Behavioral Neuroscience

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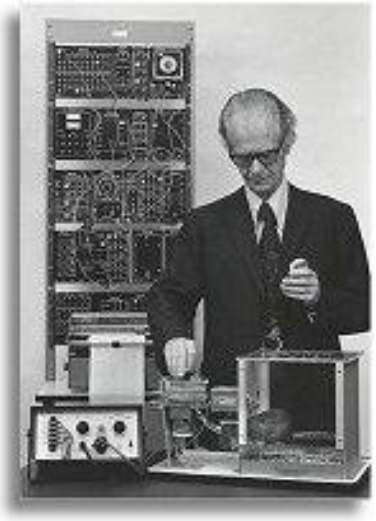
Lecture 1: Introduction to animal behavior- from classical ethology to neuroethology

Lecture 2: Social behavior and brain sexual dimorphism- Hormonal and genetic regulation

Lecture 3: The new era in the study of brain mechanisms underlying social behavior in animal models- pros and cons

Behavioral Neuroscience

Introduction to animal behavior:
from classical ethology to neuroethology



Why should we care for animal behavior

Knowledge of animal behavior = human survival

For example, understanding behavior of animals hunted for food

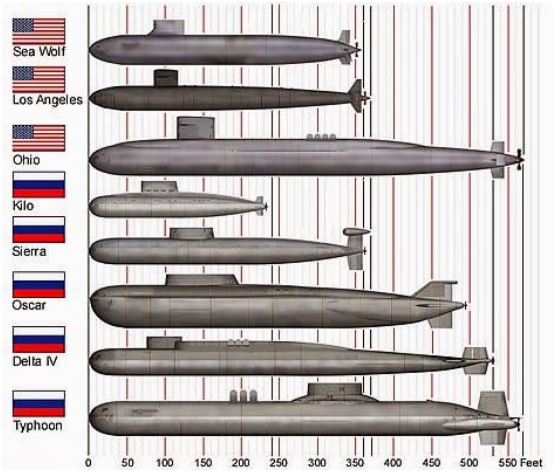
* Cave animal paintings (**ca. 30,000-10,000 BC**)

Why should we care for animal behavior

May shed light on human beings behavior- many behaviors are conserved across species
(e.g. territoriality/aggressive behavior, dominance hierarchy, sexual behavior)




Conserved behavior: aggressive behavior- size comparison



What is behavior?

- The total movements made by the intact animal (Niko Tinbergen)

- Anything an organism does that involves action (either alone or with other animals) and/or response to a stimulus" (Wallace et al 1991)

  -Stimulus can be external (environment) or internal.
  For example: Searching for food is triggered by food smell (external) when hormonal changes (internal) sign hunger state

- Behavior can be defined as innate (e.g. reflex) or learned behavior

What is behavior?

- Behavior is crucial to the survival of the individual and of all species, serving a few main purposes that allow animals to: mate, find food (eat), avoid predators, raise young

- Natural selection (Darwin) acts on behavioral traits as on other physical traits.

  -Favors animals who present beneficial behavior (promoting reproductive success/production of offspring) and disadvantages/reduces fitness to those that present unhelpful/"stupid" behaviors

Causes of Behavior

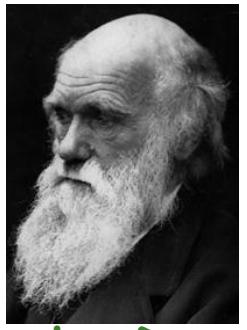
Animals behave in ways that maximize their fitness

Fitness = the ability to survive and reproduce

Behavior adapted to the animal's niche

- Animal's behavior evolved through the animal's interaction with its environment
- Animals adapt to environmental conditions they encounter in their surroundings
- **Adaptation** = any characteristic that enhances an organism's survival or reproductive success
- **Environment** = the living (biotic) and non-living (abiotic) surroundings of an organism

Darwin's theory of natural selection of behavior (evolution of behavior)



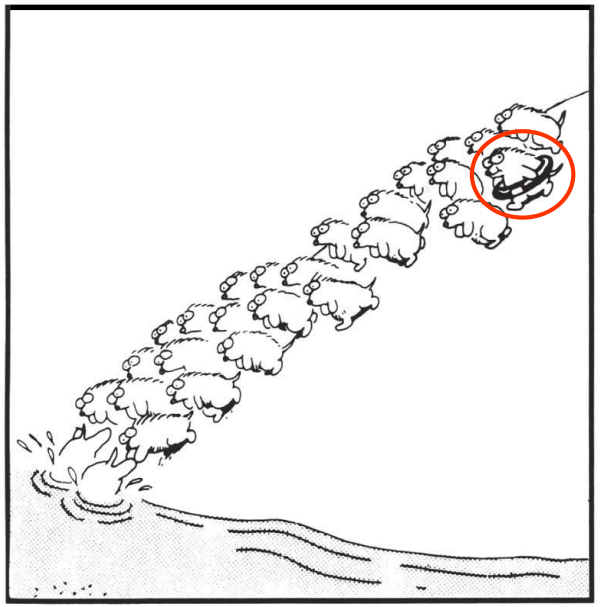
Charles Darwin
(1809-1882)

1. Variations also exist in behavioral traits

2. Some of these behavioral variations are heritable

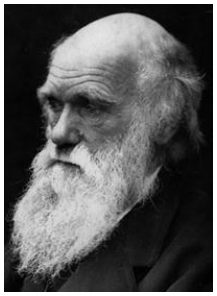
3. Certain behavioral variations make individuals better adapted to their environment

4. These individuals have the chance to survive longer and leave more offspring than those with less successful behavioral traits



ANIMAL BEHAVIOR, Eighth Edition, Figure 1.13 © 2005 Sinauer Associates, Inc.

Sexual selection of behavior



Darwin realized that some (behavioral) traits directly relate to mate acquisition and mate choice.

He termed this evolutionary process "**sexual selection**".

Sexual Selection "…depends on the success of certain individuals over others of the same sex, in relation to propagation of the species..."

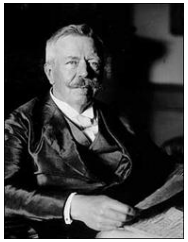
Charles Darwin 1871

Example: Sexual selection of behavior
Courtship behavior

The animal "Umwelt" (environment)

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 (behaviors) that are performed by each species.

Von Uexküll (1921) intended his idea of the *umwelt* to apply principally to physical stimuli (i.e. water, food, shelter, potential threats, reference for navigation).



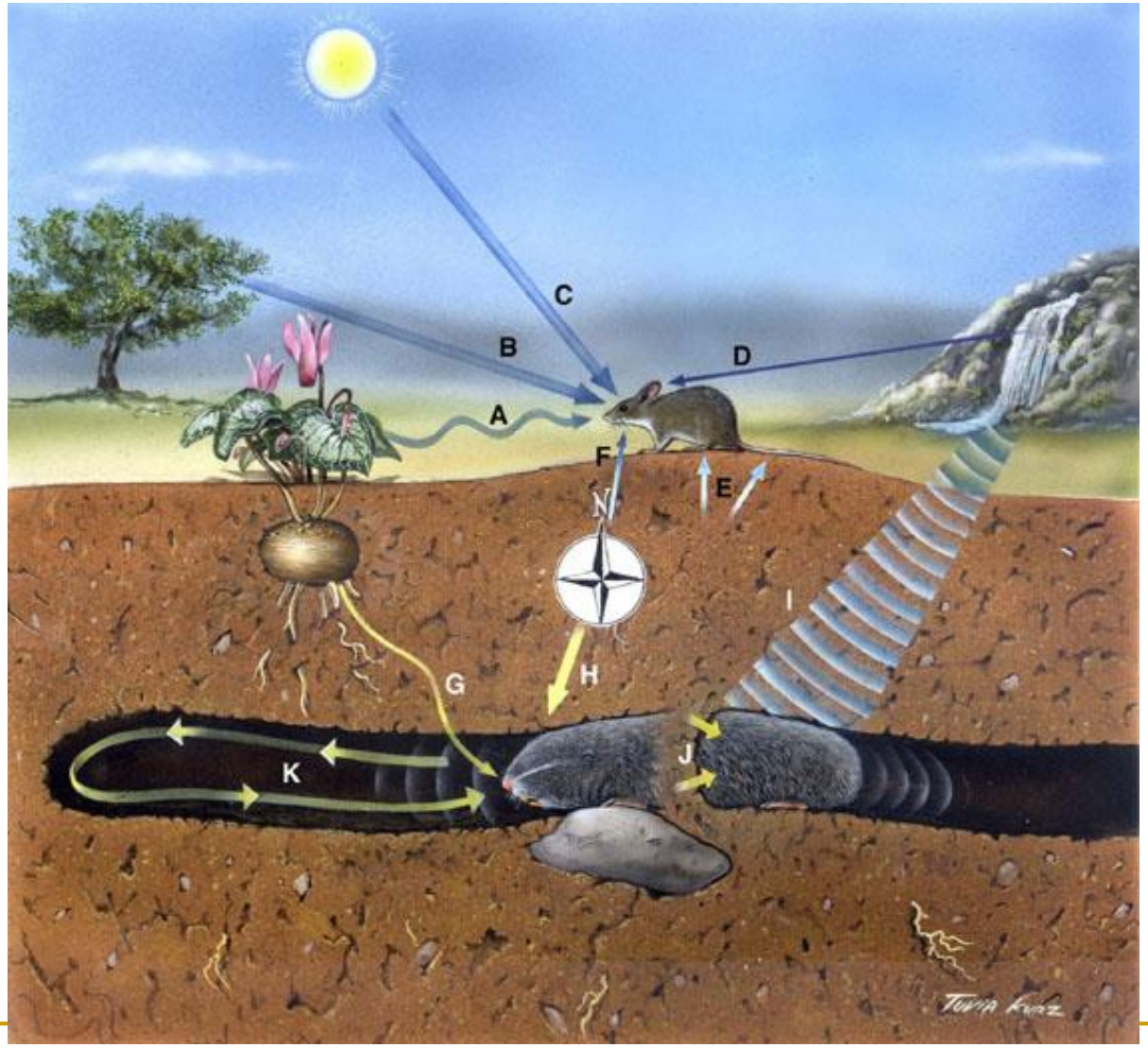
Jakob von Uexküll
(1864-1944)

Lorenz (1935) extended this concept by recognizing that animals also have a social *umwelt* since signals from other individuals can have important influences on their behavior.

Konrad Lorenz
(1903-1989)

These signals are perceived by a set of sensory channels that are adapted to the survival needs and the niche (biotic and abiotic components) of each unique species

The umwelt of a surface-dwelling rodent vs a subterranean rodent



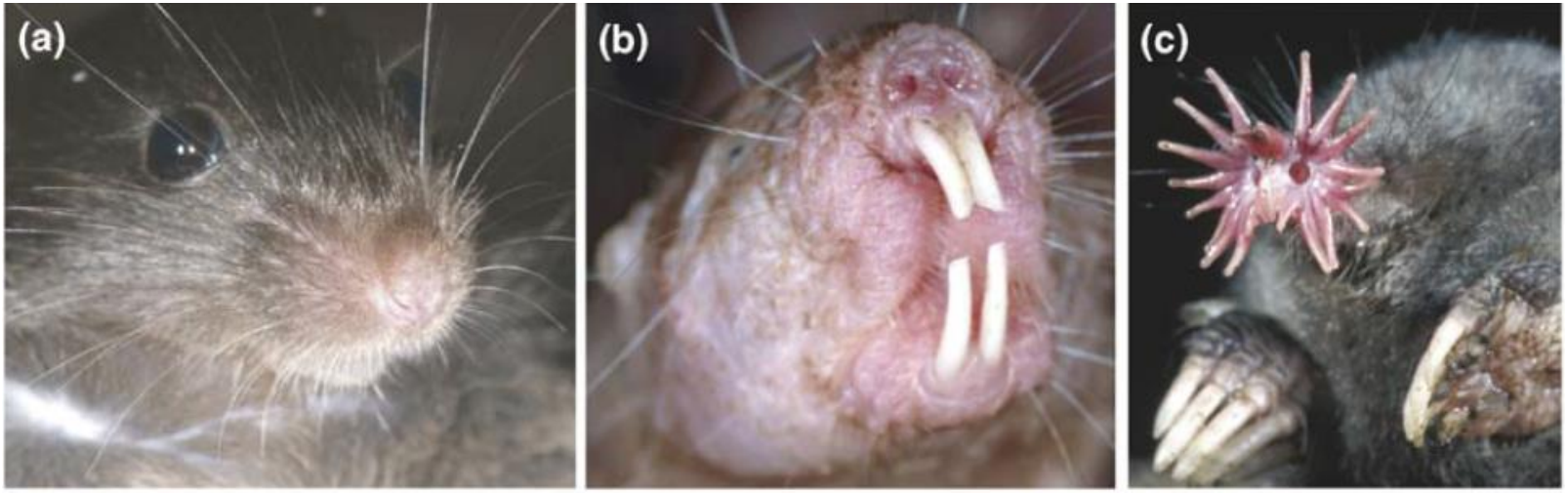
Species-specific sensory adaptation to the unique niche

