Introduction to Neuroscience: Behavioral Neuroscience

Sensory Ecology

Nachum Ulanovsky

Weizmann Institute of Science

2015-2016, 2^{nd} semester

Core courses in Brain Sciences at the Weizmann Institute

Levels of Analysis
<u>of the Nervous System</u>

<u>Four Core Courses in Neuroscience</u>

Molecular

Cellular

Synaptic

Network

System

Behavior

Introduction to Neuroscience:
Molecular Neuroscience - Genes to Behavior

Introduction to Neuroscience:
Cellular and Synaptic Physiology

Introduction to Neuroscience:
Systems Neuroscience

Introduction to Neuroscience:
Behavioral Neuroscience

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

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

Course syllabus (by week)

Part A: Introduction to Brain and Behavior (Kimchi)	
1.	Introduction to Behavior. (16/3/2016)
2.	Hormonal mechanisms of behavior. Sexual behaviors and their neural mechanisms. (23/3/2016)
3.	Animal models of social disorders. (30/3/2016)

Course syllabus (by week)

Part B: Neural mechanisms of Behavior – the Neuroethological approach (Ulanovsky)	
4.	Sensory ecology: evolutionary adaptations of animal sensory systems to their environment. (*Thursday* 14/4/2016 at 11:15 - 14:00, at *Schmidt* lecture hall -- Note unusual day & unusual location)
5.	Basic concepts: neuroscience and neuroethology. Choosing the right behavior and the right animal model. Example system #1: Introduction to Electrolocation. (20/4/2016)
6.	Example system #2: Multisensory integration in the brain of the barn owl. (Guest lecture by Dr. Yoram Gutfreund, Technion) (4/5/2016)
7.	Example system #3: The bird song system: behavior, neuroanatomy, physiology, models. (Guest lecture by Dr. Liora Las, Weizmann Institute) (18/5/2016)
8.	Example system #4: Echolocation in bats: behavior, principles of biosonar signal design, neural processing. (25/5/2016)
9.	Example system #5: Neurobiology of spatial cognition. Introduction to spatial memory, orientation and navigation: (i) Navigational strategies in different animals. (ii) Sensory mechanisms of navigation: vision, magnetic navigation, etc. The navigation circuits in the mammalian brain: Place cells, grid cells, head-direction cells. (1/6/2016)

Course syllabus (by week)

Part C: Neural mechanisms of Behavior – the Neuropsychological approach (Paz)	
10.	Introduction: Basic concepts, standard behavioral tasks. Example system #6: Fear and its representation in neural circuits. (*Guest lecture by Dr. Aryeh Taub, Weizmann Institute*) (8/6/2016)
11.	Example system #7: Reinforcement Learning. Reward and its representation in neural circuits. (*Guest lecture by Dr. Genela Morris, Haifa University*) (15/6/2016)
12.	Psychophysics: (i) Basic concepts, how to measure JND's, signal detection theory and ROC. (ii) Visual psychophysics. (iii) Other senses. (*Guest lecture by: Prof. Dubi Sagi, Weizmann Institute*) [22/6/2016]

Formalities

- **Grading:** 100% - Final exam (*open material*). NO compulsory reading.

- **Bibliography:**

We will use three main textbooks in this course:

- *Behavioral Neurobiology, An integrative approach*, 2nd ed., Zupanc G. (Oxford, 2010)
- *Behavioral Neurobiology*, Carew J. (Sinauer, 2000)
- *Learning and Behavior*, Bouton M. (Sinauer, 2007)

Additional material for some of the lectures is covered in the following books:

- *Sensory Ecology*, Dusenbery D. (Freeman, 1992)
- *An Introduction to Behavioral Endocrinology*, 4th ed., Nelson R. (Sinauer, 2011)
- *Neuroeconomics: Decision making and the Brain*, 2nd ed., Glimcher P. and Fehr E. (Academic Press, 2013)
- *Neural nets in Electric Fish*, Heiligenberg W. (MIT Press, 1991).

Sensory Ecology

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" ←

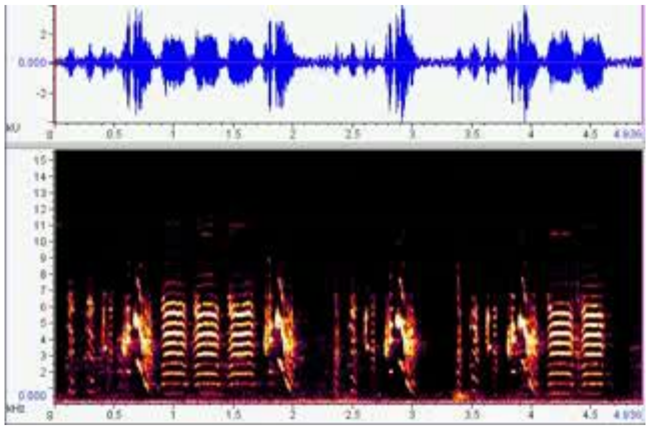
"Sensory Ecology"

Innate/Learned vs. Natural/Artificial behaviors

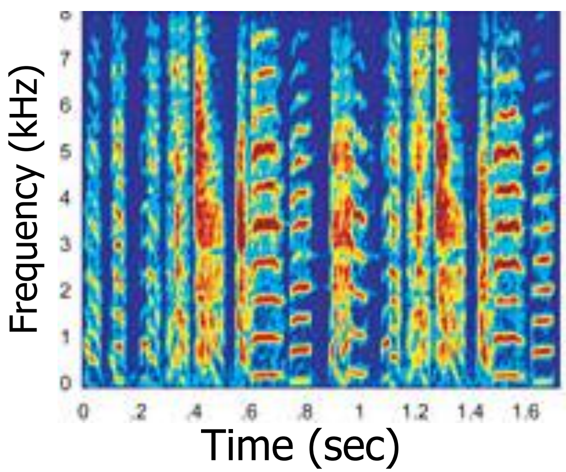
	Natural	Artificial
Learned	• Tool use in Crows & Chimpanzees • Vocal learning in songbirds	
Innate	• Sexual behaviors • Imprinting • Fixed Action Patterns	X

Vocal learning in songbirds

Adult zebra finch song (*Movie*)



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



Song of adult birds differs from the "babbles" of juveniles (*Movie*)

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 components, 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 natural behavior – and it is complex, yet very reproducible
  - A model animal that shares many aspects with vocal learning in humans (i.e. language)
  - Has many additional interesting features: Clear critical periods ; first discovery of adult neurogenesis in vertebrates…
  - *Liora Las will talk later in the course about the bird's song system.*

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 Crows & Chimpanzees • Vocal learning in songbirds	• Juggling Elephants
Innate	• Sexual behaviors • Imprinting • Fixed Action Patterns	X

Innate/Learned vs. Natural/Artificial behaviors

Vocal learning in songbirds

Juggling elephants

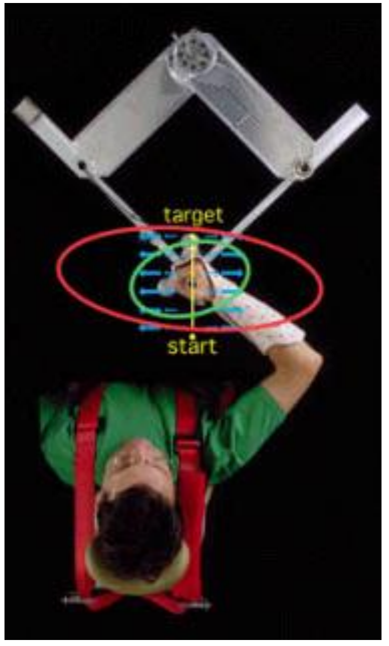
Spectrum

Innate vs. Learned = Fuzzy border:
"Innate" = if develops in all animals when reared in isolation. BUT, some innate behaviors are also followed by learning, whereby the animal improves with practice

	Natural	Artificial
Learned		
Innate		

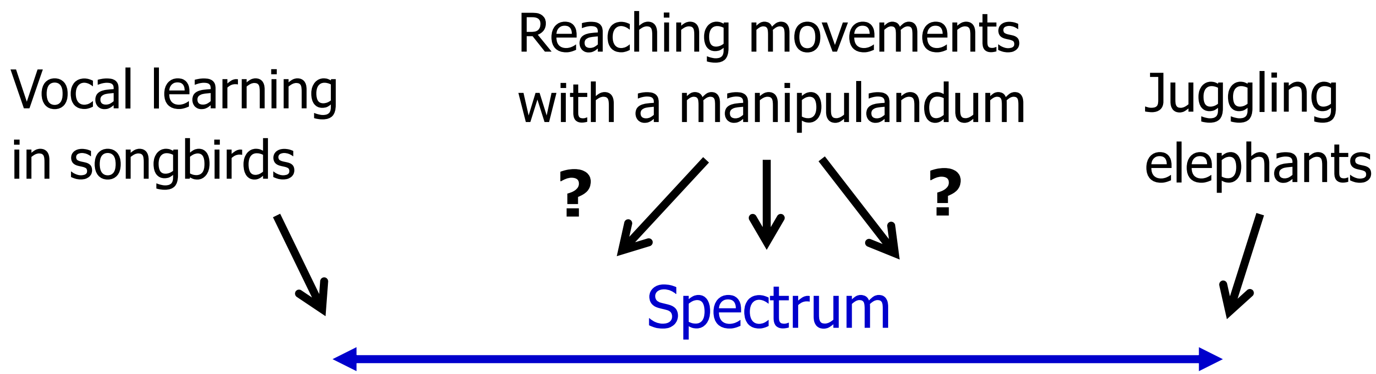
The Natural/Artificial distinction is not simple to make

What about this example?



