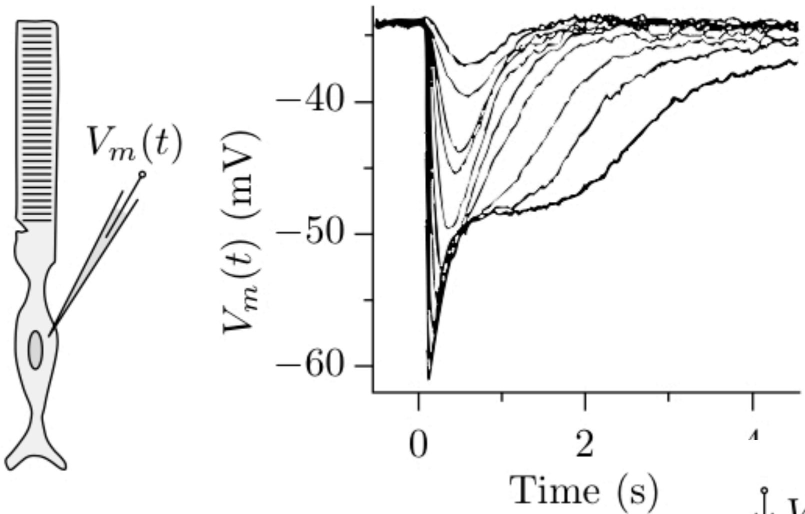
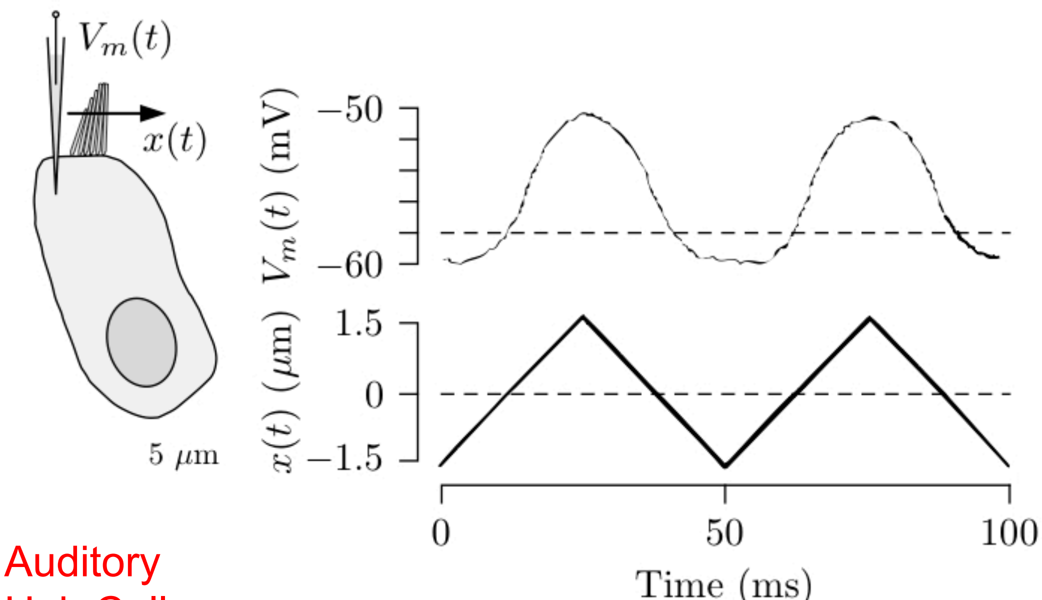


Figure 1.3

→ Not always “electrically excitable” per se, but role as “transducers” critically tied to electrical responses



Auditory Hair Cells

Figure 1.5

Cable model

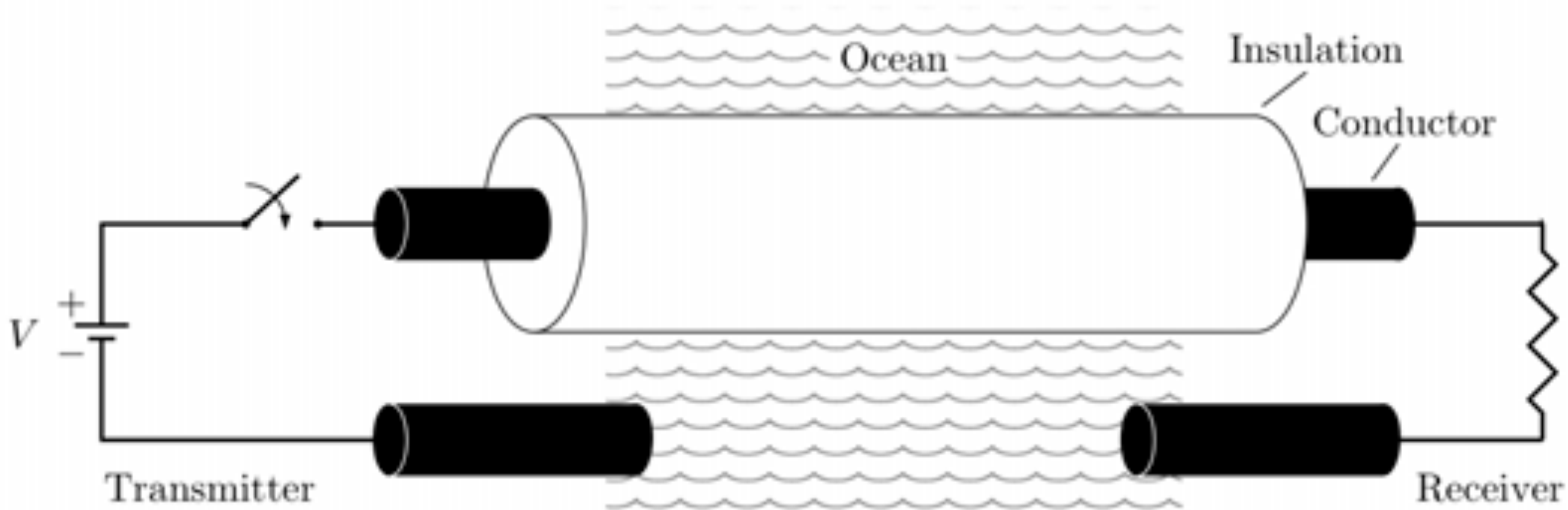


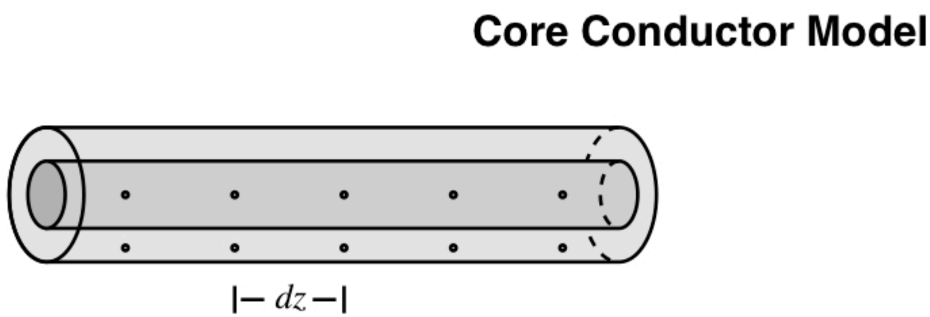
Figure 3.8

- First solved by William Thomson (aka Lord Kelvin) in ~1855

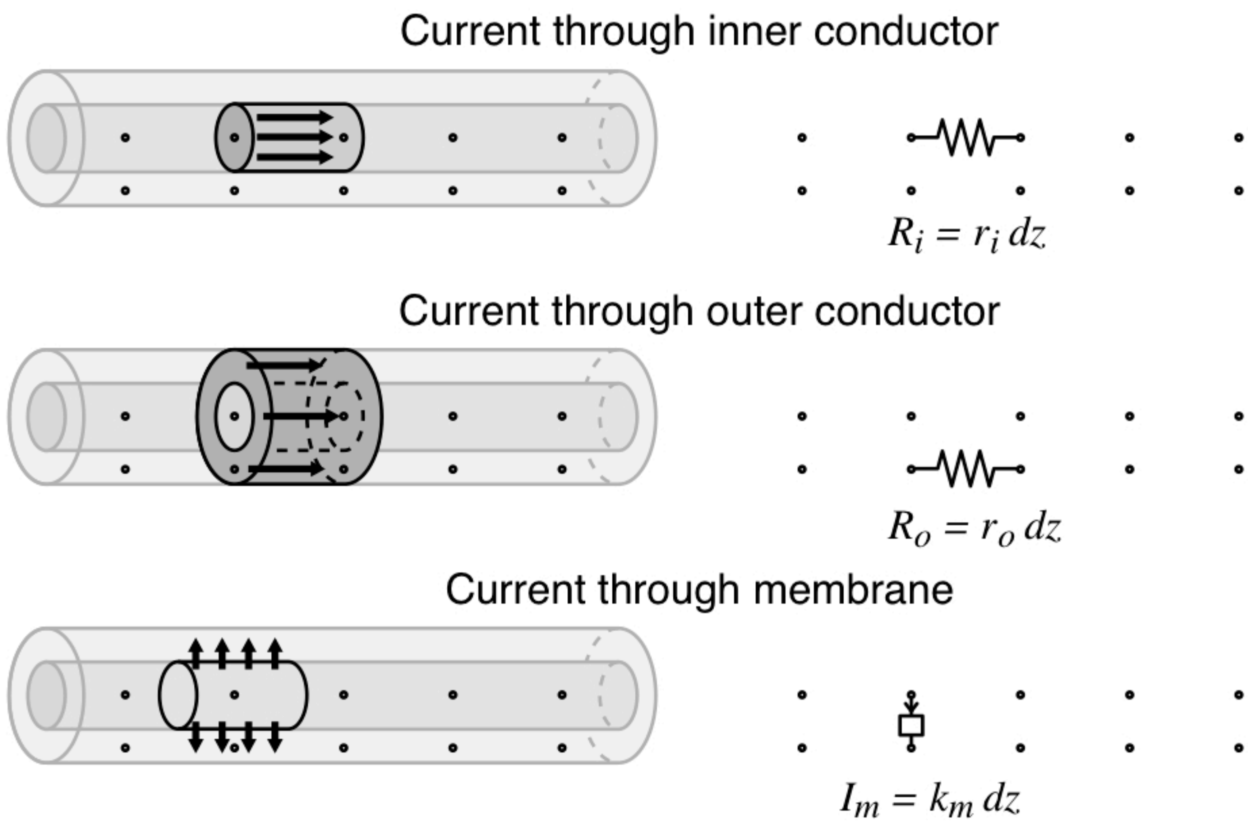
- Motivated by Atlantic submarine cable for intercontinental telegraphy

Weiss (1996)

Biophysical model of a neuron



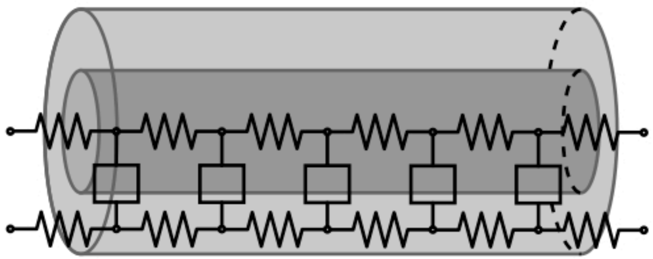
→ Model via an electric circuit



Freeman

Biophysical model of a neuron

Core Conductor Model



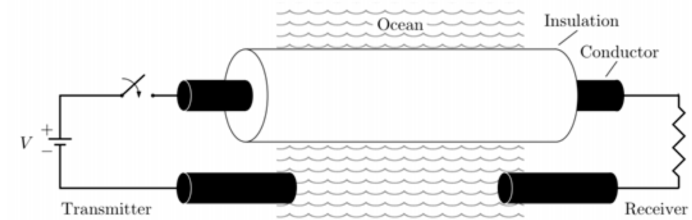


Figure 3.8

→ Cell behave like a leaky submarine cable!

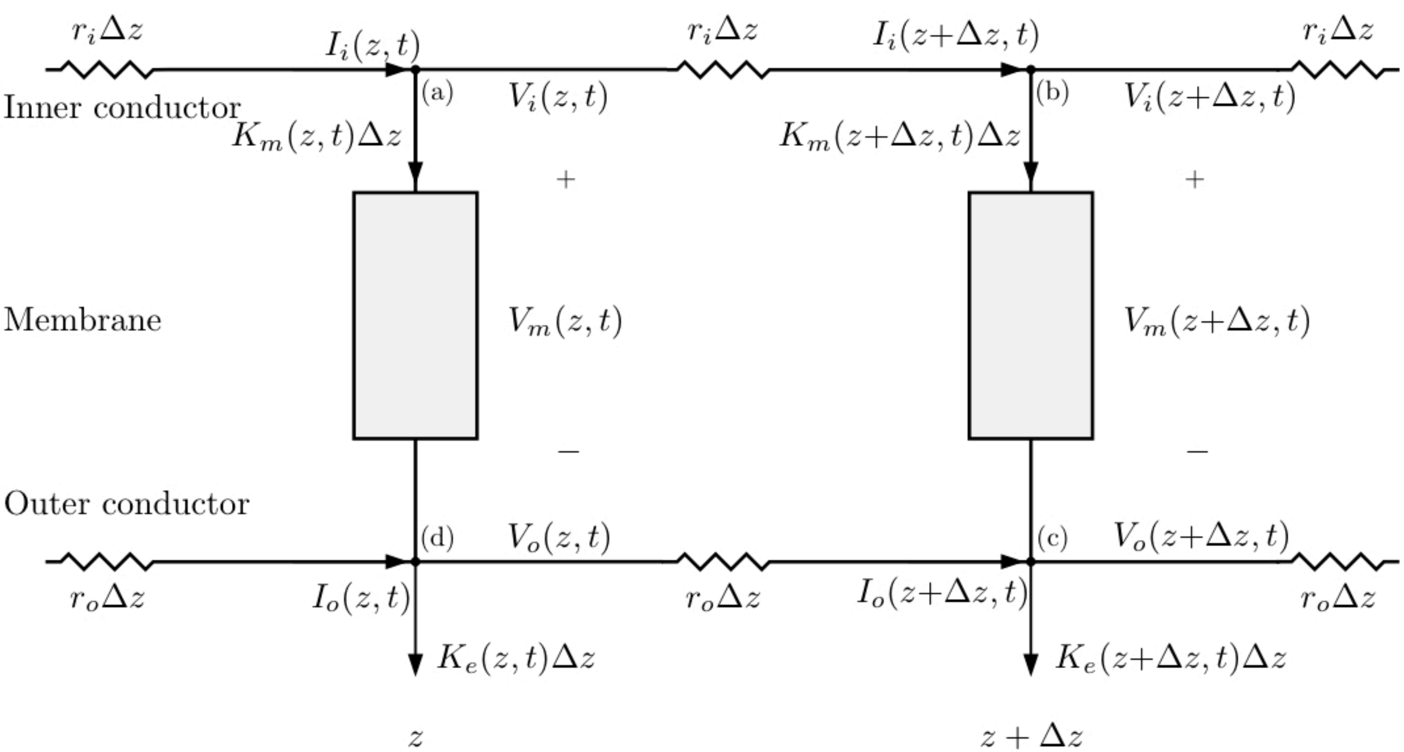
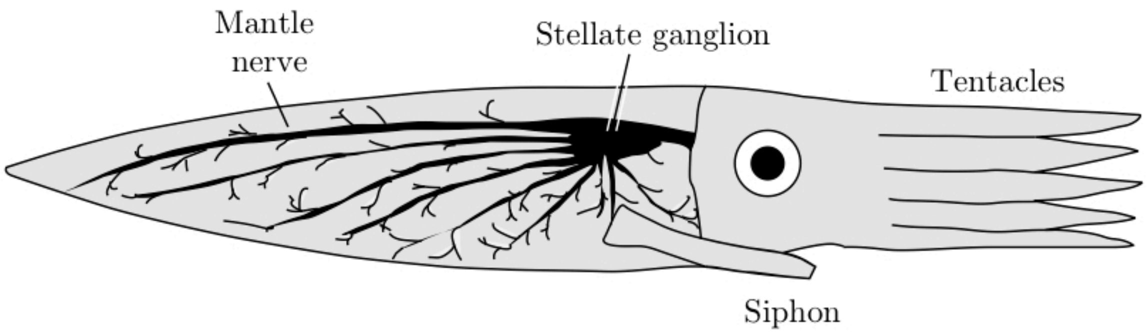


Figure 2.7

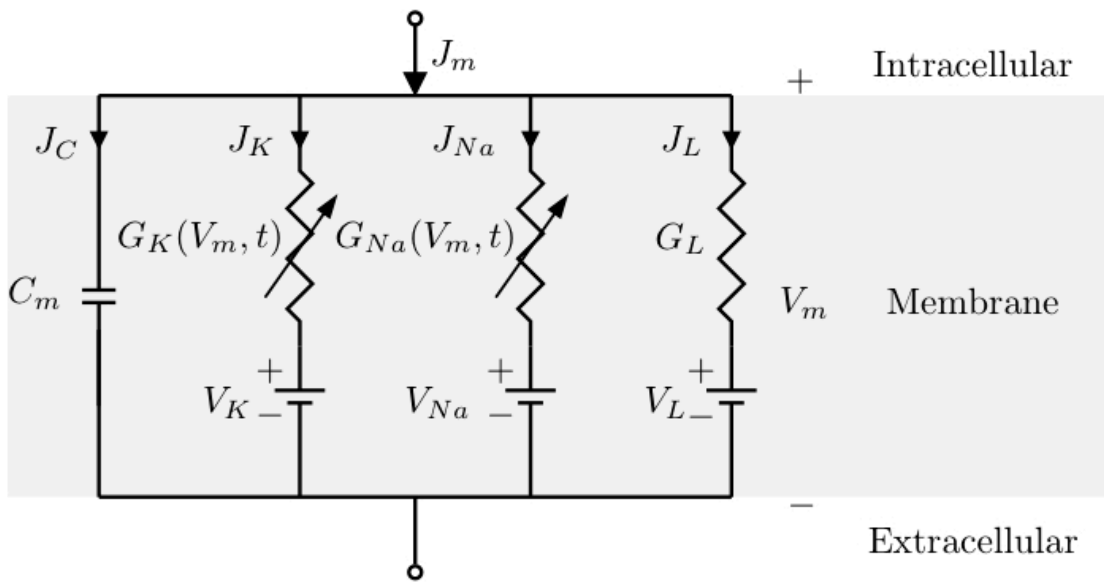
Weiss (1996)

Biophysical model of a neuron



Hodgkin Huxley model

Variable Na+ and K+ conductances



Weiss (1996)

Hodgkin-Huxley equations

$$\frac{1}{2\pi a(r_o + r_i)} \frac{\partial^2 V_m}{\partial z^2} = C_m \frac{\partial V_m}{\partial t} + G_K(V_m, t)\,(V_m - V_K) + G_{Na}(V_m, t)\,(V_m - V_{Na}) + G_L(V_m - V_L)$$

$$\tau_x \frac{dx}{dt} + x = x_\infty \qquad \frac{dx}{dt} = \alpha_x(1 - x) - \beta_x x$$

$$x_\infty = \alpha_x / (\alpha_x + \beta_x) \text{ and } \tau_x = 1/(\alpha_x + \beta_x)$$

$$G_K(V_m, t) = \overline{G}_K n^4(V_m, t)$$

$$G_{Na}(V_m, t) = \overline{G}_{Na} m^3(V_m, t) h(V_m, t)$$

$$n(V_m, t) + \tau_n(V_m) \frac{dn(V_m, t)}{dt} = n_\infty(V_m)$$

$$m(V_m, t) + \tau_m(V_m) \frac{dm(V_m, t)}{dt} = m_\infty(V_m)$$

$$h(V_m, t) + \tau_h(V_m) \frac{dh(V_m, t)}{dt} = h_\infty(V_m)$$

$$\alpha_m = \frac{-0.1(V_m + 35)}{e^{-0.1(V_m+35)} - 1},$$

$$\beta_m = 4e^{-(V_m+60)/18},$$

$$\alpha_h = 0.07e^{-0.05(V_m+60)},$$

$$\beta_h = \frac{1}{1 + e^{-0.1(V_m+30)}},$$

$$\alpha_n = \frac{-0.01(V_m + 50)}{e^{-0.1(V_m+50)} - 1},$$

$$\beta_n = 0.125e^{-0.0125(V_m+60)},$$

Finally there was the difficulty of computing the action potentials from the equations which we had developed. We had settled all the equations and constants by March 1951 and hoped to get these solved on the Cambridge University computer. However, before anything could be done we learnt that the computer would be off the air for 6 months or so while it underwent a major modification. Andrew Huxley got us out of that difficulty by solving the differential equations numerically using a hand-operated Brunsviga. The propagated action potential took about three weeks to complete and must have been an enormous labour for Andrew. But it was exciting to see it come out with the right shape and velocity and we began to feel that we had not wasted the many months that we had spent in analysing records.

—Hodgkin, 1977

Putting the pieces together....