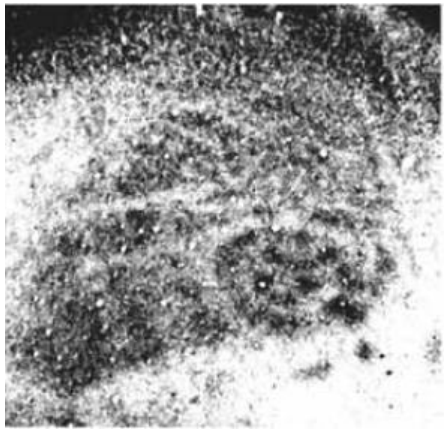
Species-specific somatosensory map in the cortex of 3 rodents

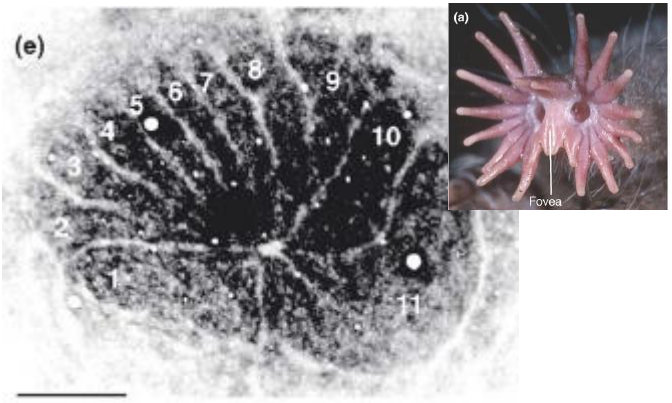
Mouse

Naked mole rat

Star mole rat





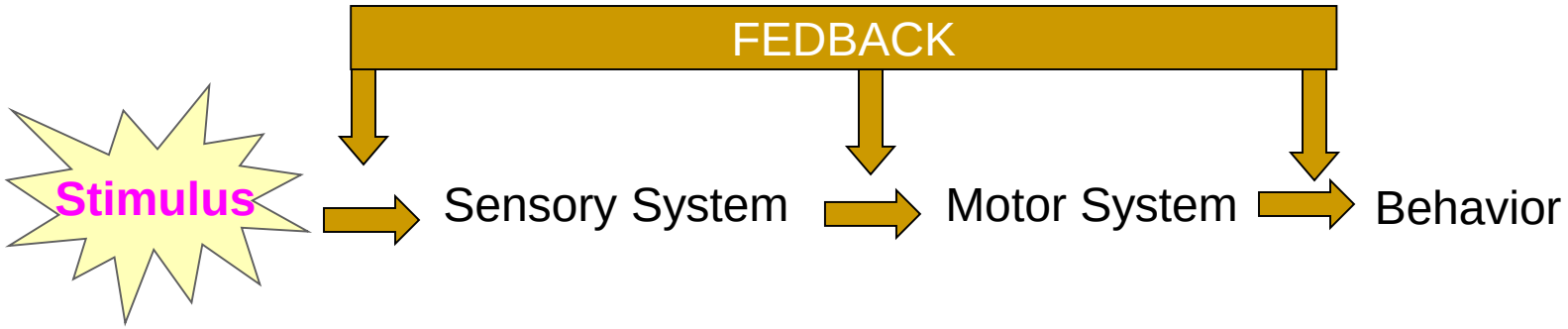


Catania and Henry 2006, Curr Opin Neurobiol

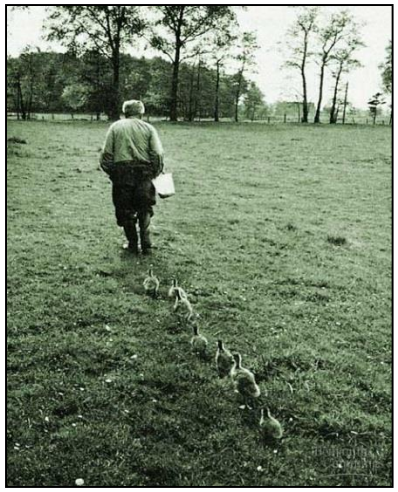
Innate versus Learned behavior

Learned Behavior

- Behavior that is modified by experience (trial and error pattern)
- Flexible. Phenotype is changing with time/experience
- Often affects even innately programmed behaviors



Learned behavior



Japanese macaques on Koshima Island

-One female started washing sand off of sweet potatoes

-Others imitated her; they later taught their offspring to do so. She later learned to do this with grain

-Her peers imitated her; the older males did not!

Instinct (innate) Behavior

- First time performance is completely functional
- Animals don't have to witness the behavior (inborn)
- Uniform, stereotyped
- Triggered by simple sign stimulus (sensory releaser)
- It has a strong genetic (inherited) basis: control by pre-programmed fixed neurological circuitries

Innate behavior

avoid predator, find mate, get food


© D.O'Daniel

Innate behavior of the Cuckoo bird

Young cats learning to hunt.

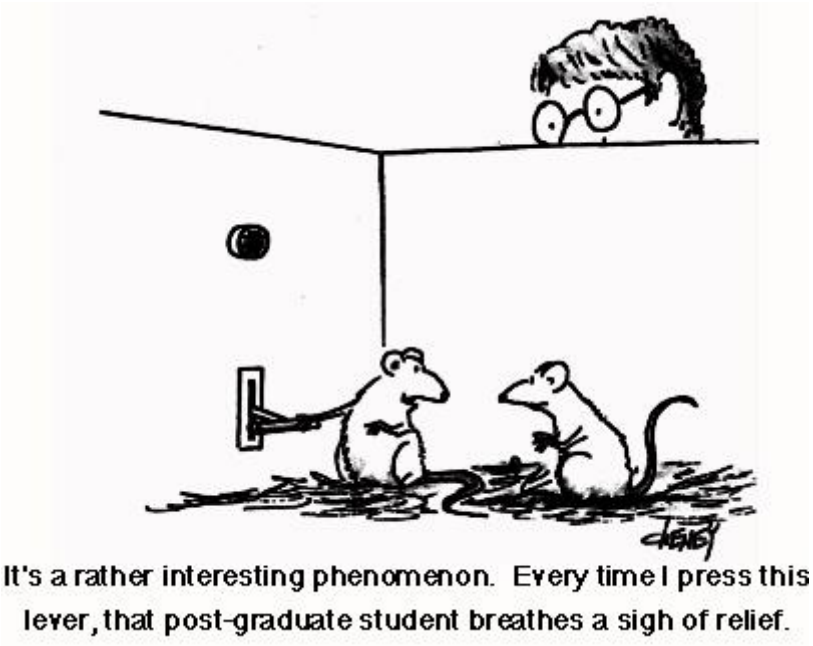
Instinct to chase (nature) combined with learning how to stalk and kill.

The only truly innate behaviors in **humans** are called **reflex behaviors**. They occur mainly in babies. Like innate behaviors in other animals, reflex behaviors in human babies may help them survive.

An example of a reflex behavior in babies is the **sucking reflex**. Newborns instinctively suck on a nipple that is placed in their mouth. It increases the chances of a baby feeding and surviving.
Another example of a reflex behavior in babies is the **grasping reflex**.

Two ways to study animal behavior

Ethology approach



Behavioral neurobiology approach

Ethology

- Study of naturalistic animal behavior and its relationship to its evolutionary origins

- Whole animal approach- the animal kept under conditions as natural as possible (preferably field observation)

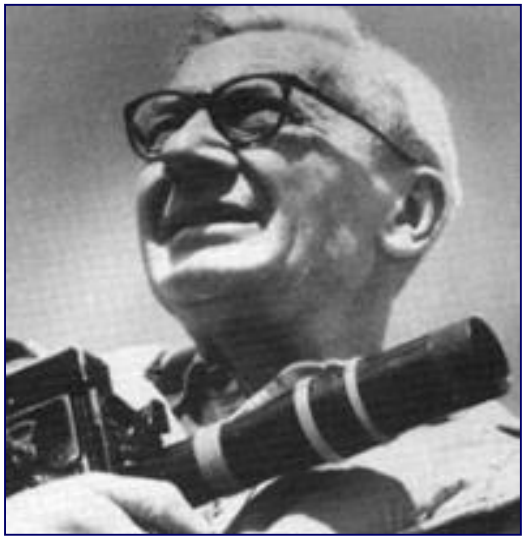
- An ethological research program starts with picking the right animal model for the research question, and it encompasses the four questions about animal behavior (Tinbergen Niko, 1963).

- These questions relate to proximate causes, that is, immediate causation and development and to ultimate causes, that is, adaptive significance and evolution

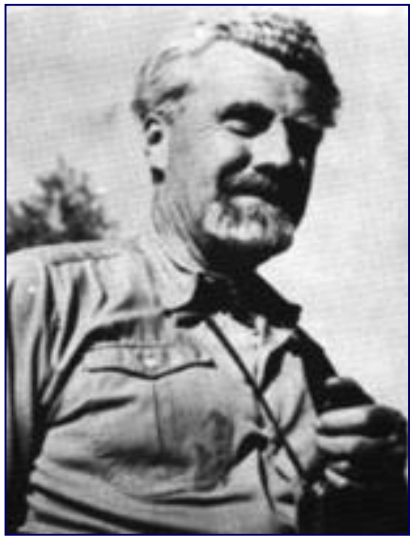
3 ethology founders:

- Karl von Frisch – Honeybee communication
- Niko Tinbergen – Fixed action pattern
- Konrad Lorenz - Imprinting

Founders of animal behavior study in the natural habitats (Ethology)



Niko Tinbergen
(1907-1988)

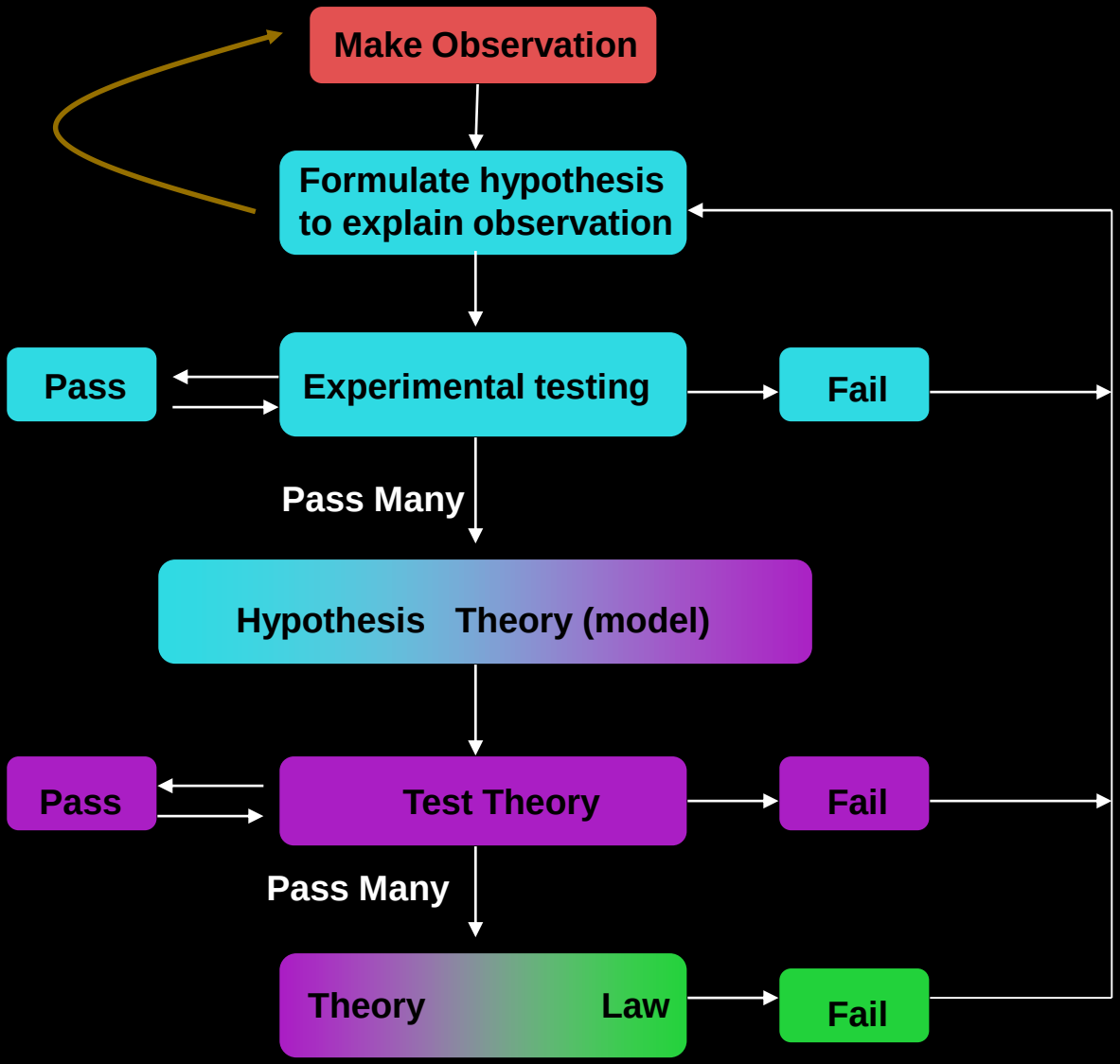


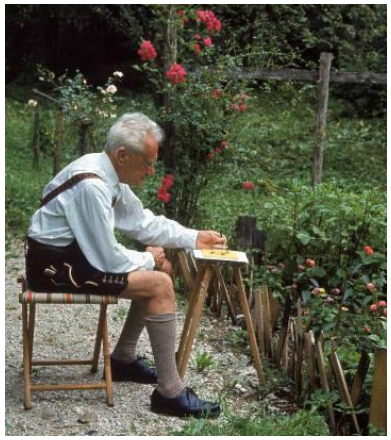
Konrad Lorenz
(1903-1989)

