Introduction to Neuroscience: Behavioral Neuroscience

Sensory Ecology

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Weizmann Institute of Science

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Before we start – some general words about the course

Formalities

- Syllabus.

- What you should expect from this course:

  - NOT as coherent as the course on cellular and synaptic physiology – because there IS NO coherent theory of Behavior, nor even coherent phenomenology

  - We will present a series of different Classical "example systems"

  - Heterogeneity of topics

- BUT (as a note of comfort): There ARE common principles and themes that generalize across different behaviors and different animal species – and we will mention some of these as we go along.

Formalities

- Course Website *(will include ALL the presentations)*:   at:

  www.weizmann.ac.il/neurobiology/labs/ulanovsky/

- Grading: Final exam. ~10% of the exam will be based on <u>book chapters</u>, which will be distributed to the students as compulsory reading material (we will distribute them a few weeks before the semester ends).

- Bibliography:

  - Behavioral Neurobiology, Carew (2000).
  - Behavioral Neurobiology: An Integrative Approach, Zupanc (2004).
  - Learning and behavior, Bouton (2007).
  - The computational neurobiology of reaching and pointing, Shadmehr & Wise (2005).
  - Sensory Ecology, Dusenbery D. (Freeman, 1992).
  - An introduction to behavioral endocrinology, 3rd ed., Nelson R. (Sinauer, 2005).

Now let's start for real...

Umwelt   (Uexküll 1920)

Two modern terms related to
the classical concept of Umwelt:

Umwelt ("surrounding world") is
The organism's model of the world:
The perceived things in the world,
the signals emitted by both the
subject and things, and the actions
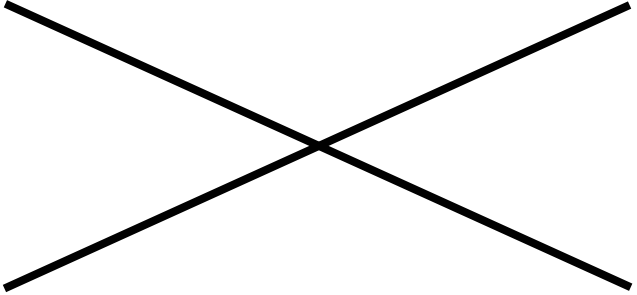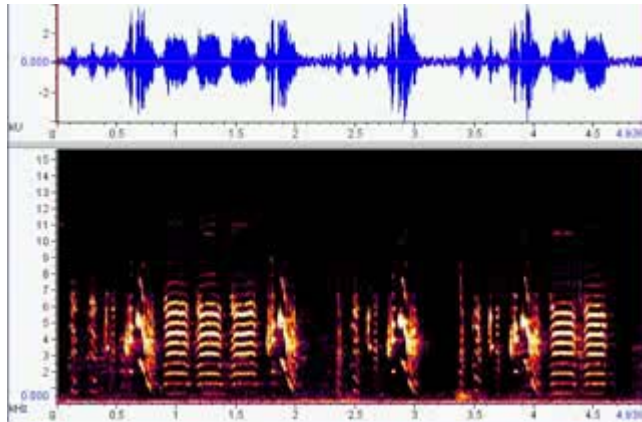that are performed by each species.
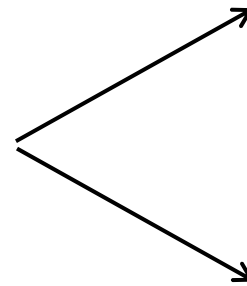
"Natural behaviors" ←

"Sensory Ecology"
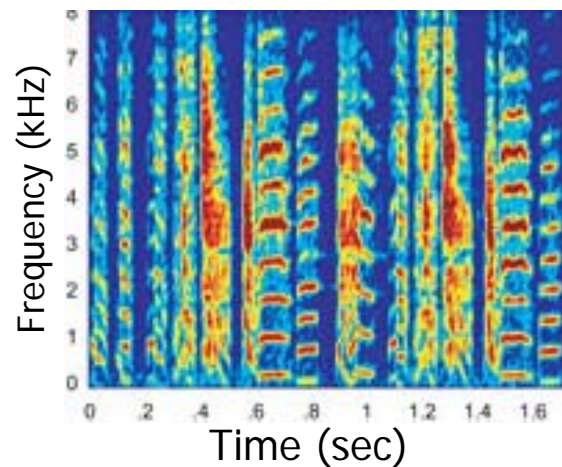
Innate/Learned vs. Natural/Artificial behaviors

	Natural	Artificial
Learned	• Tool use in New Caledonian Crows • Vocal learning in songbirds ←	
Innate	• Sexual behaviors • Imprinting • Fixed Action Patterns	✕

Vocal learning in songbirds

Adult zebra finch song (Movie)

Song of adult birds differs from the "babbles" of juveniles

Movie of an adult zebra finch singing versus juvenile zebra finch babbling

Adult zebra finch song is complex, consisting of *syllables* and *motifs*

Juvenile birds that are isolated and do not have a chance to learn singing from a tutor (= adult male) will *not* develop a full adult song, but will remain "babbling"
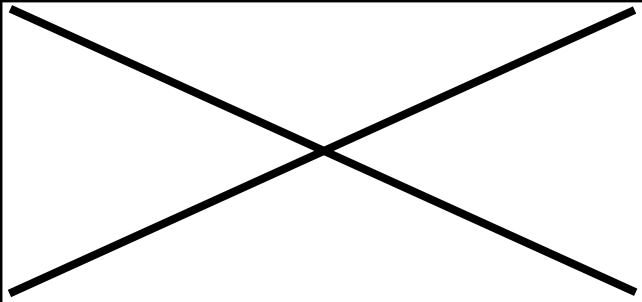
Vocal learning in songbirds

- Vocal learning in songbirds has two <u>components</u>, an innate component and a learned component: The tendency to "babble" is an *innate* behavior – but the full learning of a complex song is a *learned* behavior

- The study of the neural basis of vocal learning in songbirds has become very popular in Behavioral Neuroscience, because:

  - It is a <u>natural</u> behavior – and it is <u>complex</u>, yet very <u>reproducible</u>

  - A model animal that shares many aspects with <u>vocal learning</u> in humans (i.e. language)

  - Has many additional interesting features: Clear <u>critical periods</u> ; first discovery of <u>adult neurogenesis</u> in vertebrates...

Artificial learned behaviors

- If you are interested in studying the neural basis of Motor Coordination in elephants, this particular behavior is probably not the best choice to focus on – because it is artificial

Innate/Learned vs. Natural/Artificial behaviors

	Natural	Artificial
Learned	• Tool use in New Caledonian Crows • Vocal learning in songbirds	• Juggling Elephants
Innate	• Sexual behaviors • Imprinting • Fixed Action Patterns	

Innate/Learned vs. Natural/Artificial behaviors

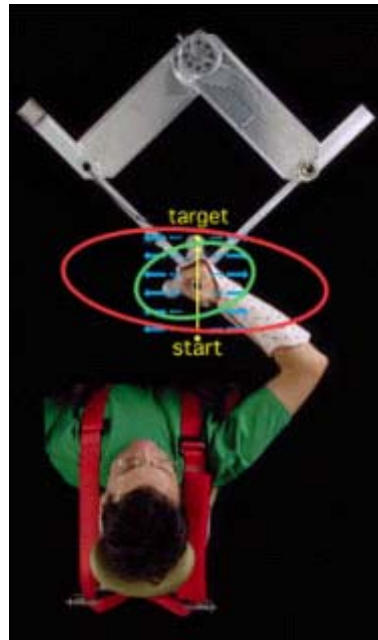Vocal learning
in songbirds

Juggling
elephants

Spectrum

Clear-cut border
························
Innate: if it develops
in all animals when
reared in isolation

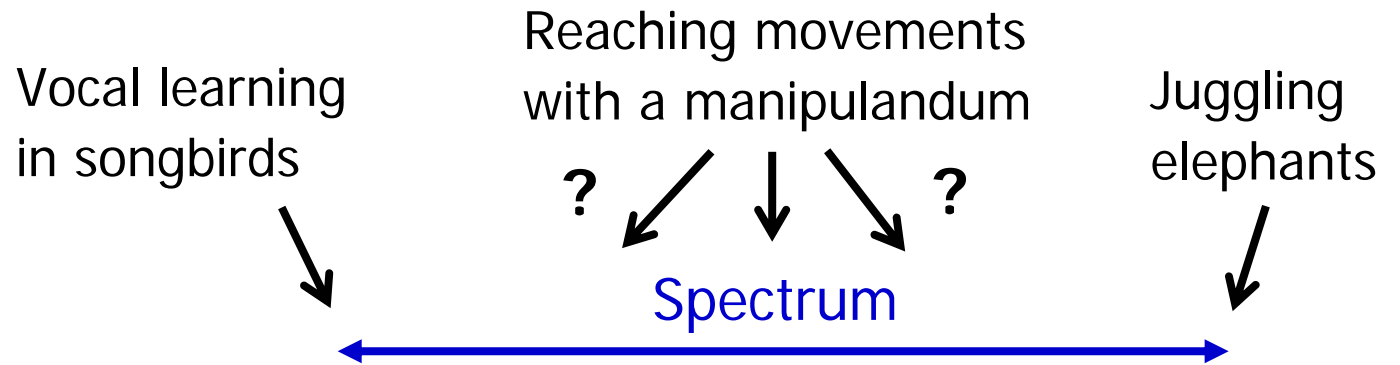|	Natural	Artificial
Learned		
Innate		✕

The Natural/Artificial distinction is not simple to make

What about this example?