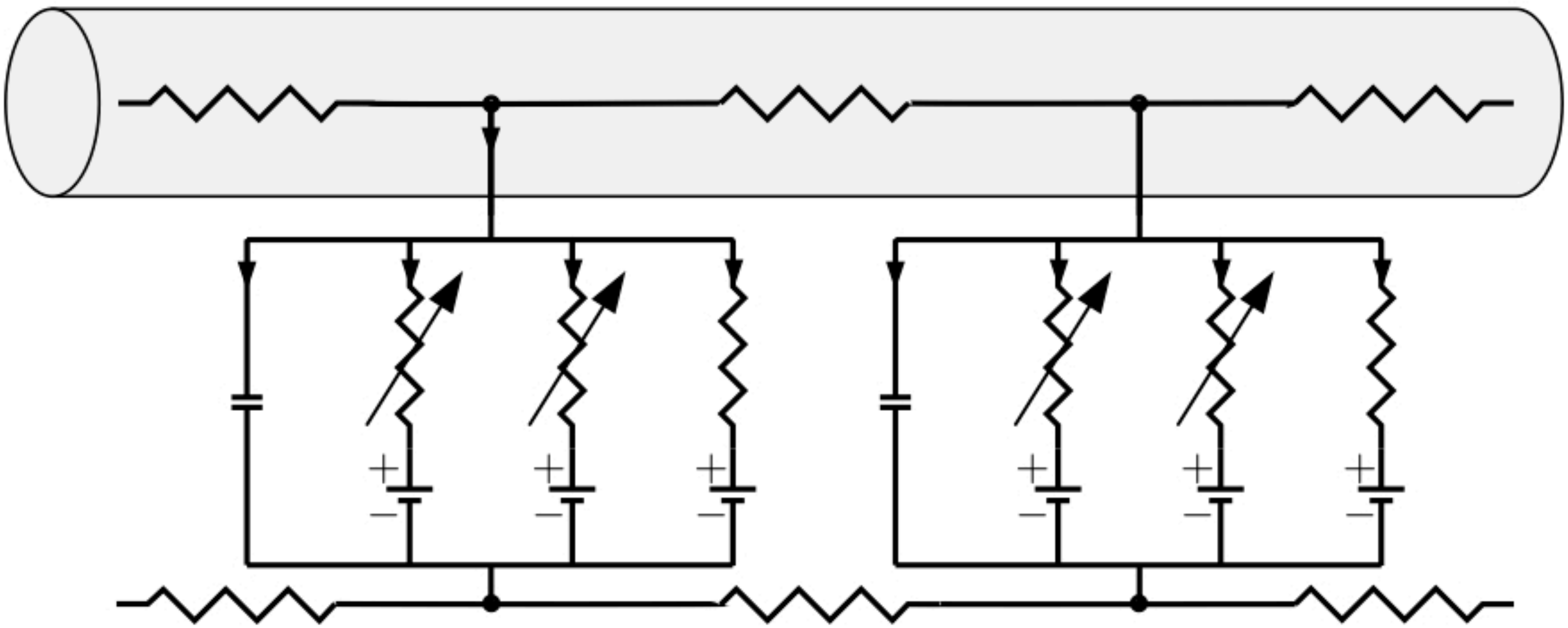


Figure 4.7

Weiss (1996)

Summary (re neurons)

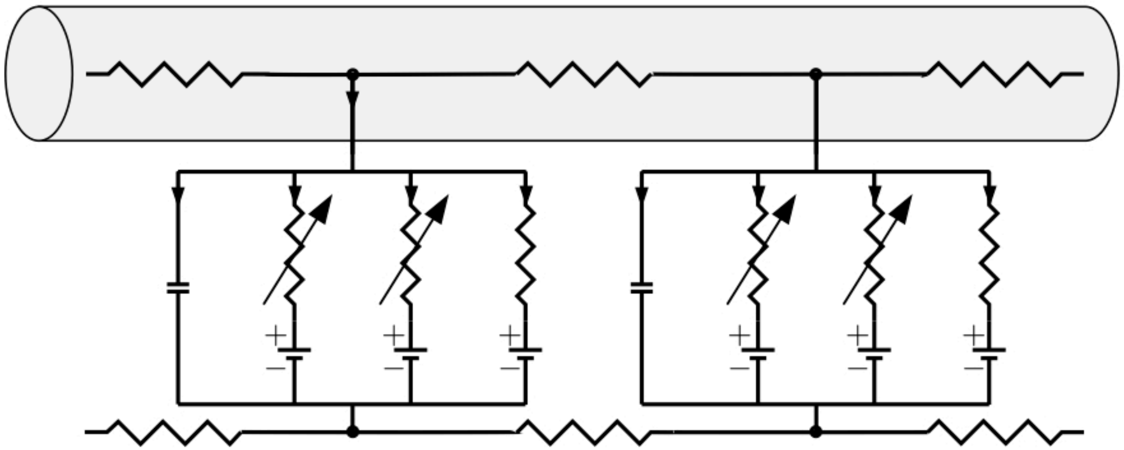


Figure 4.7

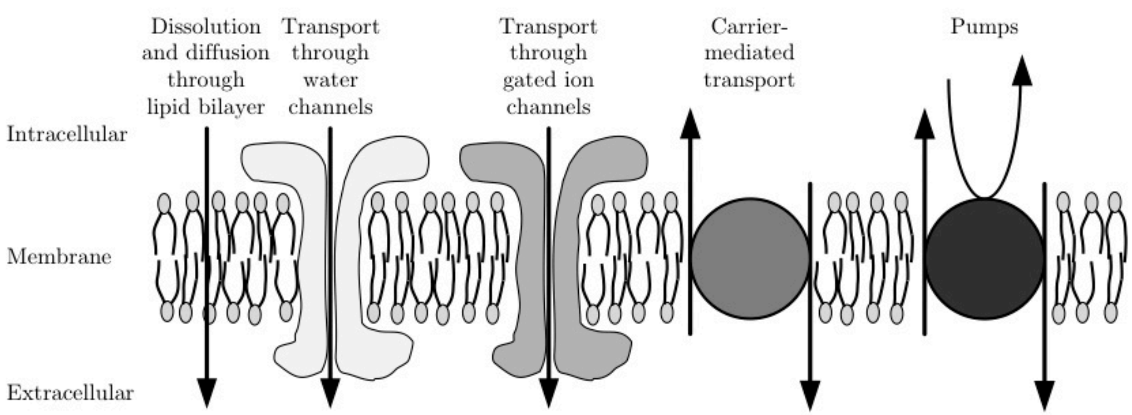


Figure 2.19

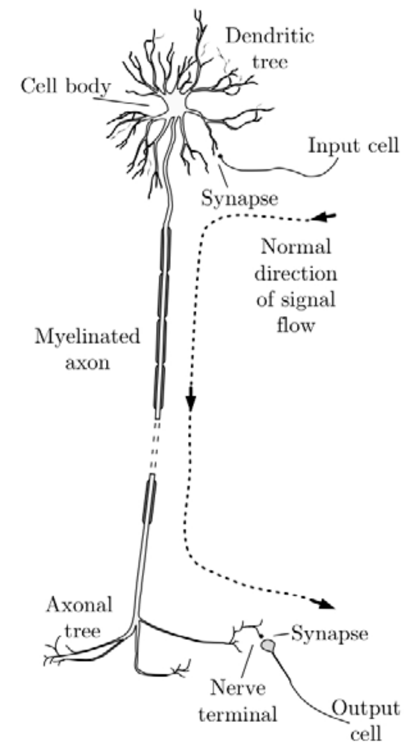
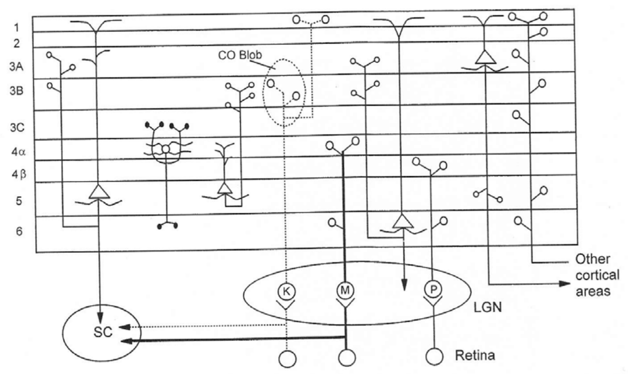


Figure 1.22

Weiss (1996)

<u>Big Picture Theme</u>
How do our sensory systems encode "information" about the world around us?



What are the basic building blocks that make up these "circuits"?

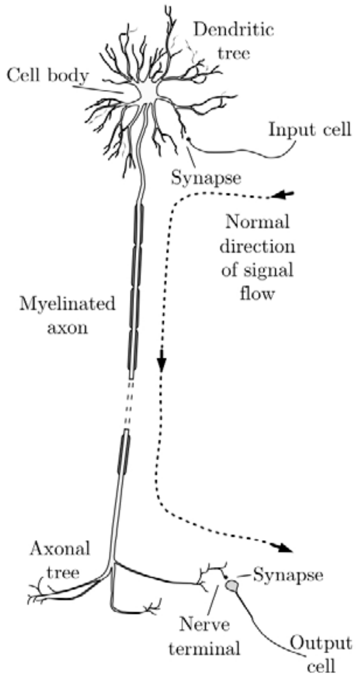
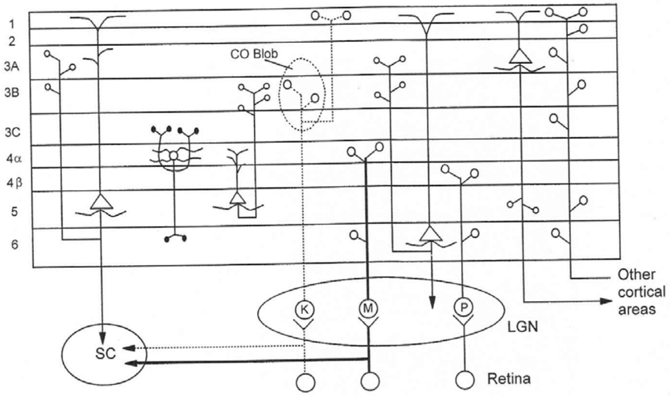


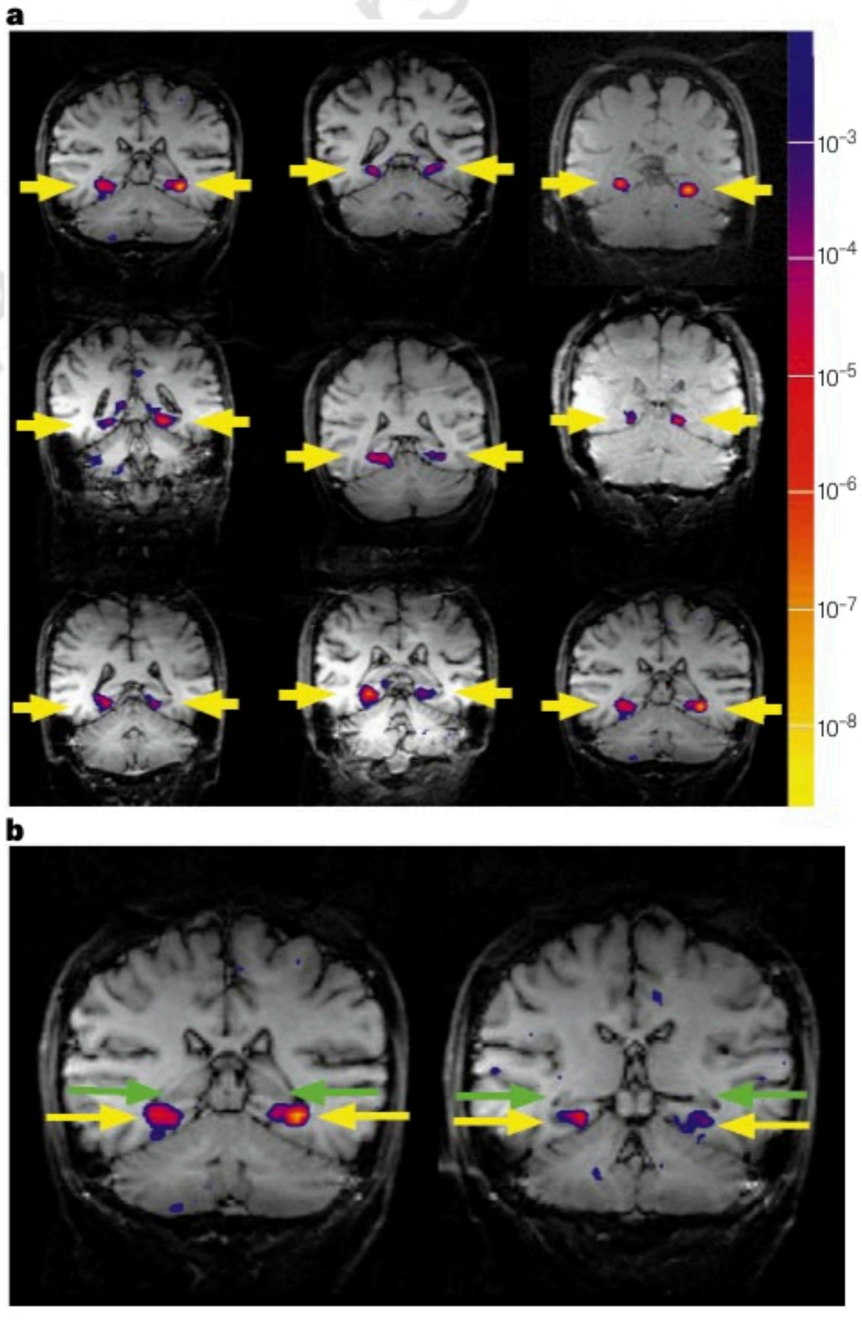
Figure 1.22

Human brain contains ~10^{11} (100 billion) neurons!
(with 100 trillion+ connections inbetween)

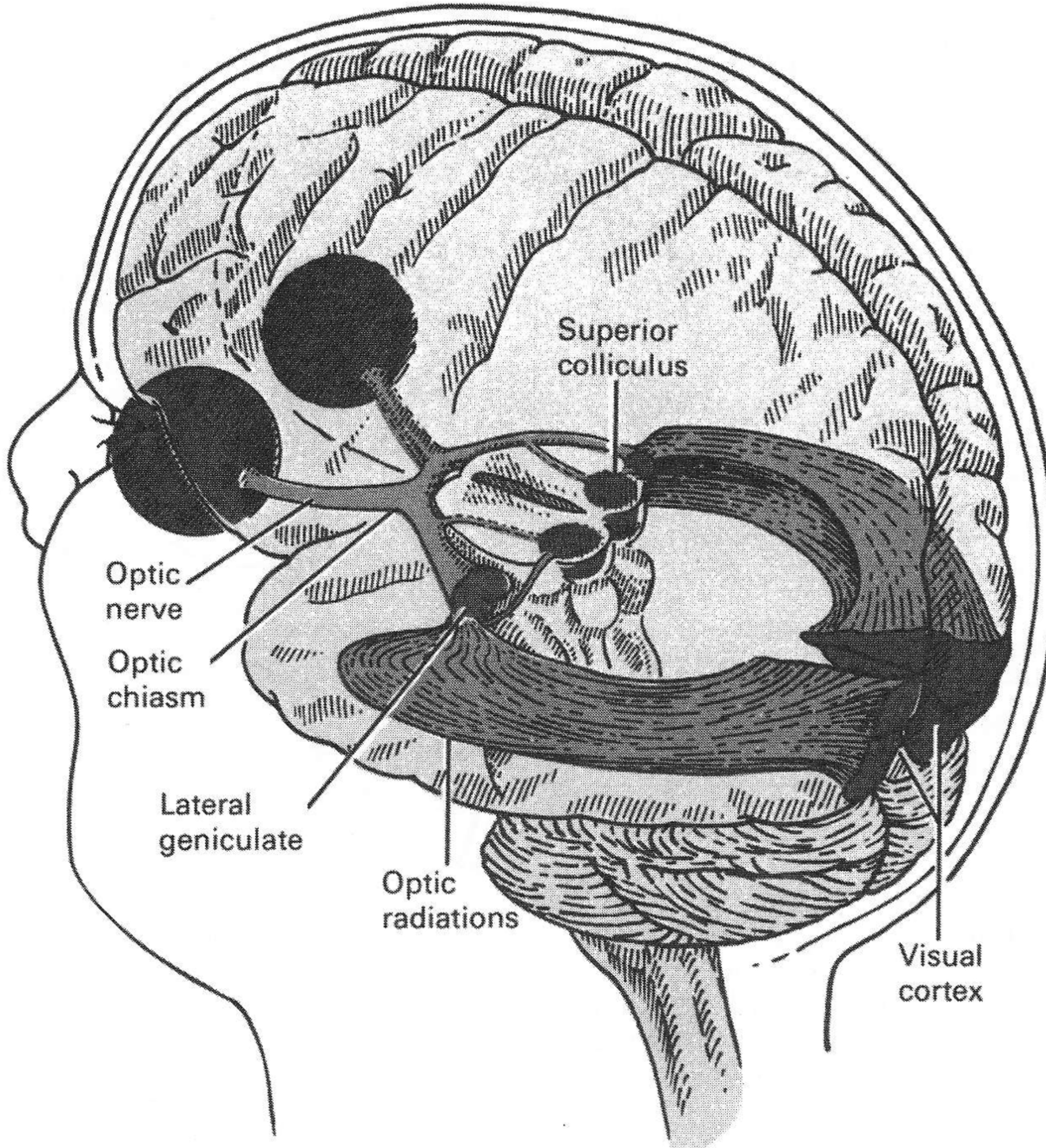


Human brain contains ~10^{11} (100 billion) neurons
(with 100 trillion+ connections inbetween)

→ This is a pretty hard problem!

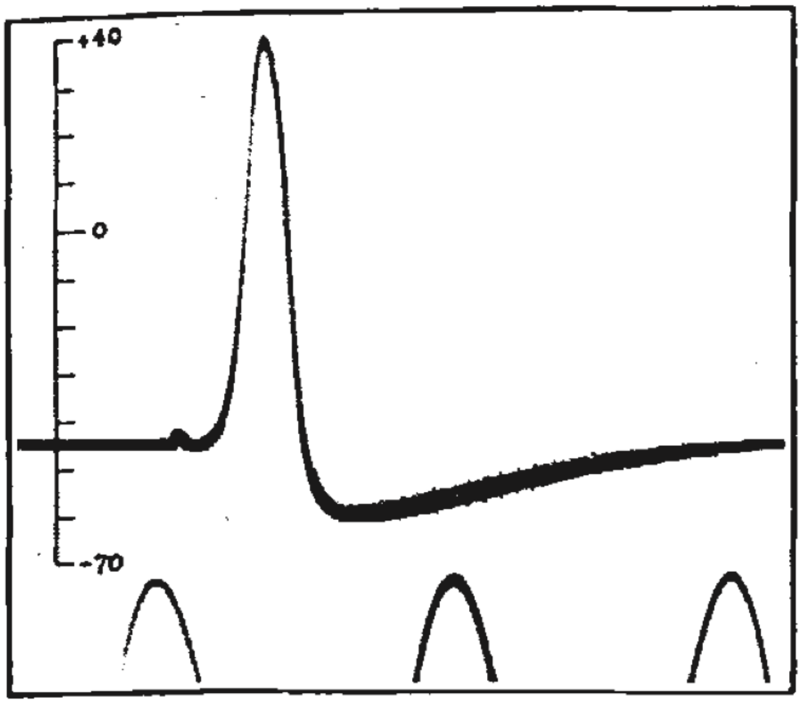


Epstein & Kanwisher (1998)


Superior
colliculus
Optic
nerve
Optic
chiasm
Lateral
geniculate
Optic
radiations
Visual
cortex

Palmer (1999)

Pop Quiz



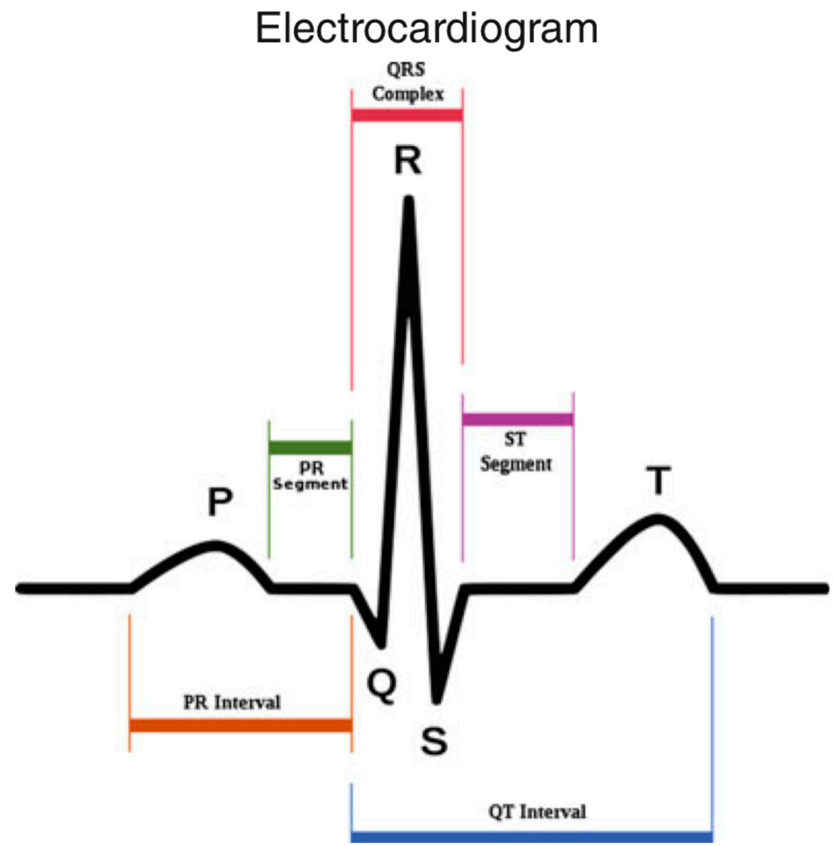


Fig. 1.2 Electrocardiogram depicting *P* wave, *QRS* complex, and *T* wave. (*Source* Wikipedia)

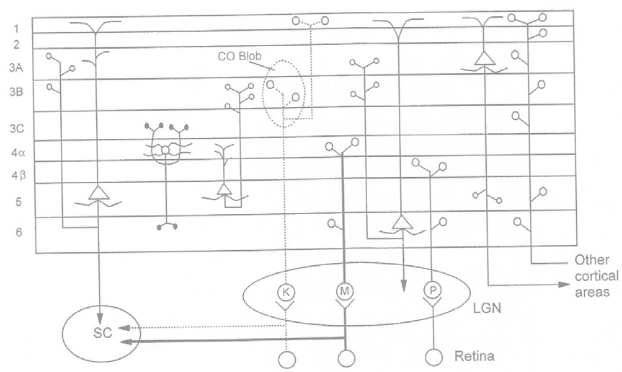
What is the difference between these two different types of "spikes"?

Fox, Pandit-Taskar, Strauss (2013)

Big Picture Theme

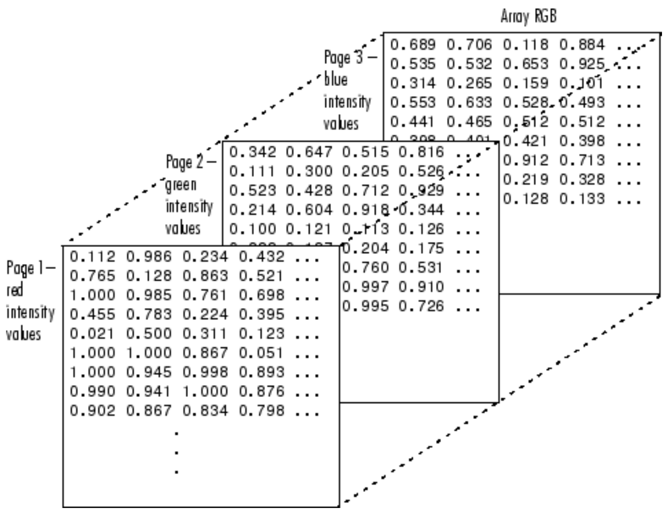
How do our sensory systems encode "information" about the world around us?

Two broad topics to cover



What are the basic building blocks that make up these "circuits"?

What are some basic (signal processing) considerations about "transforming" information?



