Human vision and the nature of light

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Three big ideas

• Understanding your own body requires some top-drawer physics ideas.

• The story isn’t over yet -- more left to understand.

• But once you understand even partially how Nature has implemented vision, you gain technological benefits.

[And anyway, it’s beautiful.]
A dropped connection

I did my undergraduate studies, majoring in Physics, at a famous university where biophysical topics never entered the undergraduate Physics curriculum at all. In fact, there were no biophysics courses offered, even to interested students. Much later I realized that sometime around the 1950s, Physics departments largely pushed Biophysics out, saying “that’s not Physics.”

Luckily, times change. But when I was asked to teach the subject, I found myself way behind other people who had studied, say biochemistry, or physiology, or neuroscience. And when I tried to read books by those people, I found it tough going, in part because of the very different culture in those fields.

And yet--it was not always so. Before my time, life science and physical science were regarded as inseparable--as *Natural Science*. Advances went in both directions:

- Electrons ----> Electron microscopy (instrumentation)
- Galvani’s frogs ----> electrochemistry (fundamental mechanisms)
- Heredity+polymer chemistry ----> DNA
- etc.

Today we’re entering another golden age of two-way exchange between life science, physical science, and even engineering. It’s time for our education to reflect that.
Discomfort is good

Educators should engage students’ “resilient preconceptions” and “provide opportunities for students to experience discrepant events that allow them to come to terms with the shortcomings of their [preexisting] models.” *

In fact, scientists are often forced to abandon long cherished models after discrepant data appear. It's not always easy to convey this fundamental aspect of science, but the particulate character of light gives a good opportunity.

* National Academies Press, 2005, How students learn
Credo

• The interesting questions in science are those where we shake our heads and ask, “How could anything like that possibly happen at all?” And biophysics is full of such questions.

• Effective science needs an act of imagination, but imagination must be coupled to discipline, often in the form of a falsifiable model, a distillation of the processes thought to be relevant.

• Quantitative models are the most falsifiable, and therefore the strongest when they survive repeated attempts to falsify them.

• But the physical world is full of randomness which gets in the way of confronting quantitative models with data.

• Far from being a mere nuisance, something that good scientists must eliminate, randomness is often fundamental and unavoidable. This means that we have got to get good at figuring out what quantitative conclusions can be inferred from noisy data, and how reliable those conclusions are.
Eyes are an ancient invention: Here is Trilobite, half a billion years old.

That design was successful: Here is a modern aphid.

But if you can afford to carry more weight around, here is a better design:
Either way, an eye looks like a planar array of pixels--superficially like a modern camera. About a hundred million photoreceptor cells in the human eye:
False sense of security

The human eye also has a lens-based focusing system, again like a camera. Already in 1625 Christopher Scheiner removed the coating from the back of an animal’s eye and looked through the transparent inner wall. Through the eye he could see miniature upside-down images that were both sharp and bright.

It made sense in terms of the budding theory of optics, e.g. Snell’s 1621 result on refraction of light. Later a Who’s-Who of scientists (Descartes, Huygens, Newton, Kepler...) developed optics into a set of powerful rules. Much later, circa 1801, Young proposed that light was a wave phenomenon, then Maxwell, Fresnel, and many others showed how all the phenomena of optics, including refraction, reflection, polarization and diffraction, can be understood starting from the hypothesis that light is a wave excitation.

A key moment was the realization that the finite size of our pupils limits the resolution we can get at the retina, due to diffraction. There’s no point having a pixel size smaller than this resolution limit, and remarkably, our photoreceptor cells really are about this size.

Looks like the wave theory of light explains everything.
We can detect very dim light with a photomultiplier tube, or (newer technology) a photodiode. Either way, light causes discrete clicks in the detector. Dimmer light gives equally big clicks, just less frequent. Here’s some data from an “avalanche photodiode”:

Uh-oh

But what happens next? What happens in those photoreceptor cells that translates light into nerve impulses?

We can detect very dim light with a photomultiplier tube, or (newer technology) a photodiode. Either way, light causes discrete clicks in the detector. Dimmer light gives equally big clicks, just less frequent. Here’s some data from an “avalanche photodiode”:

Dim illumination:

Slightly brighter:
You might imagine a mechanism something like this:

But that mechanism would give *uniformly spaced* clicks. Instead the clicks are *as random as possible* -- they are a “Poisson process.” Something about light is intrinsically random.