Reaching movements in humans <u>are</u> a natural (and important) behavior –
but the setup with the manipulandum and the chin strap is artificial
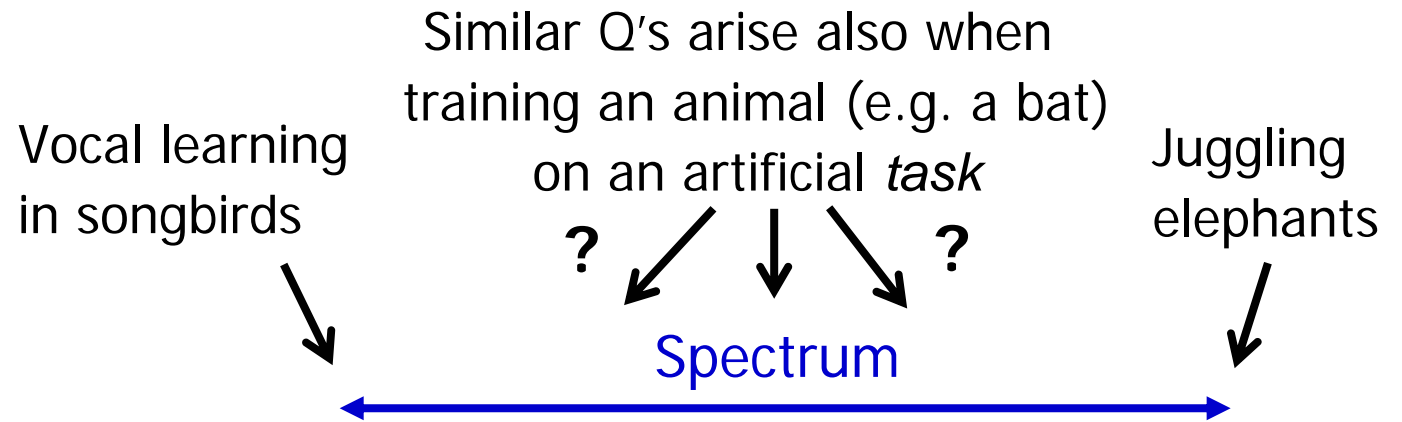
Innate/Learned vs. Natural/Artificial behaviors

Vocal learning in songbirds

Reaching movements with a manipulandum

Juggling elephants

? **?**

Spectrum

Clear-cut border

Innate: if it develops in all animals when reared in isolation

	Natural	Artificial
Learned		
Innate		✕

Innate/Learned vs. Natural/Artificial behaviors

Similar Q's arise also when
training an animal (e.g. a bat)
on an artificial *task*

Vocal learning
in songbirds

Juggling
elephants

? **?**

Spectrum

Clear-cut border

....

Innate: if it develops
in all animals when
reared in isolation

	Natural	Artificial
Learned		
Innate		✗

Innate/Learned vs. Natural/Artificial behaviors

Neuroethological approach

("more natural" experiments)

Neuropsychological approach

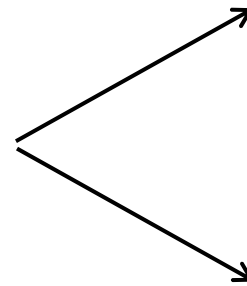("better controlled" experiments)

Spectrum

	Natural	Artificial
Learned		
Innate		✕

Umwelt (Uexküll 1920)

Two modern terms related to the classical concept of Umwelt:

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"Natural behaviors"

"Sensory Ecology" ←

Ecology

Ecology is the study of the interactions between an organism and its environment

$\longrightarrow$

"Environment":

- The physical environment
- Other organisms

Sensory Ecology is the study of how the physical environment affects the information available to the organism's sensory systems

Sensory Ecology – outline of today's lecture

- **Rationale:** Why should Neuroscientists care about Ecology?

Three aspects of Sensory Ecology:

- **The physics of the environment**: How it affects the sensory information available to the organism

- **Natural stimulus statistics**: A modern (and currently popular) look at the concept of "Umwelt"

- **Direct Perception** ("The ecological approach to visual perception" – Gibson): the surprisingly rich cues and clues that the Umwelt of humans supplies our visual system

Sensory Ecology – outline of today's lecture

Based (primarily) on the books:

- Sensory Ecology (Dusenbery, 1992)

- The ecological approach to visual perception (Gibson, 1986)

And a variety of more recent articles.

Sensory Ecology – outline of today's lecture

Types of behavioral questions:

Synthetic approach: from behavior to causes ("bottom-up")
- What do organisms do? (Description)
- How do they do it? (Proximate causes)
  - Developmental mechanisms
  - Physiological mechanisms
  - Behavioral mechanisms
- Why do they do it? (Ultimate causes)
  - Functions (adaptive values)
  - Evolution (history of the species)

Analytic approach: from problems to behavior ("top-down", e.g. Marr 1982)
- What problems must organisms solve?
- What strategies do they use to solve these problems?
- What mechanisms are used to implement the strategies?

"Behavior is complex and species-specific, but many of the problems facing organisms and the strategies for solving them are universal" (Dusenbery 1992).

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Why should neuroscientists care about ecology?

- **The evolutionary argument:** Because brains in general, and sensory systems in particular, have evolved so as to maximize the animal's fitness in the face of *natural* stimuli, in the *natural* world.

- **There are many examples suggesting that ecology matters.**

Example 1: Moth hearing and bat echolocation

Co-evolution of the auditory system of moths and the echolocation calls of bats: The Umwelt of moths (which prominently includes echolocation calls of bats) strongly affected the evolution of moths' auditory system
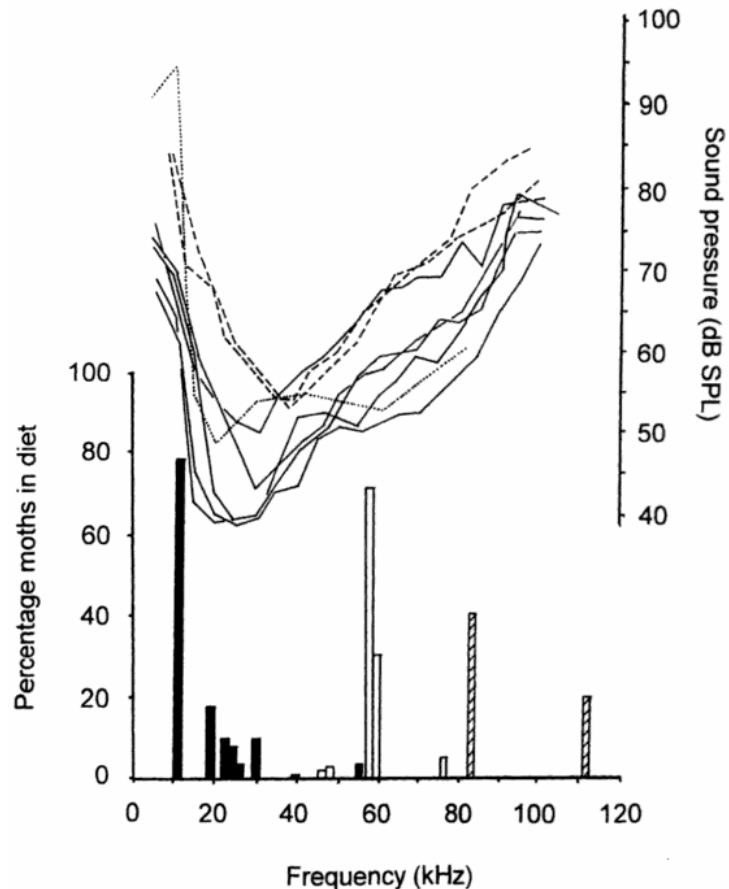
- Audiograms of 8 moth species: note that bats with frequencies 20–50 kHz eat less moths; these are also the frequencies of moths' best hearing

- Moth hearing matches the local population of bats: may differ for the *same* moth/bat species in different locations (graph not shown)

... we will talk more about bat echolocation later in the course.