Karl von Frisch
(1886-1982)

The Nobel Prize in Physiology or Medicine 1973
"for their discoveries concerning organization and elicitation of individual and social behavior patterns"

Scientific approach



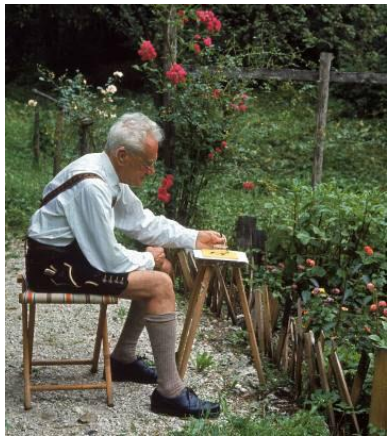


Bee communication- Karl von Frisch

- Pioneered studies in bee communication and foraging
- Demonstrated that honey bees use a dance language to communicate the location of food resources to other bees
- The waggle dance is used to communicate the position of a distant food source
- This dance communicates both the distance and direction using the sun, the hive, and the food source as reference points

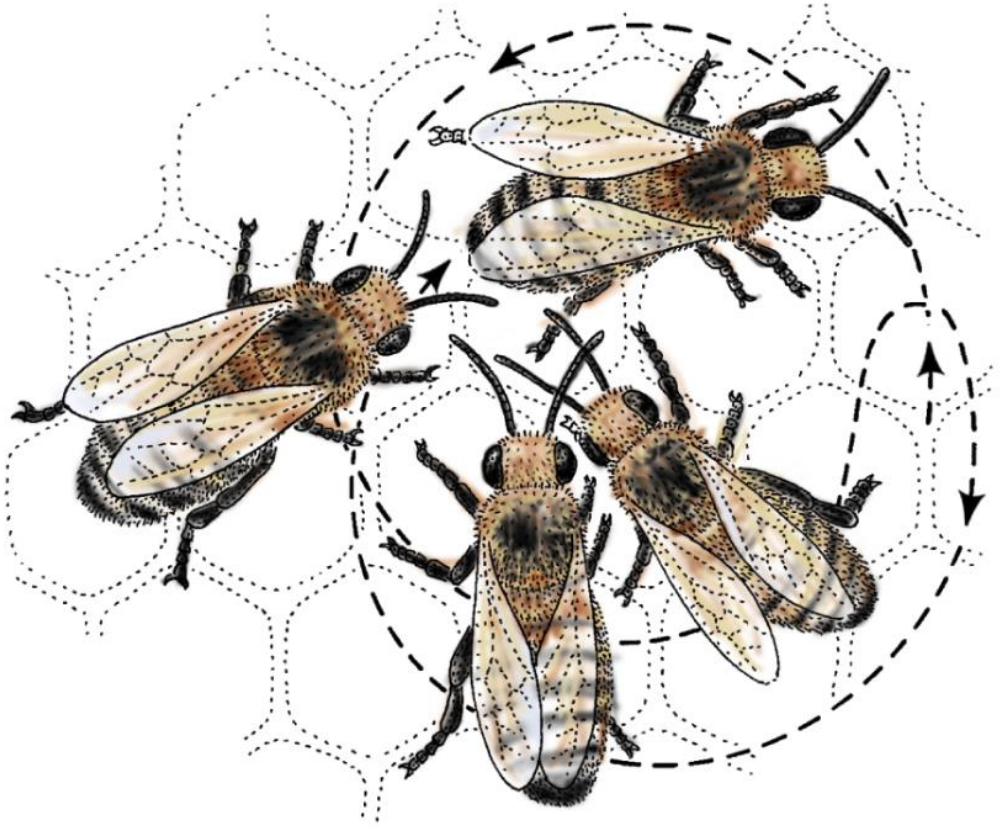
Bee communication- Karl von Frisch

- Trained European honey bees to feeders
- First believed bees used flower scents or other odors to find food sources
- Began to pay close attention to the dances performed by returning foragers
  - Dances very precise, with varying tempo and direction

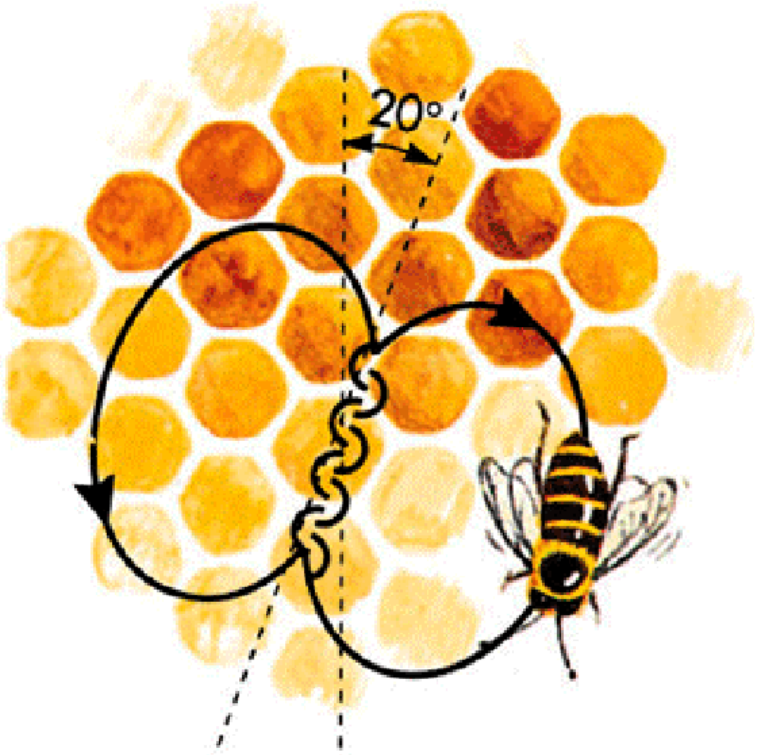


"Round dance"

When food source is
< 50 m from hive



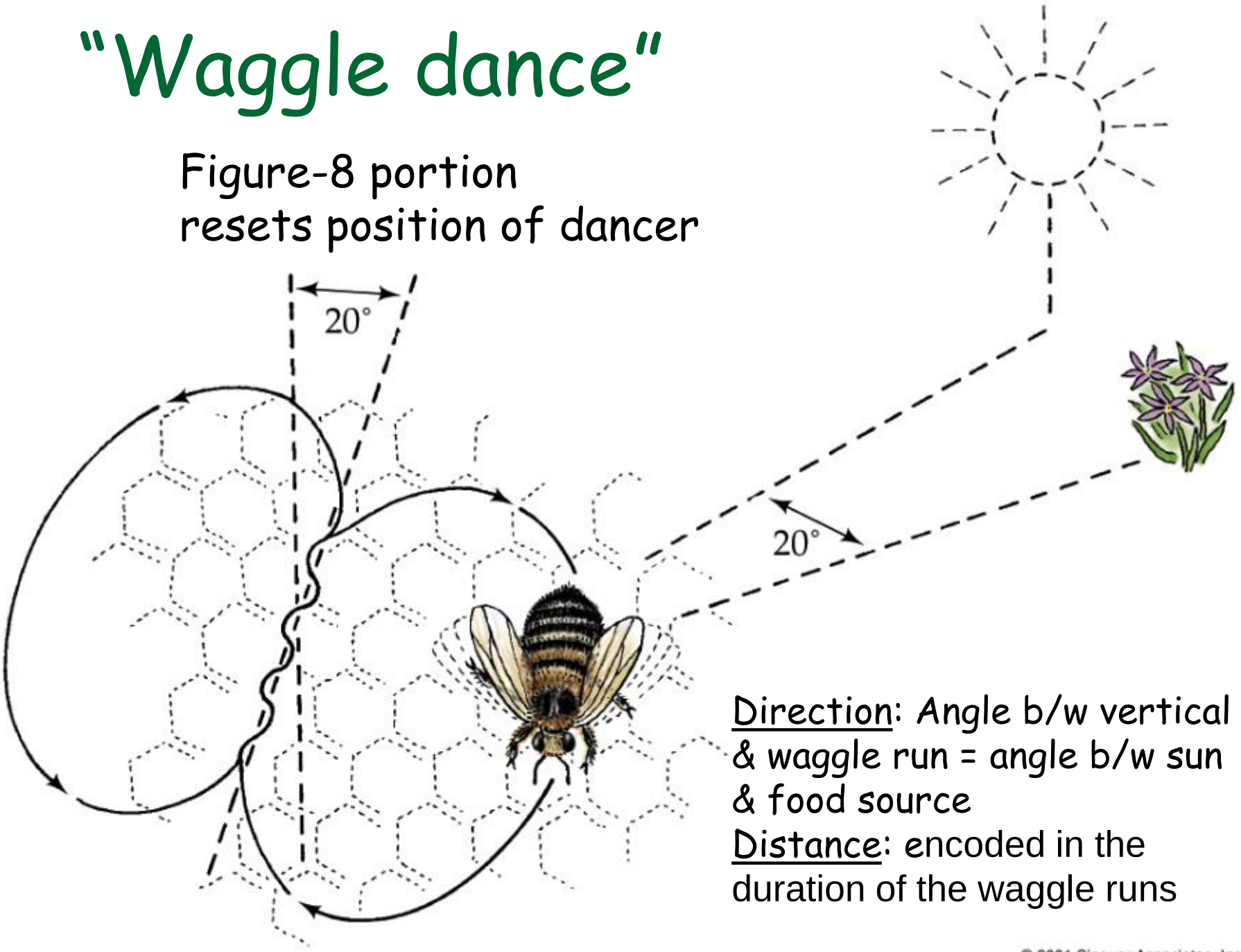
"Waggle dance"



When food source is
>50 m away from hive

"Waggle dance"

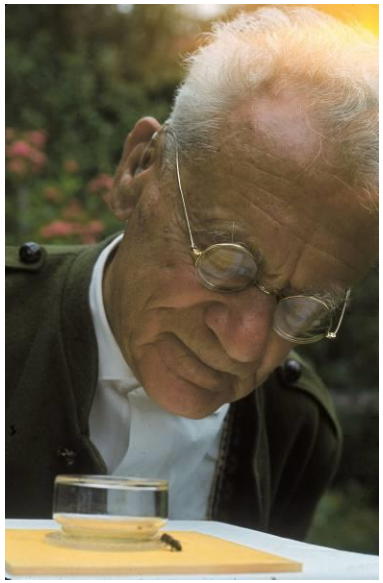
Figure-8 portion
resets position of dancer