Reaching movements in humans are a natural (and important) behavior – but the setup with the manipulandum and the chin strap is artificial

Innate/Learned vs. Natural/Artificial behaviors



	Natural	Artificial
Learned		
Innate		X

Innate/Learned vs. Natural/Artificial behaviors

Vocal learning in songbirds

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

? **?**

Juggling elephants

Spectrum

	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		X

Umwelt (Uexküll 1920)

Two modern terms related to
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→ **"Natural behaviors"**

→ **"Sensory Ecology"** ←

Ecology

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

→

"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?

<u>Three aspects of Sensory Ecology:</u>

- **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.

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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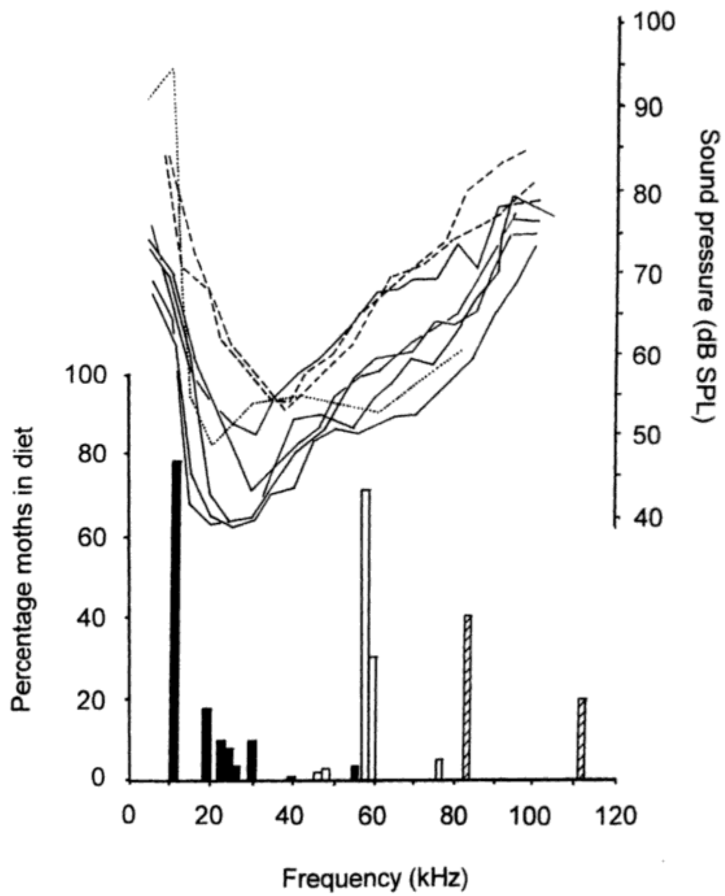
Why should neuroscientists care about ecology?

- **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

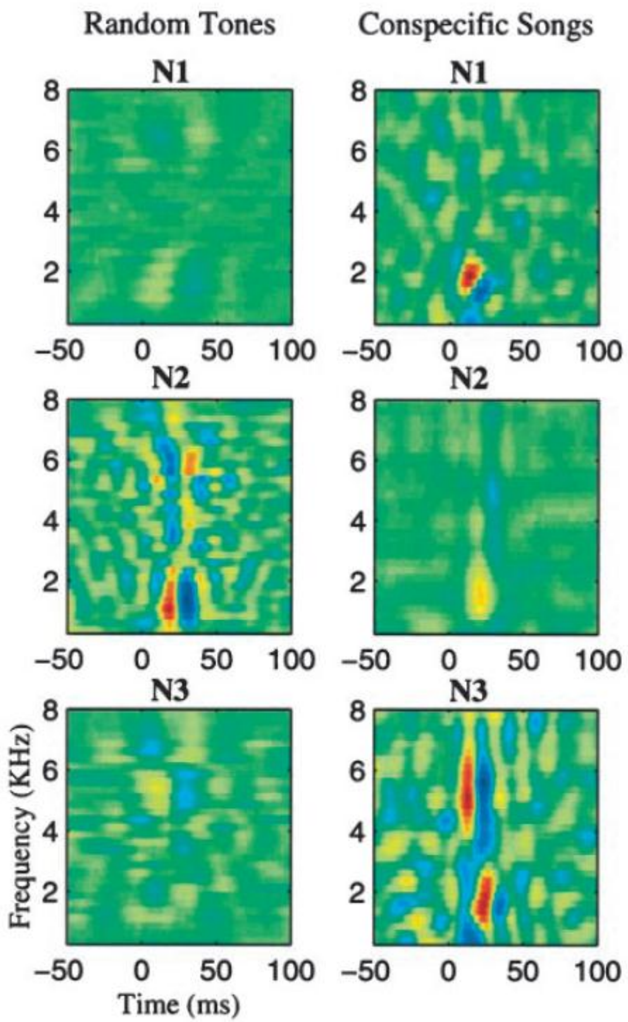


- Audiograms of 8 moth species: note that bats with frequencies 20–50 kHz eat less moths; these are also the frequencies of moths' best hearing
- Moth hearing matches the local population of bats: may differ for the *same* moth/bat species in different locations (graph not shown)

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

Example 2: Natural stimulus statistics and neural activity

Neurons respond <u>differently</u> 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)

→ This means that using artificial sounds to study the auditory system – as has been done for the last half century – has a limited utility if we want to understand how the auditory system processes real-world, natural sounds.

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

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Stimulus transmission

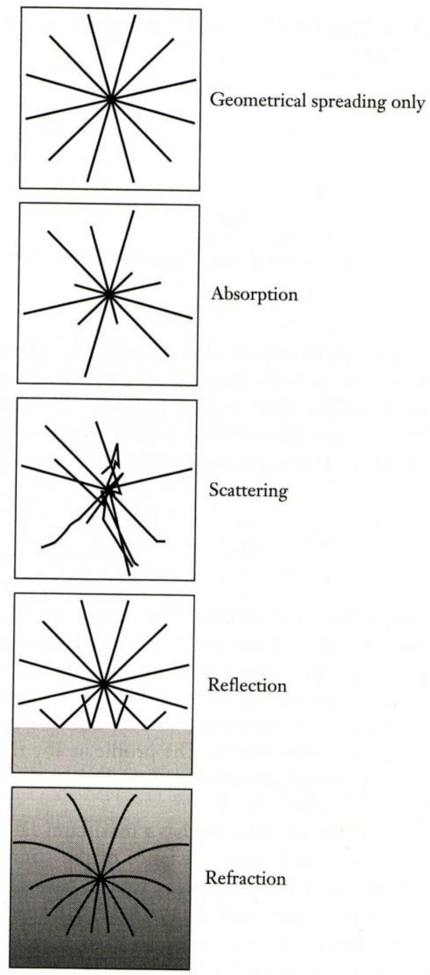
Sensory information is transmitted over long distances by one of 3 mechanisms *("long distance" does not include touch*):

- **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**

1. Wave propagation (light and sound)

Several physical properties of waves:

- **Geometric spreading**
  - For point source in three dimensions (3-D), intensity (I) decreases as $1/R^2$, where R is the distance from the source: $I \sim 1/R^2$. For point source & for a spread limited to 2-D → $I \sim 1/R$ (examples soon).
- **Absorption**
- **Scattering**