Example 2: Natural stimulus statistics and neural activity

Neurons respond differently to ensembles of natural stimuli compared to artificial stimuli: example from the auditory system
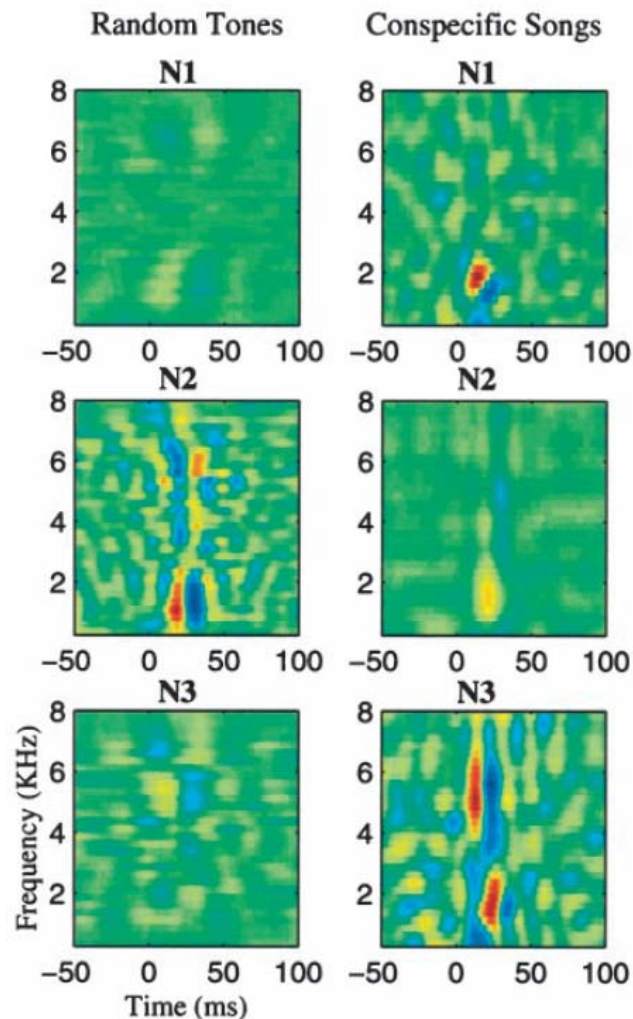
Spectro-temporal receptive fields of 3 auditory neurons (Theunissen et al. 2000)

… we will talk more about Natural Stimulus Statistics later today.

Sensory Ecology – outline of today's lecture

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Stimulus transmission

Sensory information is transmitted over long distances by one of 3 mechanisms *("long distance" does not include touch*):

- **1. Propagation:** Light and Sound

- **2. Diffusion:** Heat and Chemicals (olfactory and gustatory)

- **3. Flow:** Heat and Chemicals (olfactory and gustatory)
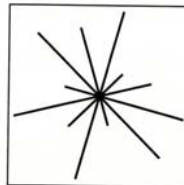
1. Wave propagation (light and sound)

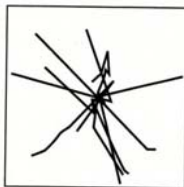**Several physical properties of waves:**
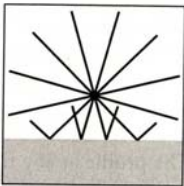
- **Geometric spreading**

- **Absorption**

- **Scattering**

- **Reflection**

- **Refraction**   *** diffraction**
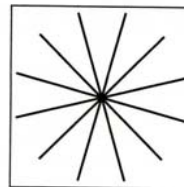
Geometrical spreading only

Absorption

Scattering

Reflection

Refraction

1. Wave propagation (light and sound)

Several physical properties of waves:

- **Geometric spreading**

    - For point source in three dimensions (<u>3-D</u>), intensity (**I**) decreases as $1/R^2$, where R is the distance from the source: <u>**I** ~ $1/R^2$</u> . For point source & for a spread limited to <u>2-D</u> → <u>**I** ~ 1/R</u> (examples soon).

- **Absorption** ⎫
- **Scattering** ⎬ **Attenuation**

- **Reflection**

- **Refraction**

- **diffraction**

We will talk in detail about Geometric Spreading and about Attenuation when we will discuss Echolocation in Bats later in the course.
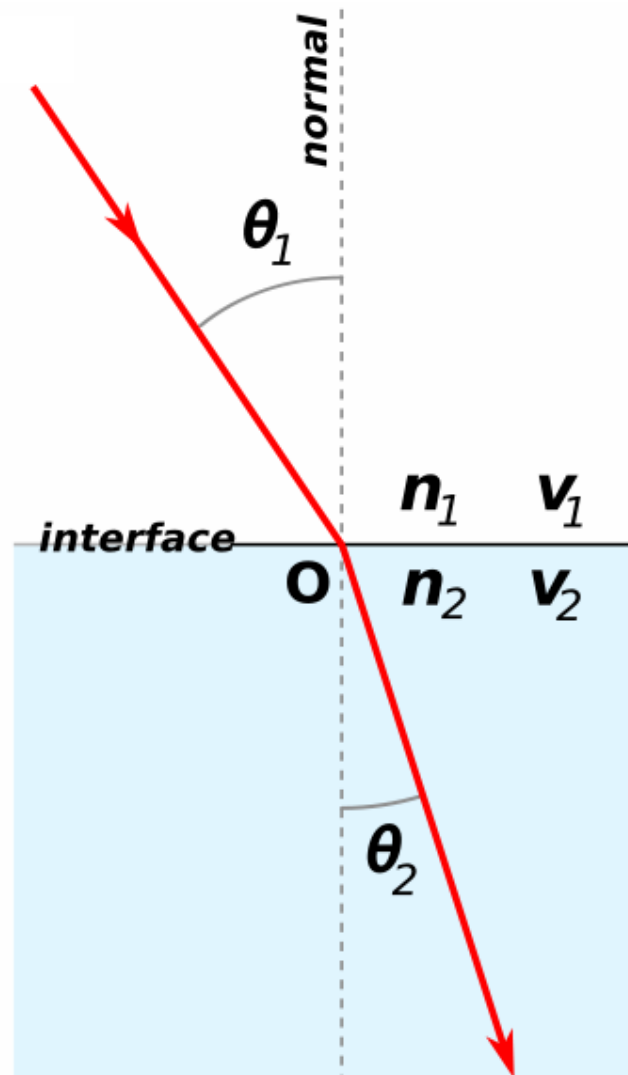
1. Wave propagation (light and sound)

<u>Example:</u> Implication of **Reflection** & **scattering** in the ocean's midwater. Scattering in the midwater (depth > ~ 100 m) is uniform around the vertical axis – allowing usage of **Mirror Camouflage** by silvery fish.

Mirror

Reflected light

Background light
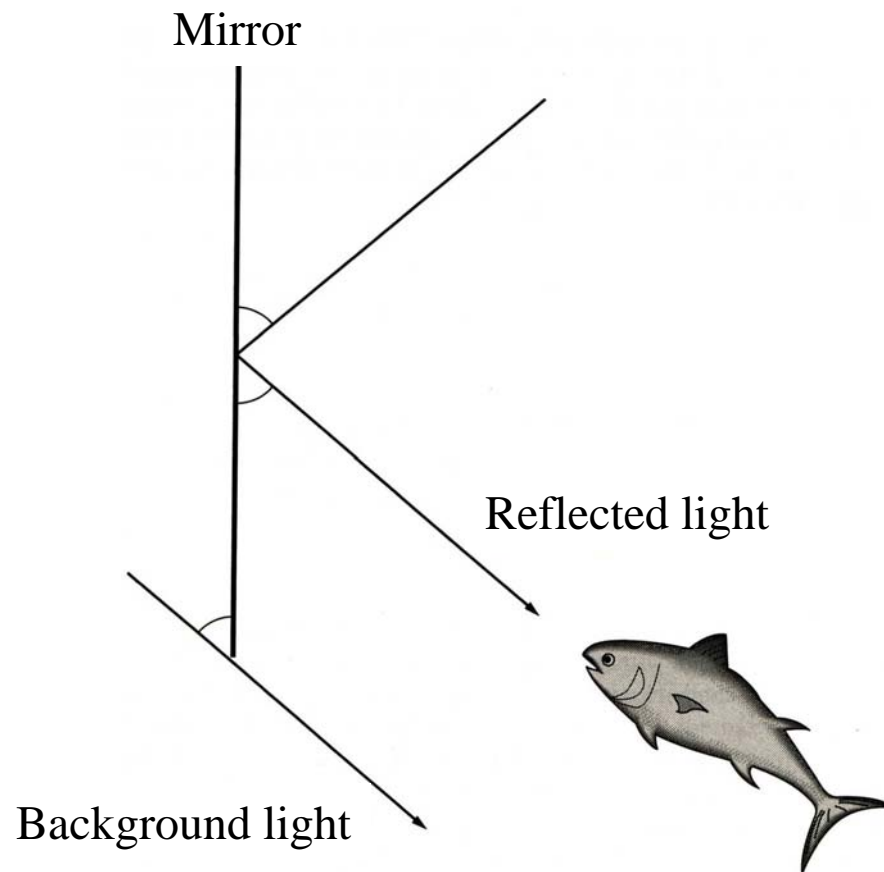
1. Wave propagation (light and sound)

<u>Example:</u> Implication of **Reflection** & **scattering** in the ocean's midwater. Scattering in the midwater (depth > ~ 100 m) is uniform around the vertical axis – allowing usage of **Mirror Camouflage** by silvery fish.