Direction: Angle b/w vertical & waggle run = angle b/w sun & food source

Distance: encoded in the duration of the waggle runs

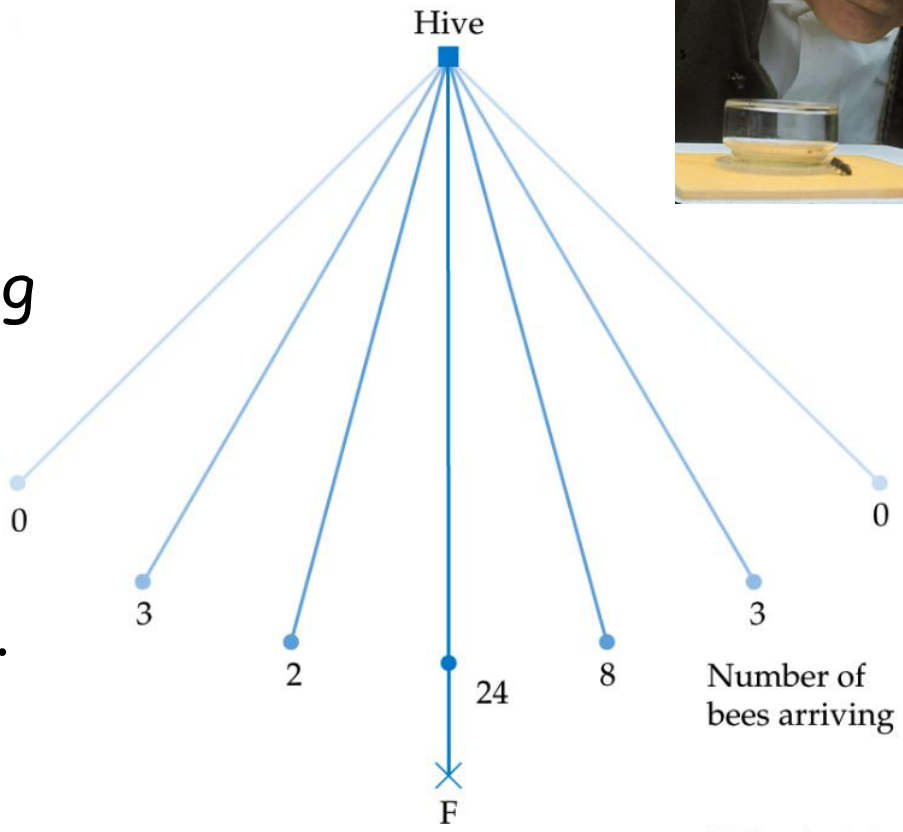
von Frisch's Experimental evidence



DIRECTION

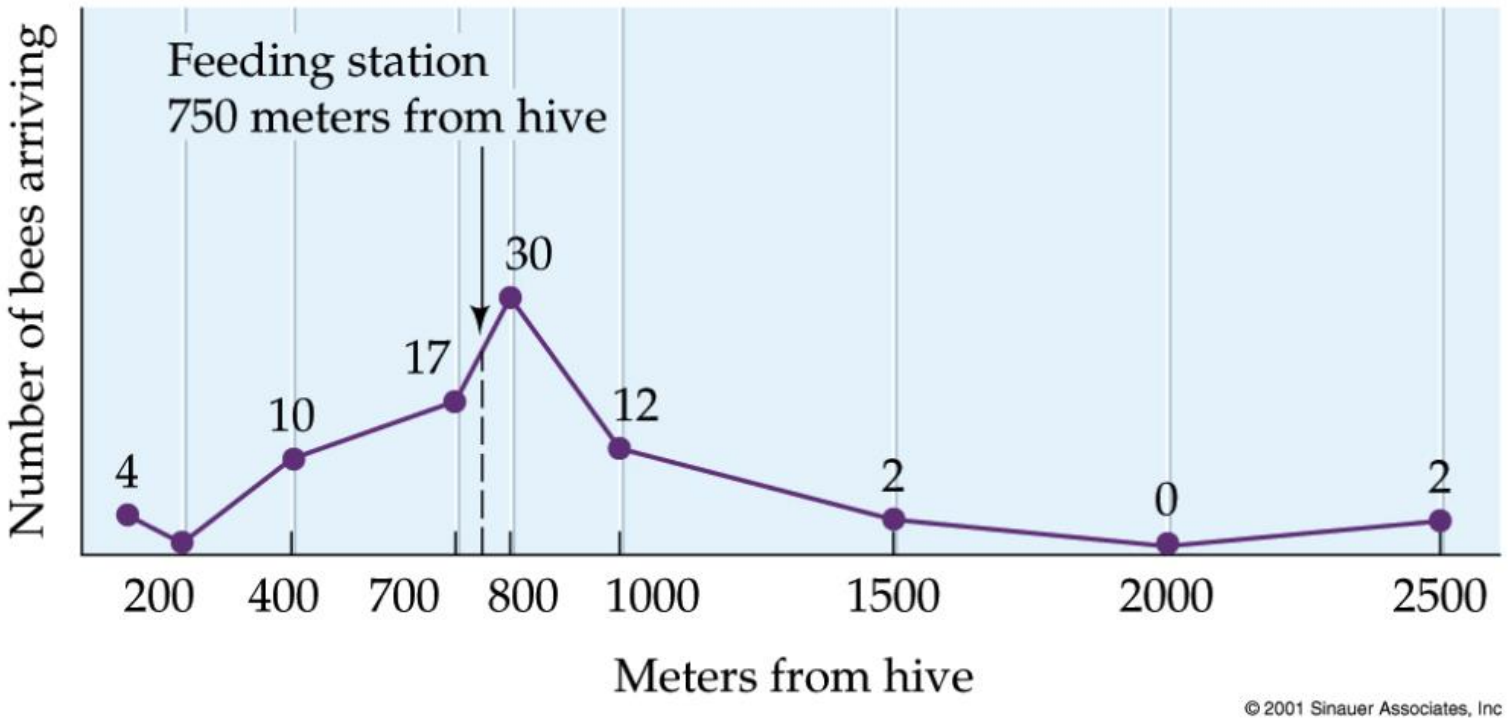
Train foragers to feeding station F.

Then, collect new recruits to all feeding stations (same distance).



DISTANCE

Train foragers to come to a feeding station 750 meters from the hive. Look at number of recruits to stations at various distances (same direction).

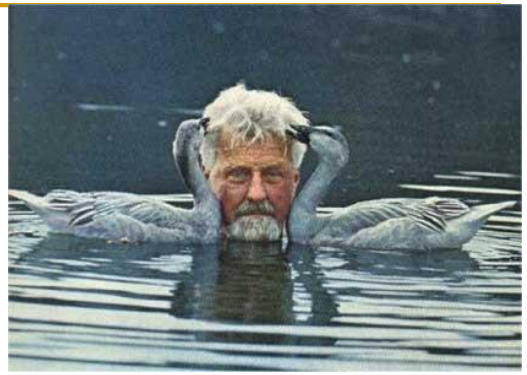


Learning who is your mother- Imprinting behavior

Imprinting Lorenz's testing

- Konrad Lorenz & Geese hatchlings
  - Behavioral observation: geese hatchlings closely follow their mother
  - Explanation: Mother-offspring bonding in animals is crucial to safety & development of the offspring
  - Hypothesis: Geese hatchlings follow the first thing they see that moves

Imprinting Lorenz's testing



Experiment: *A clutch of goose eggs was divided between the mother goose and an incubator (treated by Lorentz). Lorenz ensured that he was the first moving organism seen by the hatchlings.*

Results: *Goslings reared by the mother behaved normally and mated with other geese.*
-Goslings that spent their first hours of life with Lorenz followed him wherever he went, preferred humans for the rest of their lives and even tried to mate with humans.

Conclusions: *Greylags goose have no innate sense of "mother" or "gooseness". They identify with and respond to the first object with certain characteristics they encounter. The ability or tendency to respond is innate.*

Imprinting- Konrad Lorenz

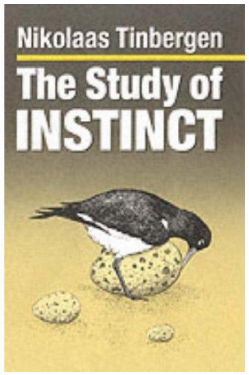
- Learned behavioral pattern that is dependent on innate mechanisms
- Learning that occurs during a sensitive or critical period in the early life of an individual
- Irreversible

Lorenz's work provided one of the first experimental evidence that there are critical learning periods in life where a specific type of stimulus is necessary for normal development.
-We could consider that imprinting is a kind of learning, albeit with a very strong innate element.

Imprinting for conservation

Conservation biologists have taken advantage of imprinting by young whooping cranes as a mean to teach the birds a migration route.

A pilot wearing a crane suit in an Ultralight plane acts as a surrogate parent.

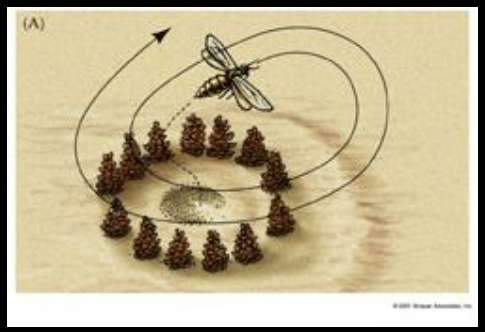


Fixed Action Pattern (Instinct) Nikolas Tinbergen

Nikolaas Tinbergen (left), Konrad Lorenz (right)

- Highly stereotypic behavior
- Triggered by a **sign stimulus** (external stimuli)
- When stimuli are exchanged between members of the same species, the stimuli are called **releasers**
- Once begun, the behavior will continue to completion
- In some cases, aspects of the FAP need to be learned (trained) in order to master the behavioral repertoire

Tinbergen's Observations on the Bee Wolf

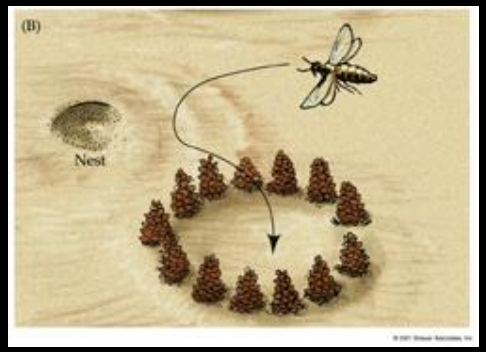


1. Observation - Female flies in a circle before going to hunt?

2. Hypothesis - Female is using landmarks to find the nest

3. Prediction - Female will return to a landmark to find the nest

4. Test - Place an artificial landmark around the nest and move it when the female is away



5. Result - Female orients to new landmark

6. Confirm hypothesis √

Tinbergen's Observations on the Bee Wolf

1. Question – Is the female responding to the cones or their scent

2. Hypothesis - Female is using visual cues to find the nest

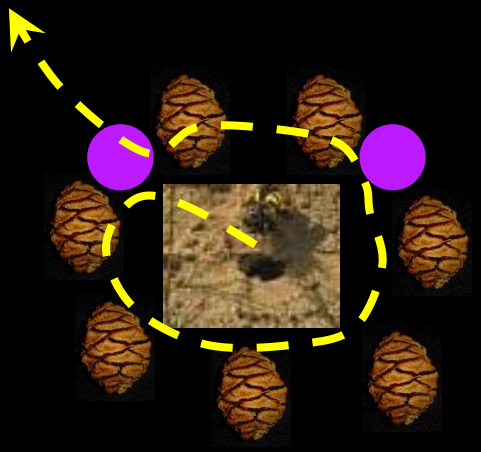
3. Prediction - Female will return to a landmark to find the nest

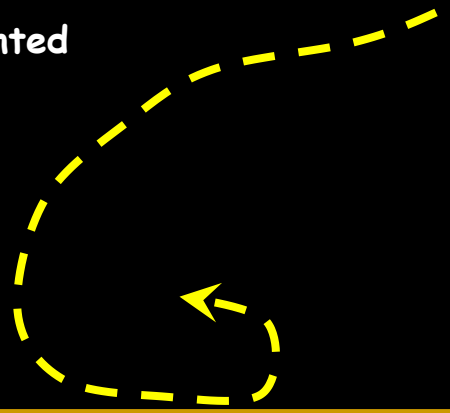
4. Test - Place an artificial landmark around the nest and include scented (pine oil) pads

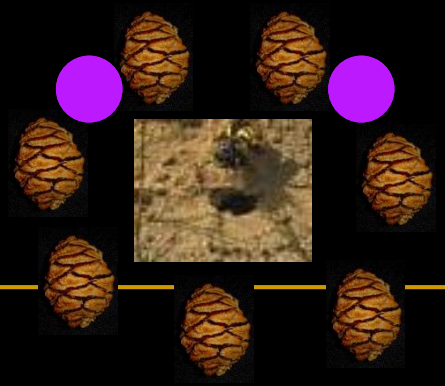
5. Move the cones and add unscented pads when the female is away but leave the scented pads at the nest

6. Result - Female orients to pine cones and not scented pads

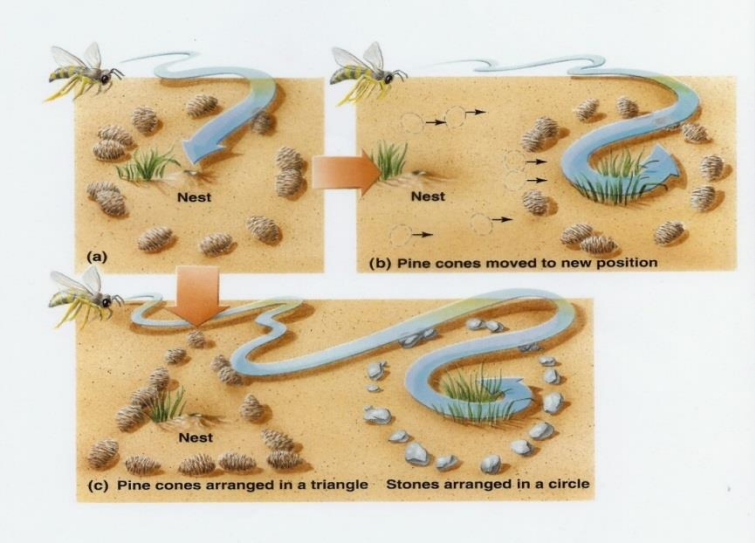
7. Confirm hypothesis √







Tinbergen's Experiment:
Fixed action pattern in nest finding behavior in wasp



Fixed Action Patterns:
Egg-rolling behavior of the greylag goose

FIG. 69. Grey lag goose retrieving egg. After Lorenz and Tinbergen, 1938.