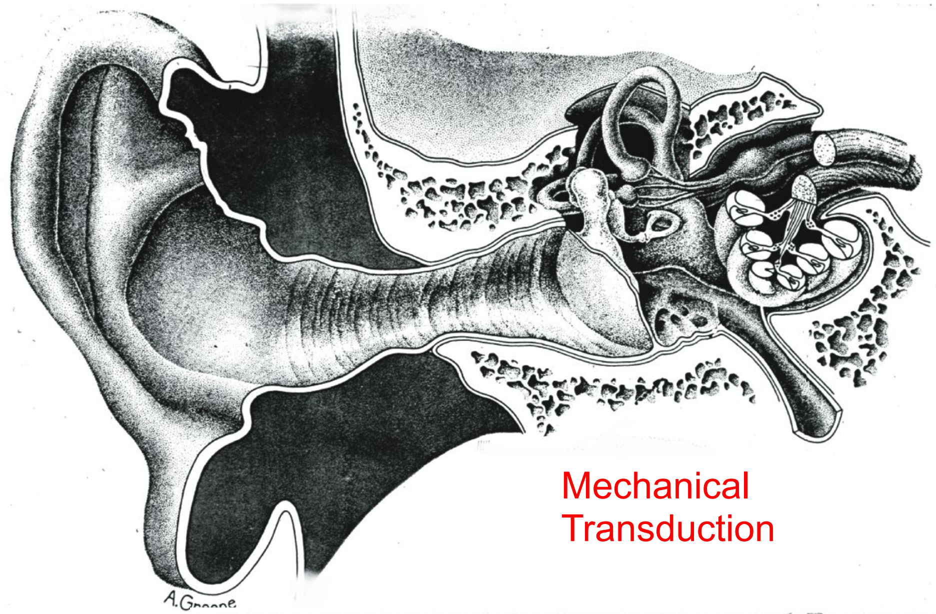
Transduction

1. the transfer of genetic material from one organism (as a bacterium) to another by a genetic vector and especially a bacteriophage

2. the action or process of converting something and especially energy or a message into another form

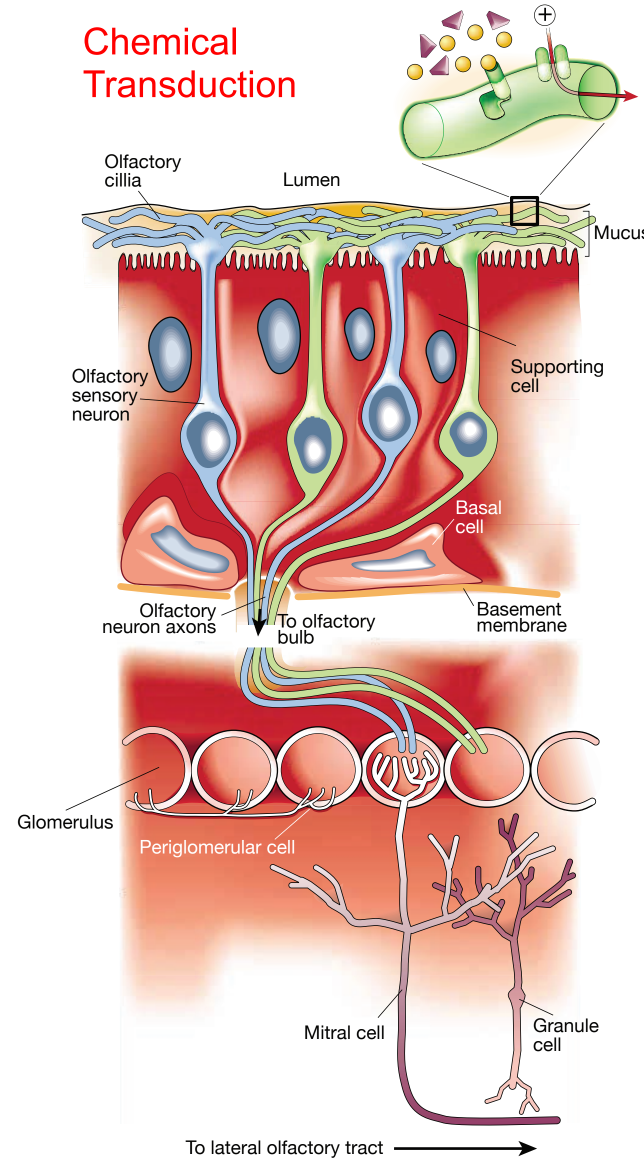
Merriam-Webste
http://www.jungleae.com/how-to-hold-a-microphoner

Peripheral sensory transduction



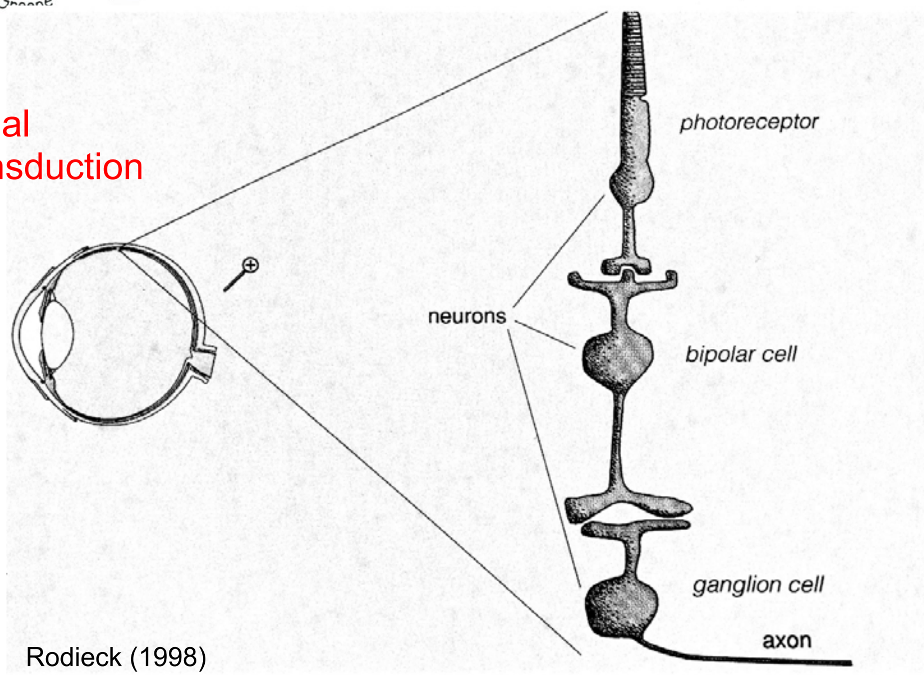
Mechanical Transduction

Chemical Transduction

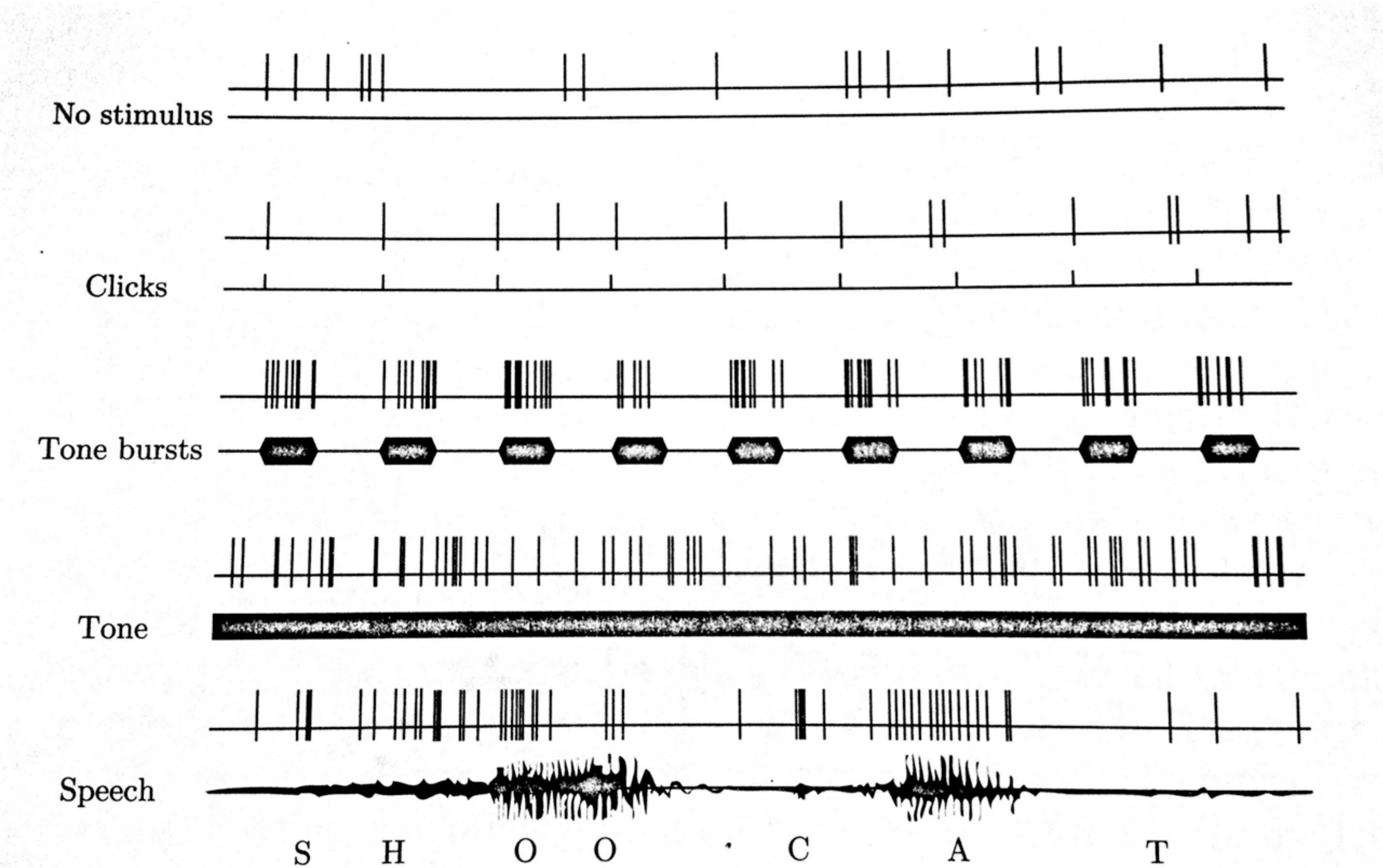


Firestein (2001)

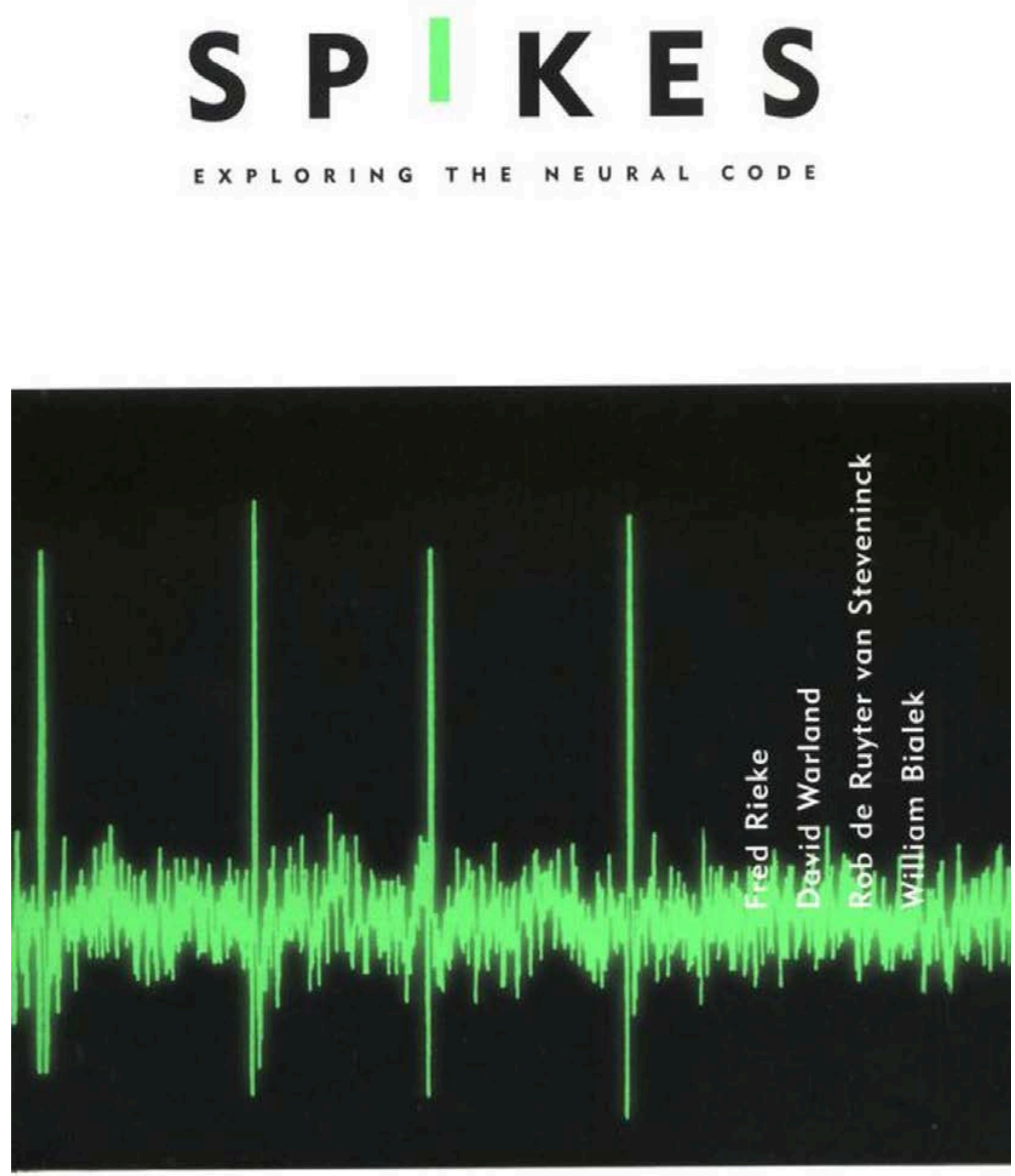
Visual Transduction



Rodieck (1998)

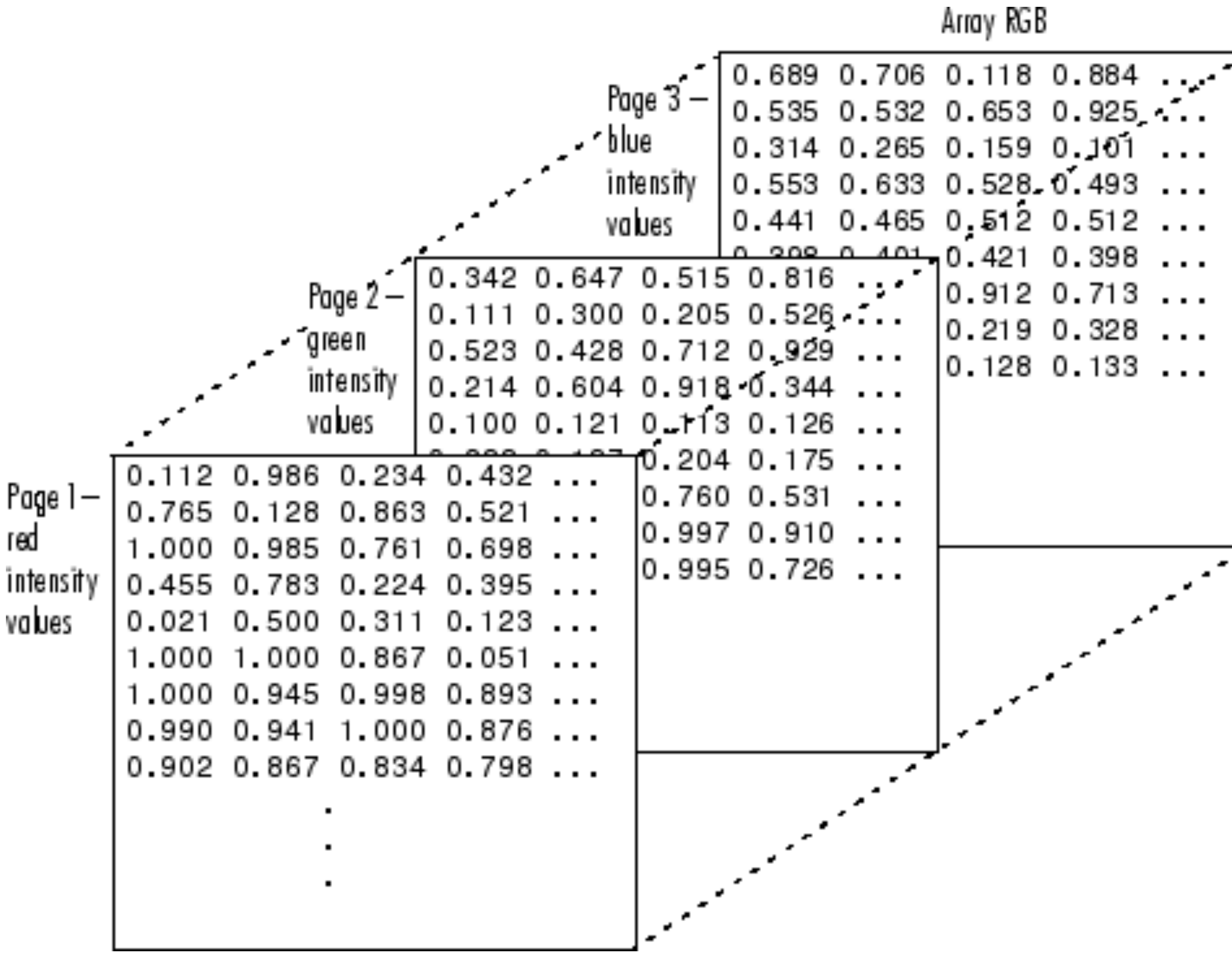


Question: How similar/different is the “input” versus the “output”?



Somehow, the information is “transformed”, encoded into some other “language”....

Aside: Images as numbers (i.e., a "bitmap")

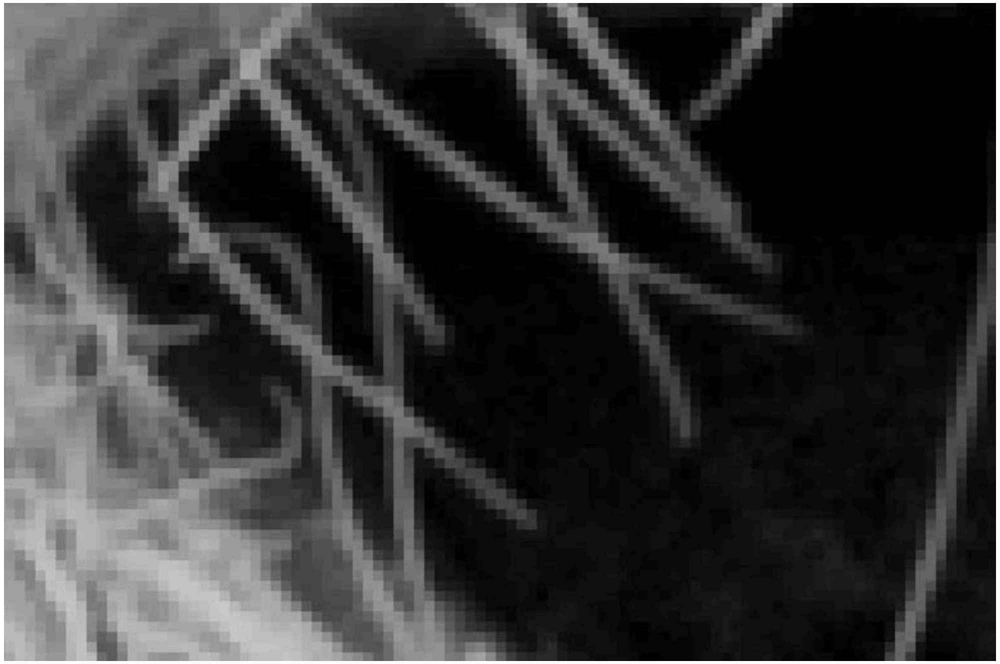


http://i.stack.imgur.com/kI65e.gif

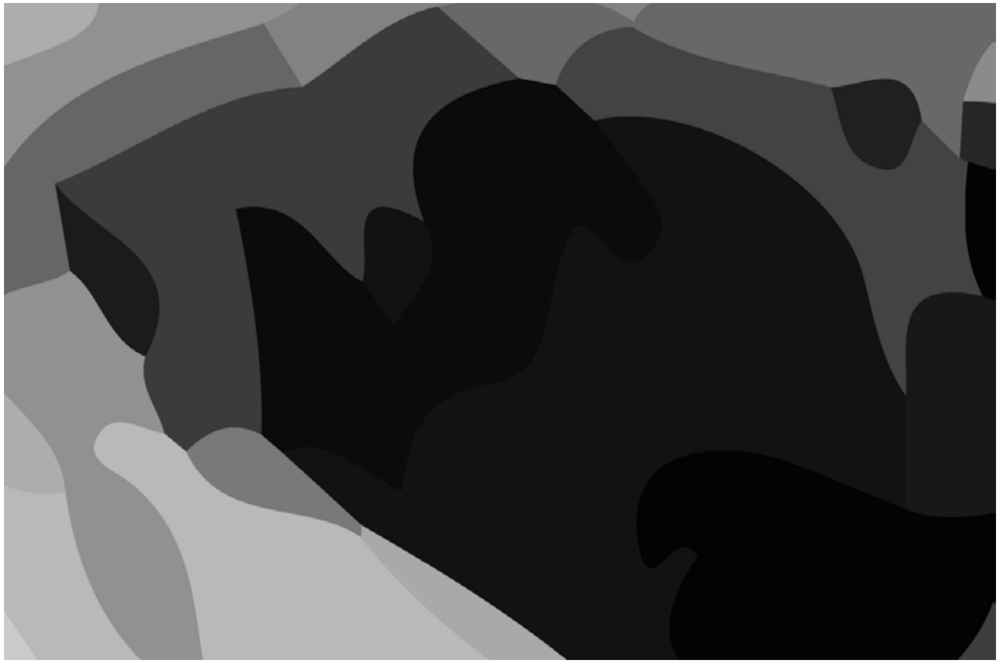
Many ways to “encode” something....

Many ways to "encode" something....