*click for uniform clicks audio*                      *click for shot noise*

Moreover, when we shine dim light on *several* photodetectors, they never respond in unison: Each click comes from just *one* detector, even if the beam of light is spread out to cover them all.

Friday, April 1, 2011
Both digital and film cameras also expose one pixel at a time, at random: 3.6x10^6 photons
Even classic diffraction effects turned out to be particulate in character.
Light is lumpy

All these phenomena are related to the “photoelectric effect.” Starting from its discovery by Heinrich Hertz, people found that:

- Light can discharge a negatively-charged electroscope.
- But not a positively-charged one.
- Ability of light to discharge an electroscope does not depend on the intensity (brightness) of the light, although brighter light discharged it faster.
- But it does depend on color: for most metals, only ultraviolet light works.

Einstein found he could only understand these phenomena, and especially the photoelectric effect and thermal radiation, by postulating that light consists of tiny lumps called “quanta” or “photons.”
Intolerable

Normally we don’t notice this graininess, because it’s so fine, but very sensitive detectors can respond to individual photons. Amazingly we’ll see that our human eyes can do it too!

And yet, light also shows many other properties long thought to be slam-dunk evidence of wavelike behavior. Examples: Diffraction from a slit, diffraction from a grating, and Newton’s Rings. How could any of that possibly happen at all in the particle picture? Einstein didn’t know.

Now, in physics we often put a box around a set of issues and say, “We can't understand that today,” and move on. But this is an intolerable contradiction. It's too big to put a box around it. We have to understand it before we have any business moving on.

Generally we physics teachers say, “You’re not ready for that. You’ll understand that some day.”

Yeah, right. Students would have to wait till they were halfway through a PhD in high-energy particle physics (which they’re not going to do anyway) before we’d get around to telling them.

Is it really so hard to say it? Can we say it in a biological context? Some students will hear it better that way.
Here is the hypothesis we will be exploring: the **Light hypothesis:**

- “Light” is an interaction that comes in lumps, each of which carries a precisely defined amount of energy.
- A photon interacts with matter by dumping all its energy on a *single* electron (and disappearing). Or, a photon can pass by an electron without disturbing it in any way. Which of these options happens is a *random* choice, whose *probability* is given by the absolute square of a certain complex number.
- There is a recipe for calculating that number, which we’ll explore.
- When the intensity is high, then it may seem as though the light is continuous. But really, such effects as interference, image formation, and so on all reflect modulations in the *probability* of receiving discrete photons at various places on our detector.

It’s quite a job to see how this hypothesis can reproduce all the familiar phenomena of light, while also embracing the unfamiliar ones. But that’s what physicists try to do.
Whoa

But first -- do eyes really work the same way that photodetectors work? If not, then it’s not biophysics. People could have waited until the proper electronics had been invented, the patch-clamp method, etc. But some people can’t wait. Hecht, Shlaer, and Pirenne got the answer almost half a century earlier than that, by being clever.

Here are some of Hecht et al’s data. Seeing a faint flash of light is unreliable; there’s intrinsic randomness, just as predicted by the Light Hypothesis.

In fact, the Light Hypothesis says that the detection of a photon should follow a cumulative Poisson probability distribution. Can you work out the consequences of that hypothesis for this experiment yourself? Of course you can.
%% pcn 10/07 hecht.m
% hecht experiment
% data from hecht et al page 835 table V 4th column
p=[0,0.12,0.44,0.94,1]; nphoton=[23.5,37,59,93,149,239];lnphoton=log10(nphoton);
plot(lnphoton,p,'o');
xlabel('log10 nbar','FontSize',16);ylabel('P_{see}','FontSize',16);title('probability of seeing','FontSize',16)
%%
figure
plot(lnphoton,p,'--');hold on
for mstar=1:2:12,
 q=0.12;
 for j=1:46,
     photons=20+5*j;
     mbar=q*photons;
     total=0;
     for i=mstar:50
         total=total+exp(-mbar)*(mbar^i)/factorial(i);end
     ptheory(j)=total;lphotontheory(j)=log10(photons);end
plot(lphotontheory,ptheory,'r');
end
xlabel('log10 nbar','FontSize',16);ylabel('P_{see}','FontSize',16);title('probability of seeing, q=.12, various mstar','FontSize',16)
%%
figure; plot(lnphoton,p,'--');hold on
for q=.04:.01:.10,
  mstar=7;
 for j=1:46,
     photons=20+5*j;
     mbar=q*photons;
     total=0;
     for i=mstar:50
         total=total+exp(-mbar)*(mbar^i)/factorial(i);end
     ptheory(j)=total;lphotontheory(j)=log10(photons);end
plot(lphotontheory,ptheory,'r')
end
xlabel('log10 nbar','FontSize',16);ylabel('P_{see}','FontSize',16);title('probability of seeing, mstar=7, various q','FontSize',16)