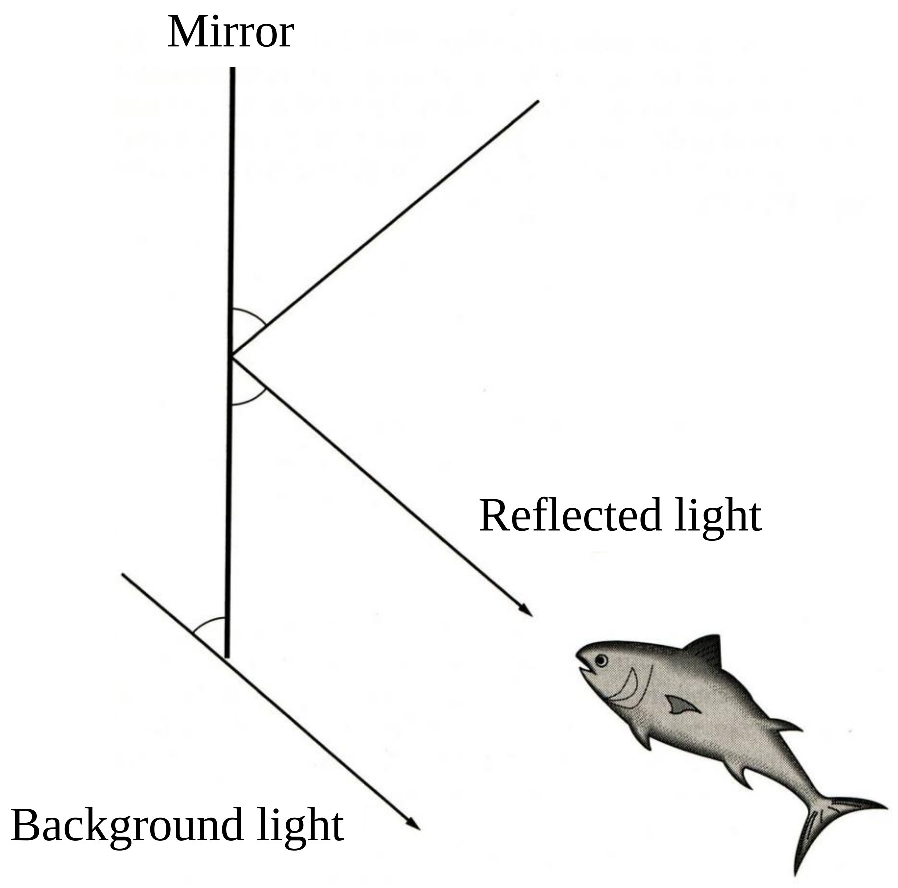
} **Attenuation** (Absorption + Scattering)

- **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.



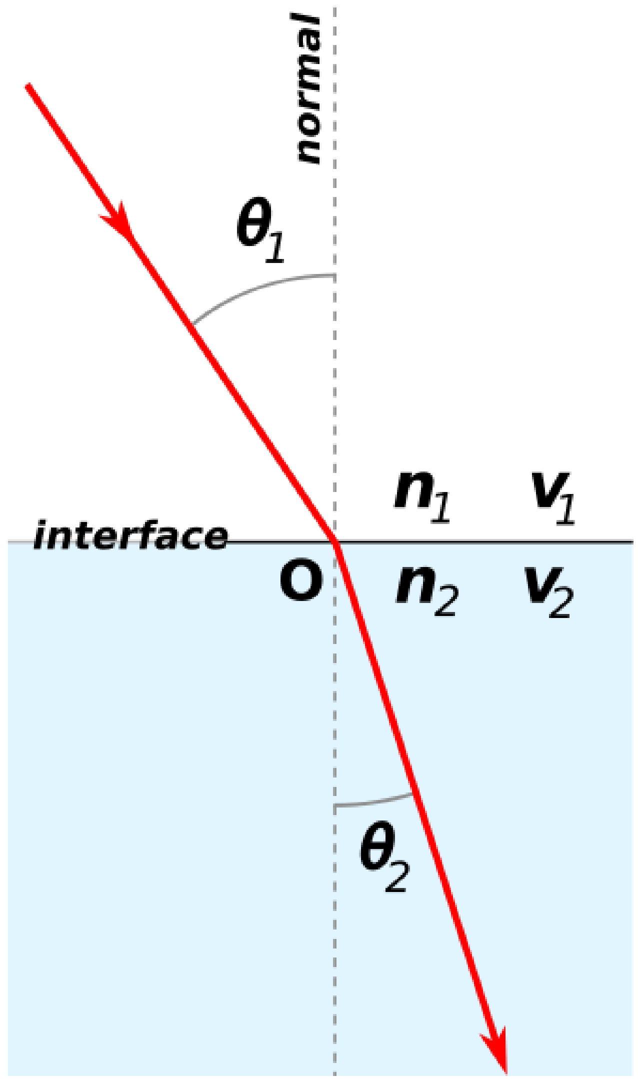
1. Wave propagation (light and sound)

Example: 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:

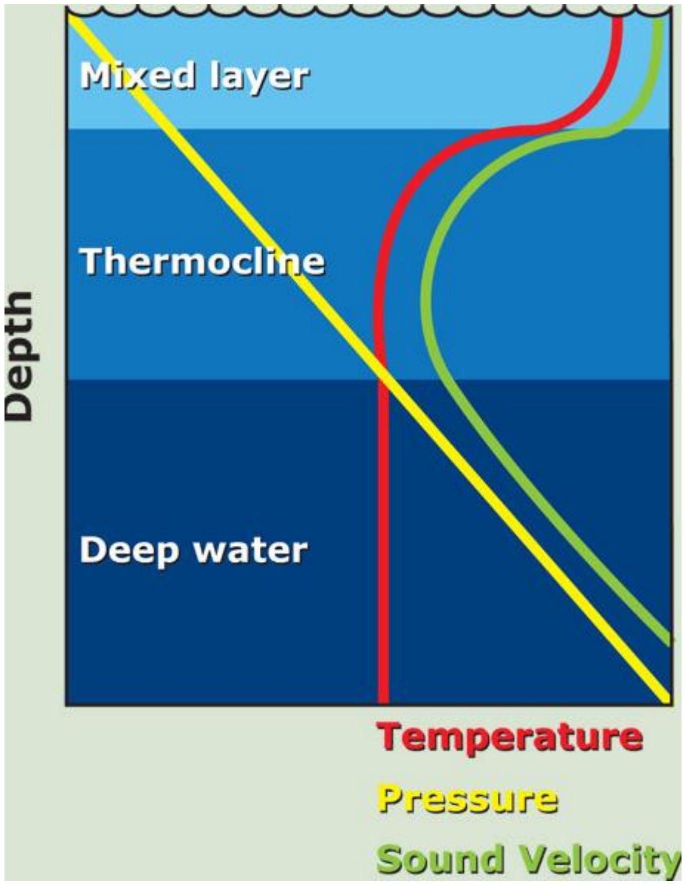
$$\frac{\sin \theta_1}{\sin \theta_2} = \frac{v_1}{v_2} = \frac{n_2}{n_1}$$

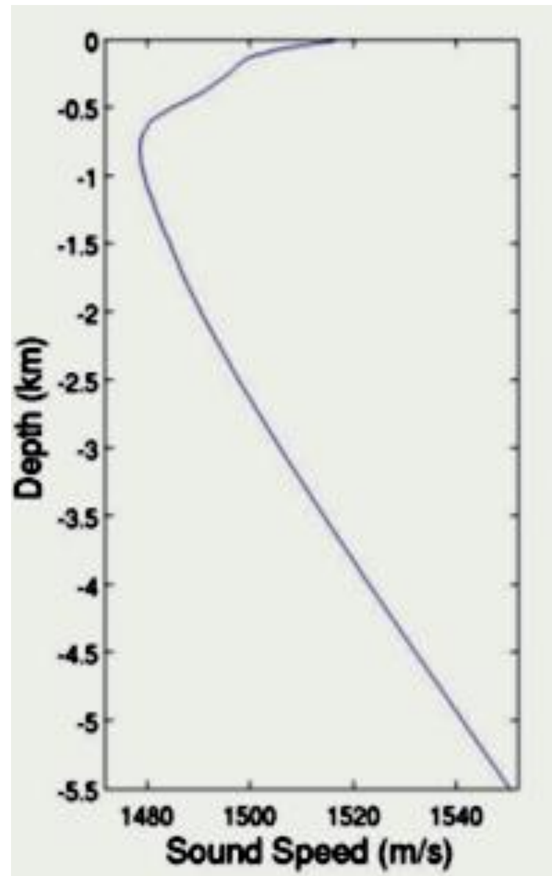
1. Wave propagation (light and sound)

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.