Bitmap version

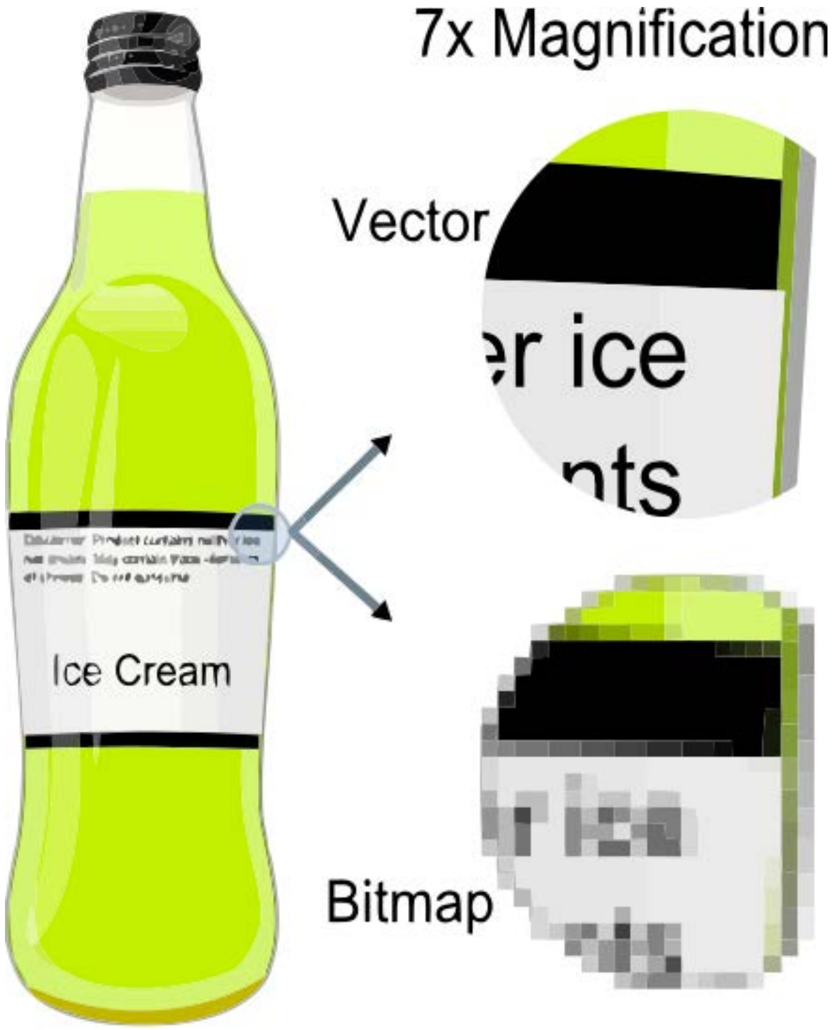


Vector version



zoom-in about corner of eye

Many ways to "encode" something....

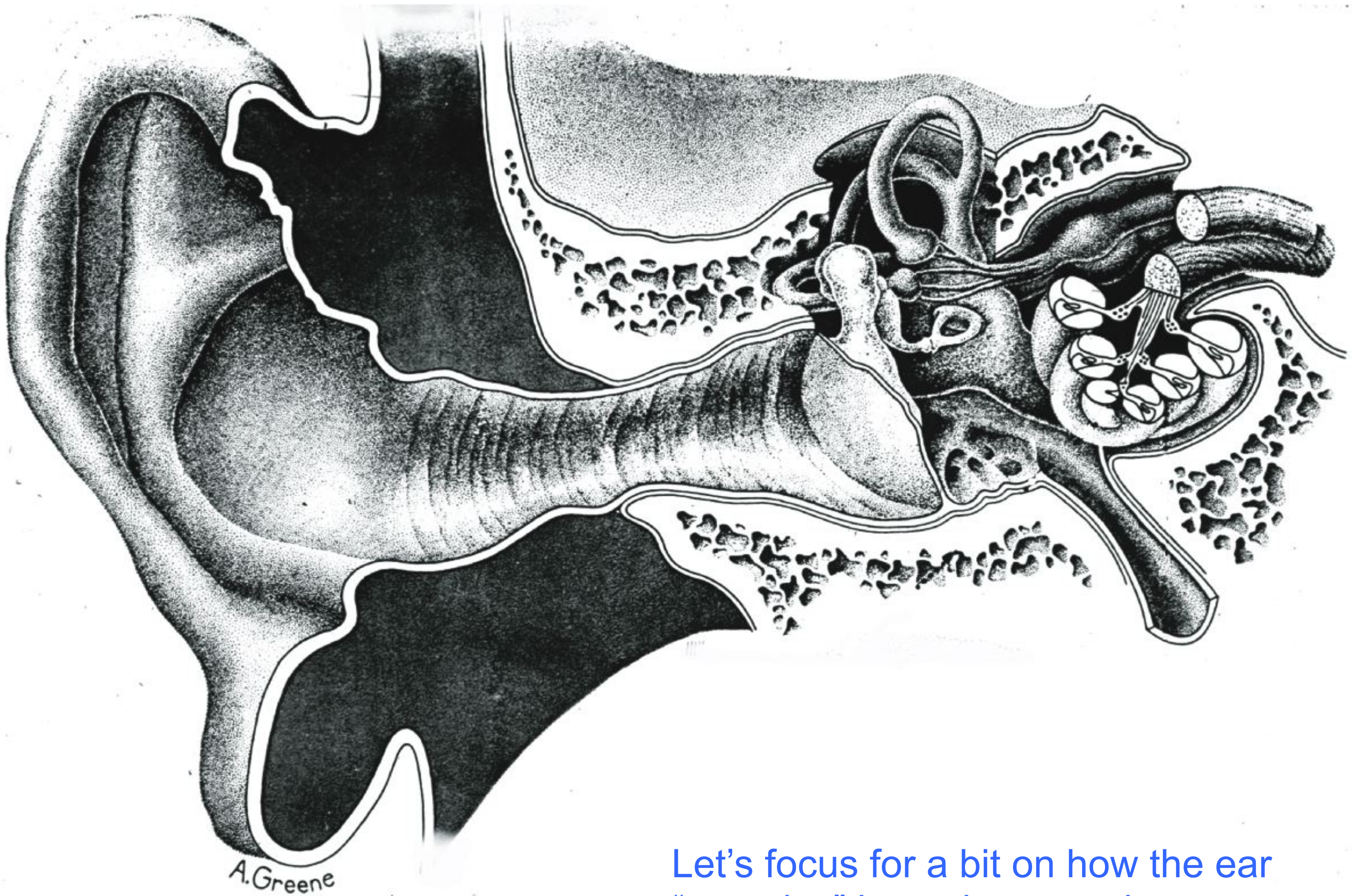


Bitmap version

Vector version

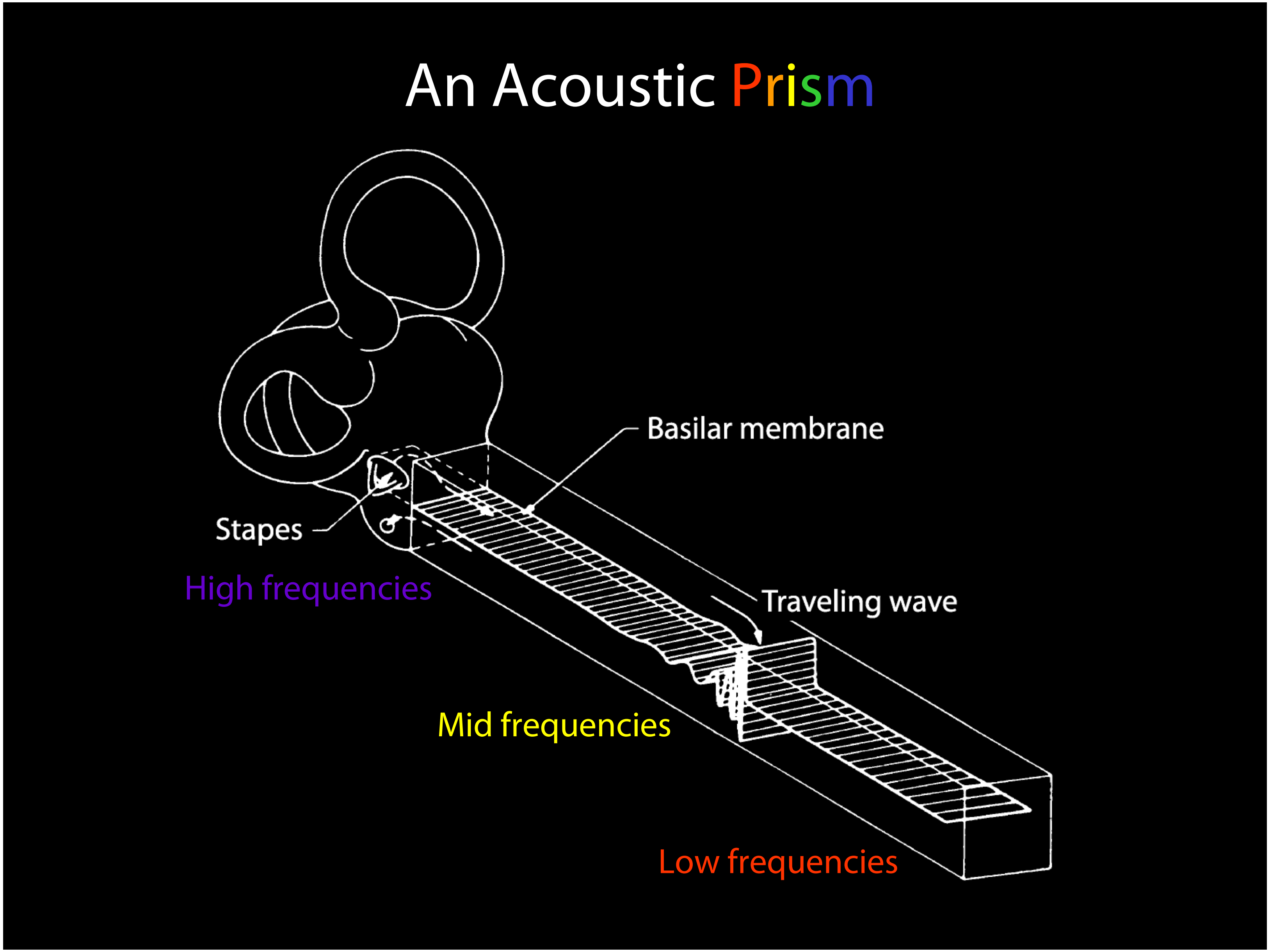
→ "Same" image, two very different representations

Wikipedia



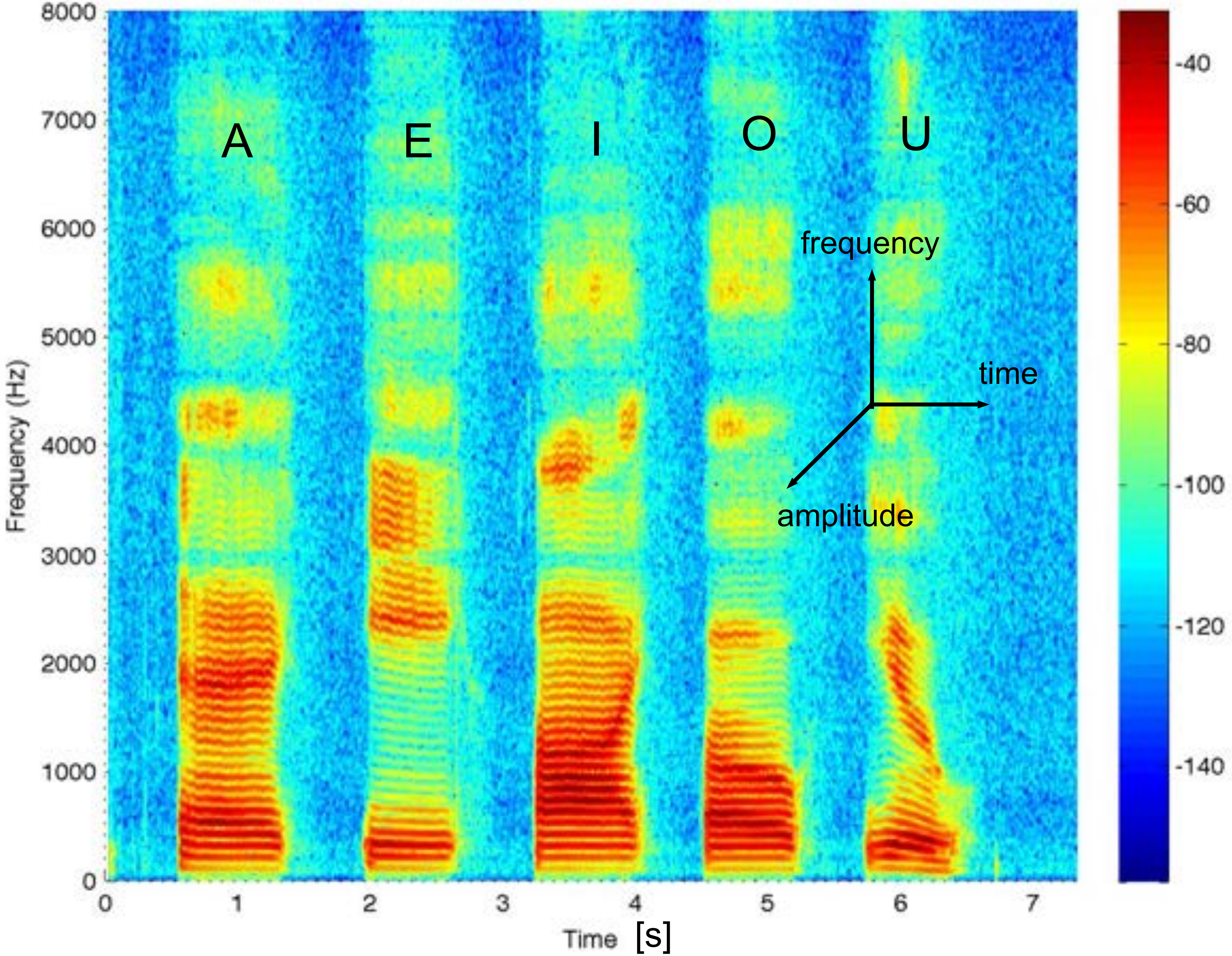
Let’s focus for a bit on how the ear “encodes” incoming sounds

Spectral Decomposition



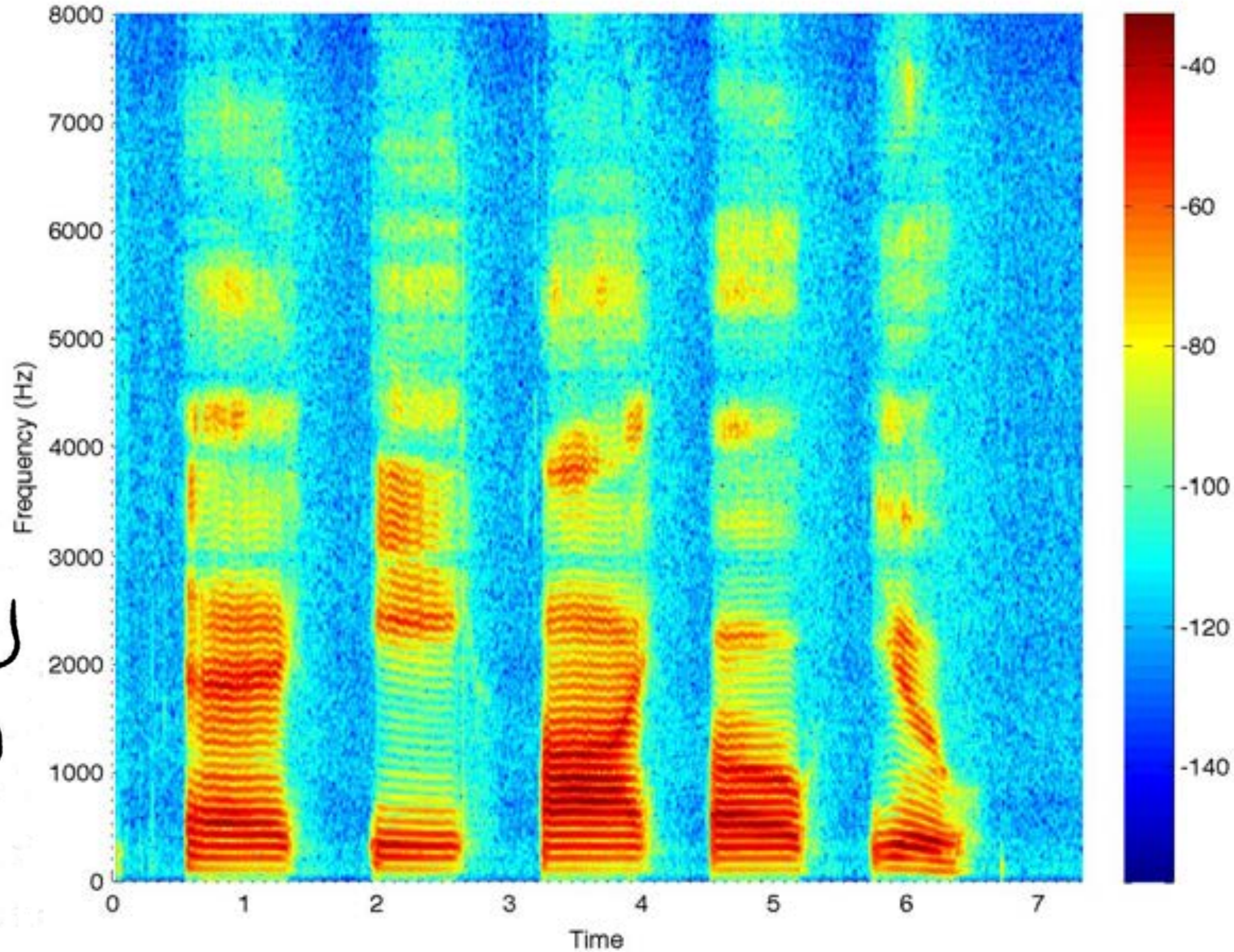
Zweig et al. (1976)

Aside: Fourier analysis



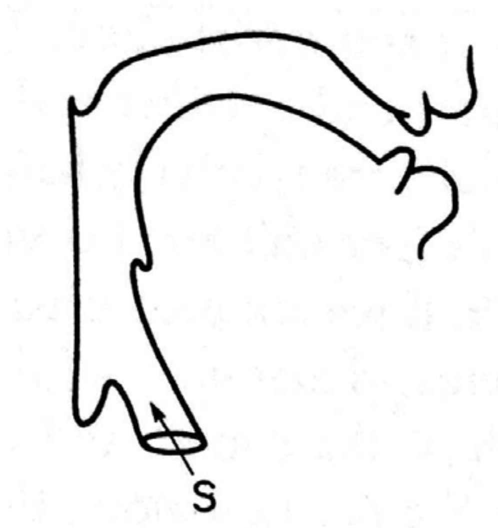
Aside: Acoustic phonetics

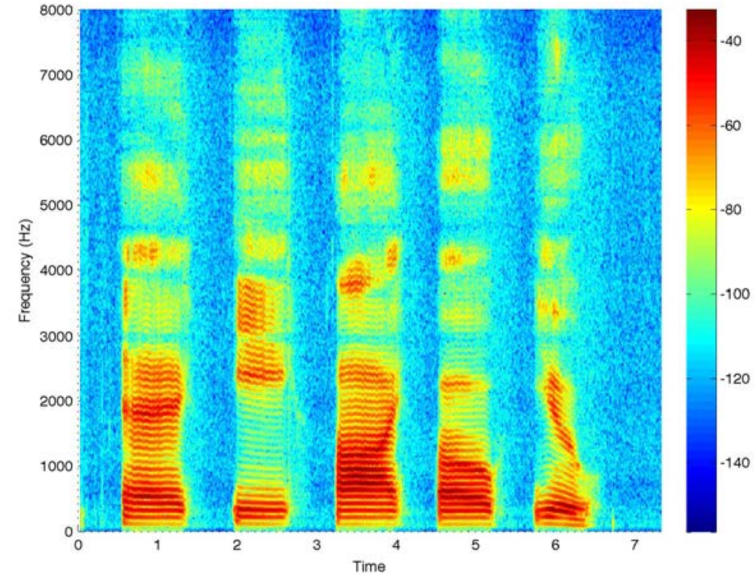
Human vocal tract cross-section

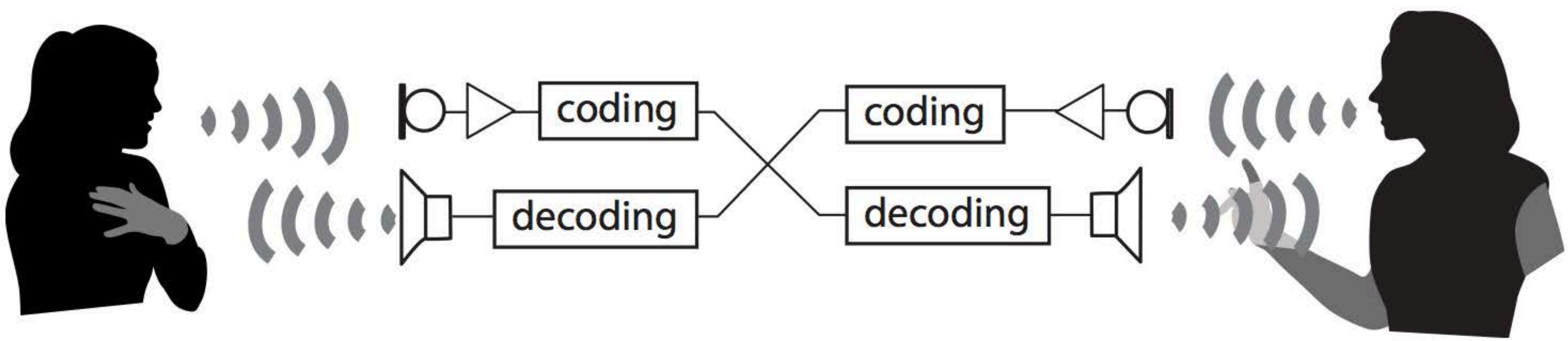


EXspectrogram.m

Aside: "Speech chain"