Above: threshold=7 fits the data well.
Modern Methods

Direct measurements on single rod cells confirm that they can respond to single photons, and confirm the inherent randomness of the response. An individual rod or cone cell’s response can be measured by gently sucking its outer segment into a pipette electrode and stimulating it with 500 nm light (green). Scale: outer diameter of pipette about 6 micrometers.

Inset: pulses of light give rise to current blips with a Poisson distribution of the number of photons absorbed. Single-photon blips are clearly discernible.
Get Serious

So, OK -- our eyes respond to photons. So what about that intolerable contradiction? How can little bullets display the diffraction and refraction needed to explain physiology (and much more)?

*Light hypothesis, continued:*

- The probability to observe a photon is the length-squared of a certain complex number $\psi$.

- If there are multiple routes (or processes) by which a photon could make the trip, and we don’t directly observe which one was taken, then they *all* make additive contributions to the total amplitude. These contributions are all complex numbers with equal *lengths*, but different *angles*, so they may reinforce or cancel.

- The angle (phase) of any one contribution equals the angular frequency of the light (related to its color) times the transit time for the path. In vacuum, light travels at the fixed speed $c$, so transit time may be written as (path length)/$c$.

- In a transparent material, it gets complicated by all those electrons, but for some purposes it’s a good approximation to say that in water, etc. the speed is reduced to $c/n$, where $n$ is the “index of refraction.”

*That’s it.*
So how does that help?

It’s incredible, but with that additional info we can reproduce all of the familiar classical optics results, including focusing by the lens of the eye. And you don’t need to trust some authority figure on that -- you can do the calculations for yourself.

The key question is, Why does light (usually) (seem to) go on (pretty) straight lines?
After all, a penny held in the sunlight casts a sharp shadow. And yet our Light Hypothesis says that photons take all possible paths between source and detector!
We need a digression to see how, and when, this familiar behavior emerges from the Light Hypothesis.

In the pictures below, we approximate the integrals as sums and drew little arrows to represent each term in the sum. The full integral (red arrow) is the vector from one end of the chain to the other end, times dx.

\[ \int_{-5}^{5} e^{ix^2} \, dx \]
\[ \int_{-1}^{9} e^{ix^2} \, dx \]

A similar integral whose range of integration contains no stationary-phase point will have a small total value:

\[ \int_{1}^{11} e^{ix^2} \, dx \]

Again: Near \( x = 0 \) the arrows point mainly to the right and they add up to something significant. If the range of integration contains that stationary-phase point, we’ll get a large total (long red arrow). Otherwise, we won’t.

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The concept we found -- “stationary phase” -- explains why we sometimes get sharp edges, other times not.

Left: wide slit, sharp edges.
Lower left: medium slit, medium edges.
Lower right: narrow slit, fuzzy edges.

That gives us the “diffraction limit” on resolution (how well we can see) of an optical system. You can now understand other optical phenomena (like focusing) with similar principles.

See:
R. Feynman, *QED*
“Is that all?”

Is anything *new* going on?”

Oh, yes. Perhaps you are tired of the diffraction limit? Perhaps you want to image things smaller than the wavelength of light? Perhaps you want to invent a method that gets named “Method of the year 2008” by *Nature Methods*?

Understanding the statistical character of light has led to microscopy methods like PALM, STORM, FIONA... Now we can see.
“OK, OK…

I guess I believe that what everybody says is possible. We learned about the true character of light, we reconciled its wave and particle aspects... Is that all? Can’t we learn something new about biophysics once we’ve got this master key? I don’t want to learn physics just for the (alleged) fun of it!”