1. Wave propagation (light and sound)

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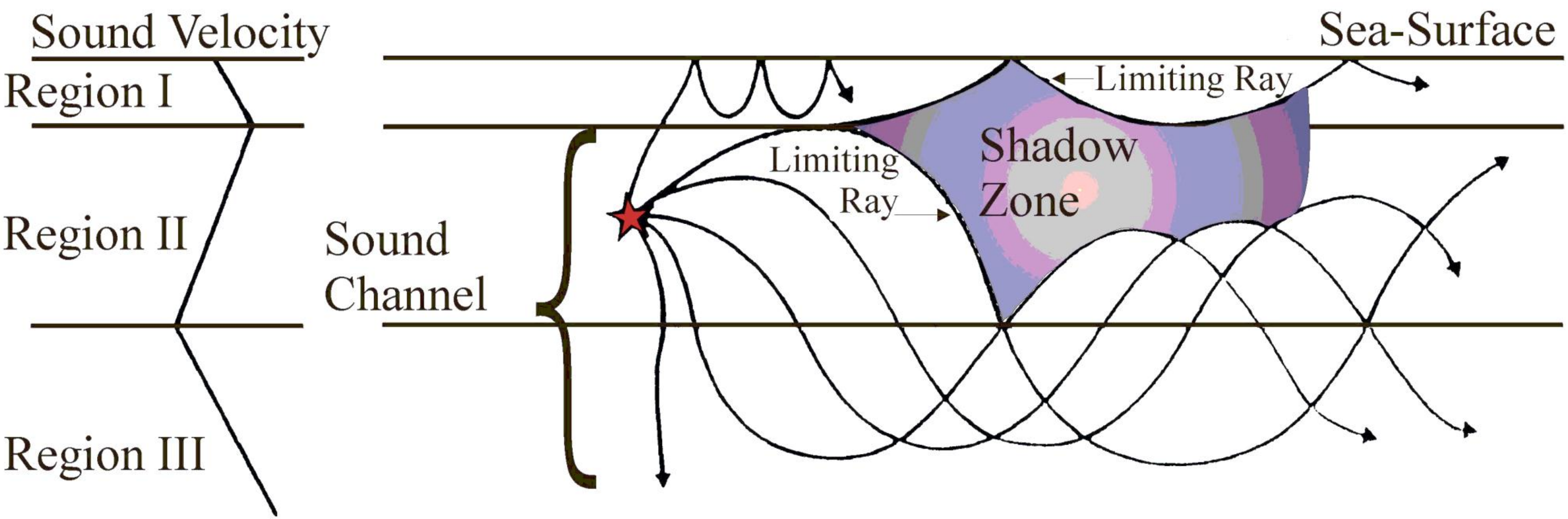


1. Wave propagation (light and sound)

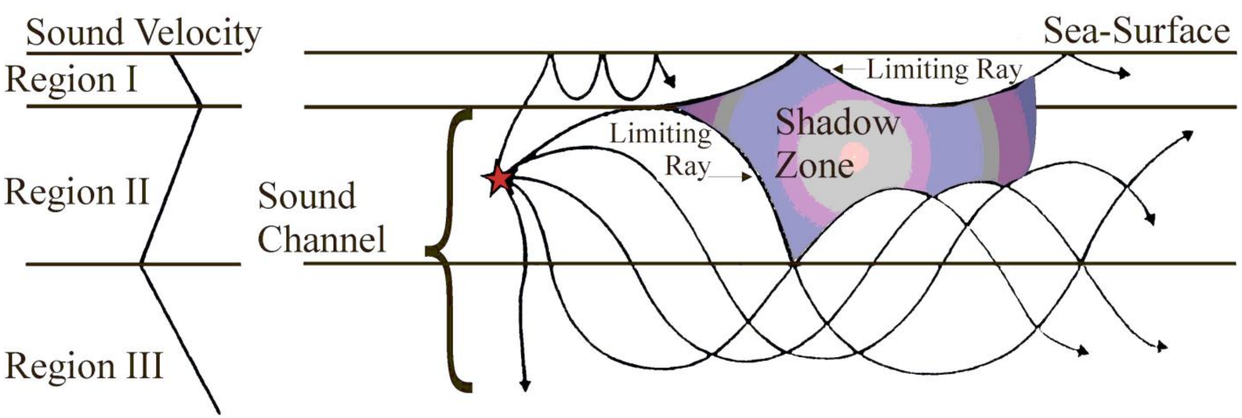
Refraction – Deep Sea Sound Channel creates a ~ 2-D acoustic waveguide at a certain depth where sound velocity in the ocean is minimal, and thus allows sound to spread for thousands of kilometers through the combined actions of **refraction** and ~1/R **geometric spreading** (remember that for 2-D, waves 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 surface sound channel, 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

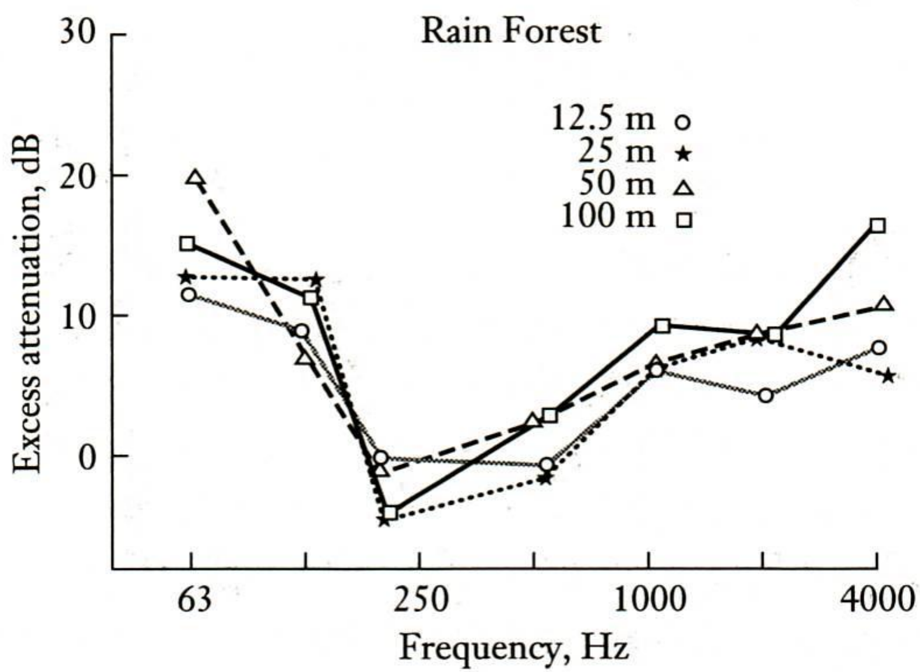
Deep sea channel:
Refraction + 1/R spreading

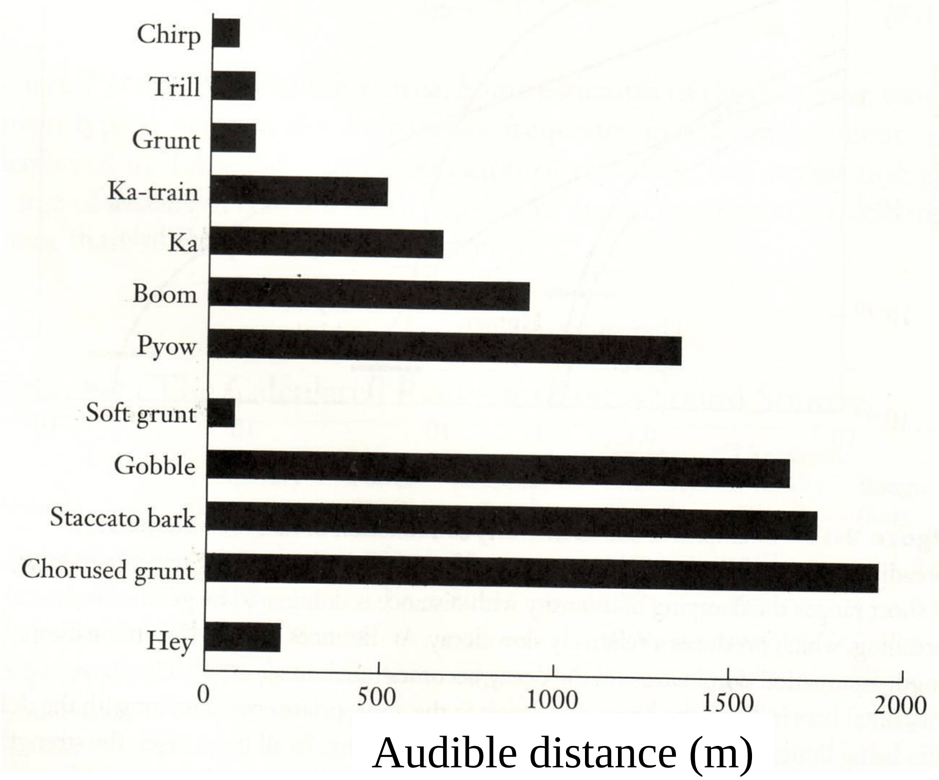
100 km

1. Wave propagation (light and sound)

Refraction – "Sound window" @ 200 – 500 Hz 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.