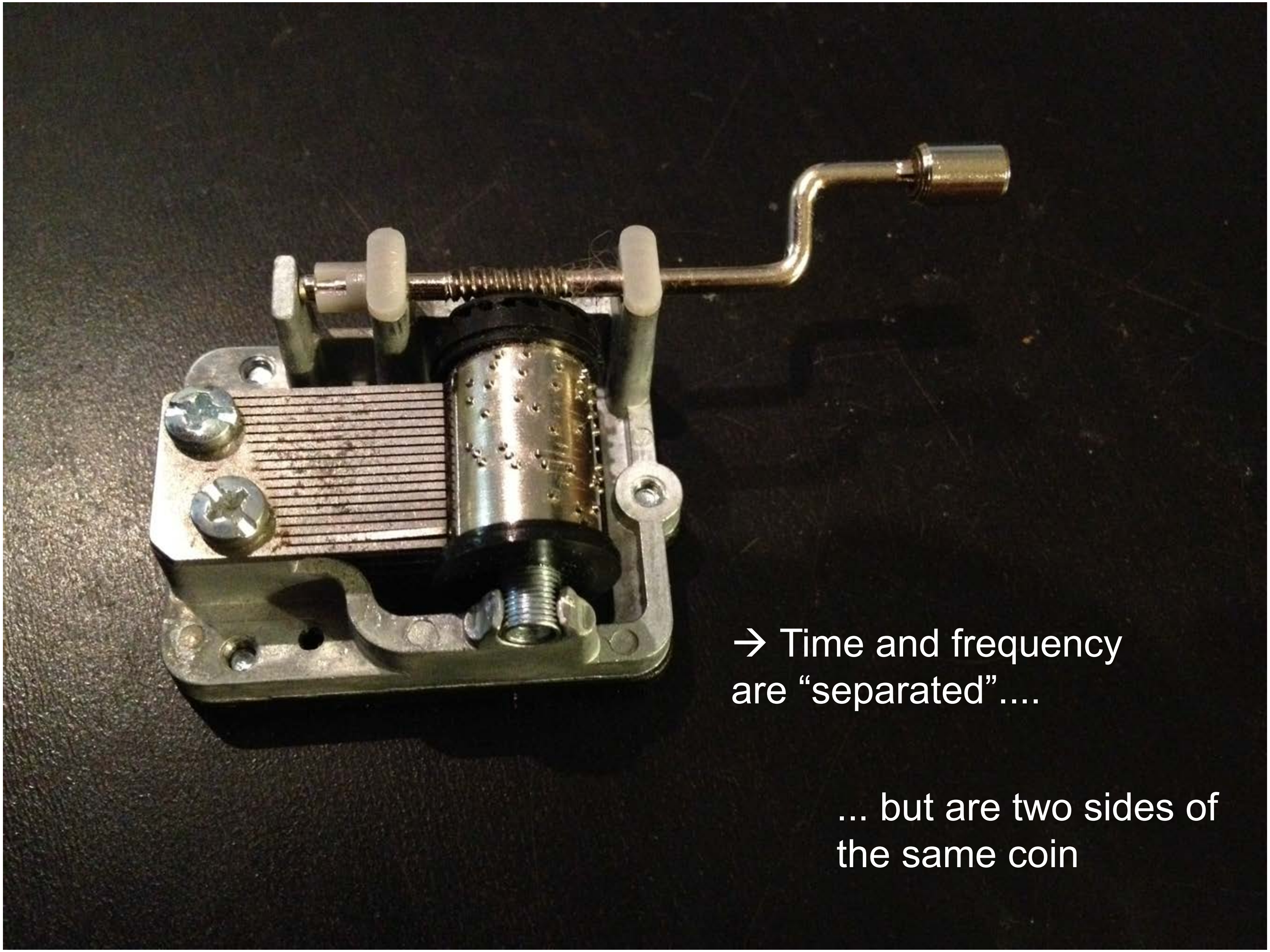




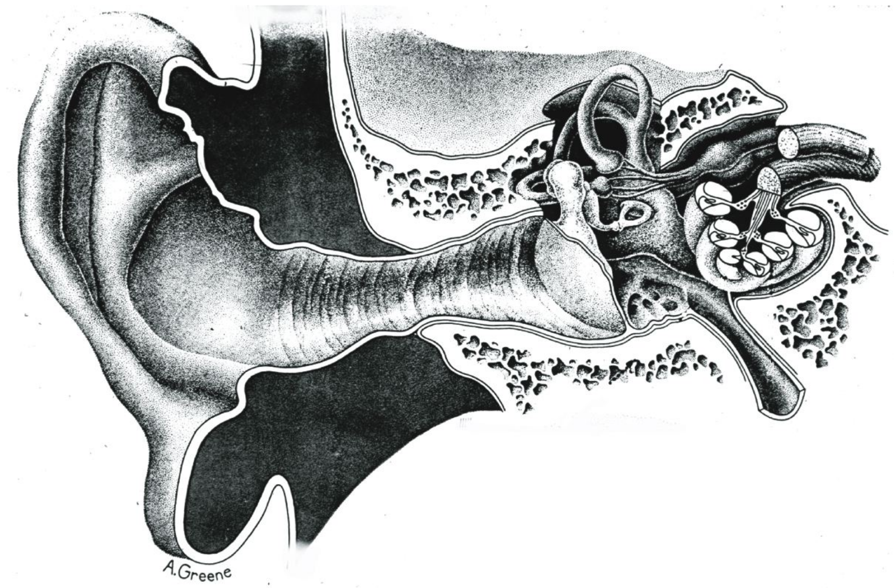


Pulkki & Karjalainen (2015)

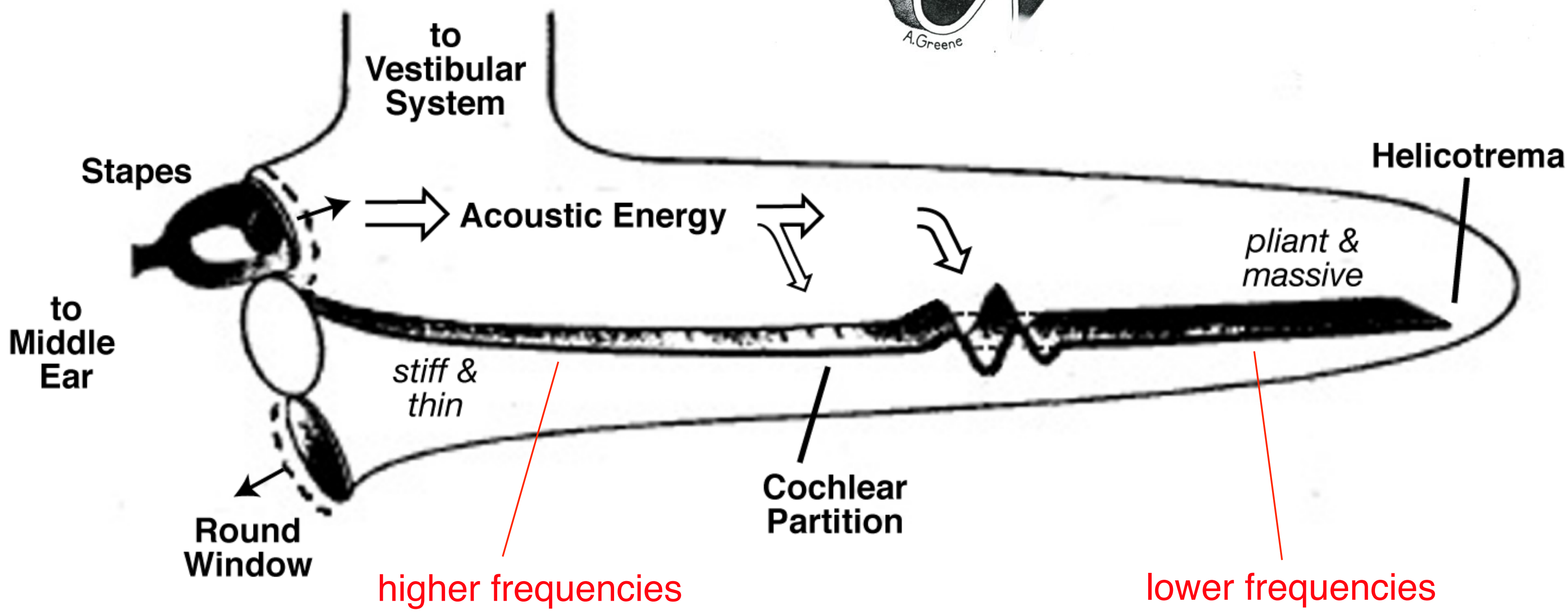
Aside: Fourier analysis



Ear is a Fourier analyzer (*Tonotopicity*)

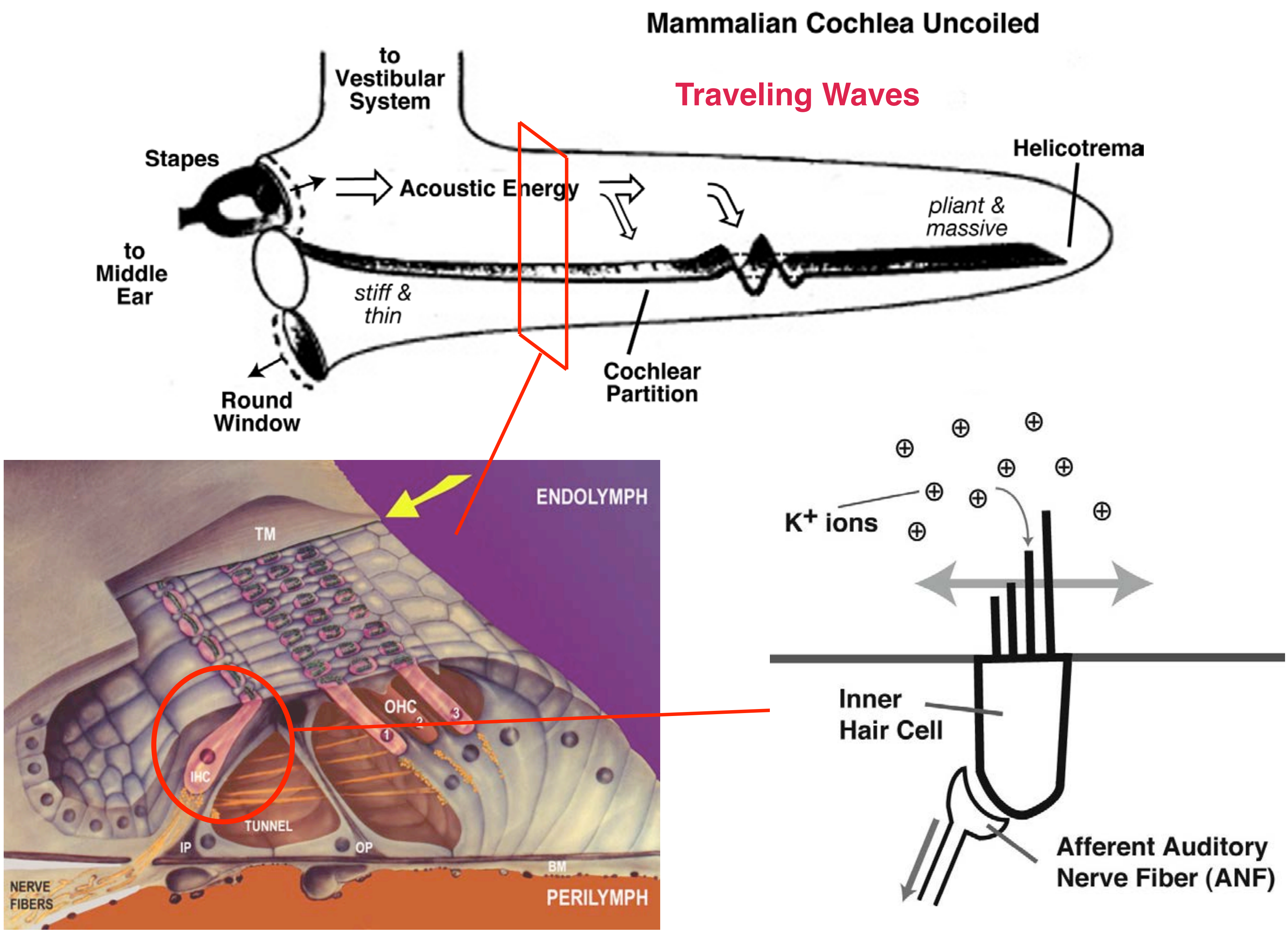


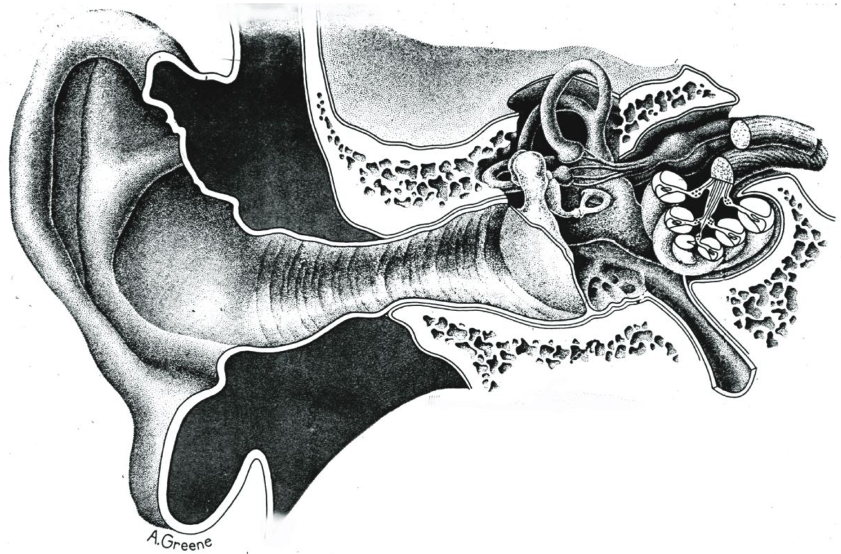
Basilar membrane (BM)

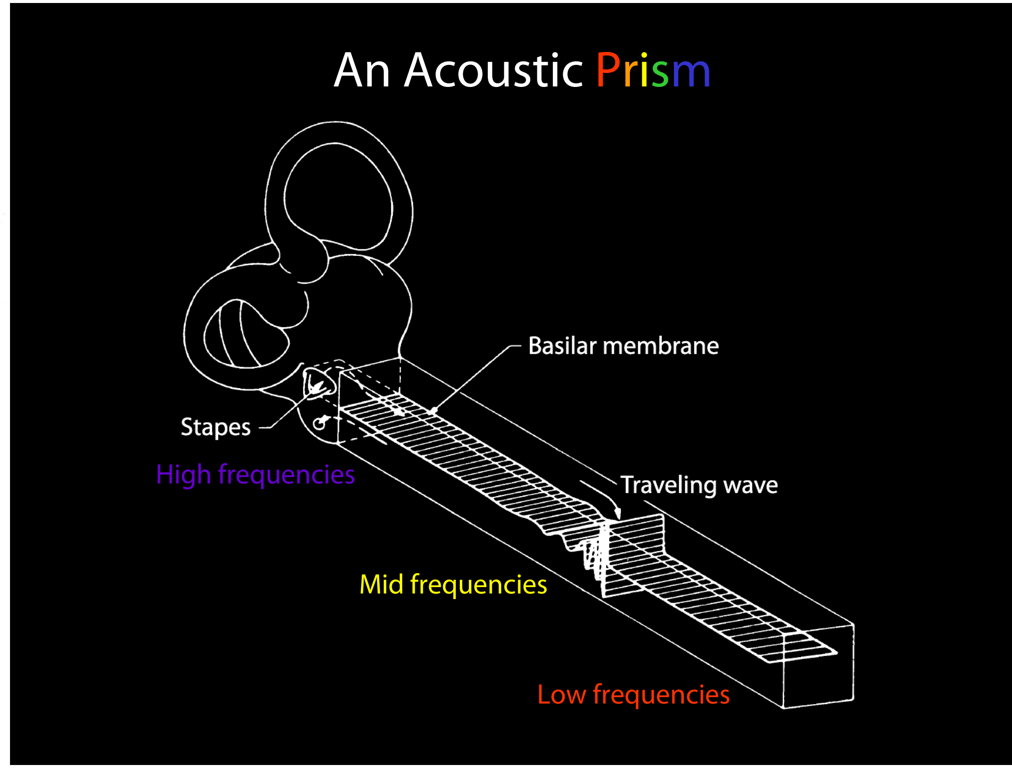


Geisler (1996)

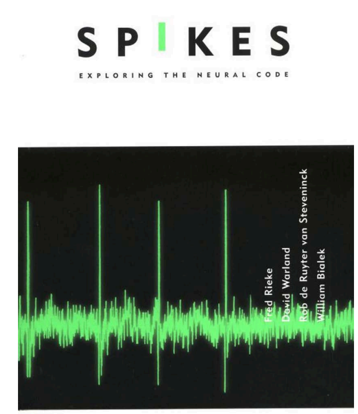
Hair cell = ‘Mechano-electro’ transducer







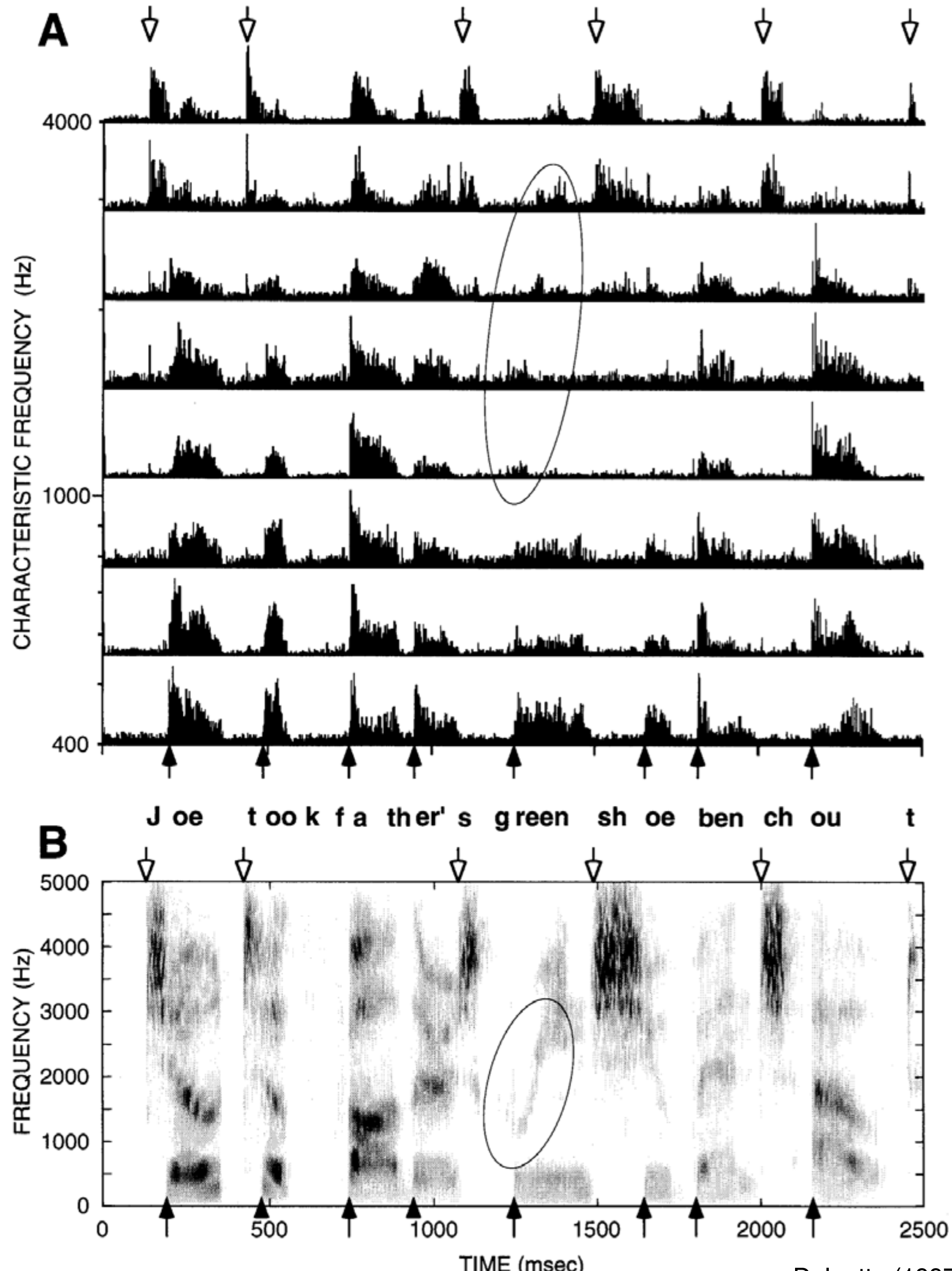
- Ear acts as a hydrodynamic spectrum analyzer
  (spatial location ←→ frequency)



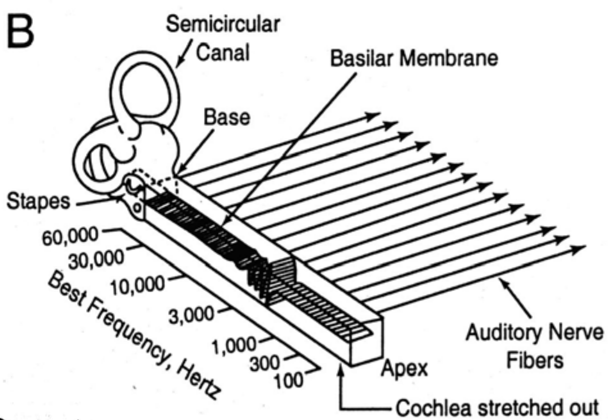
- Spectral decomposition serves as an underlying basis for auditory “neural code”

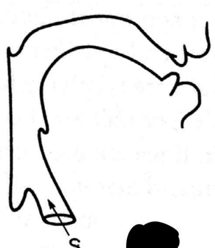
Neural coding of speech

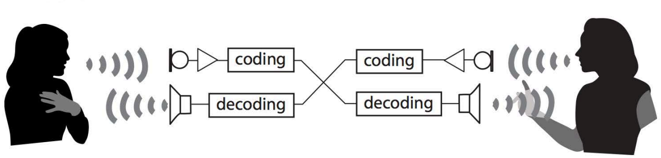
Fig. 1. Neurogram and spectrogram for a speech utterance produced by a female speaker. A. Neurogram display of the activity of the cat auditory nerve in response to the utterance. Each trace represents the average post-stimulus-time histogram for 2-7 auditory-nerve fibers whose CFs are located in a 1/2 octave band centered at the vertical ordinate. All histograms were computed with a bin width of 1 msec, and have been normalized to the same maximum in order to emphasize temporal patterns. The stimulus level was such that the most intense vowels were at 50 dB SPL. B. Broadband spectrogram of the utterance. Filled arrows point to rapid increases in amplitude in the low frequencies (and their neural correlates on top), while open arrows point to rapid increases in amplitude in the high frequencies. The ovals show the second-formant movement in "green" and its neural correlate.



Delgutte (1997)







Aside: Imaging & Fourier Analysis

Medical/Biological/Neural Imaging

(e.g., MRI, CT, OCT, x-ray crystallography, spectroscopy, microscopy, interferometry, ...)