Yes. Somehow or other, the reception of a single photon gets converted to a neural impulse. By the time that impulse reaches the optic nerve, it has become a spike.

Spiking neurons, e.g. in the optic nerve, have limited dynamic range. They represent their signal by the times of individual spikes, each of which is exactly like any other. There are upper and lower bounds on this rate. The eye must make the best possible use of this limited range of representing the intensity of light at each pixel.

And the problem is even more acute than that: you have $10^8$ photoreceptors, but only $10^6$ optic nerve fibers!
Meet Emily.
At high illumination, truncation to 1-bit depth destroys a lot of detail (top right). But we can do much better than this, at the same high level of compression. To do so, we first apply a filter (bottom). The filter is called “center/surround;” it is the difference of two concentric Gaussians. Truncating in this way vastly reduces the image size, or the bandwidth needed to transmit it in a given amount of time. (In this case we went from 8 bits per pixel to just one.) Can you do that for yourself? With Matlab, yes you can.
Although the bands are uniform, each appears to lighten right next to a darker band and vice versa.
If you fixate on one intersection, other intersections appear gray, darker than the streets.
“Oh, Please

... Spare us the psychology. Is there some objective data on this?”
Meet *Limulus*:

Fig. 4. The discharge of impulses from a single receptor unit in response to a simple “step” pattern of illumination in various positions on the retinal mosaic. The pattern of illumination was rectangular, covering an area 1.65 mm. × 1.65 mm. on the eye. It was obtained by projecting the demagnified image of a photographic plate on the surface of the eye. The insert shows the relative density of the plate along its length as measured, prior to the experiment, by means of a photomultiplier tube in the image plane where the eye was to be placed. The density of the plate was uniform across its entire width at every point. The measurements illustrated were made over the central 1.5 mm. of the image on the eye.

The upper (rectilinear) graph shows the frequency of discharge of the test receptor, when the illumination was occluded from the rest of the eye by a mask with a small aperture, minus the frequency of discharge elicited by a small “control” spot of light of constant intensity also confined to the facet of the test receptor. Scale of ordinate on the right.

The lower (curvilinear) graph is the frequency of discharge from the same test receptor, when the mask was removed and the entire pattern of illumination was projected on the eye in various positions, minus the frequency of discharge elicited
But how does it work?

Anatomically we find this in *Limulus*:

It’s a big grid with mutually inhibitory couplings, which can be measured. Can you (yes you) make quantitative, testable predictions based on that? **Yes you can.**
Here’s a real simple solution on a grid of just 8 points:

\[
\begin{align*}
    a & = 0.7; \\
    b & = a^4; \\
    c & = a^9; \\
    M1 & = \begin{bmatrix}
        a & b & c & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
        b & a & b & c & 0 & 0 & 0 & 0 & 0 & 0 \\
        c & b & a & b & c & 0 & 0 & 0 & 0 & 0 \\
        0 & c & b & a & b & c & 0 & 0 & 0 & 0 \\
        0 & 0 & c & b & a & b & c & 0 & 0 & 0 \\
        0 & 0 & 0 & c & b & a & b & c & 0 & 0 \\
        0 & 0 & 0 & 0 & c & b & a & b & c & 0 \\
        0 & 0 & 0 & 0 & 0 & c & b & a & b & c \\
        0 & 0 & 0 & 0 & 0 & 0 & c & b & a & b \\
    \end{bmatrix}; \\
    E & = \begin{bmatrix}
        0 & 0 & 0 & 0 & 0 & 1 & 1 & 1 & 1 & 1 \\
    \end{bmatrix}'; \\
    F & = (\text{eye}(10) + 0.5\times M1)\times E;
\end{align*}
\]

Hartline and Ratliff’s model was a bit more elaborate than that -- but not a lot more. We have exploited an analogy to a physics subject: antiferromagnetism.
Hello again, Emily.

At low illumination we have a lot of Poisson noise (top left), but we can still see detail. Truncation to 1-bit depth again destroys detail (top right), but this time it's *even worse* if preceded by the same filter that was so helpful before (bottom).

(In these pictures the whitest pixels are taken to contain just 30 absorbed photons.)

Friday, April 1, 2011
Rescue

The problem is a familiar one in statistics: “The difference of two noisy variables is itself a very noisy variable.”