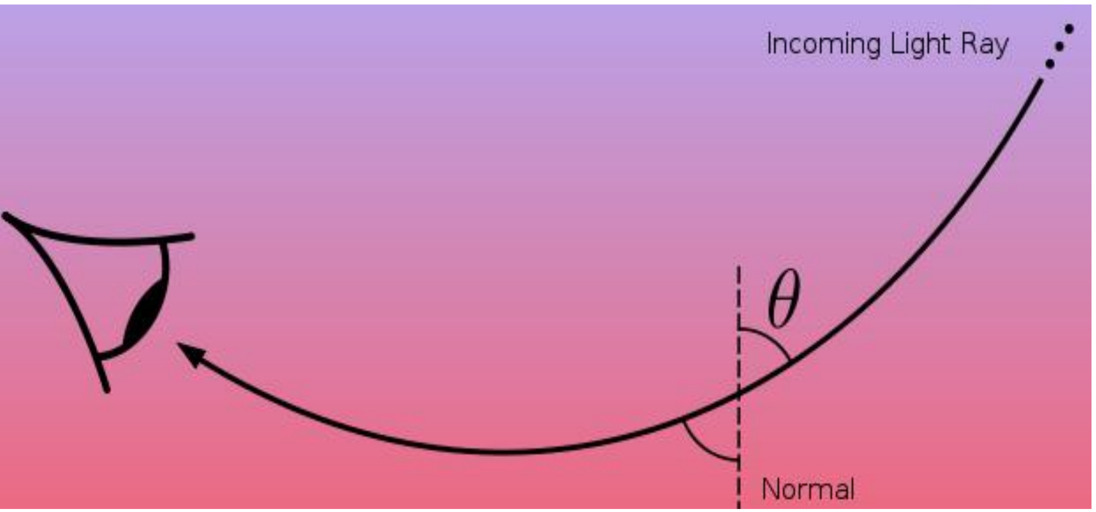
Many of the long-distance monkey vocalizations are @ 200 – 500 Hz, utilizing this sound window.





1. Wave propagation (light and sound)

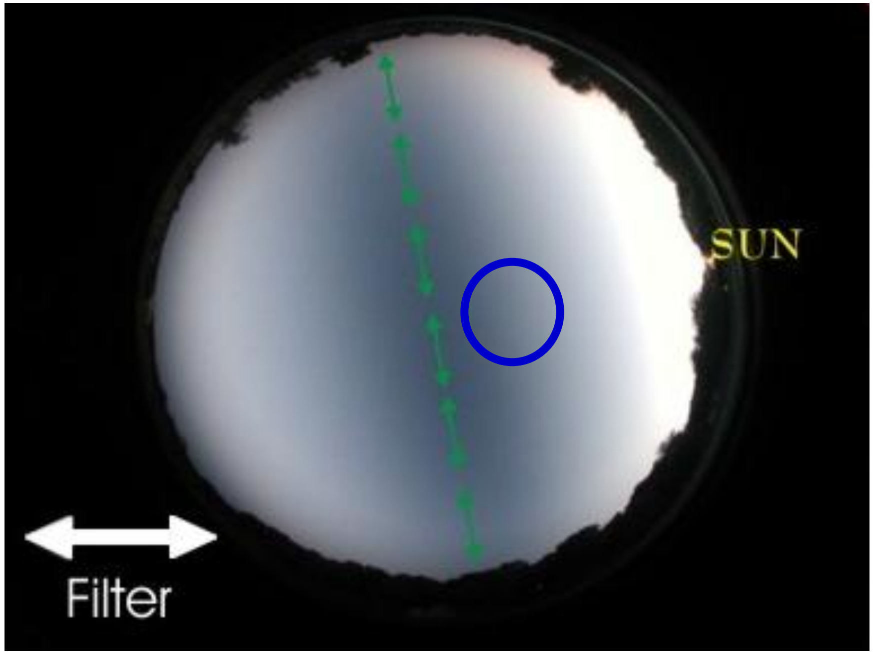
Refraction – Mirage.



1. Wave propagation (light and sound)

Scattering – creates two interesting effects:

- **Why is the sky blue?** Because scattering ~ $1/\lambda^4$ (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)



Fish-eye sky photo through horizontal polarization filter

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.

Stimulus transmission

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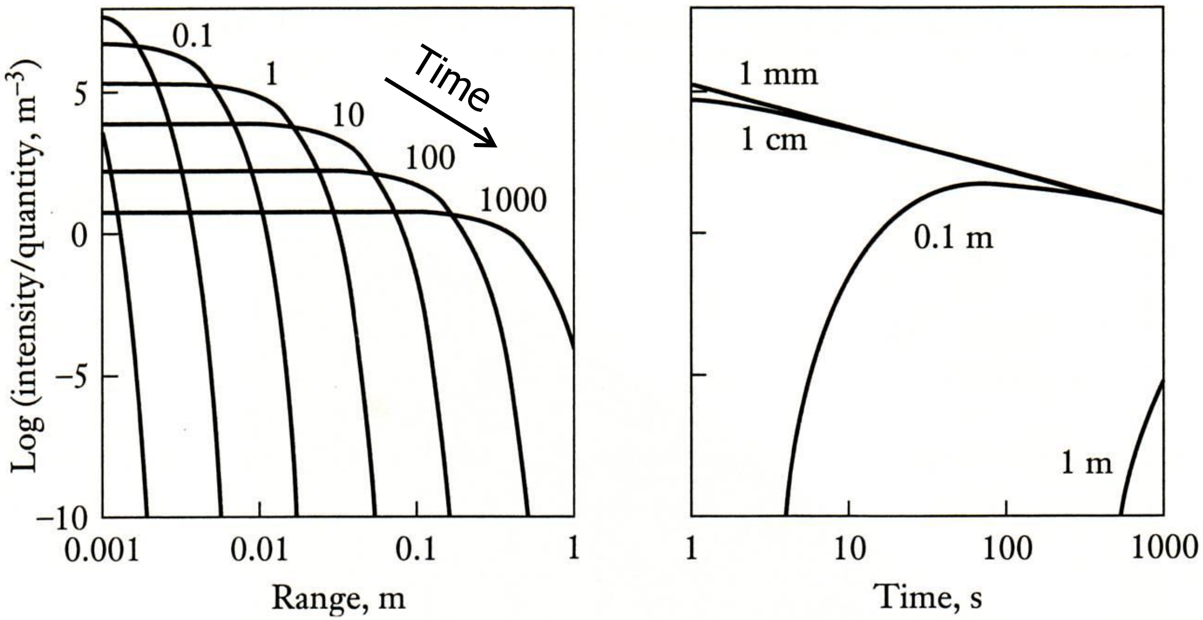
- **3. Flow:** Heat and Chemicals (olfactory and gustatory)

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 flow 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 – using air bubbles