- Fourier transform is a key foundation in imaging (e.g., “k-space” in MRI)
- Also the backbone of modern signal processing

Wikipedia

Aside: Fourier analysis (REVISITED)

Intuitive connection back to Taylor series:

$$y(x_1 + \Delta x) \approx y(x_1) + \sum_{n=1}^{N} \frac{1}{n!} \left. \frac{d^n y}{dx^n} \right|_{x_1} (\Delta x)^n. \qquad \text{(D.2)}$$

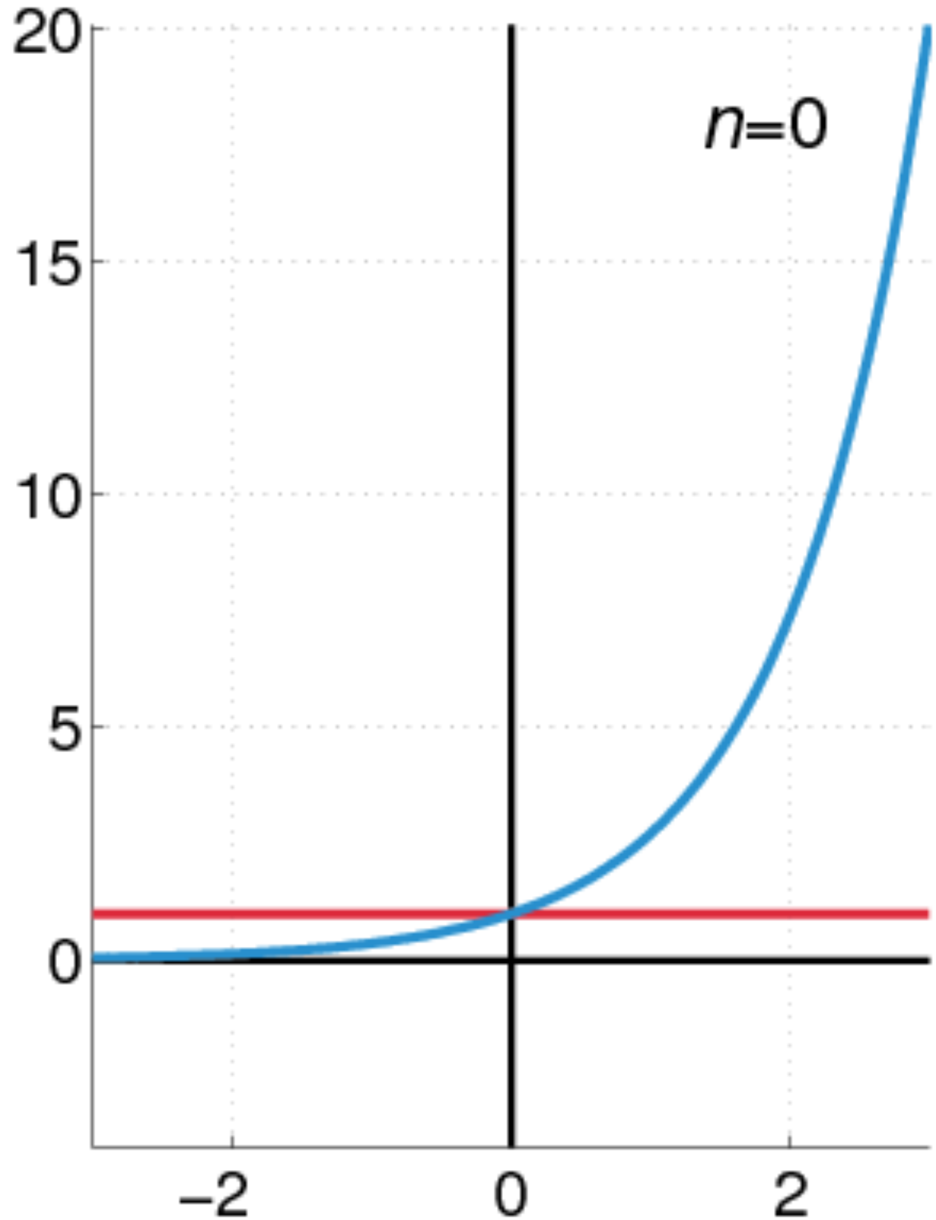
$$f(x) = f(x_o) + f'(x_o)(x - x_o) + \frac{f''(x_o)}{2!}(x - x_o)^2 + \cdots + \frac{f^{(n)}(x_o)}{n!}(x - x_o)^n + \cdots$$

$$= \sum_{n=0}^{\infty} \frac{f^{(n)}(x_o)}{n!}(x - x_o)^n$$

Taylor series → Expand as a (infinite) sum of polynomials

Different Idea: Fourier series → Expand as a (infinite) sum of sinusoids

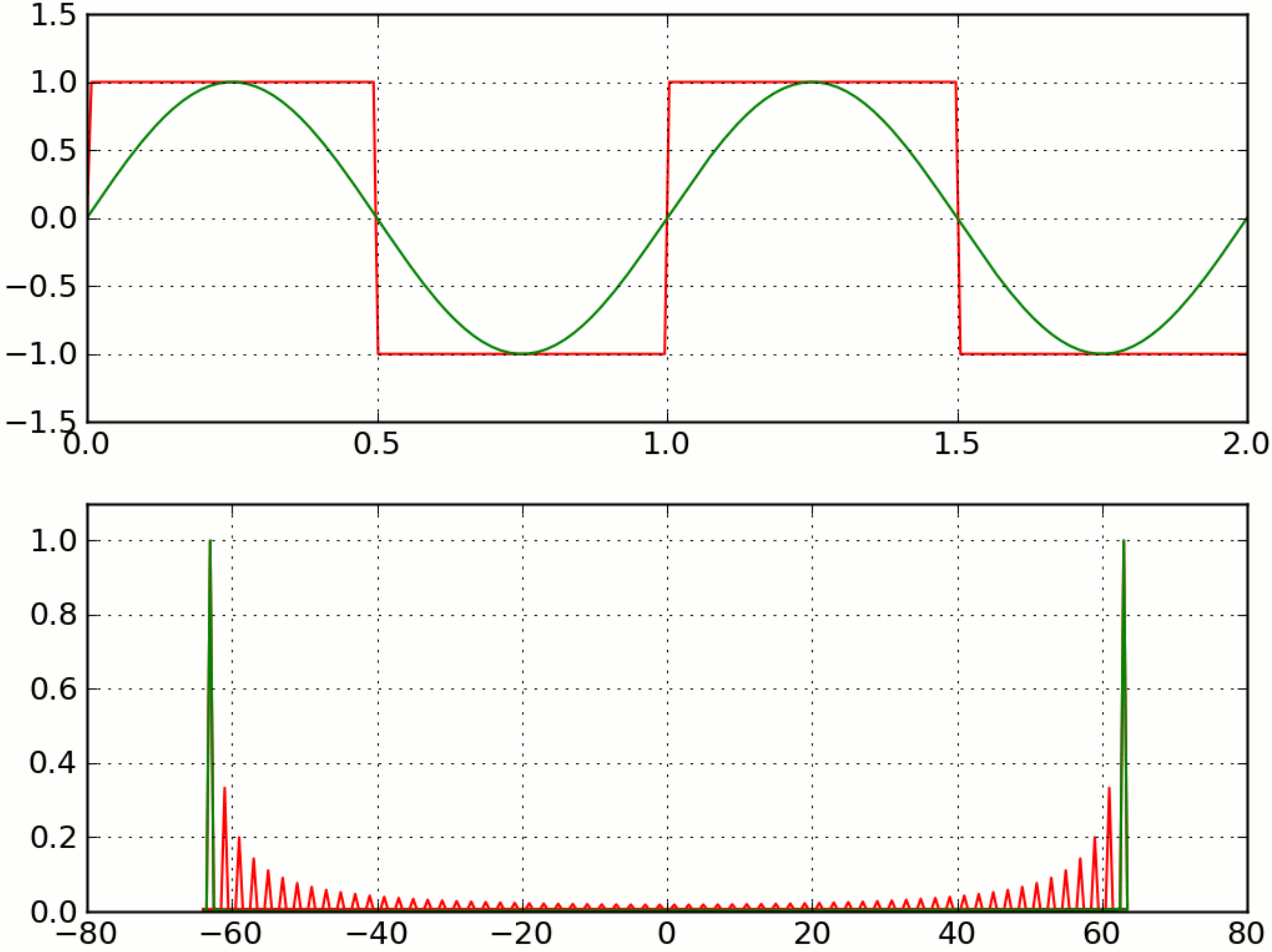
Aside: Fourier analysis (REVISITED)



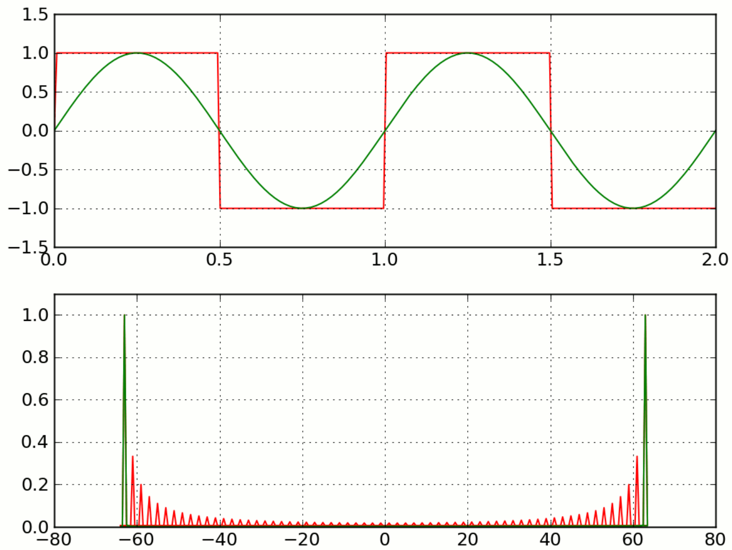
"The exponential function e^x (in blue), and the sum of the first n+1 terms of its Taylor series at 0 (in red)."

wikipedia (Taylor

Aside: Fourier analysis (REVISITED)



wikipedia (square



"Animation of the additive synthesis of a square wave with an increasing number of harmonics."

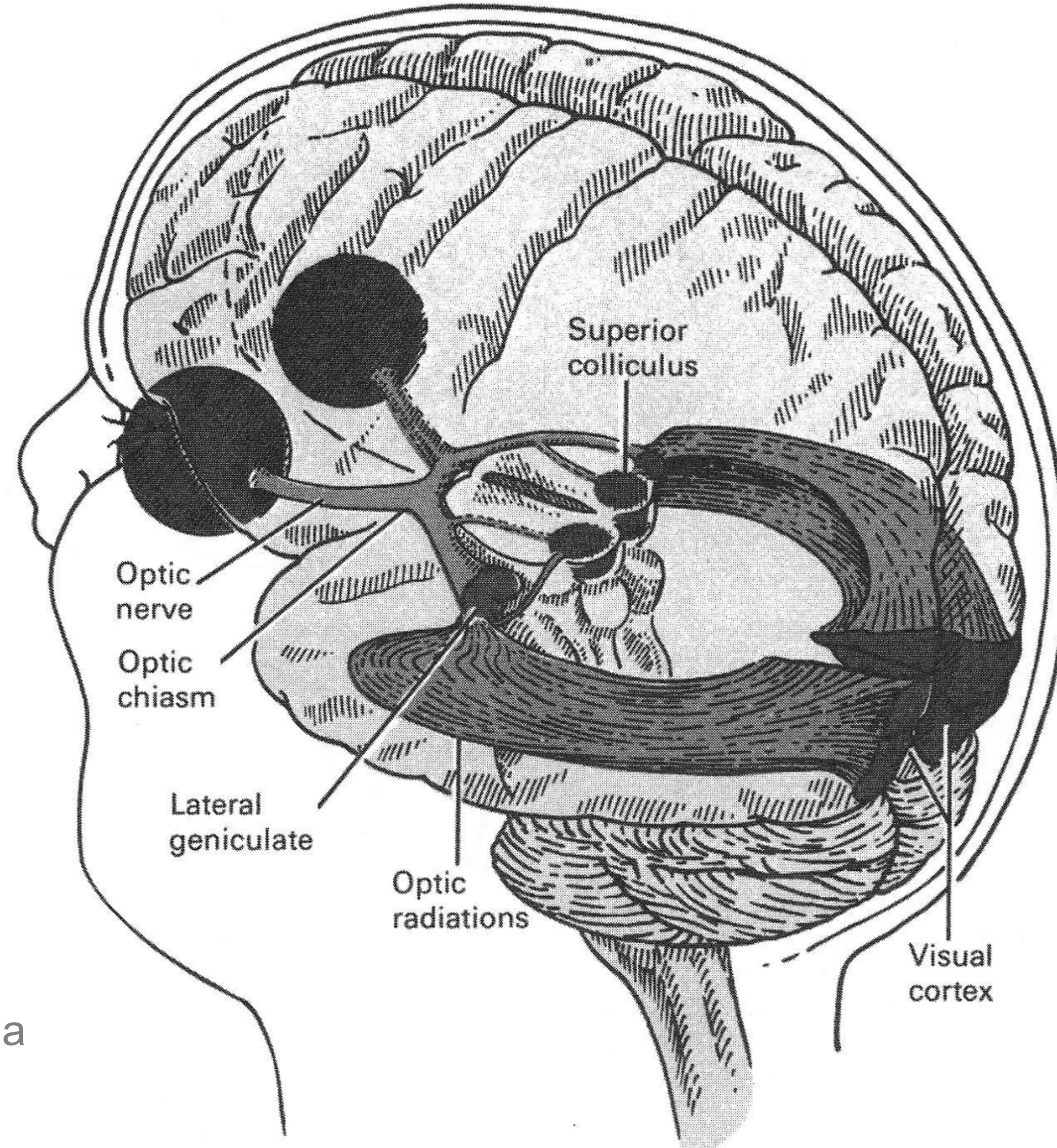
"The six arrows represent the first six terms of the Fourier series of a square wave. The two circles at the bottom represent the exact square wave (blue) and its Fourier-series approximation (purple)."

wikipedia (square

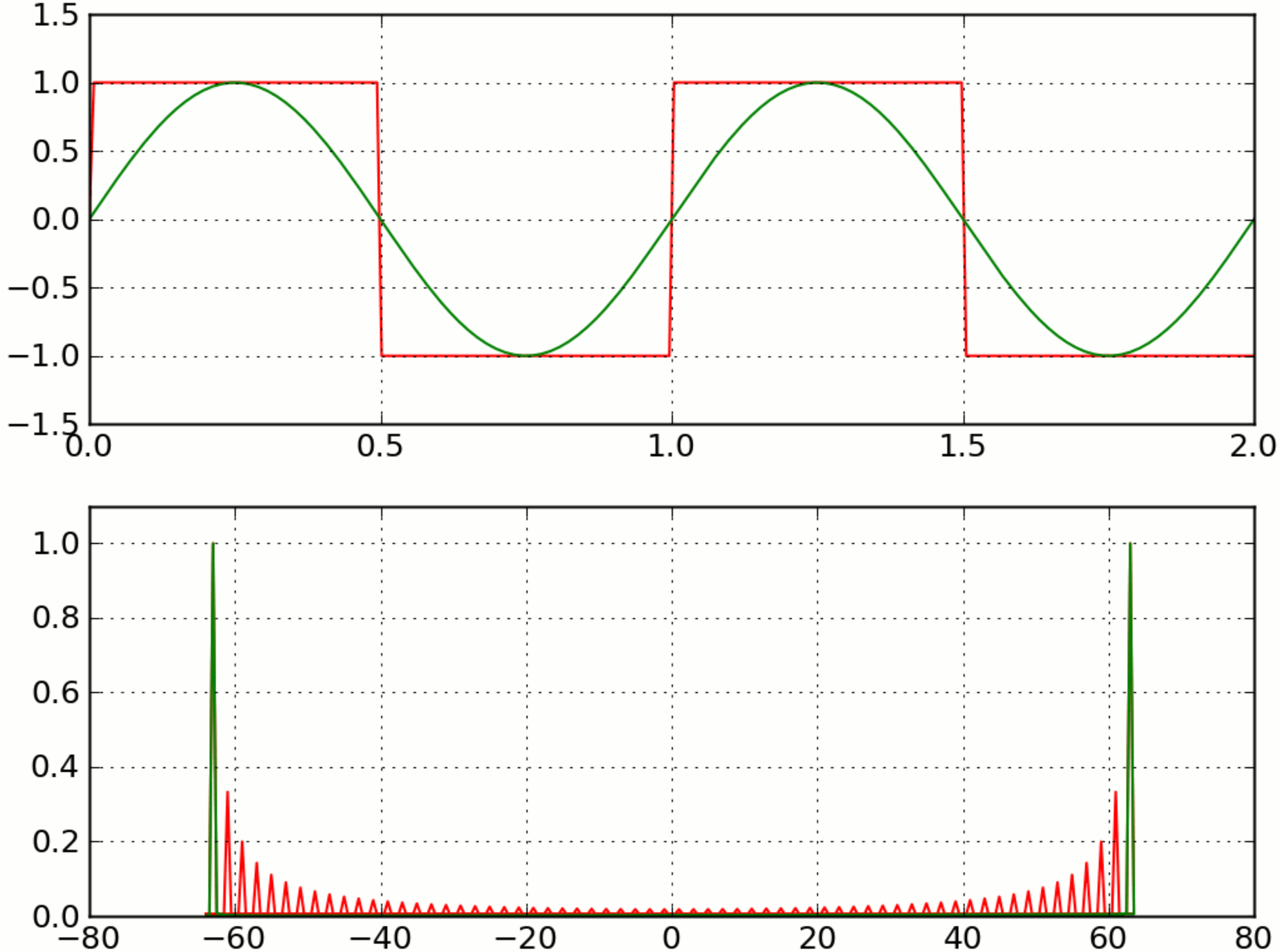
But what about vision?
What is the basis for the underlying neural code?

Harder questions I don't know the answers to....

... but spectral analysis is a useful starting point!



Palmer (1999)



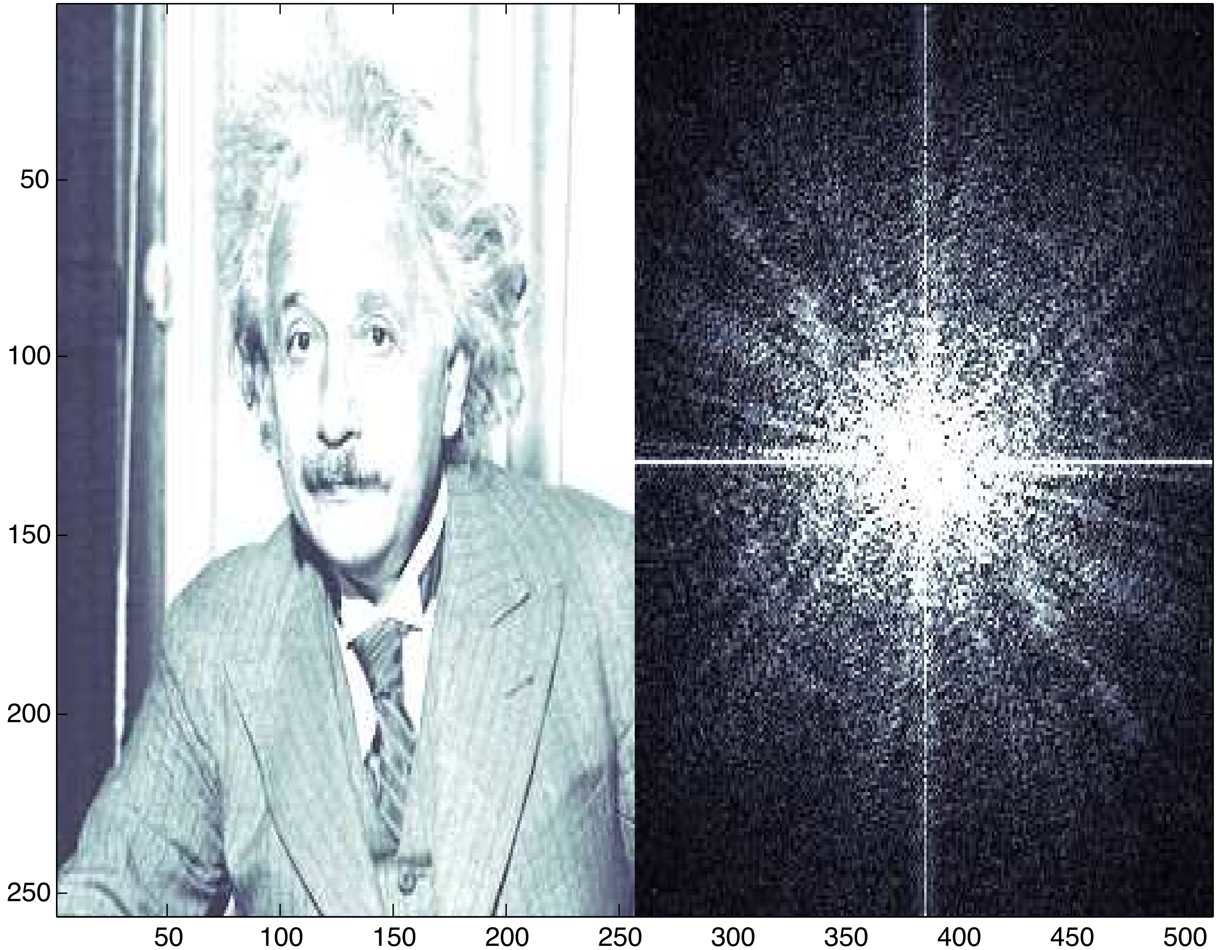
Consider: What makes an edge and “edge”?

wikipedia (square

2-D Fourier Transforms

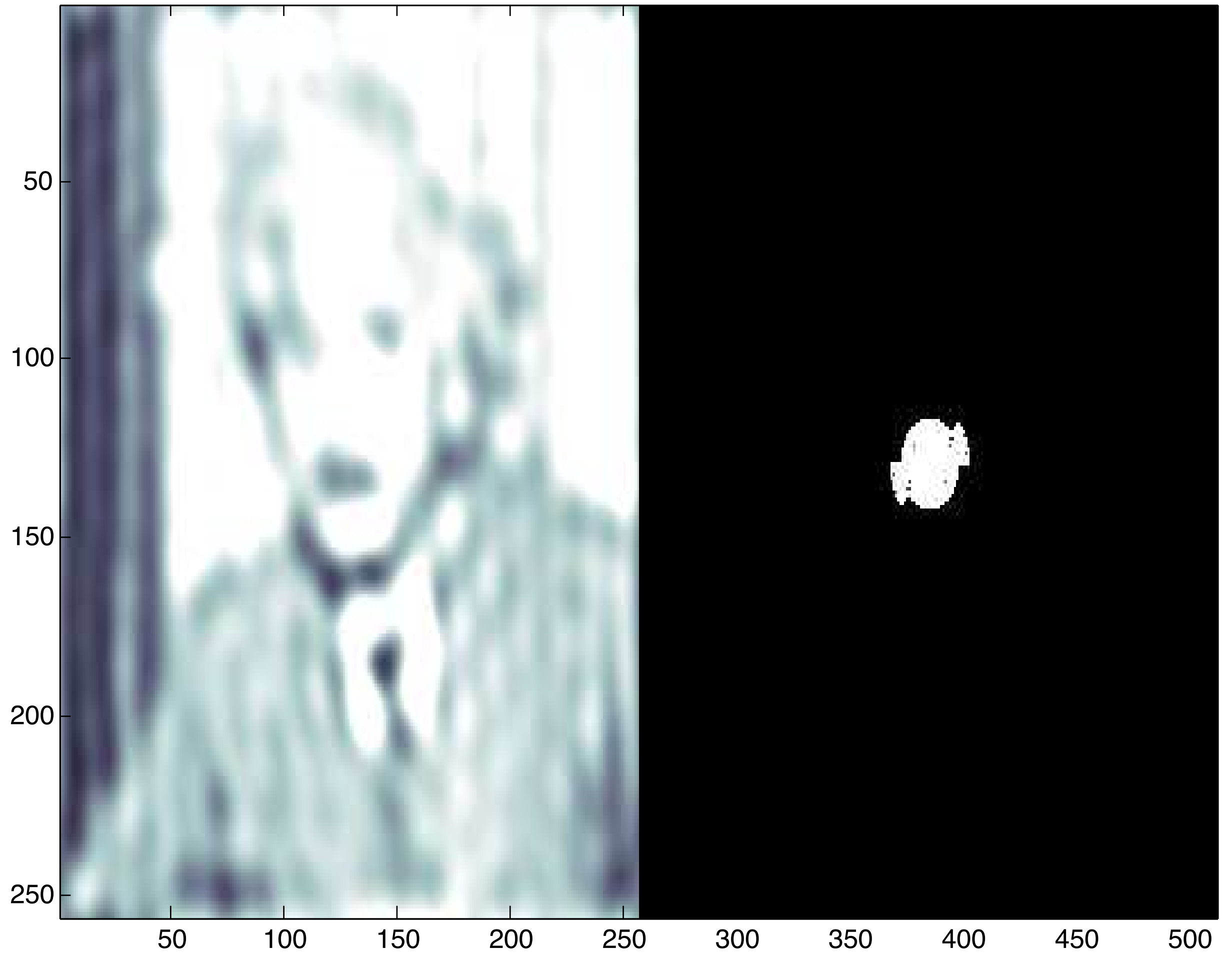
EXfourier2D.m
(Richard Murray, CVR)