This is why fishes such as sardines and piper have silvery sides.

1. Wave propagation (light and sound)

Refraction

Snell's Law:

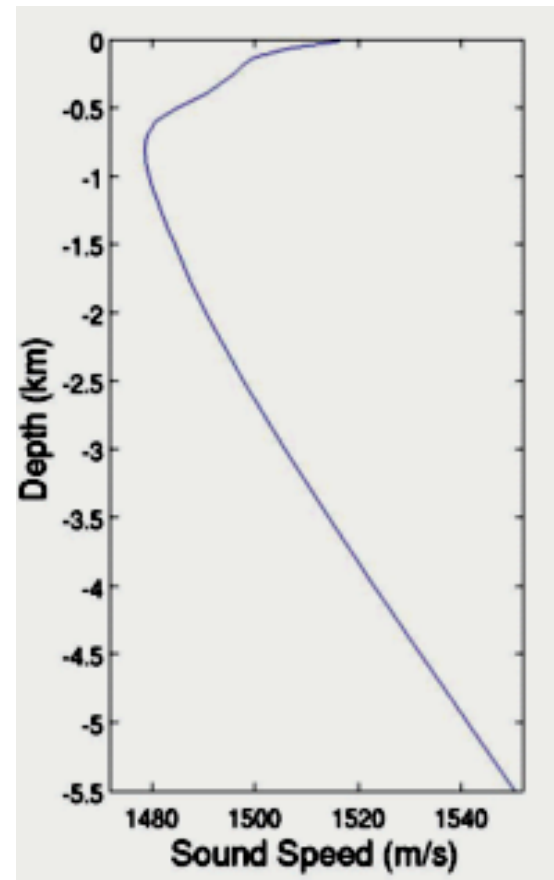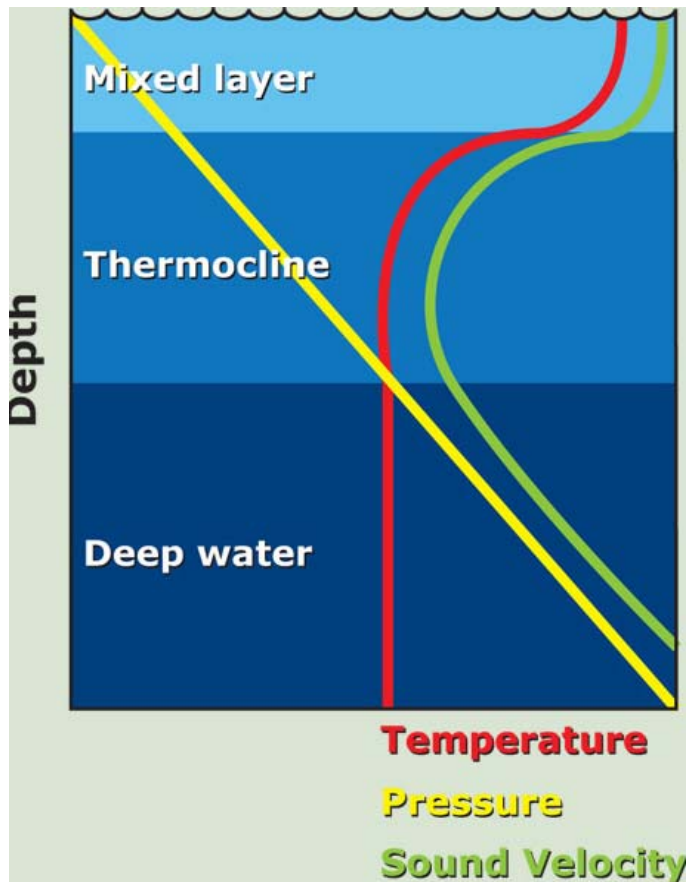$$\frac{\sin \theta_1}{\sin \theta_2} = \frac{v_1}{v_2} = \frac{n_2}{n_1}$$

1. Wave propagation (light and sound)

Refraction – Implications for the hunting behavior of the Archerfish
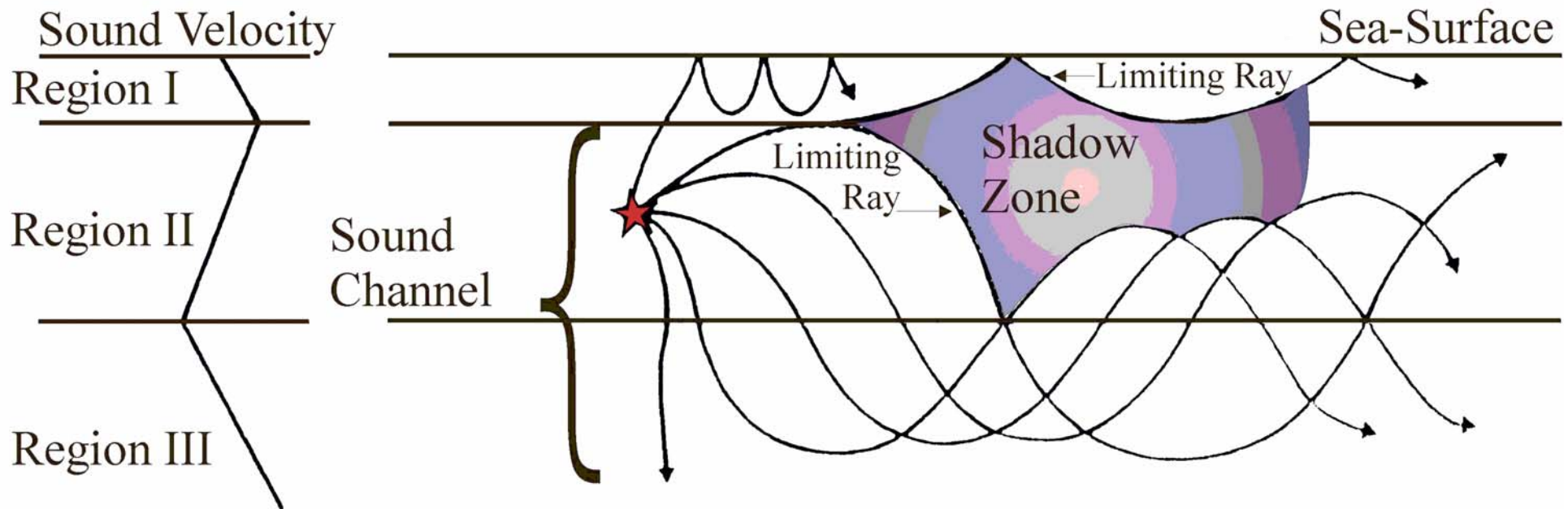
1. Wave propagation (light and sound)

Refraction – Deep Sea Sound Channel creates a ~ 2-D acoustic waveguide at a certain depth where sound velocity in the ocean is minimal.

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Refraction – Deep Sea Sound Channel creates a ~ 2-D acoustic waveguide at a certain depth where sound velocity in the ocean is minimal.