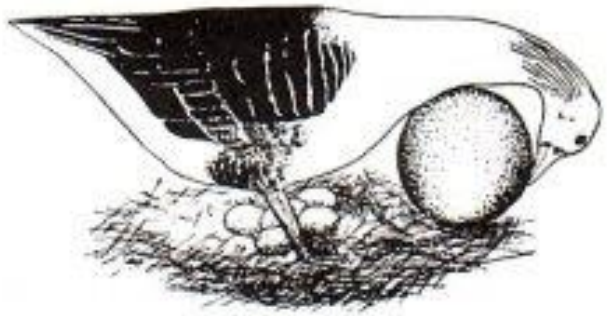
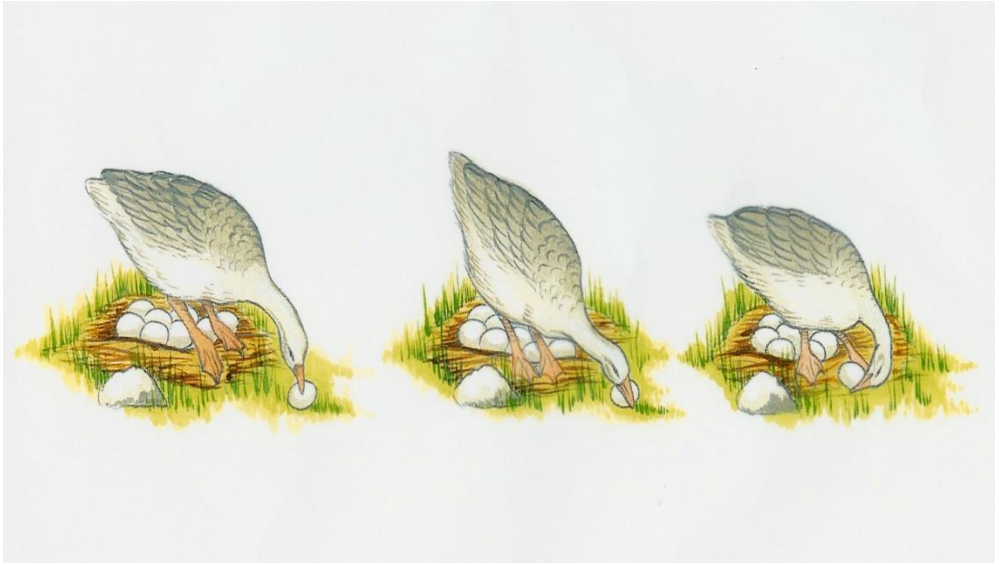
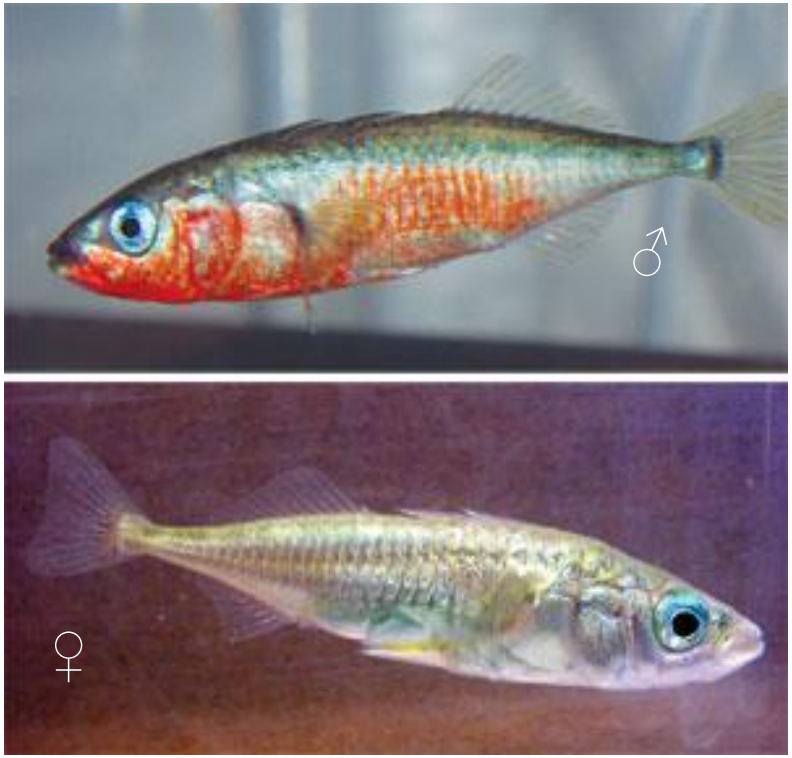


FIG. 70. Grey lag goose attempting to retrieve giant egg. After Lorenz and Tinbergen, 1938.



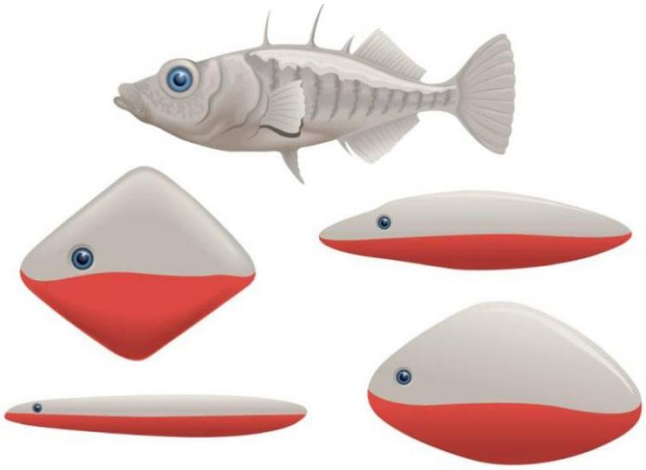
- The goose will roll an egg that is outside the nest back into the nest in the same manner every time.
- The goose will do this with any round object placed outside the nest.
- Each time this action pattern is initiated, it is carried through to completion.

FAP social behavior in three-spined stickleback
(Key visual sign stimulus releasing)



Fixed action pattern in three-spined stickleback

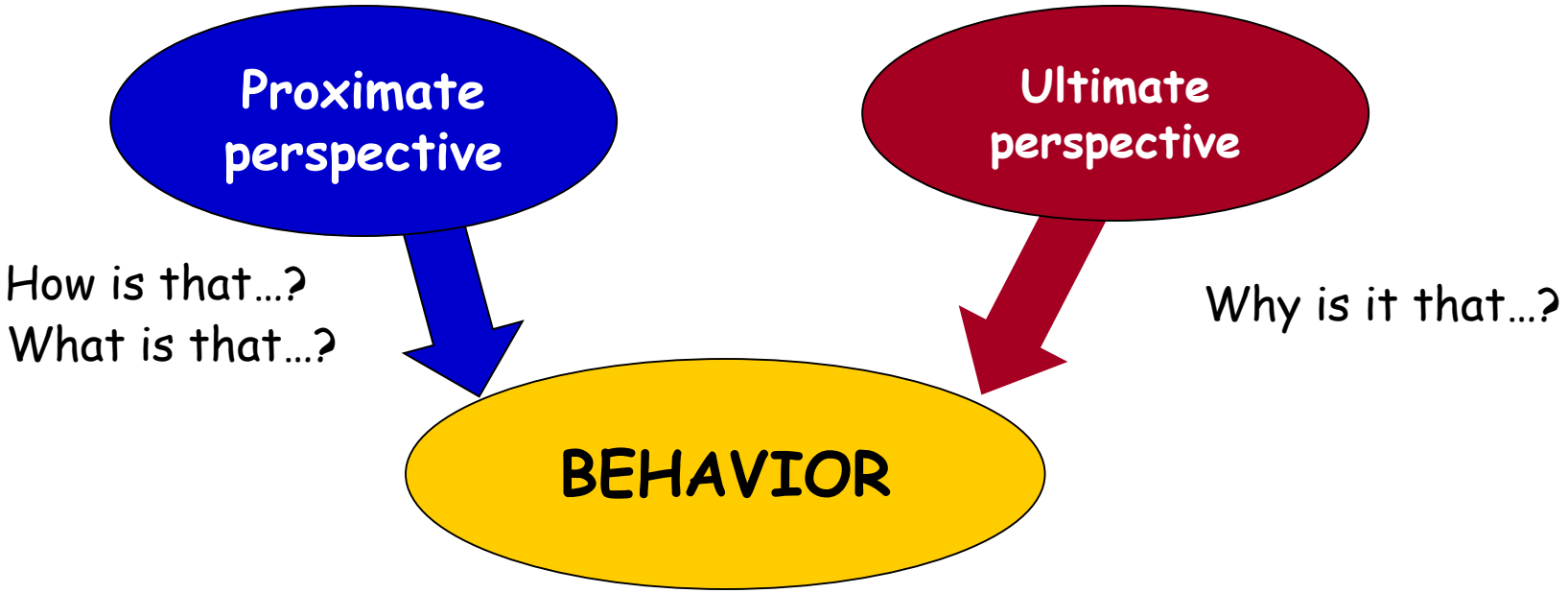
- Will attack as long as a red spot is present on the ventral body part



- Will court if white swollen belly (i.e. a pregnant female)

2 Levels of Behavioral (Ethology) Studies

The study of *how* and *why* animals interact with each other (both within and among species) and their environment.



Studying the mechanisms of the immediate causation and development of the behavior

Studying what is the adaptive significance and evolution of the behavior: How it influences survival and reproduction

Proximate and ultimate perspectives on aggressive behavior by male sticklebacks

BEHAVIOR: A male stickleback fish attacks other male sticklebacks that invade its nesting territory

PROXIMATE CAUSE:

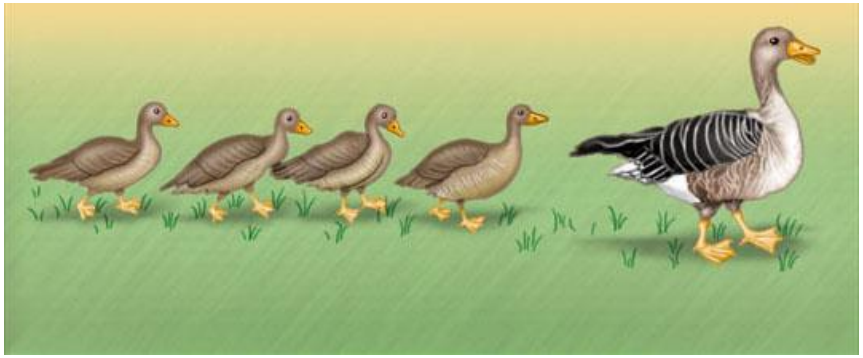
The red belly of the intruding male acts as a sign stimulus that releases aggression in a male stickleback

ULTIMATE CAUSE:

By chasing away other male sticklebacks, a male decreases the chance that eggs laid in its nesting territory will be fertilized by another male

Proximate and ultimate perspectives on imprinting in graylag geese

BEHAVIOR: Young geese follow and imprint on their mother



PROXIMATE CAUSE:

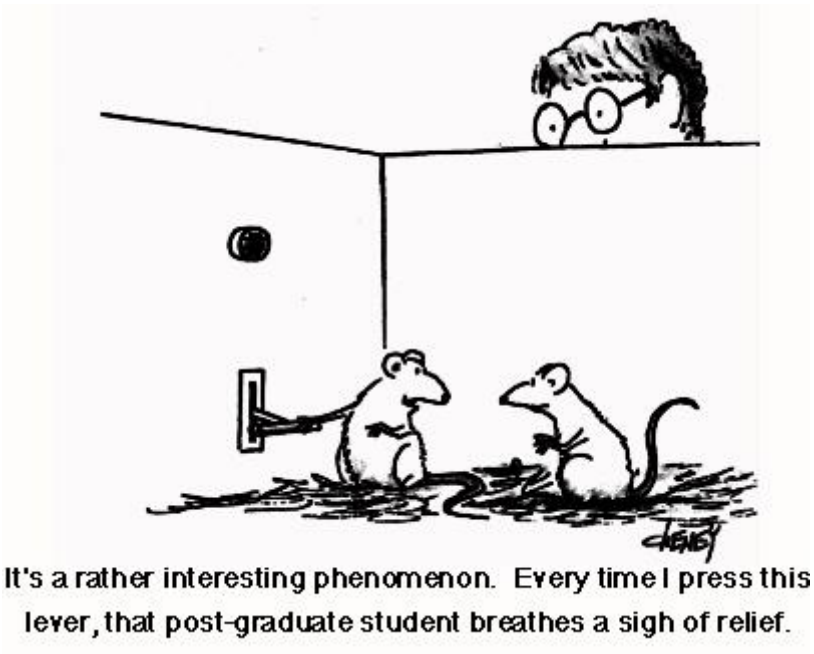
During an early, critical developmental stage, the young geese observe their mother moving away from them and calling

ULTIMATE CAUSE:

On average, geese that follow and imprint on their mother receive more care and learn necessary skills, and thus have a greater chance of surviving than those that do not follow their mother