‘Spatial domain’ ‘Frequency domain’

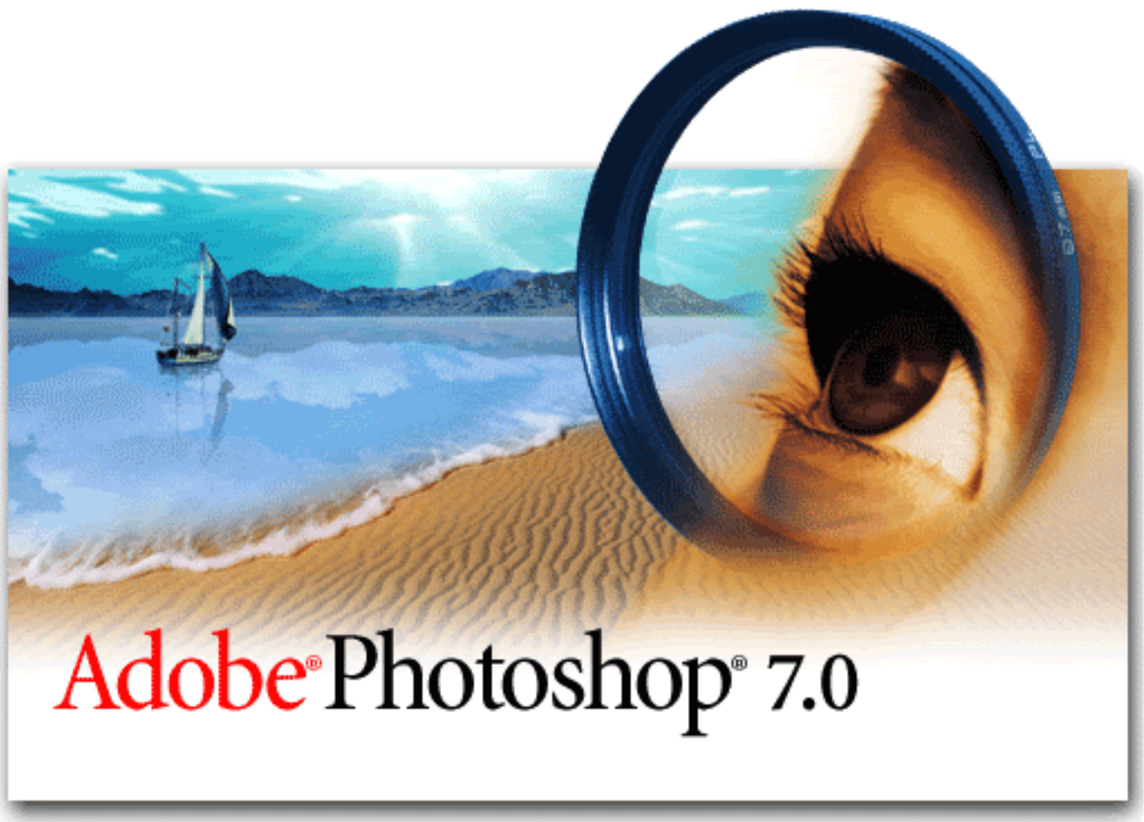


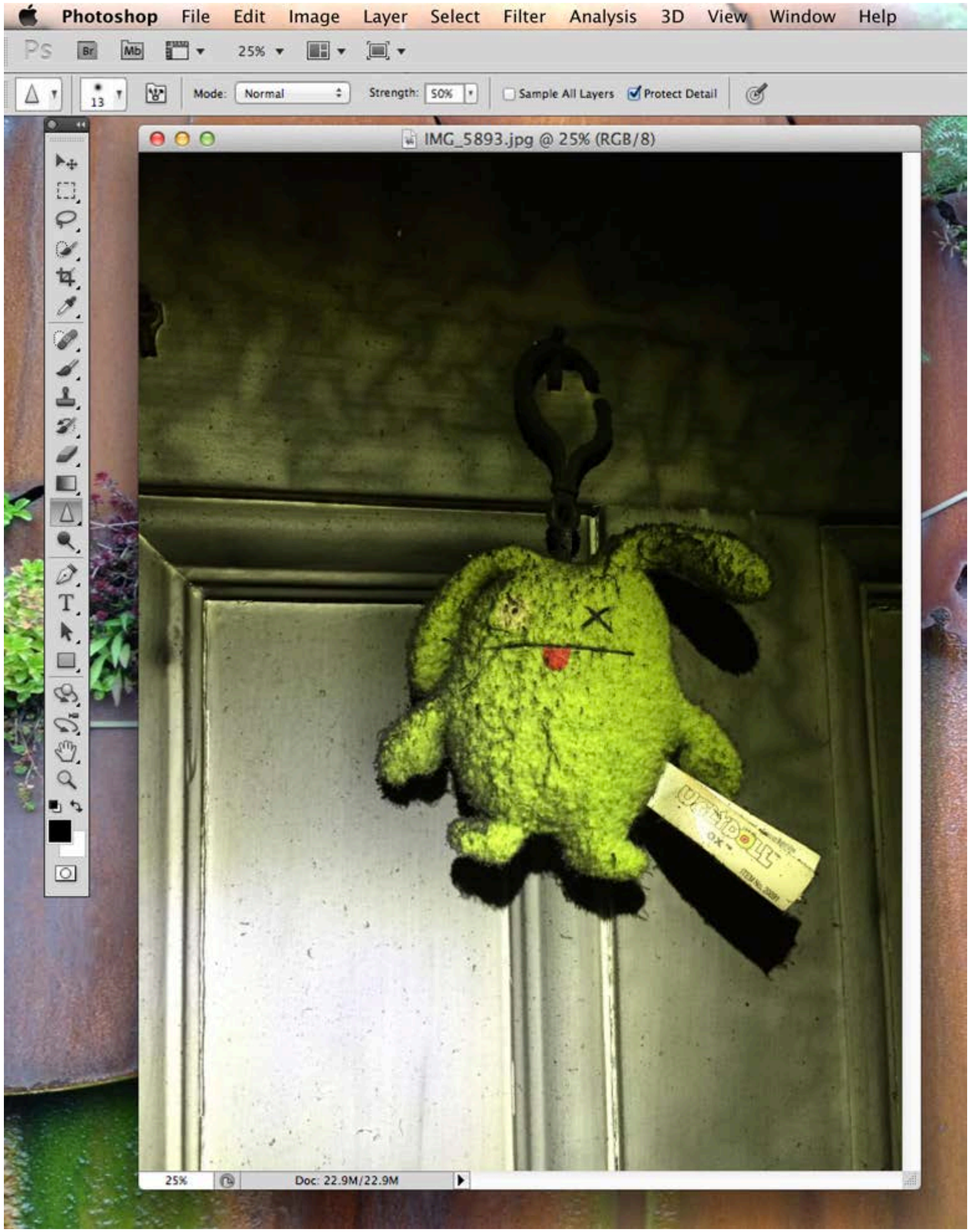
Note: Only ½ of the information is shown on the right (amplitude only; phase not shown)

EXfourier2D.m
(Richard Murray, CVR)

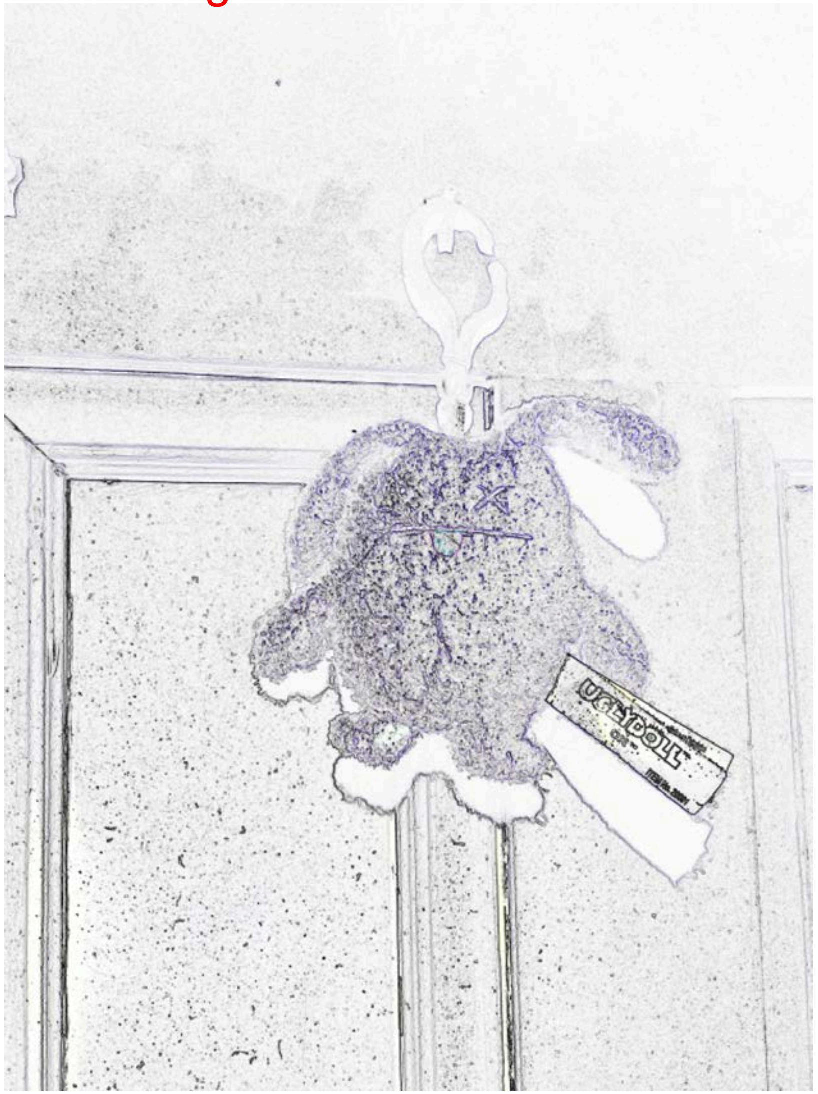


→ 'Low-pass filtered' version of the image


Adobe® Photoshop® 7.0

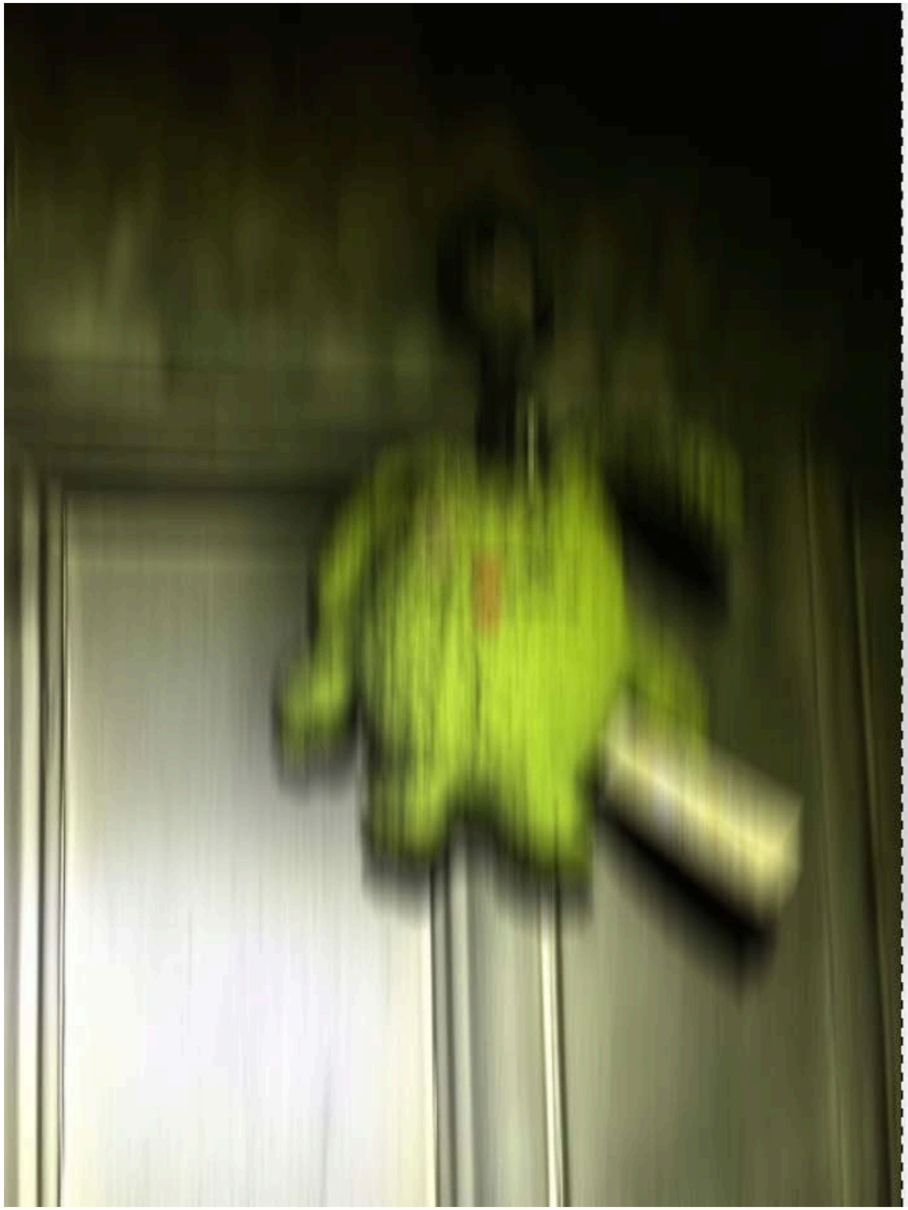

Photoshop File Edit Image Layer Select Filter Analysis 3D View Window Help
Mode: Normal
Strength: 50%
Sample All Layers
Protect Detail
IMG_5893.jpg @ 25% (RGB/8)
25%
Doc: 22.9M/22.9M

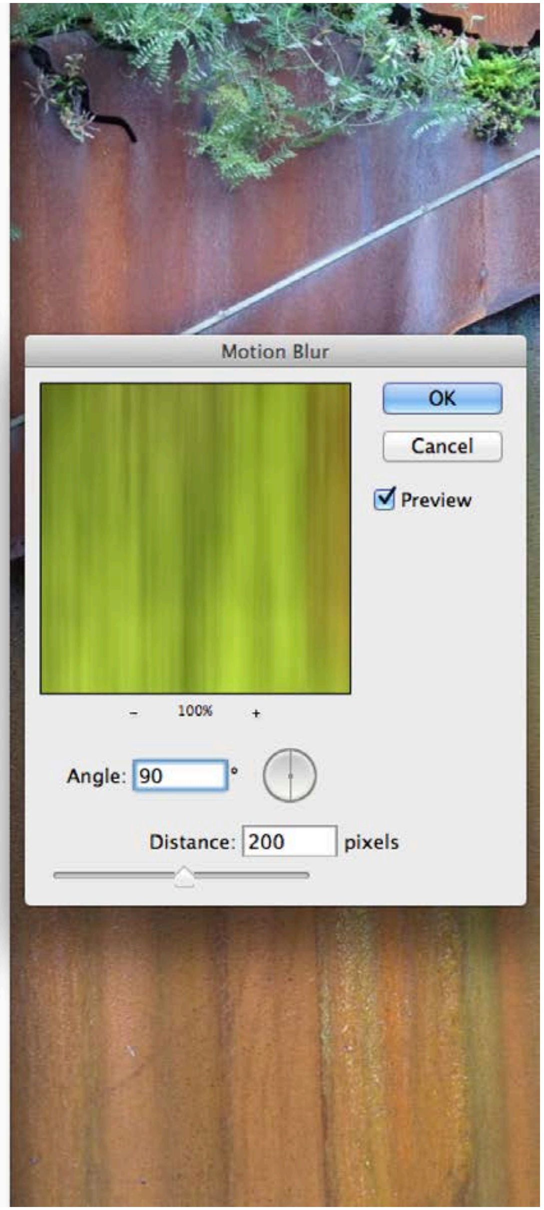
Find Edges



Stained Glass

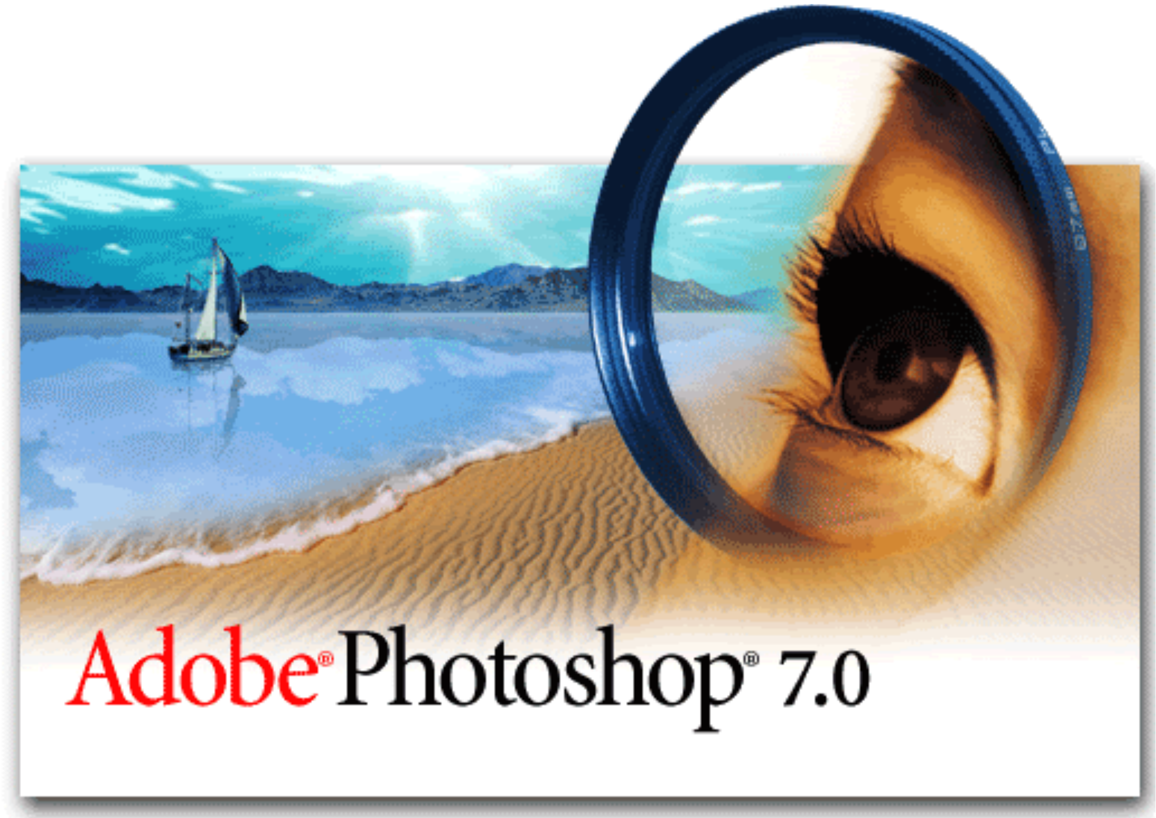
Motion Blur



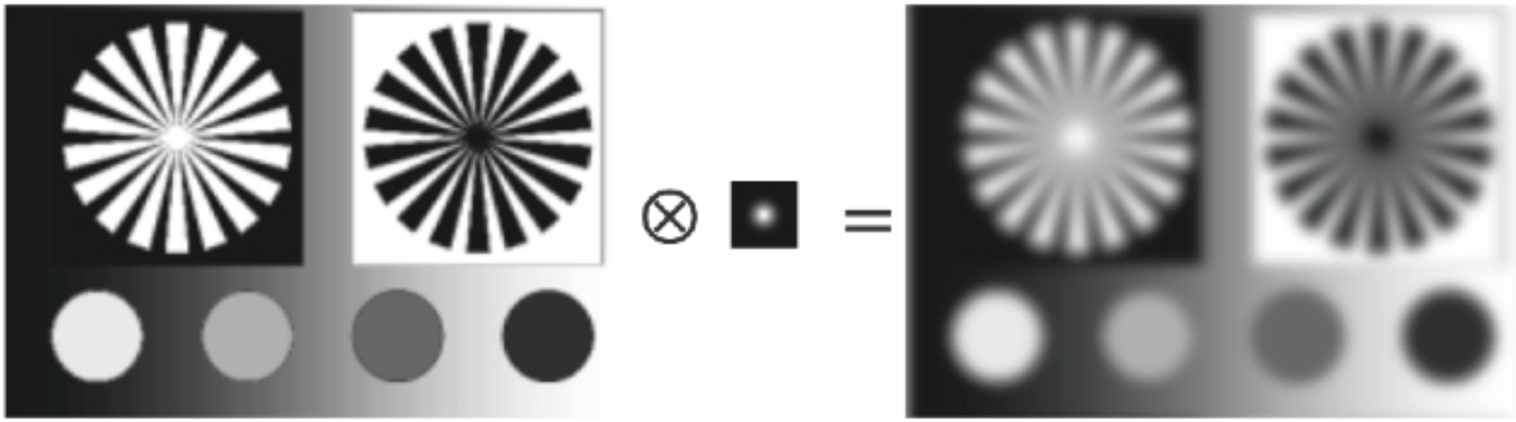

Motion Blur
OK
Cancel
Preview
100%
Angle: 90 °
Distance: 200 pixels

How does Photoshop “work”?