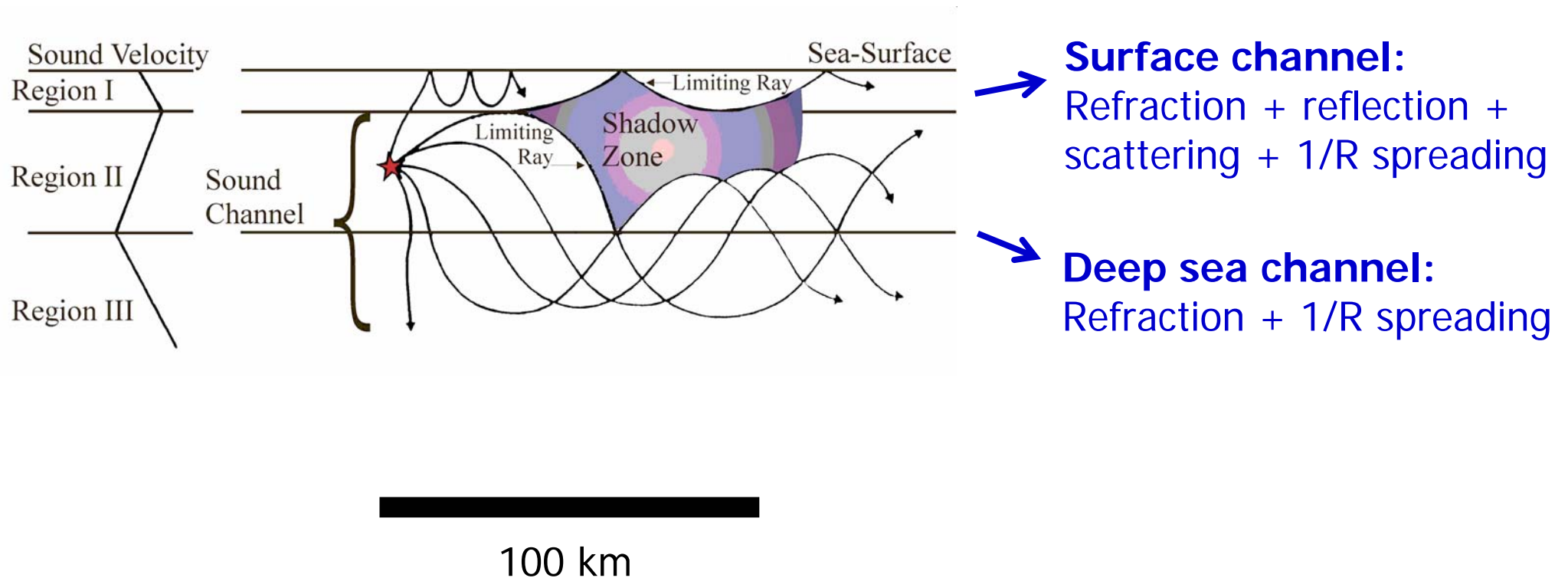# 1. Wave propagation (light and sound)

Refraction — <u>Deep Sea Sound Channel</u> creates a ~ 2-D acoustic waveguide at a certain depth where sound velocity in the ocean is minimal, and thus allows sound to spread for thousands of kilometers through the combined actions of **refraction** and ~1/R **geometric spreading** (remember that for 2-D, waves spread as ~1/R instead of the usual ~1/R^2 geometric spreading).

At high latitudes the depth of the sound channel is quite shallow, and it is thought to be important for **acoustic communication of whales**.

Another, sound channel is the <u>surface sound channel</u>, at the sea surface; it acts through the combined actions of **refraction** and **reflection** from the sea surface. It's also thought to be important for acoustic communication, but is less efficient due to **scattering** from the rough sea surface.
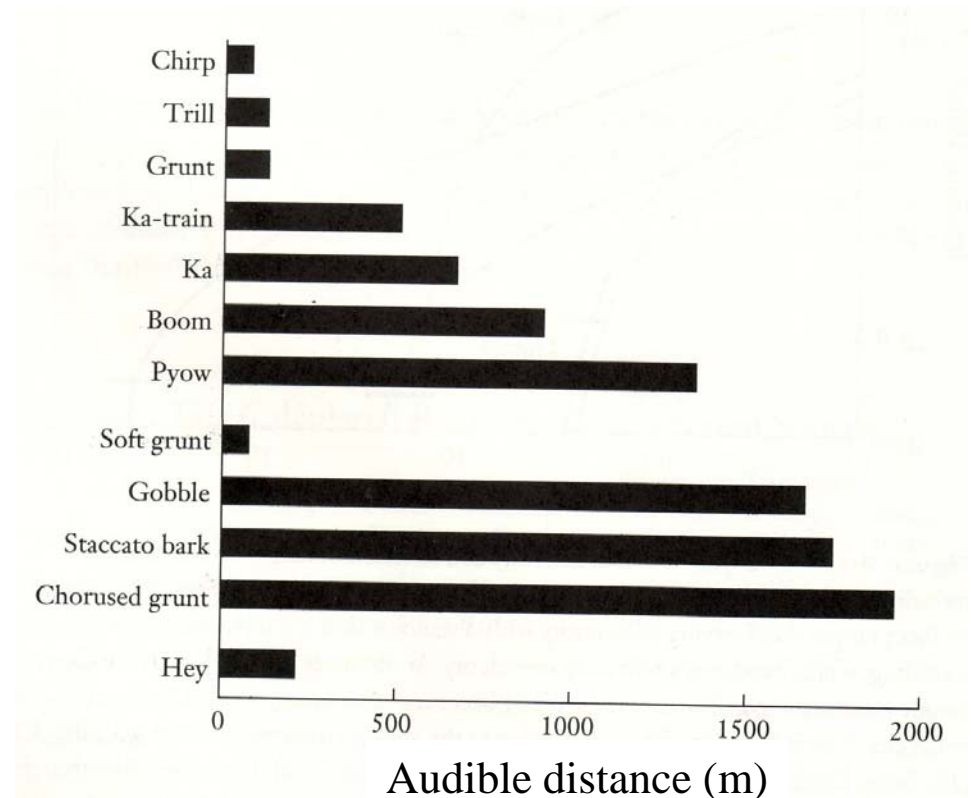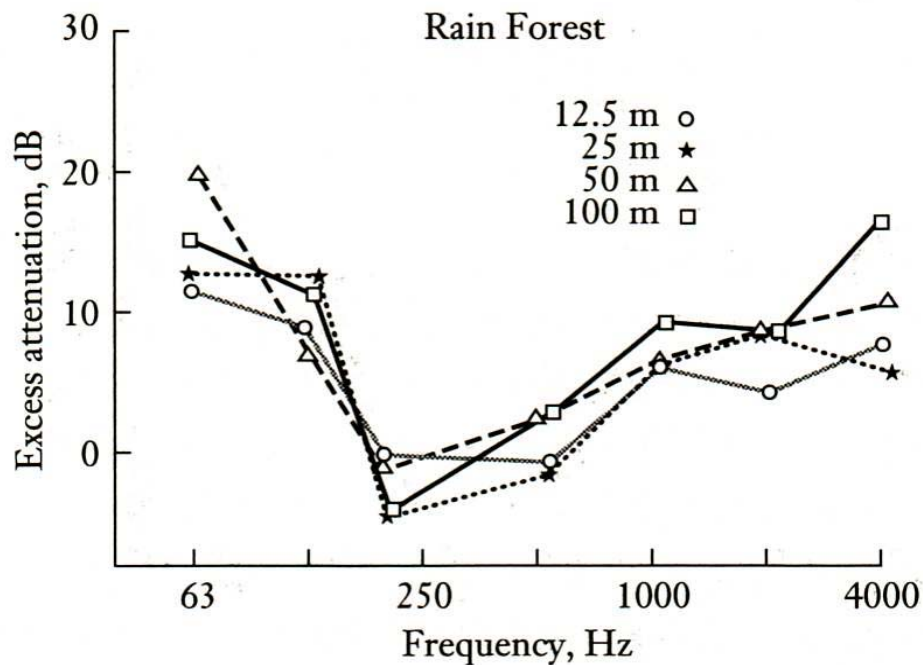
1. Wave propagation (light and sound)

Refraction – Deep Sea Sound Channel creates a ~ 2-D acoustic waveguide at a certain depth where sound velocity in the ocean is minimal.

Surface channel:
Refraction + reflection + scattering + 1/R spreading

Deep sea channel:
Refraction + 1/R spreading

100 km

1. Wave propagation (light and sound)

Refraction — "Sound window" @ <u>200 – 500 Hz</u> in the rainforest is caused by **refraction** from the sun-heated air layer at the upper canopy – in combination with **scattering** and **diffraction** from trees and branches.