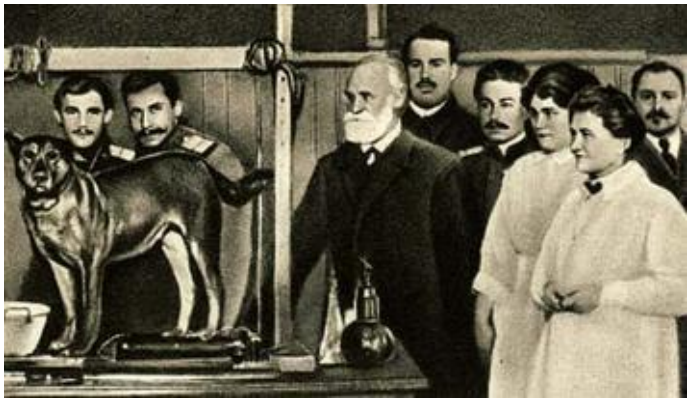
Two ways to study animal behavior

Ethology approach

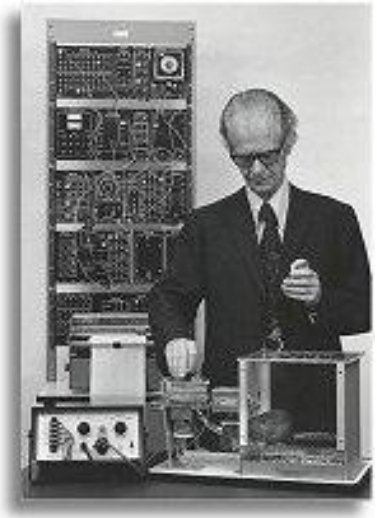


Behavioral Neurobiology

Experimental studies of animal behavior in laboratory conditions



Ivan Pavlov
(1849-1936)



Burrhus Frederic Skinner
(1904-1990)

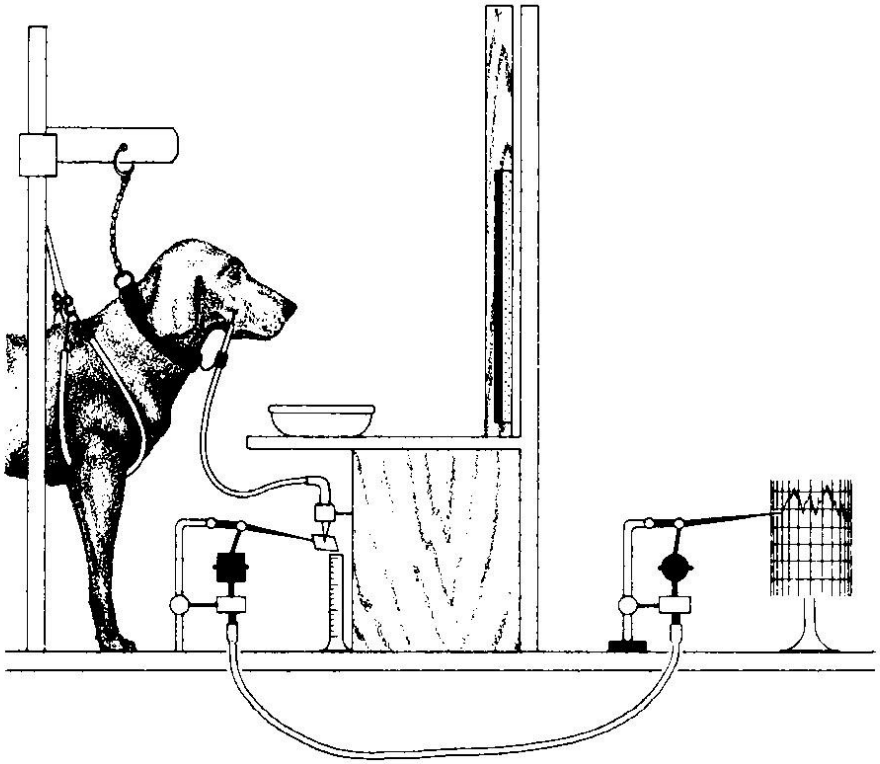
Ivan Pavlov

The Nobel Prize in Physiology or Medicine 1904

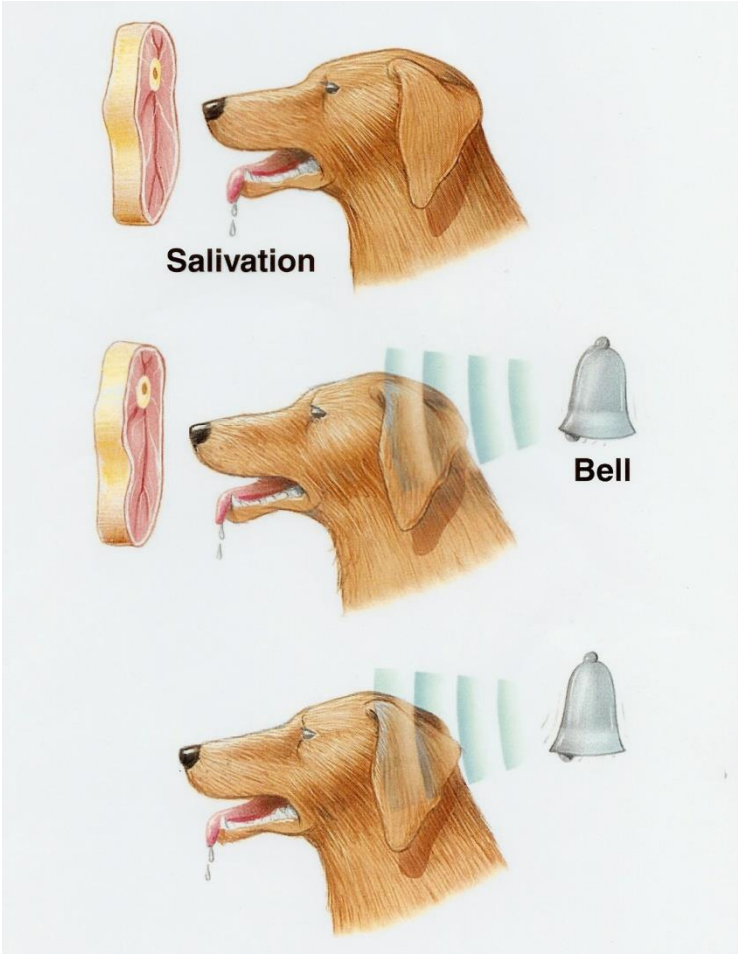
For his research in temperament, conditioning and involuntary reflex actions of the digestive glands

Pavlov's experiment:
The original and most famous example of classical conditioning involved the salivary conditioning reflex of Pavlov's dogs.

Pavlov's Classical Conditioning experimental setup



Pavlov's Classical Conditioning



Before Training/Conditioning

Food ⟶ Salivation

Tone ⟶ ???? (nothing)

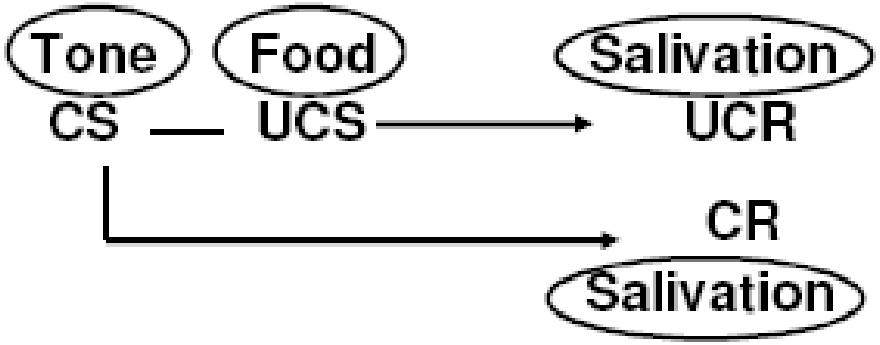
During Training/Conditioning

Tone — Food ⟶ Salivation

After Training/Conditioning

Tone — Food ⟶ Salivation

Salivation



Definitions:

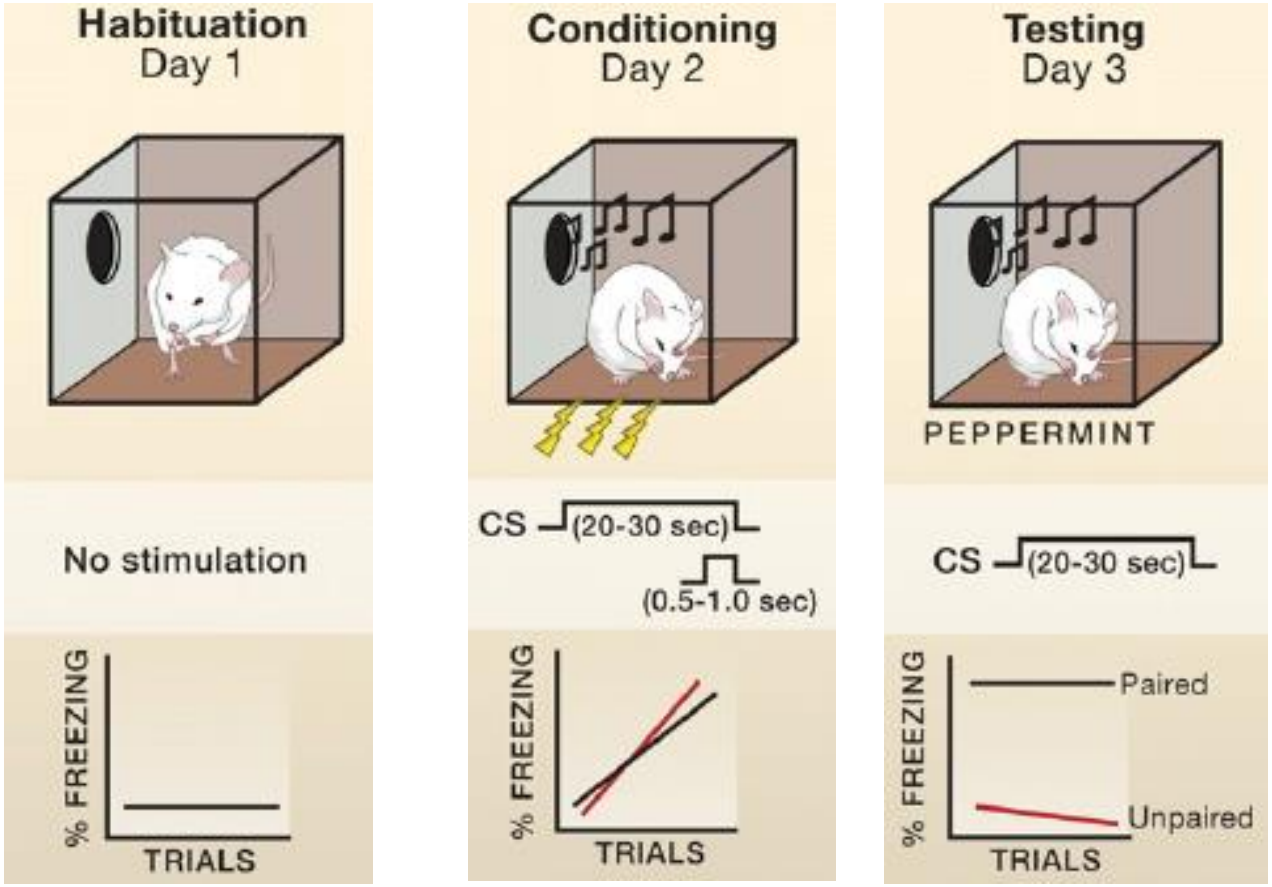
Unconditioned Stimulus (UCS): A stimulus that automatically elicits a response without any prior conditioning/learning

Unconditioned Response (UCR): That unlearned reaction/response to an UCS without previous conditioning.

Conditioned Stimulus (CS): Is a previously neutral stimulus that, through pairing with the UCS, also eventually elicits a response.

Conditioned Response (CR): That reaction/response that occurs to the CS.