(at least in very basic terms)



<u>2-D Convolutions</u>: Images & ‘Filtering’



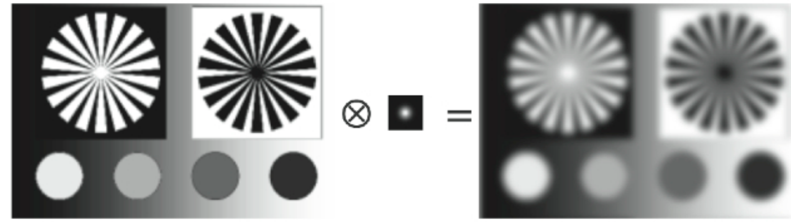
- Two basic ingredient: “image” and “kernel” (or filter)
- Kernel is tied back to an “impulse response”
- Convolution is an operation that ties the two together

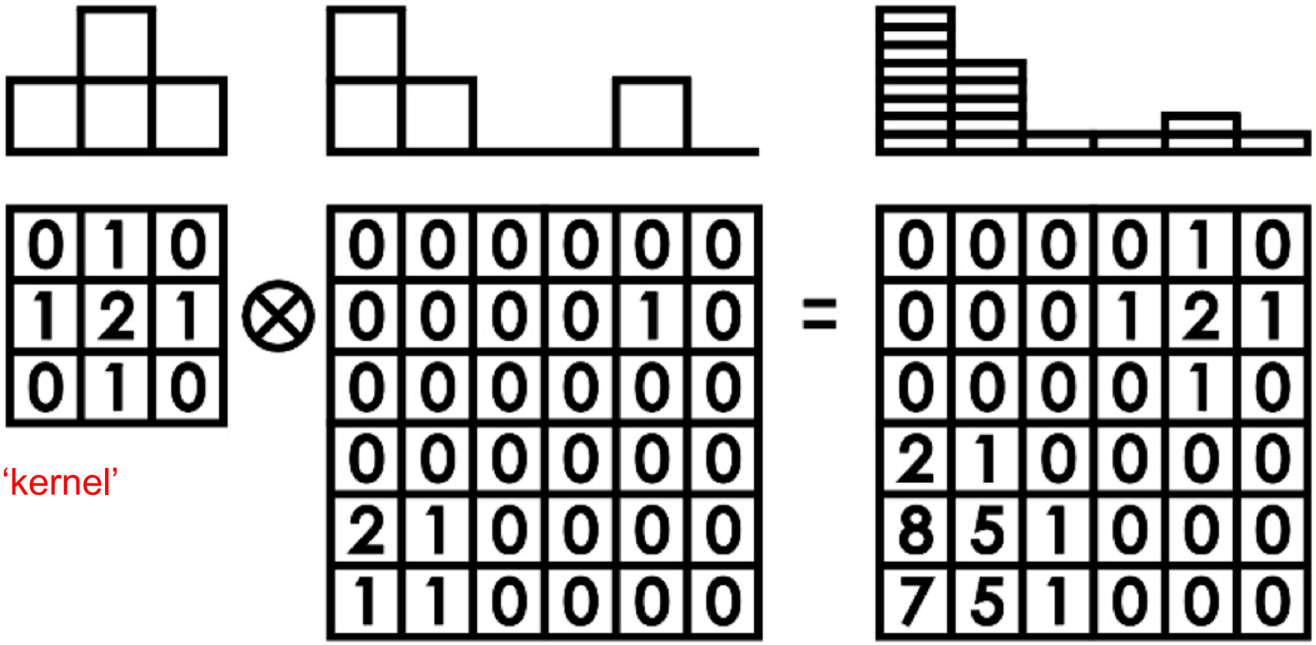
(surprisingly universal consideration throughout science)

Pawley (ch.25)

Image Processing: Filtering

Convolution → Blurring





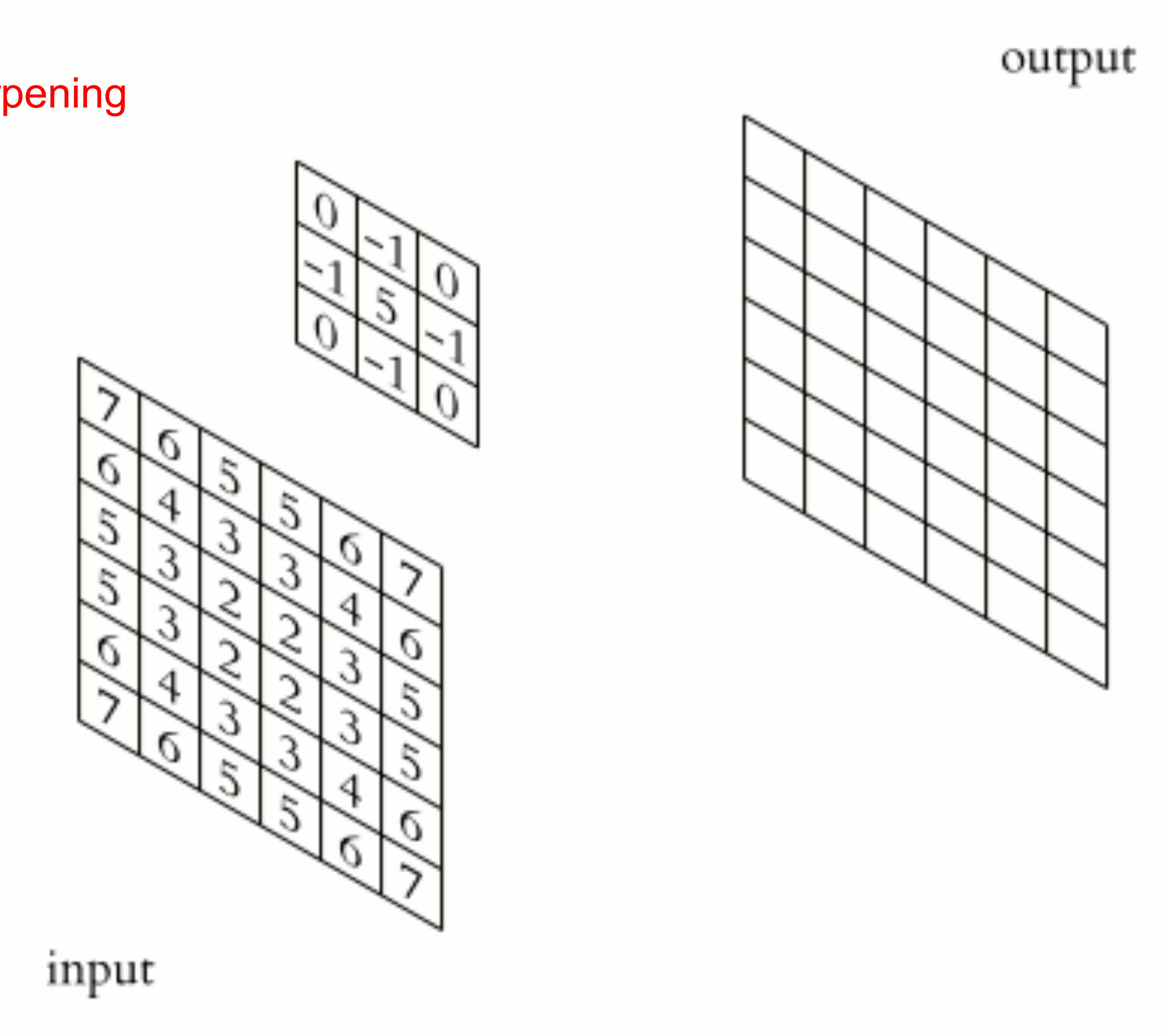
Blurring ‘kernel’

FIGURE 25.2. Schematic diagram demonstrating the convolution (⊗) operation with a 6 × 6 pixel object and a 3 × 3 pixel blurring kernel. The profiles above show the maximum projection of the two-dimensional grids as would be seen looking across the planes from above. Note how the contrast of the peaks in the image is reduced and smeared across the image.

Pawley (ch.25)

Image Processing: Filtering

Convolution → Sharpening



Basic idea is that a convolution is a numerical operation between image and kernel

Wikipedia
[see page for Kernel (image processing)]

Connection to Fourier Transforms

- Consider the Fourier transform of the (1-D) convolution:

$$\begin{aligned}\mathcal{F}[p \otimes q] &= \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} [p \otimes q] e^{-i\omega t}\, dt \\ &= \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} \left[\frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} p(\tau) q(t-\tau)\, d\tau \right] e^{-i\omega t}\, dt \\ &= \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} p(\tau) \left[\frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} q(t-\tau) e^{-i\omega t}\, dt \right] d\tau.\end{aligned}$$

- Making use of the 'shifting property', the term in the square brackets is:

$$\frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} q(t-\tau) e^{-i\omega t}\, dt = e^{-i\omega\tau} Q(\omega)$$

$Q(\omega)$ is the Fourier transform of $q(t)$

$$\begin{aligned}\mathcal{F}[p \otimes q] &= \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} p(\tau) e^{-i\omega\tau} Q(\omega)\, d\tau \\ &= P(\omega) Q(\omega),\end{aligned}$$

$P(\omega)$ is the Fourier transform of $p(t)$

Convolution theorem

$$\mathcal{F}[p \otimes q] = \mathcal{F}[p]\, \mathcal{F}[q]$$

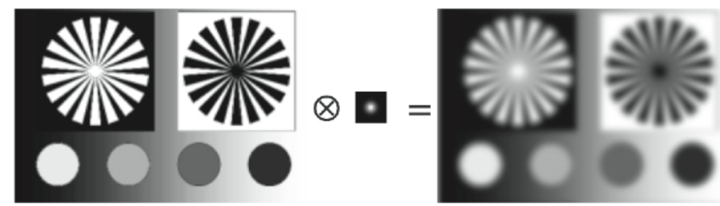
Devries (1994)

<u>Convolution Theorem</u>

- Simple but powerful idea:
Convolution in the time domain is simply a multiplication in the spectral domain

$$\mathcal{F}[p \otimes q] = \mathcal{F}[p]\,\mathcal{F}[q]$$

- Door swings both ways: From the output, if we know the impulse response, we can *deconvolve* (i.e., divide in spectral domain) to get the original input!



$$V_{out} = V_{in} \otimes r$$

$$\mathcal{F}[V_{out}] = \mathcal{F}[V_{in} \otimes r] = \mathcal{F}[V_{in}]\,\mathcal{F}[r]$$

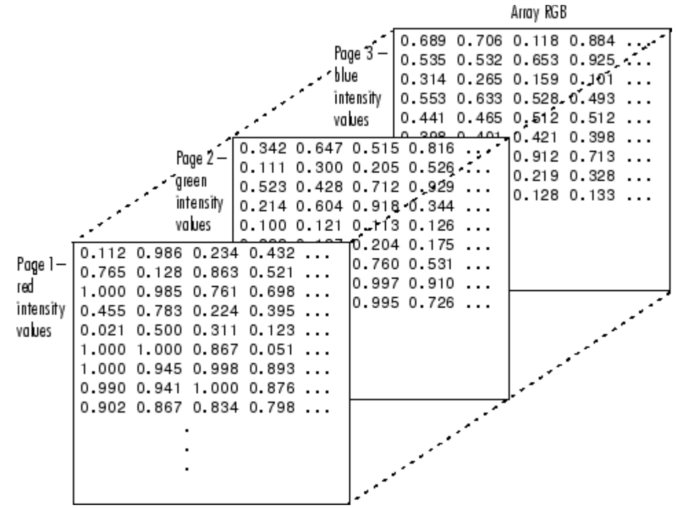
$$\mathcal{F}[V_{in}] = \frac{\mathcal{F}[V_{out}]}{\mathcal{F}[r]}$$

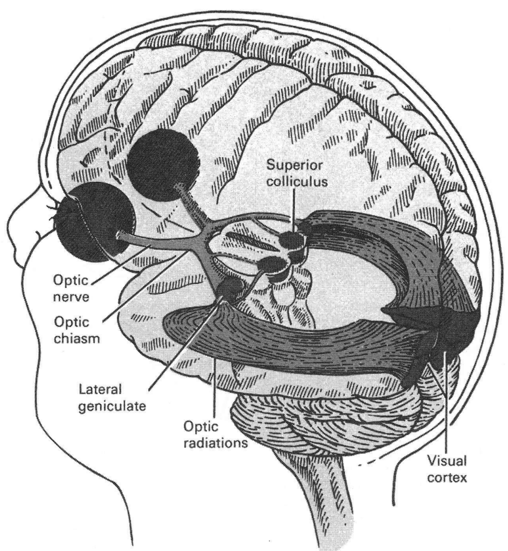
$$V_{in}(t) = \mathcal{F}^{-1}\left[\frac{\mathcal{F}[V_{out}]}{\mathcal{F}[r]}\right]$$

<u>Short version</u>: Numerically this is easy to do!

Devries (1994)

What are some basic (signal processing) considerations about “transforming” information?





- Does Photoshop and the visual system operate in the same way?

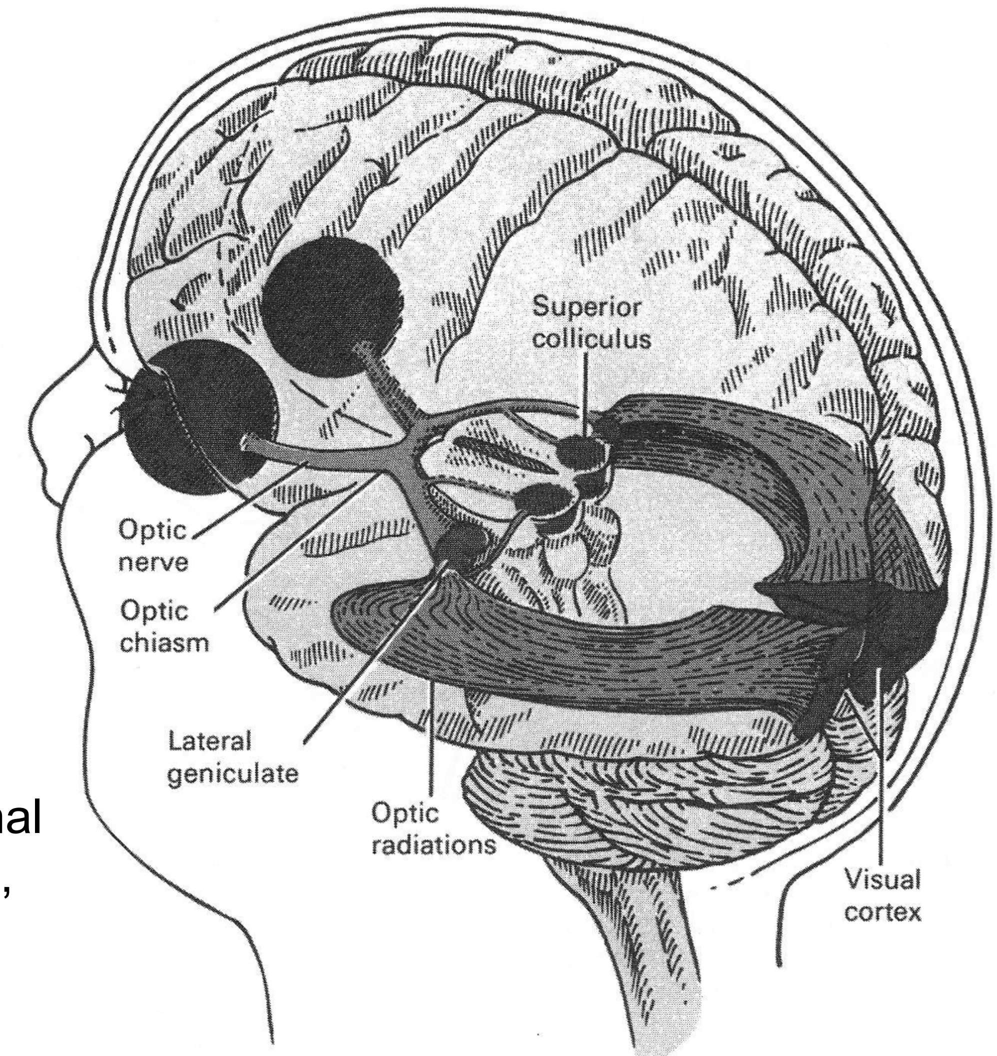
→ No. But there are likely basic “signal processing” facets (e.g., spectral decomposition) universally at work

Question:
How do our sensory systems encode “information” about the world around us?

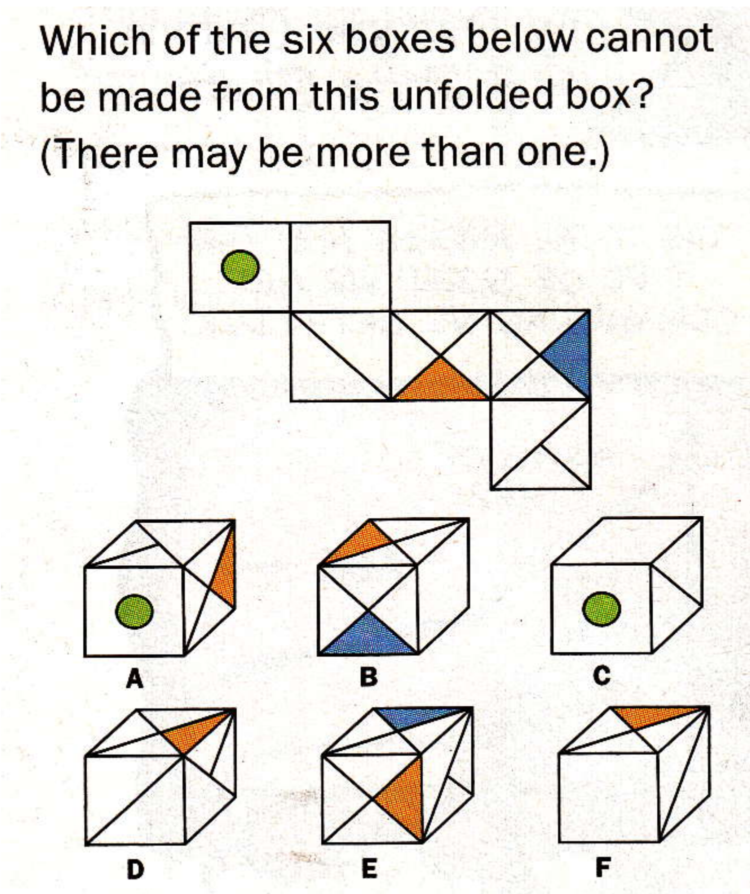
Consider how you “process” this picture....

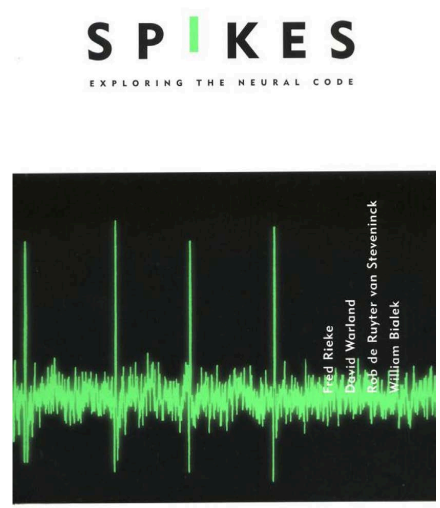
- Transducers and neurons as the basic building blocks

- Transformation into a “neural code” involves abstract-ish signal processing considerations (e.g., spectral analysis, convolution)



Palmer (1999)





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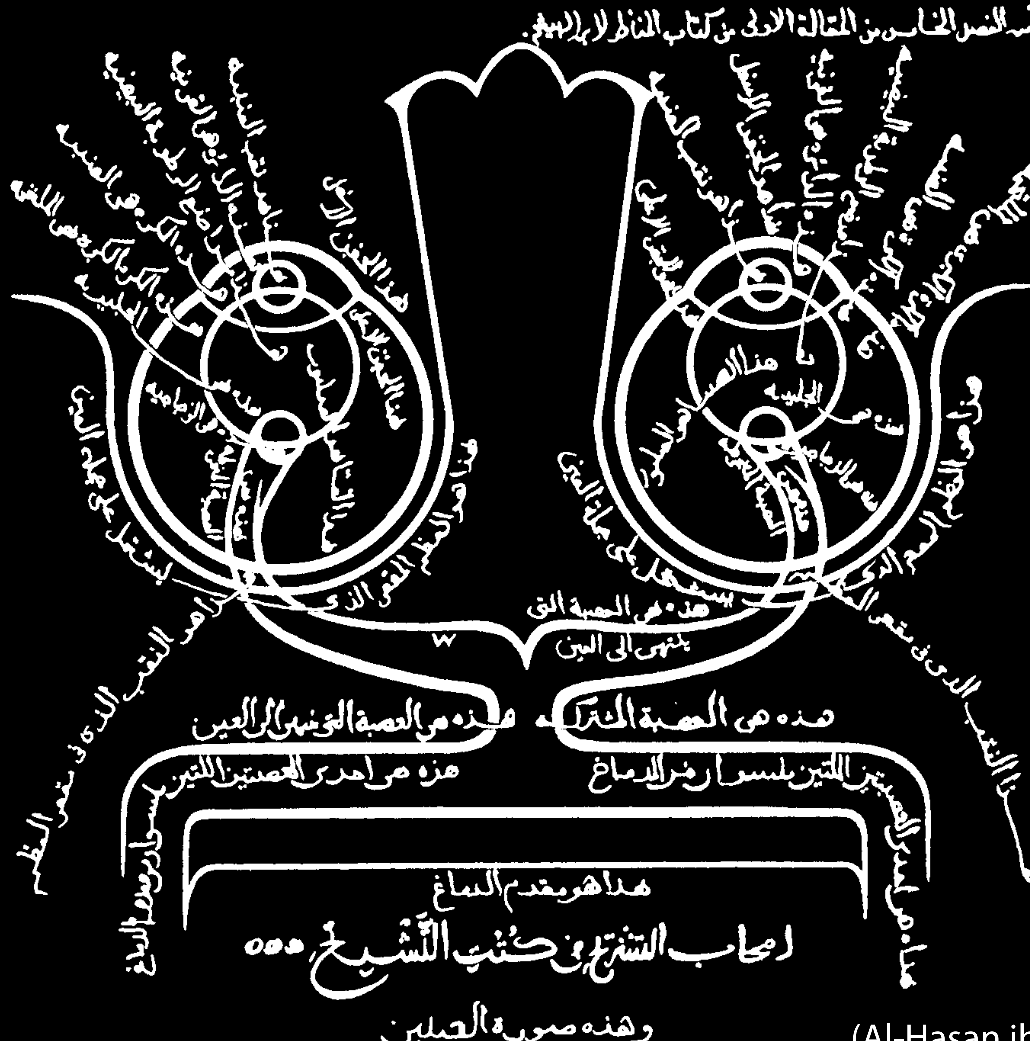

(Al-Hasan ibn al-Haitham 1083)