Many of the long-distance monkey vocalizations are @ 200 – 500 Hz, utilizing this sound window.
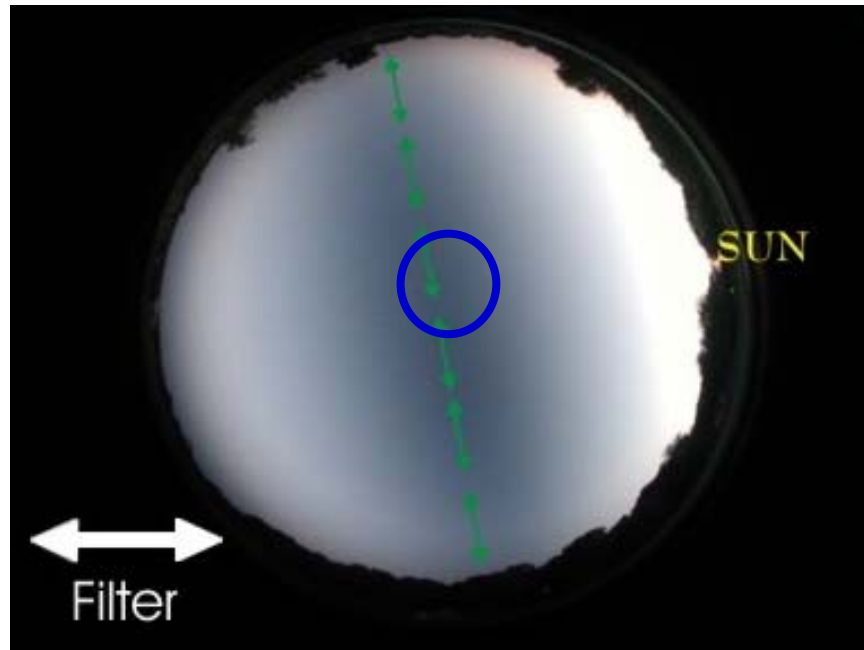
1. Wave propagation (light and sound)

**Refraction – ** Mirage.
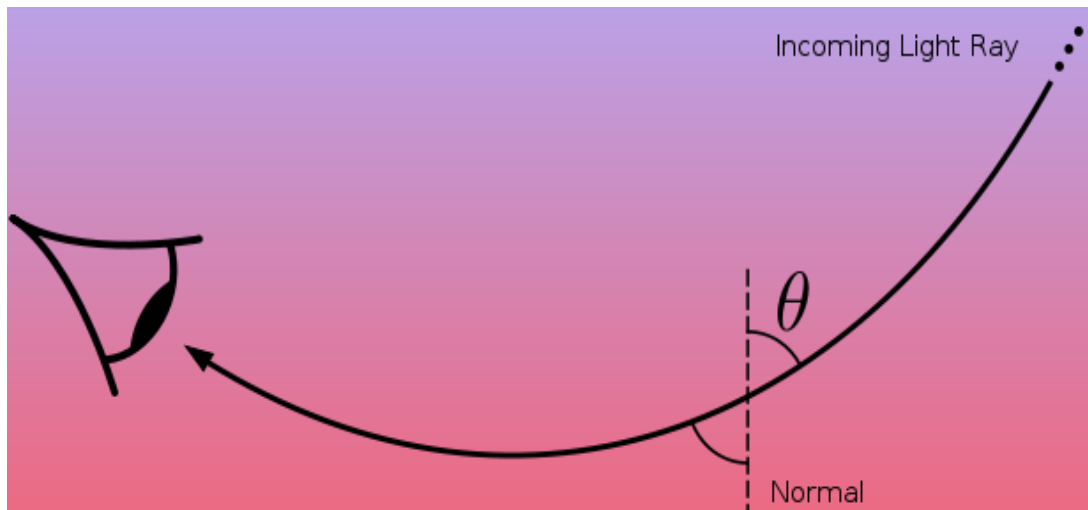
1. Wave propagation (light and sound)

Scattering – creates two interesting effects:

- **Why is the sky blue?** Because scattering $\sim 1/\lambda^4$ (λ = wavelength)

- Scattering polarizes the sun's light – which forms the basis of insect's **polarization compass** (we'll discuss this later when talking about Navigation)

Even if only a patch of the sky is visible (e.g. via forest canopy), this may be enough for an insect to compute the direction of the sun = perpendicular to the polarization pattern.

Fish-eye sky photo through horizontal polarization filter

Stimulus transmission

Sensory information is transmitted over long distances by one of 3 mechanisms *("long distance" does not include touch*):

✓ • **1. Propagation:** Light and Sound

➡ • **2. Diffusion:** Heat and Chemicals (olfactory and gustatory)

➡ • **3. Flow:** Heat and Chemicals (olfactory and gustatory)

2. Diffusion

Diffusion is a very slow process: not efficient over long distances.
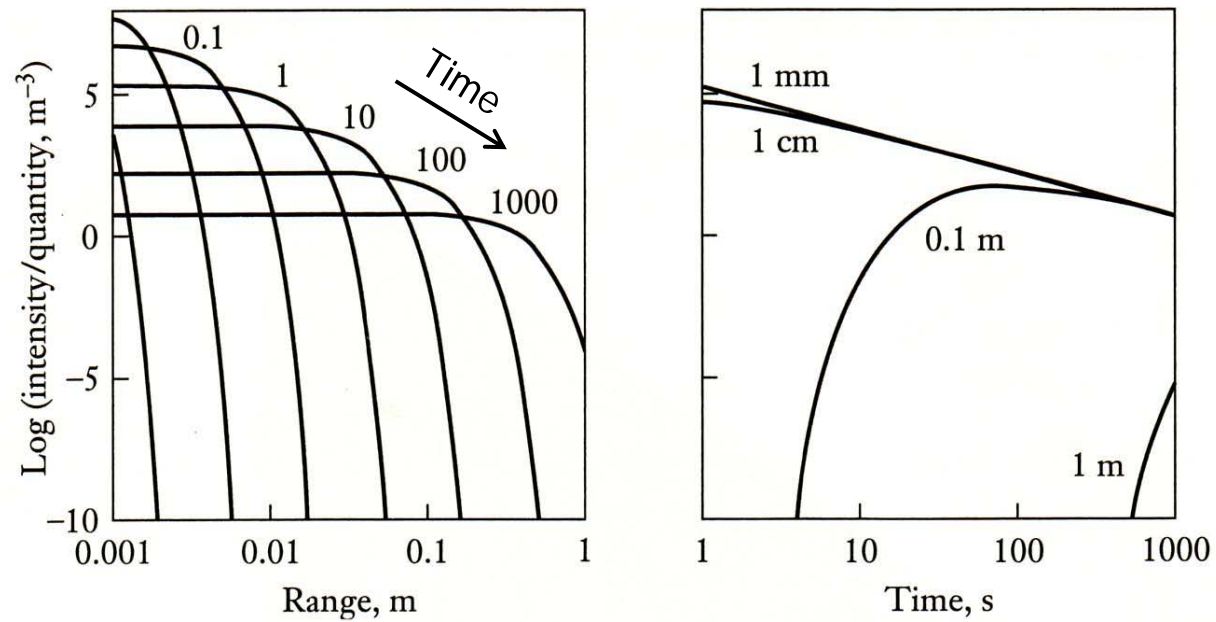
3. Flow

Because diffusion is inefficient, in order to transmit olfactory information over long distances it is crucial to have <u>flow</u> of air (or of water for aquatic animals)

- **Sniffing** = Flow created by the animal (inhaling)

- **Wind**

3. Flow

Sniffing by dogs and humans

Porter et al., *Nature Neurosci.* (2007)