Movie 1

Movie 2

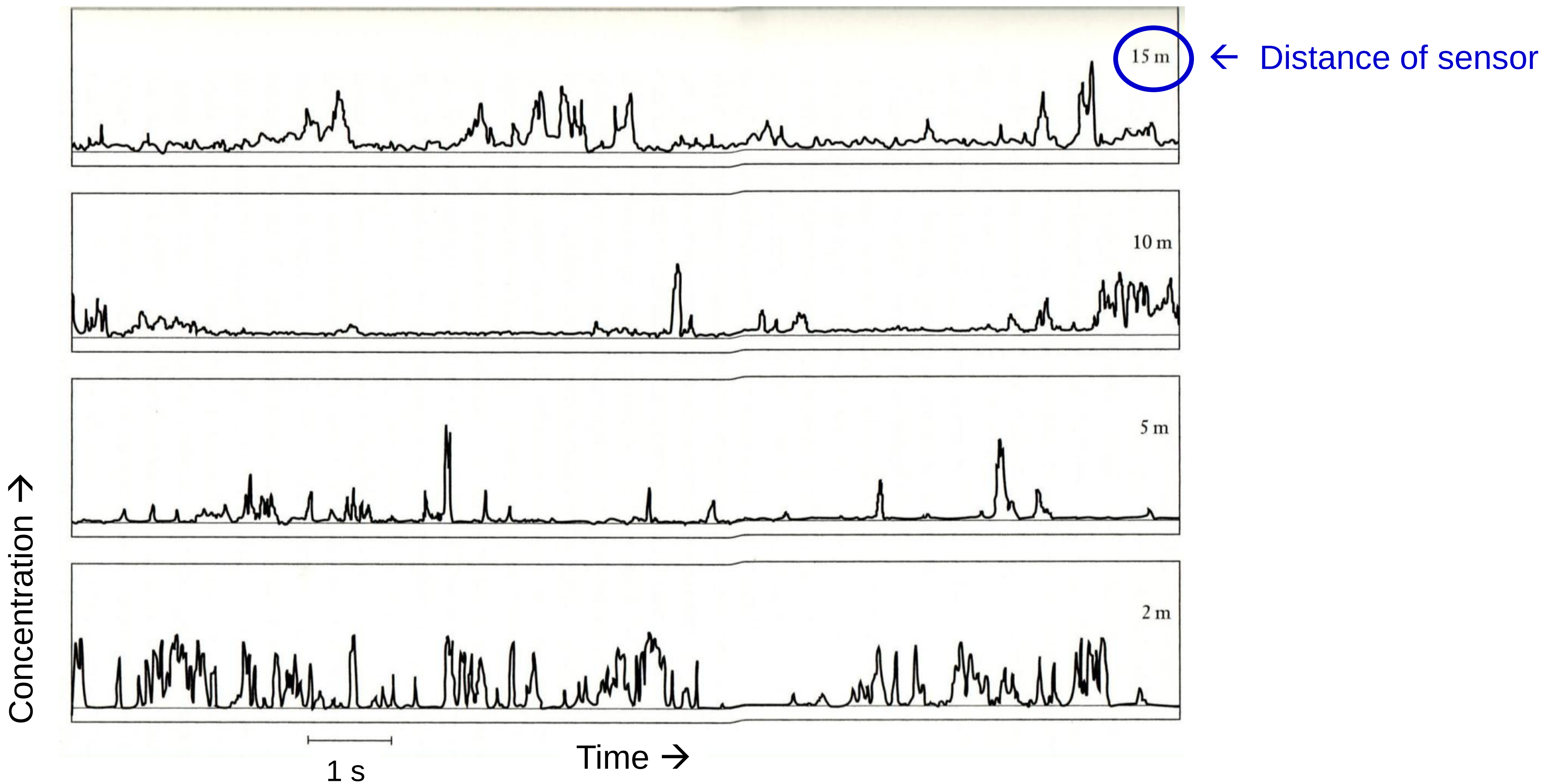
K. Catania, *Nature* (2006)

3. Flow

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

3. Flow

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



3. Flow

Wind: The problem with wind is that it creates turbulent flow = intermittent 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 for olfactory search (Vergassola et al., *Nature* 2007)
- When studying the neural basis of olfaction, you need to understand the **natural stimulus statistics** of odors

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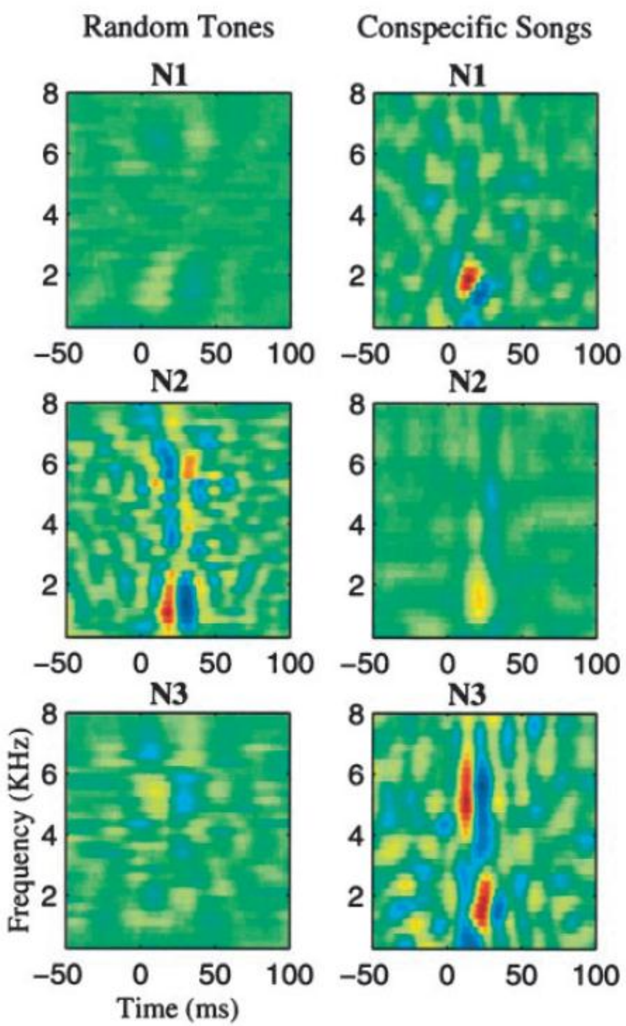
Natural stimulus statistics and neural activity

Neurons respond <u>differently</u> 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)

→ This means that using artificial sounds to study the auditory system – as has been done for the last half century – has very limited utility if we want to understand how the auditory system processes real-world, natural sounds.

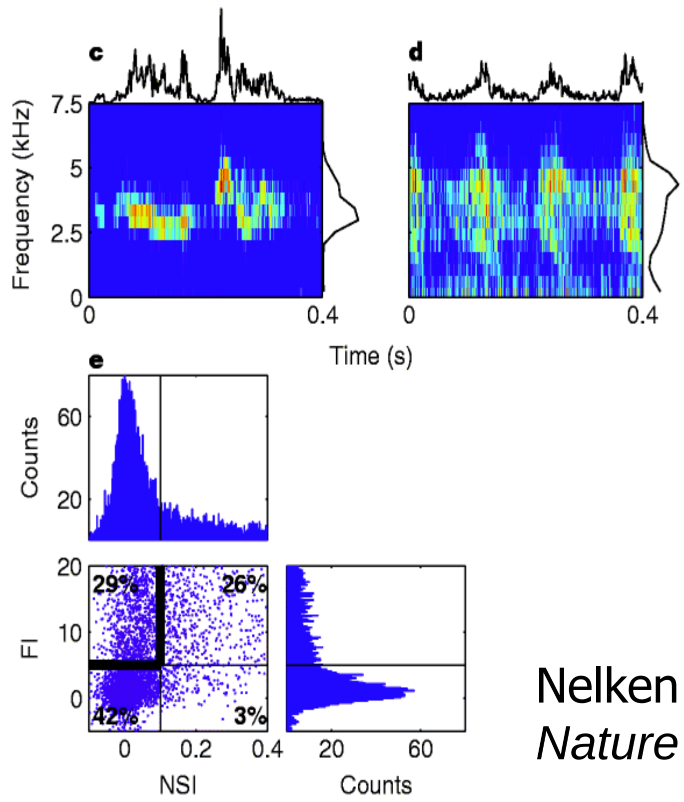
→ We must understand in-depth the natural stimulus statistics of auditory soundscapes.

→ similar results were found also for Vision.