We can gain back some detail by using a filter with slightly wider center and much wider surround, which averages out some of the noise.

Looks like lateral inhibiton is not such a good idea after all, if we want to see in dim light. But an engineer might say, “Simply turn it on only at high illumination.”

Can our eyes do that?

Why, yes.
Below left, the center-surround structure of fly visual field (solid curves) changes with changing S/N ratio: At high signal the most inhibition is at 2.5 degrees, whereas at lower signal it moves out to 3 degrees. Below right, at high illumination (top curves) there’s a peak in sensitivity (circles) at 5 cycles/degree. At lower illumination this peak moves to lower spatial frequency (wider center), until at very low illumination there’s no peak at all.

Fly

Mammal

Primate

![Figure 4. Measured contrast sensitivity. The data in the left figure are reproduced from Enroth-Cugell and Robson (1966), while that on the right are from De Valois et al (1974). In both cases, the luminance level I₀ decreases by one log unit each time we go to a lower curve.](image)
Color

Color has always fascinated humans.

Color perception is *useful* to humans, and other animals:

- Image segmentation (separating objects in a scene).
- Object recognition, including fine shades of ripe/unripe fruit.
- Sexual selection.
- Emotional signaling.

Even the ancient Greeks knew that color is not an objective quantity like mass. Similarly Galileo in 1630: Color “resides only in consciousness.”

But it’s a cop-out: Color has *something* to do with the physical stimuli entering your eyes! And those stimuli consist of... photons. Can that knowledge shed any “light” on this extremely complex subject?
Any color light can be synthesized by mixing red, green, and blue. For example, the "white" light from a fluorescent bulb has a spectrum (bottom) quite different from that of sunlight (top):

When this image is scaled down (and maybe you take off your glasses), both panels look sort of yellow.

But when I blow it up you see that actually the left panel consists of vivid green and red!

• *How could anything like that possibly happen at all?*
We know about light. Light is a stream of photons, etc. We can characterize a beam of light physically by splitting it into different frequency photons and separately measuring the rate of arrival of each photon type. Or equivalently, we could give the probability density function $F(\nu)$ that any one photon will have frequency $\nu$. Even a scientist with no color vision could do that.

But that says nothing about sensations like color, and certainly doesn’t explain the phenomena on the previous slide.

Young and Helmholtz devised a simple hypothesis to account for these phenomena. We can modernize it a bit in the light of later discoveries, to get what I will call the **Color Hypothesis**. Each assumption is reasonable, but more importantly each can be experimentally established.
Color Hypothesis:

1. Primates like us have three distinct types of cone cells. Each type of cone cell is packed with layers containing solely one of three different rhodopsin molecules, and each cell type is wired to the rest of the retina (and ultimately the brain) in a distinct way.

2. Each rhodopsin type is characterized by a sensitivity function, which describes its probability to absorb a photon, based on that photon’s color (frequency). More precisely, the entire cone cell has a sensitivity function, which gives the probability that an incident photon will be productively absorbed, i.e. that it will contribute to a signal, as a function of its color.

3. Each productive absorption event is statistically independent of the others. That’s reasonable because each rhodopsin molecule individually has a small chance of absorbing any given photon, so successive absorptions are likely to be located far from each other in the cone cell. Nonproductive absorptions are independent of productive ones.

4. The population of rhodopsins in a cell may fluctuate depending on the observer’s recent history, differences between observers, etc. However, such fluctuations affect only the overall scale of the sensitivity functions; they are independent of frequency $\nu$. All (normal) observers have identical rhodopsins in each class, and hence identical sensitivity functions.

5. Each cone cell reports a rate to the next layer of retinal nerve cells: How many productive absorptions are occurring per second. The signal that reports that rate is the sum of independent, identical impulse responses to every productively absorbed photon, regardless of that photon’s color (the univariance principle).