3. Flow

Underwater Sniffing by the star-nosed mole

<div style="border: 2px solid green; color: green;">

**Movies of star-nosed mole sniffing
underwater using air bubbles
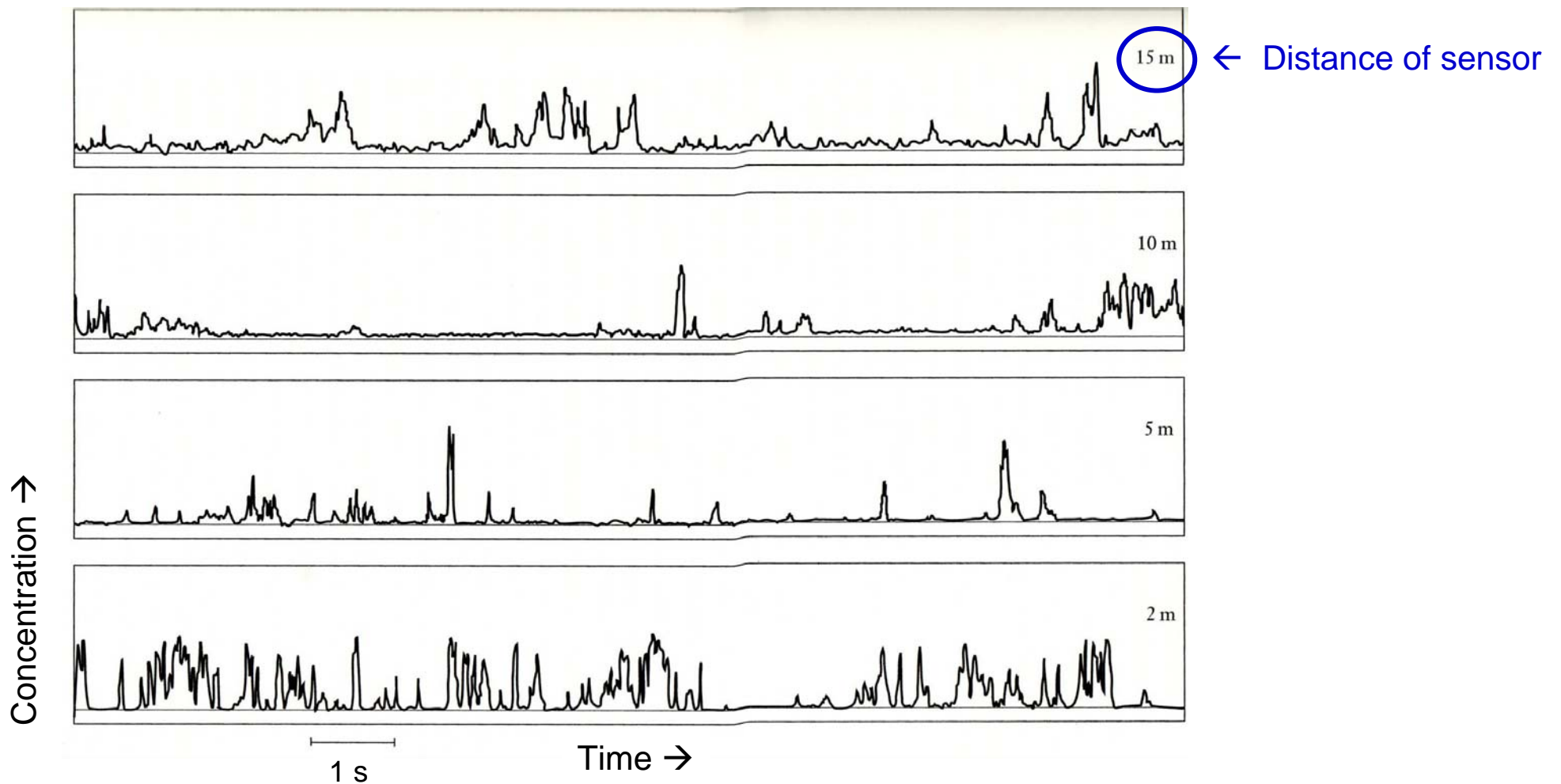(mov1, mov2)**

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K. Catania, *Nature* (2006)

3. Flow

Wind: The problem with wind is that it creates <u>turbulent</u> flow = <u>intermittent</u> olfactory input

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Wind: The problem with wind is that it creates <u>turbulent</u> flow = <u>intermittent</u> olfactory input

- Nevertheless, moths can detect pheromone odors from > 1 km

- It may be better NOT to use a **chemotaxis** strategy, which tries going up the gradient – as there is *no* continuous gradient – but to use an **infotaxis** strategy (Vergassola et al., *Nature* 2007) – this topic will likely be discussed next year in the course on "Systems Neuroscience"

- When studying the neural basis of olfaction, you need to understand the **natural stimulus statistics** of odors

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- **Natural stimulus statistics**: A modern (and currently popular) look at the concept of "Umwelt"

- **Direct Perception** ("The ecological approach to visual perception" – Gibson): the surprisingly rich cues and clues that the Umwelt of humans supplies our visual system

Natural stimulus statistics and neural activity

Neurons respond differently to ensembles of natural stimuli compared to artificial stimuli: example from the auditory system
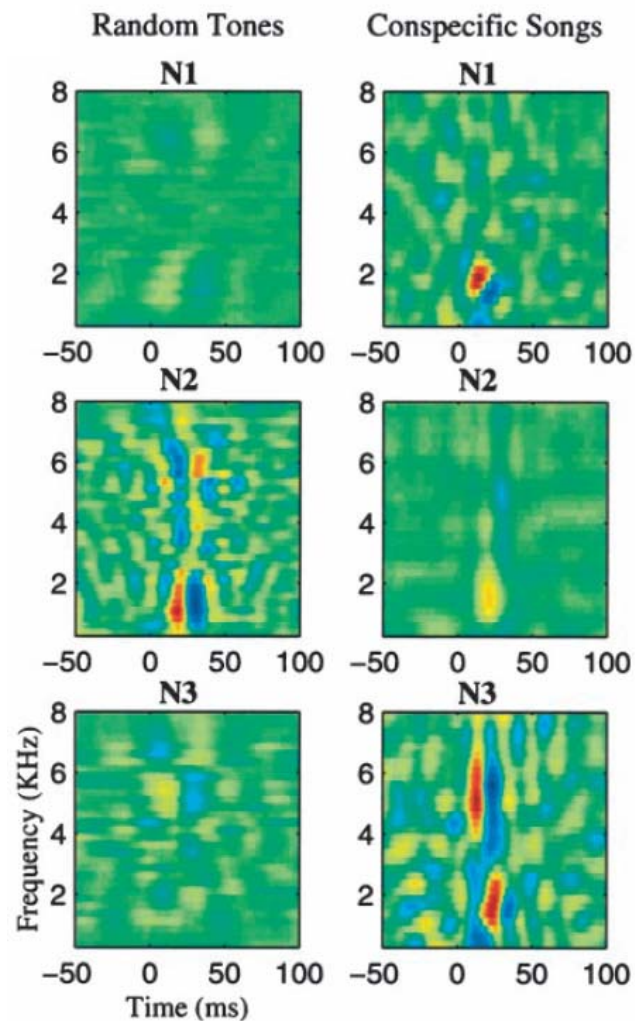

Spectro-temporal receptive fields of 3 auditory neurons (Theunissen et al. 2000)
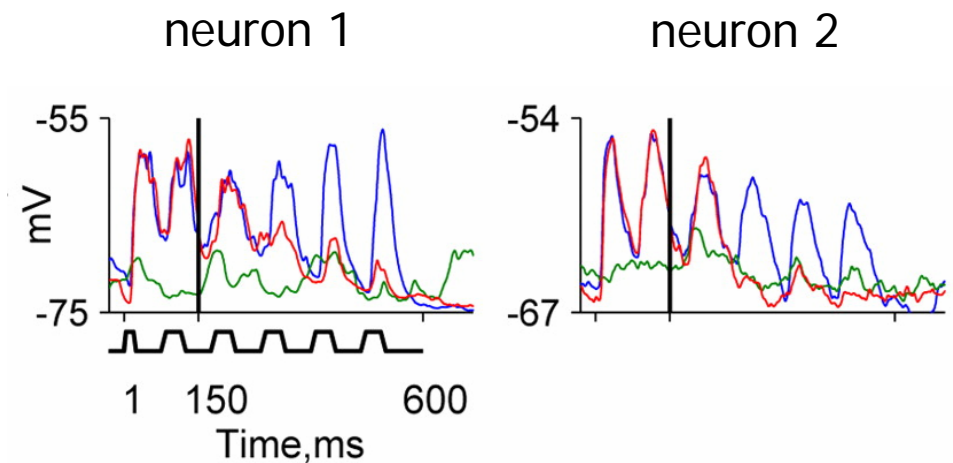
Natural stimulus statistics and neural activity

Natural soundscapes often contain wideband sounds with strong amplitude modulations – and it turns out that:

- Humans are particularly good at detecting tonal sounds over such modulated background ("CMR effect")

- Neurons in auditory cortex are very sensitive to such naturalistic sounds + tones
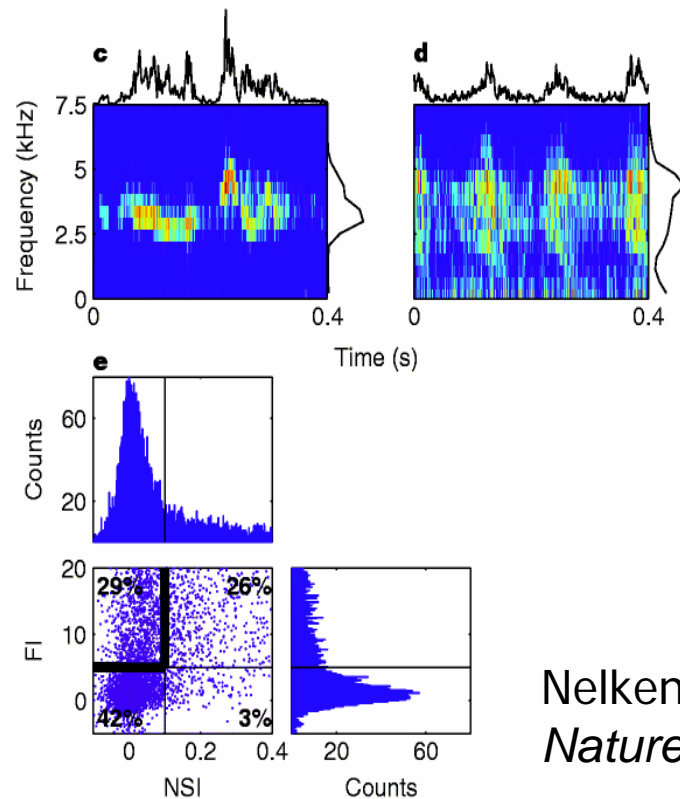