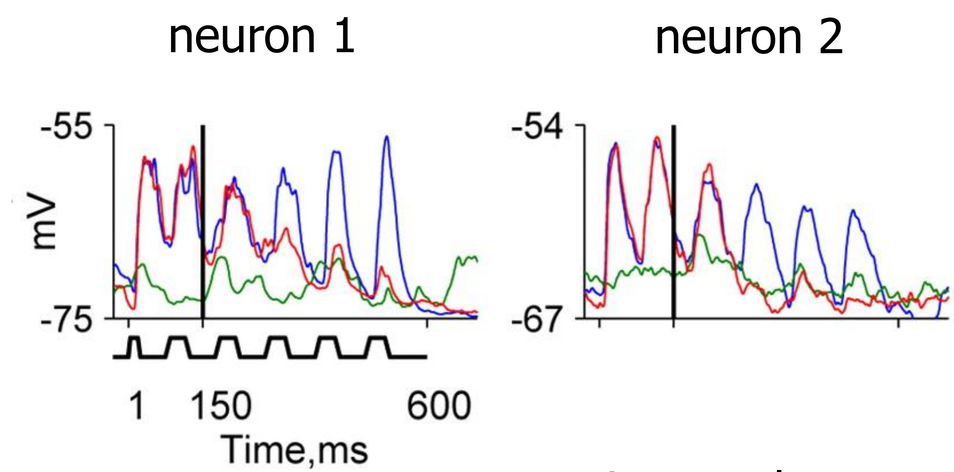
Natural stimulus statistics and neural activity

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)

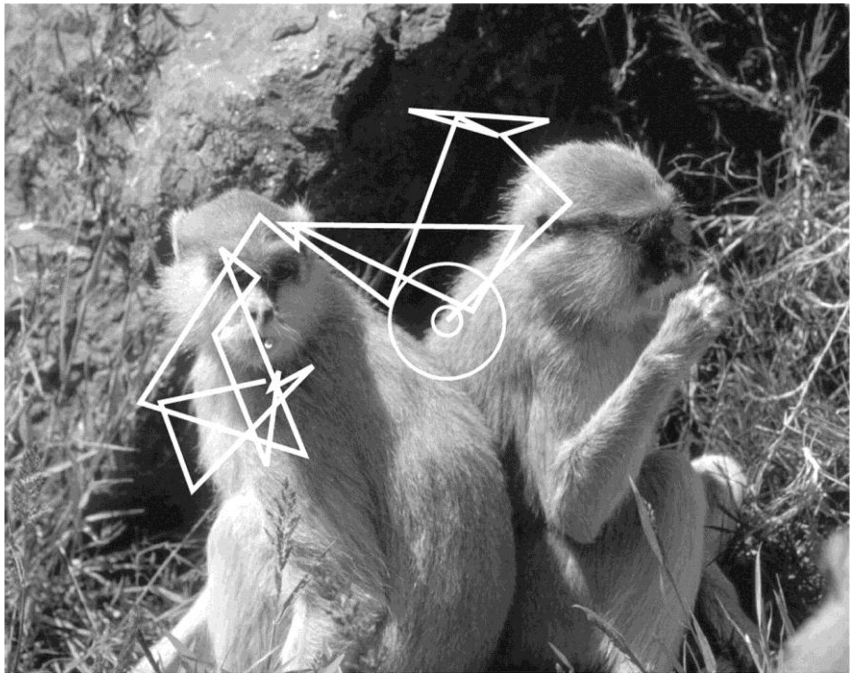


Las et al.
J. Neurosci. (2005)

Natural stimulus statistics and neural activity

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

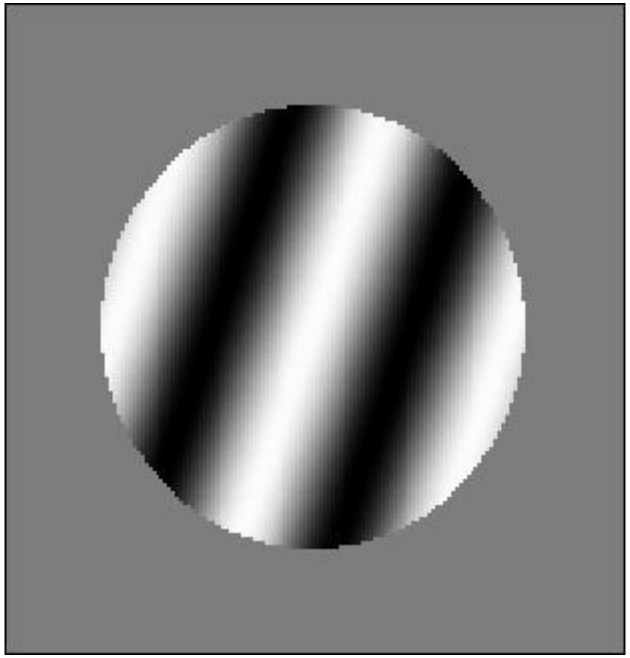
- **Responses** of visual neurons
- Modeling the **development** of response properties (receptive fields) of visual neurons
- Visual system **function**: The large eye movements (saccades) and microsaccades pose a serious problems for classical theories of vision – while active-sensing theories suggest that vision works *through* the eye movements.



Vinje and Gallant, *J. Neurosci.* (2002)

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

Natural *stimulus* statistics is also tightly linked to natural *movement* statistics



Question: When do you ever have, in the natural environment, moving-grating or moving-bar stimuli as were used by Hubel & Wiesel, and as used to this day in most studies of visual neuroscience ?

Answer: Almost exclusively due to the animal's *own* movements.   It is only then that the trees, houses are other line-elements in the scenery start moving coherently on the retina.

→ Perhaps, then, motor signals are represented in V1 ?

Natural *stimulus* statistics is also tightly linked to natural *movement* statistics

Dissociating visual inputs from movements in a virtual (VR) setup:

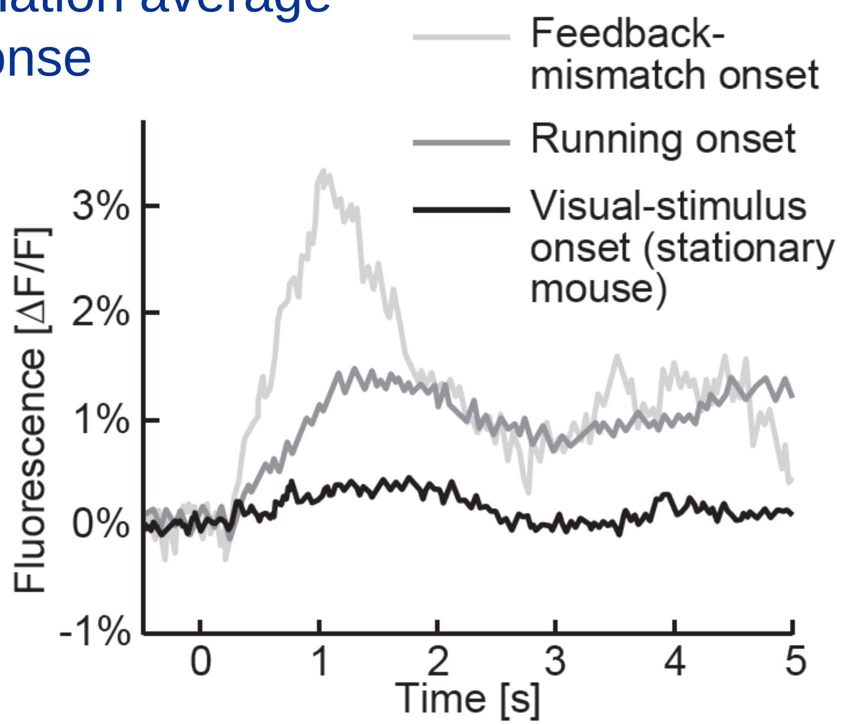
Movie 1 – Mouse behavior in VR

Movie 2 – Calcium imaging of neural activity

Keller et al., *Neuron* (2011)

Natural *stimulus* statistics is also tightly linked to natural *movement* statistics – and this coupling affects neurons