Example: Negative Classical Conditioning



Jonathan et al 2011; Cell

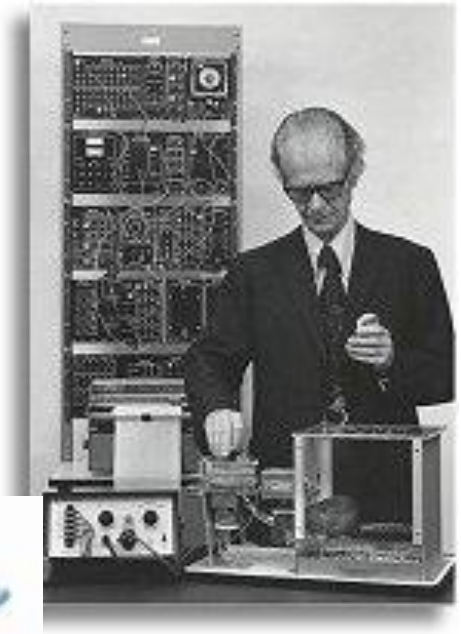
Skiner's Operant Conditioning learning

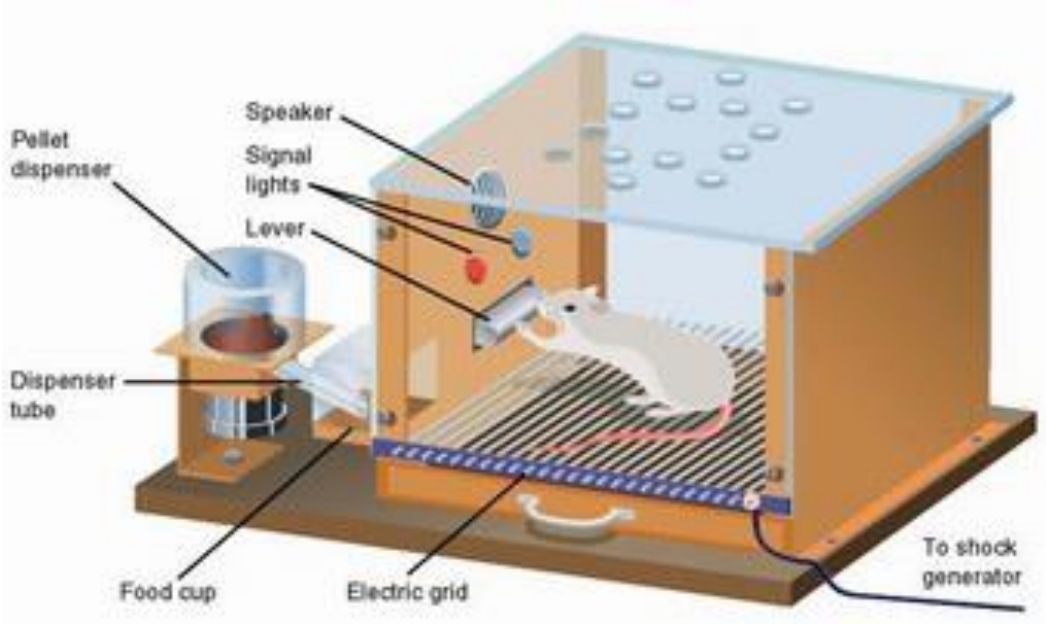
"Everything we do and are is determined by our history of rewards and punishments."-BF Skinner

- A process where an animal learns to associate one of its behaviors with a reward or punishment and then tends to repeat or avoid that behavior

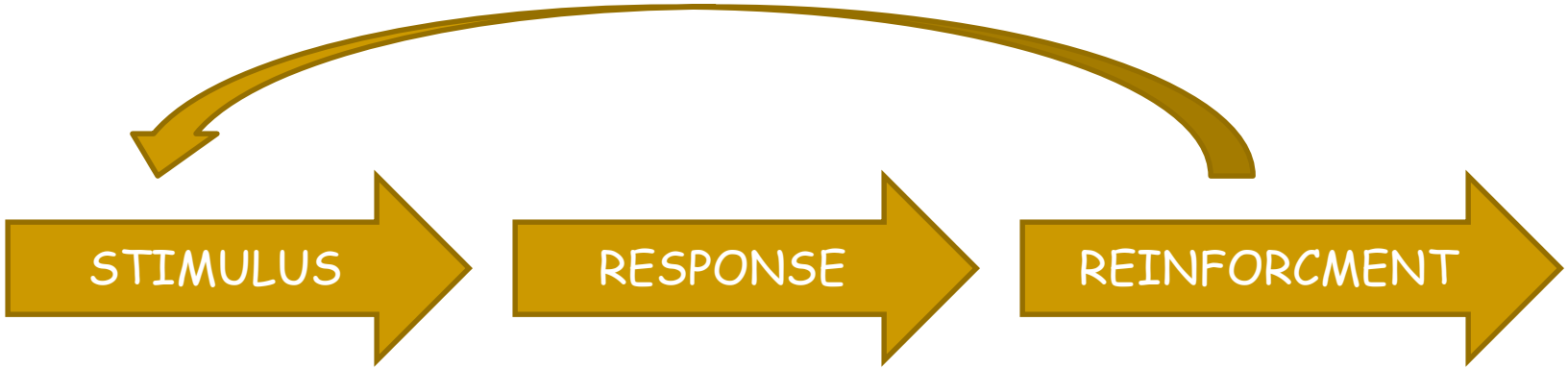
- In contrast to classical conditioning the response is voluntary (it is NOT a reflex) and the animal must do something to gain a reward (or avoid punishment)

Operant Conditioning: The Skinner Box



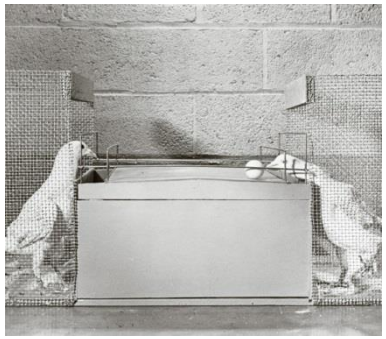


Skiner's Operant Conditioning



If your behavior is followed by a positive consequence, you are more likely to repeat the act in the future;
if it is followed by a negative consequence, you are less likely to repeat it.

Example: Positive Operant Conditioning



From Ethology to Neuroethology

A discipline that combines the study of animal behavior and study of neuroscience to inquire how the brain controls behavior in wild-derived animals, using lab conditions mimicking natural environment.

Example 1: The neural basis for seismic social communication

The blind mole rat (*Spalax ehrenbergi*)