Nelken et al.
Nature (1999)

Las et al.
J. Neurosci. (2005)

Natural stimulus statistics and neural activity

Natural vision has complex statistics – due to the long-range correlations within the images themselves, and the complex scanning movements by the eyes – both of which turn out to have important implications for:

- **Responses** of visual neurons

- Modeling the **development** of response properties (receptive fields) of visual neurons
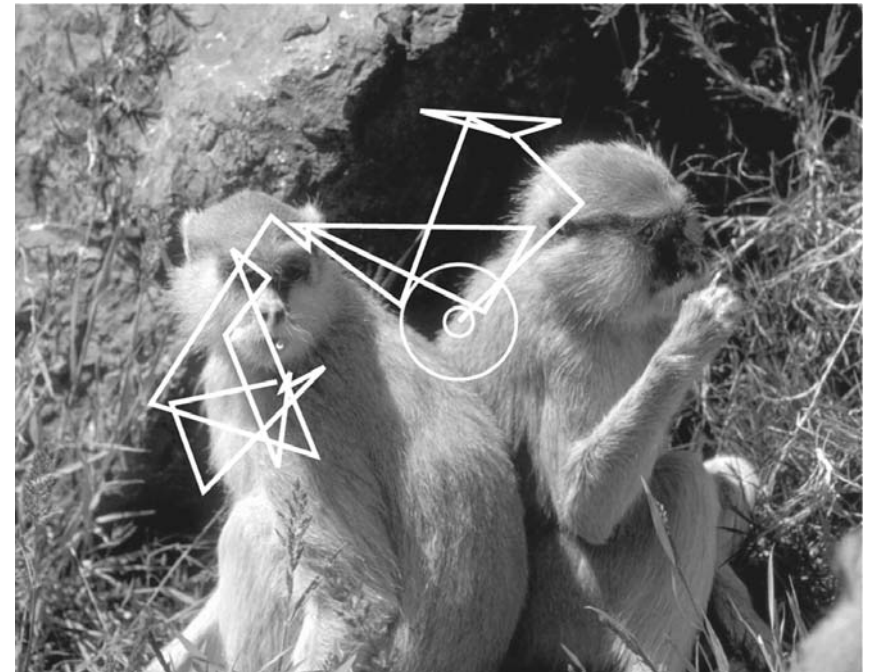
Vinje and Gallant, *J. Neurosci.* (2002)

… you will learn more about Natural Stimulus Statistics in the course "Systems Neuroscience".

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"The ecological approach to visual perception" – Gibson

- You will likely get reading from this book, and/or from some related articles, as it is impossible to cover here all of Ecological Vision.

Example #1: **Optic Flow** :

- The zero-point of optic flow allows estimating the **point of collision**, independent of cross-winds

- Geometric methods for directly estimating **time-to-collision** without complex calculations

- Optic flow is the main cue used by:

  - Pilots landing on aircraft carriers in rough seas

  - Honeybee odometer (distance meter)
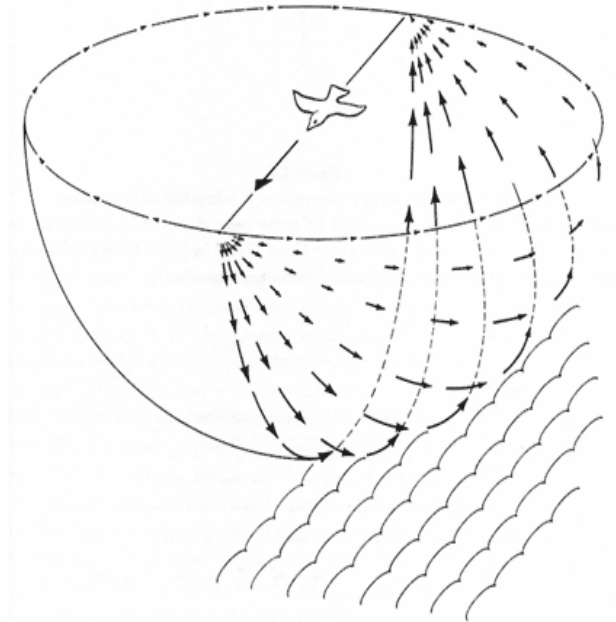
"The ecological approach to visual perception" – Gibson

Example #2: **The invariant horizon ratio of terrestrial objects**
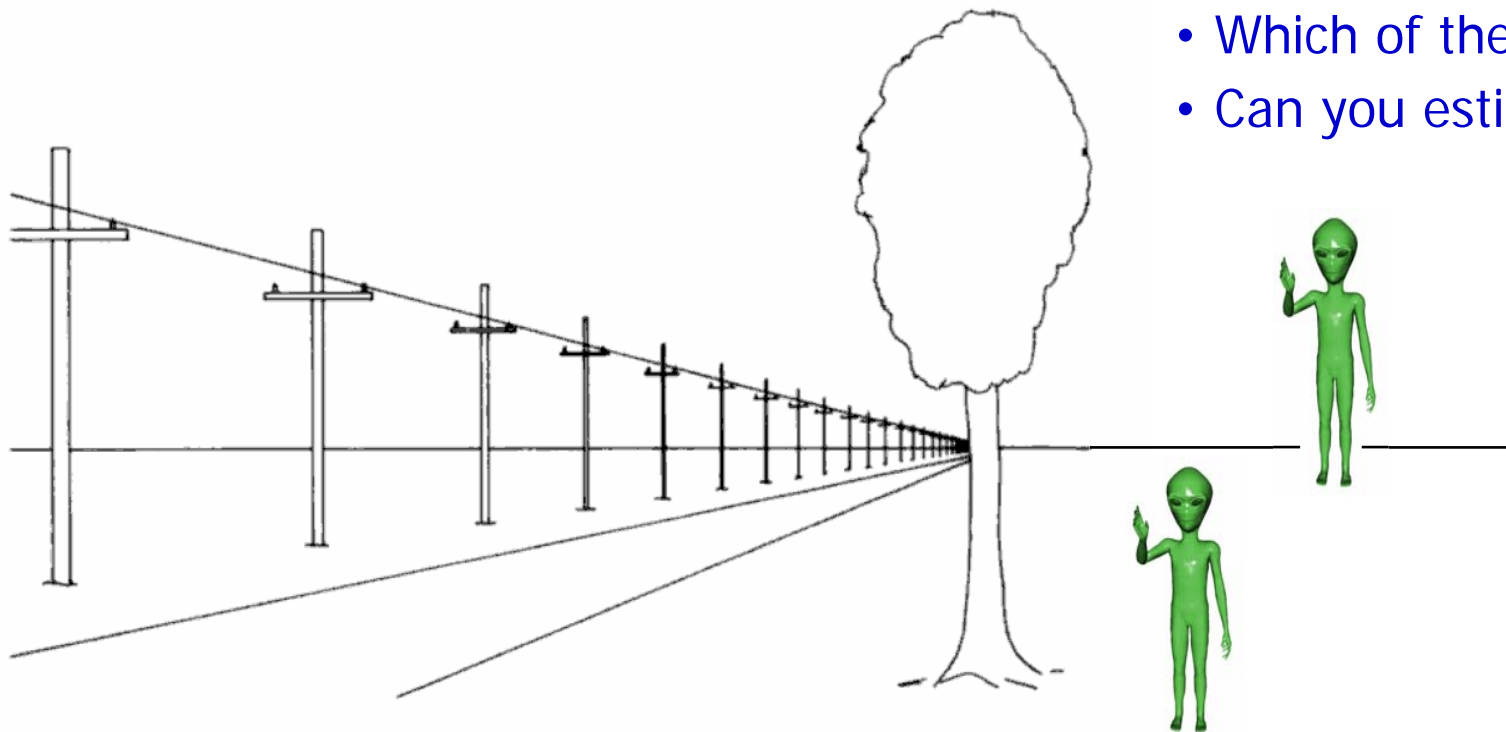
- Who is taller: the tree or the aliens?
- Which of the aliens is taller?
- Can you estimate the tree height?

- The line where the horizon cuts the object is just as high above the ground as your eye. Note that all telephone poles are "cut" at the same height, and their above:below horizon ratio is ~ 2:1, implying a total height of 6 m. For the tree, we can estimate 5 m.

Take home message

When studying the neural basis of behavior in a certain animal species, it is important to <u>control</u> the animal's Umwelt (surrounding world) in the laboratory – but it is also very important to fully <u>understand</u> this animal's Umwelt in its natural environment → because the natural environment is what the animal's brain evolved to cope with, and hence we must incorporate these considerations when studying brain function.