Population average response

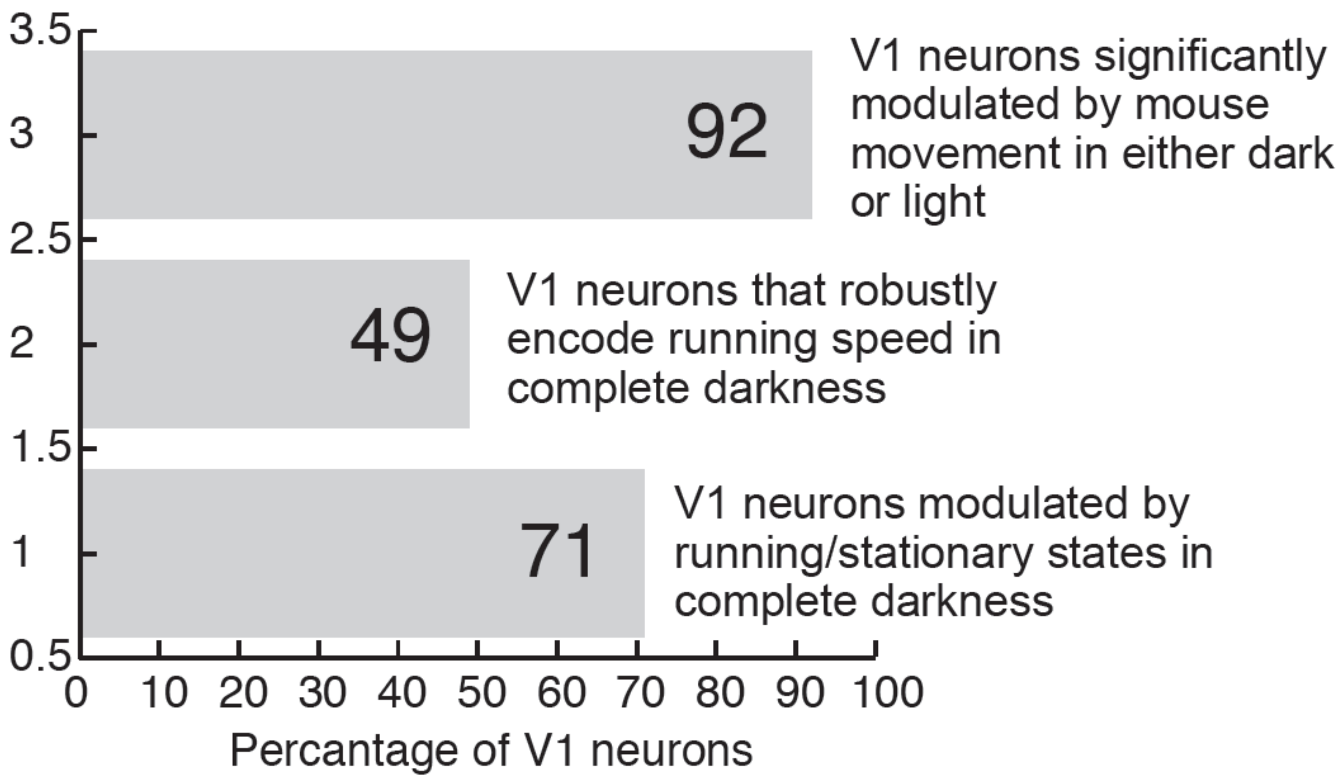


→ Surprisingly, the majority of neurons in mouse V1 did *not* encode purely passive visual stimuli, but responded to either congruence or incongruence ("feedback-mismatch") between vision and the animal's own movements.

→ How many of Hubel and Wiesel's original neurons were in fact Mismatch cells – and *not* pure visual cells ?!

Keller et al., *Neuron* (2011)

Natural *stimulus* statistics is also tightly linked to natural *movement* statistics – and this coupling affects neurons



→ Several additional VR studies showed similarly strong effects of locomotion on V1 responses: e.g. Saleem et al. (2013).

Numbers Based on:
Saleem et al., *Nature Neurosci.* (2013)

Sensory Ecology – outline of today's lecture

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

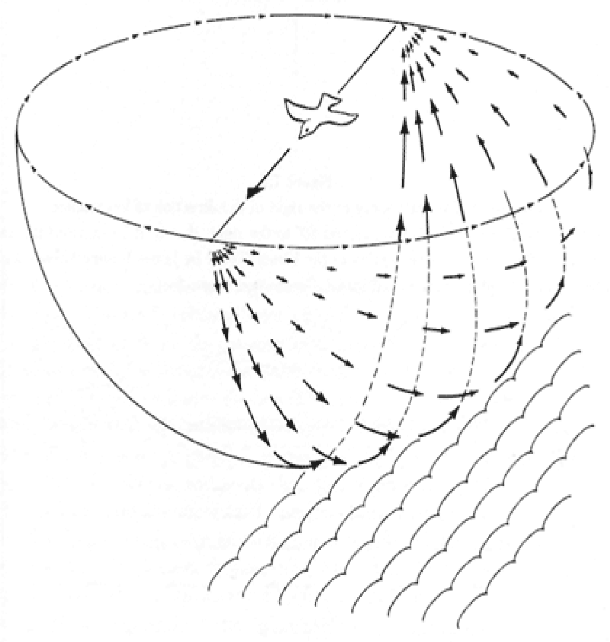
Three aspects of Sensory Ecology:

- **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

"The ecological approach to visual perception" – Gibson

Example #1: **Optic Flow** :

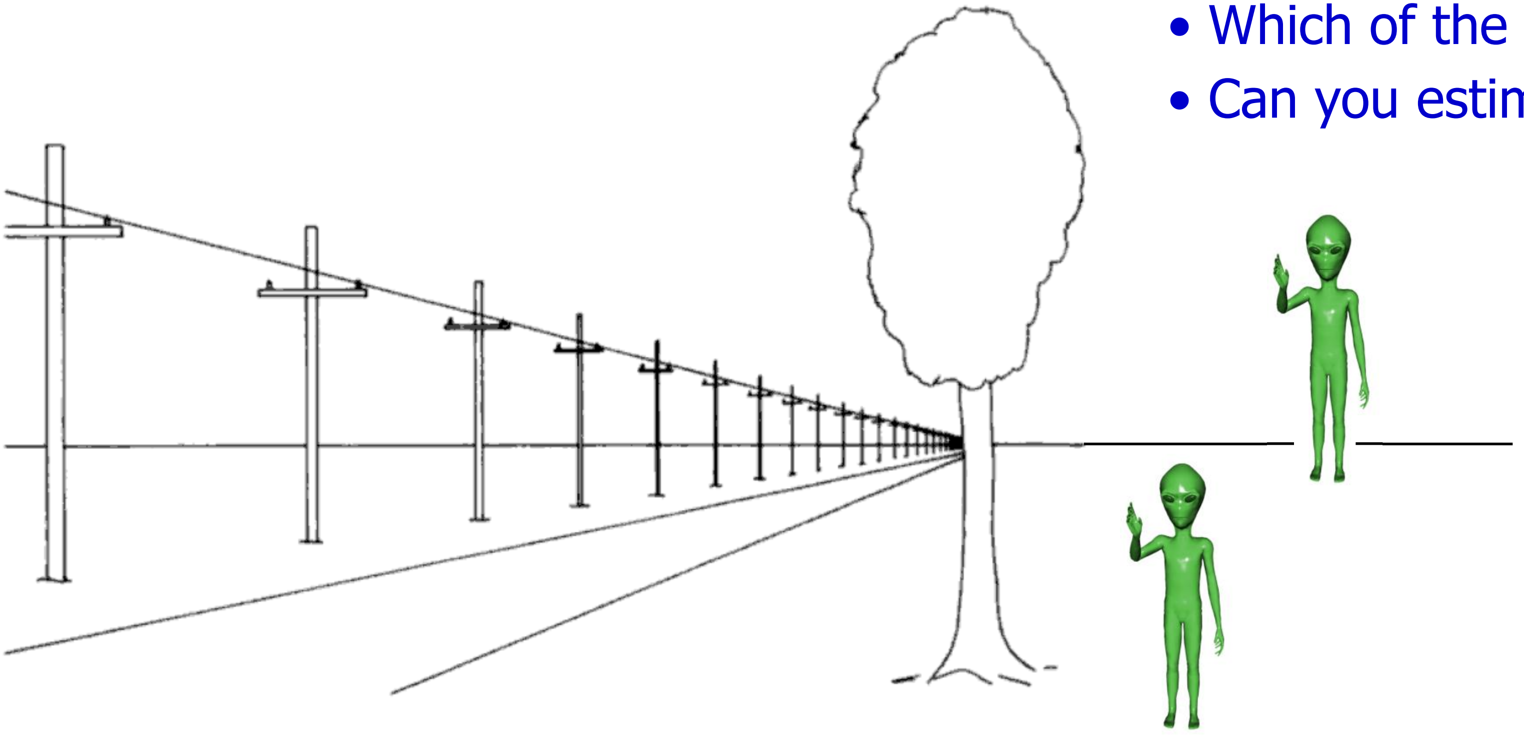
- The zero-point of optic flow allows estimating the **point of collision**, independent of cross-winds
- Geometric methods for directly estimating **time-to-collision** without complex calculations
- Optic flow is the main cue used by:
    - Pilots landing on aircraft carriers in rough seas
    - Honeybee 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 control the animal's Umwelt (surrounding world) in the laboratory – but it is also very important to fully understand 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.