We don’t care (yet) about how the photoreceptors make their reports to the brain; nor do we care about how the brain later interprets those reports.
What tunes a molecule to a particular optical frequency? It’s got to do with *resonance*, which in turn involves having electrons with significant but limited mobility (“restoring force”). Small changes in the protein surrounding a retinal group affect the spatial range of that mobility. By analogy, here are solutions of “quantum dots” (nanoscale crystals of CdSe), differing only in the physical *size* of the crystals. (Photo from **Marija Drndic, Penn Physics**).
**Left:** Baylor et al. found that the spectral response (sensitivity) curves of cones fall into three well-separated classes. Notice the big overlap between the “red” and “green” curves. (Later Nathans et al. found three distinct genes for the rhodopsin analogs in cone cells, each nearly identical to the others and to the rod-cell rhodopsin, but not quite the same.*)

**Right:** Once those curves are known, the color-matching functions can be predicted, and they agree with psychophysical measurements.

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*Figure 6* Spectral sensitivities of cone cells of the macaque monkey. The y-axis shows the relative sensitivity to a quantum of light on a logarithmic scale. The x-axis is wavelength (upper scale) and its reciprocal, wavenumber (lower scale).

*Figure 7* Colour-matching, observed and predicted. Above: arrangement for experiments. A monochromatic test light of selectable wavelength was projected in the left field. On the right were three monochromatic matching lights of fixed wavelength. Below: intensity of the matching lights as a function of the wavelength of the test light. Continuous curves: Stiles and Burch’s results. Points: results predicted from monkey cone spectral sensitivities given in Figure 6. A dip below zero indicates that the matching light had to be applied to the left rather than the right half of the field.
Technology payoff: You can fool the eye into thinking that a wide range of colors is present by using just three pixel types…

Our compromise is to have just 3 cone types with separate circuitry. That’s why mixing 3 colors is enough to match almost any perception.

But to say it a different way: Our eyes *discard* a lot of information about the spectrum of light entering any given visual field! Can an artificial visual system discriminate better than that?
Enhanced, artificial color vision

Yuval Garini, Physics Department & Bar-Ilan Institute of Nanotechnology, Israel
$I(x,y,\lambda)$
Spectral Karyotyping principle

![Graph showing fluorescence intensity vs. wavelength for different fluorescent proteins. The graph indicates peak intensities at different wavelengths for Cy3, TR, and Cy3 + TR, with peaks at 700 nm, 650 nm, and 580 nm respectively.]

![Images of karyotypes stained with fluorescent proteins showing chromosomes in different colors. The images illustrate the application of spectral karyotyping in cytogenetics.]
Wrap

Nobody argues any more with the proposition that living organisms are made of the same stuff as “physical” devices, but they do many amazing things we’re not accustomed to seeing artificial objects do.

How?

• We can learn new things about life science by recalling that physical principles offer opportunities, as well as constraints, to organisms. Sometimes this approach has betrayed the existence of actors and mechanisms decades before their explicit biochemical isolation (DNA, ion channels, motor proteins, photoreceptor molecules...). It can even help us figure out how to intervene when something’s going wrong.

• We can learn new things about physical science by studying How Nature Does It. Those lessons can be useful for other purposes.

• Both physical and life science want to see previously invisible things. People who know both are the ones who will invent the next wave of cool methods.
Why I like biophysics

What did you learn in this talk?

Well, strictly speaking... *nothing*. I believe you don’t learn till you do things yourself. But many of the most important calculations in biophysics really are things you can do for yourself, using modern tools unavailable to the Ancients. *I like that.*

It turned out we could not understand vision at all without some top-drawer ideas from fundamental physics (like quantum theory). Other cool ideas entered too (stationary-phase, antiferromagnetism...).

When properly fleshed out, the discussion also makes use of probability theory, biochemistry, evolution... (plus a little information theory, physiology, kinetic theory, physical chemistry, cell biology, neuroscience...). *I like that too.*

Well, I've done my best to share with you my conviction that Biophysics is a unified whole, best approached without artificial, outdated discipline boundaries. That's the Deep Program.
Read More

I realize this was a whirlwind tour. You will enjoy reading…

**Light:**
R. Feynman, *QED* <-- suitable for high school students

**Vision:**
1. *Feynman Lectures* vol 2
2. Benedek and Villars, *Physics with illustrative examples from medicine and biology* vol 2
3. David Hubel, *Eye, brain, and vision* (also available free online from [http://hubel.med.harvard.edu/index.html](http://hubel.med.harvard.edu/index.html)). <-- suitable for high school students

**Teaching:**
National Academies Press, 2005, *How students learn*
Thanks

These slides will appear at
www.physics.upenn.edu/~pcn