Mole-Rat

Rodentia


Blind mole rat


Naked mole rat

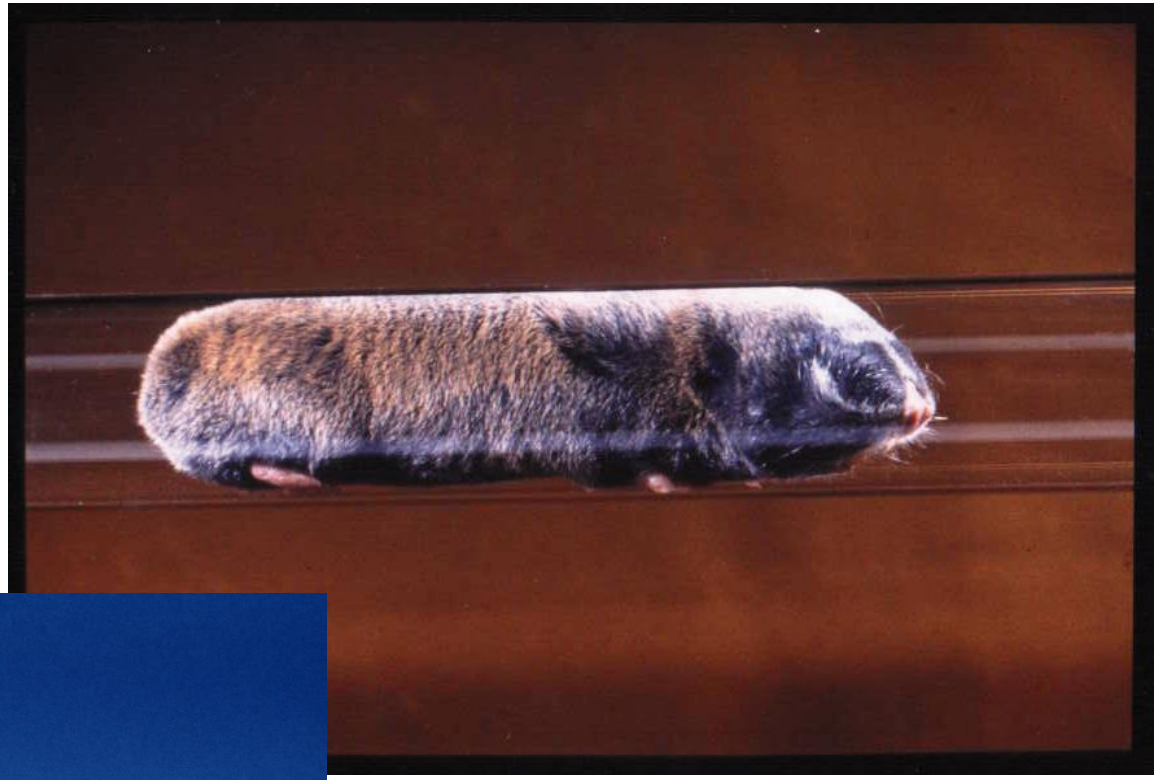
Mole

Insectivora


Star nose mole

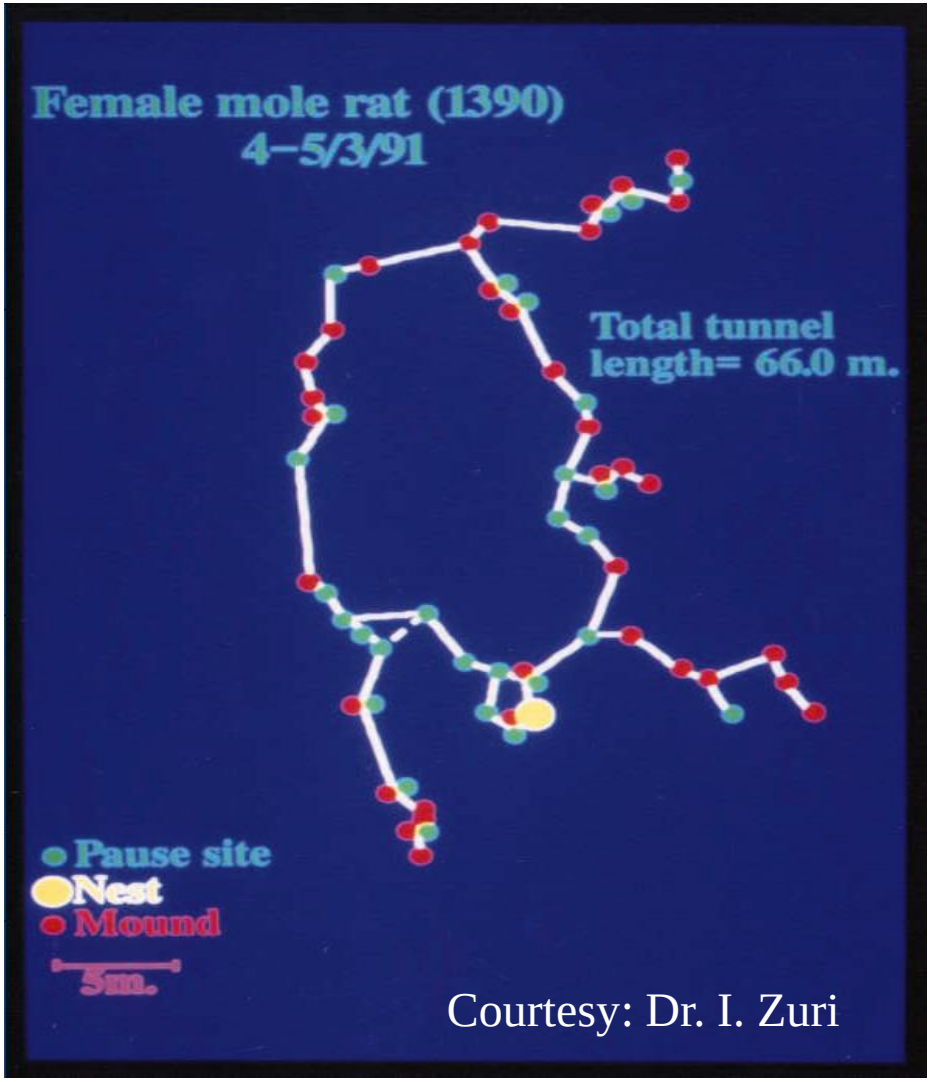

European mole

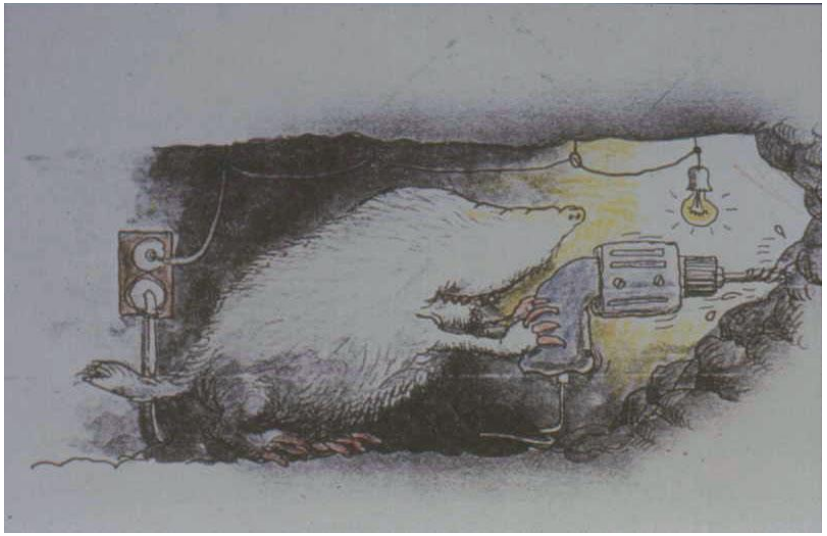
Mole rat - side view



Two patterns of mole rat mounds in Israel


10

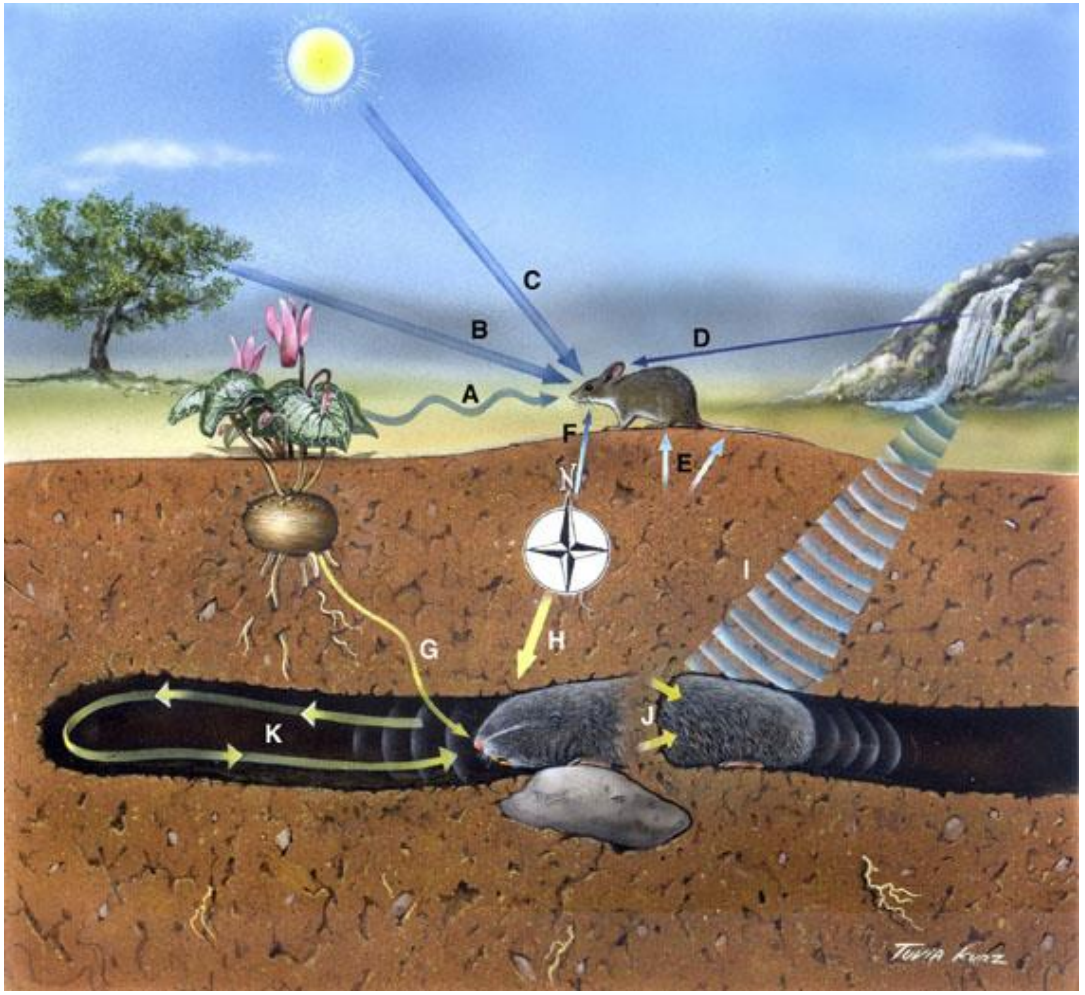

Female mole rat (1390)
4–5/3/91
Total tunnel
length= 66.0 m.
Pause site
Nest
Mound
5m.
Courtesy: Dr. I. Zuri



Burrow excavation is both costly and difficult

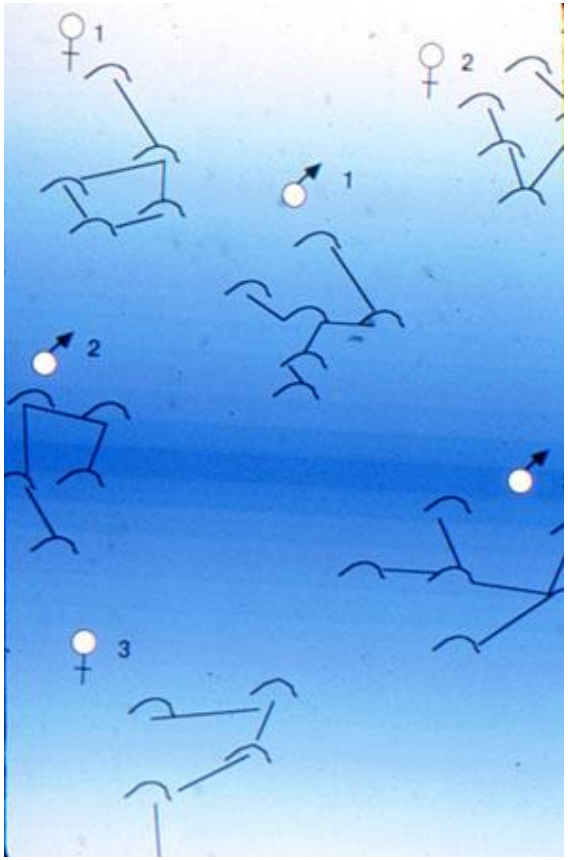
- **High energy cost: up to 3400 times more than moving on surface**
- **High CO_2 pressure (~13.5%) and low O_2 pressure (~5.5%)**
- **High risk of body overheating (unventilated niche)**
- **High risk of losing water and consequent dehydration (food is the only water source)**

Mole rats are exposed to unique environmental conditions

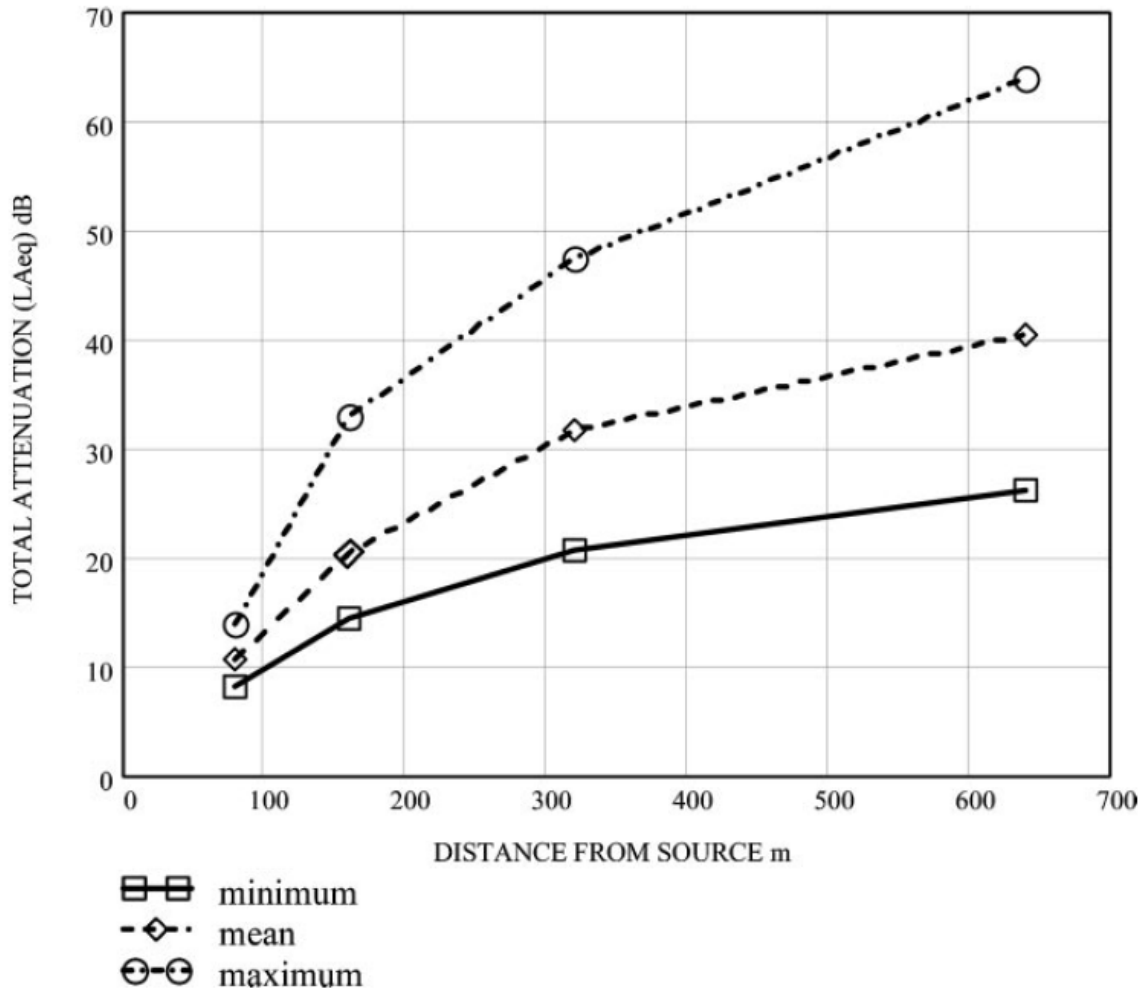


Sensory adaption to the underground niche

How do blind mole rats communicate with each other (find their mate/ avoid aggressive males)?



Airborne Sound is Quickly Attenuated in Soil



Attenborough 2002; *Annu Rev Fluid Mech*

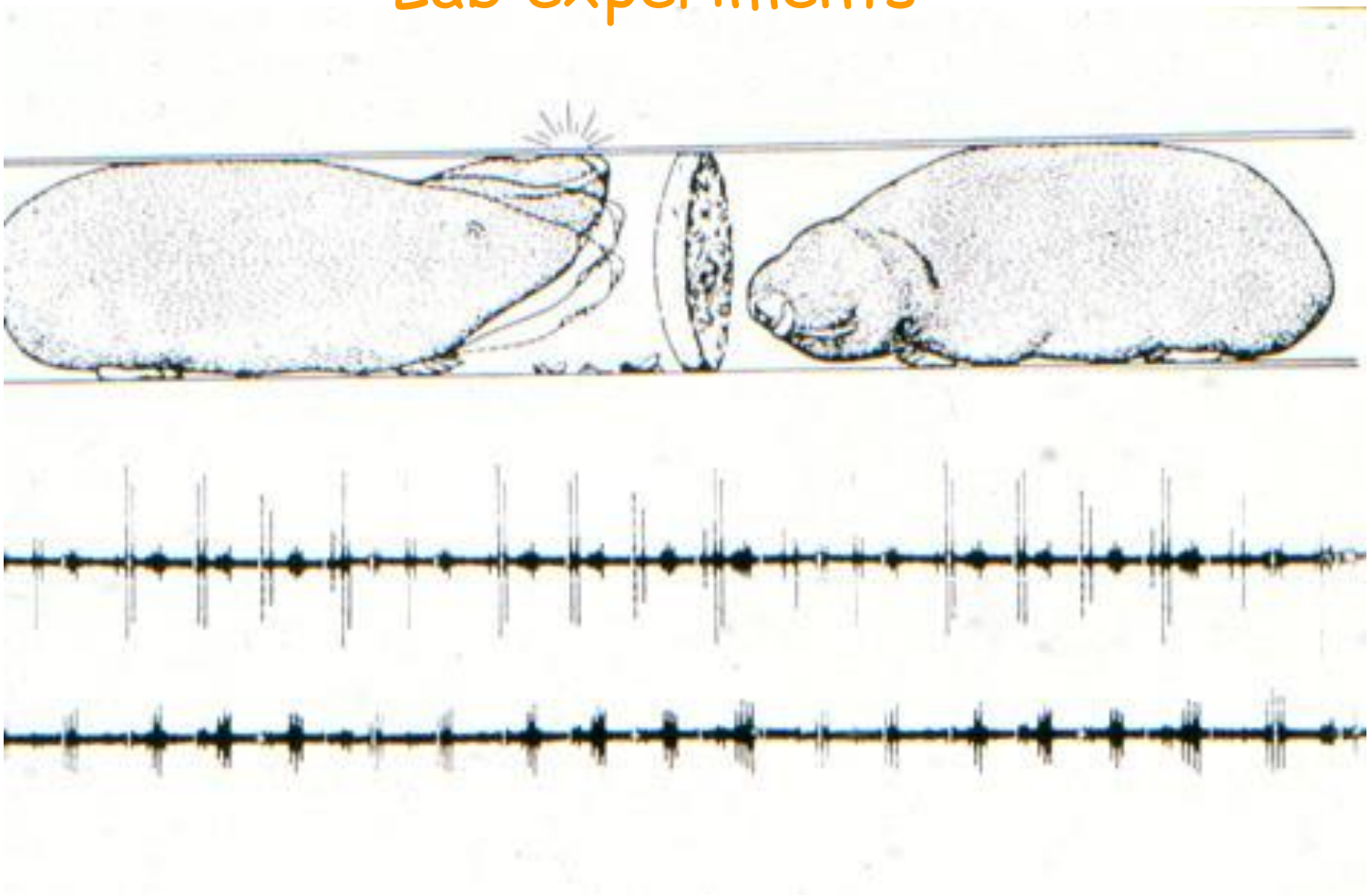
Behavioral observations:

Mole rats produce head drumming
Mole rats often press their lower jaw to the tunnel side

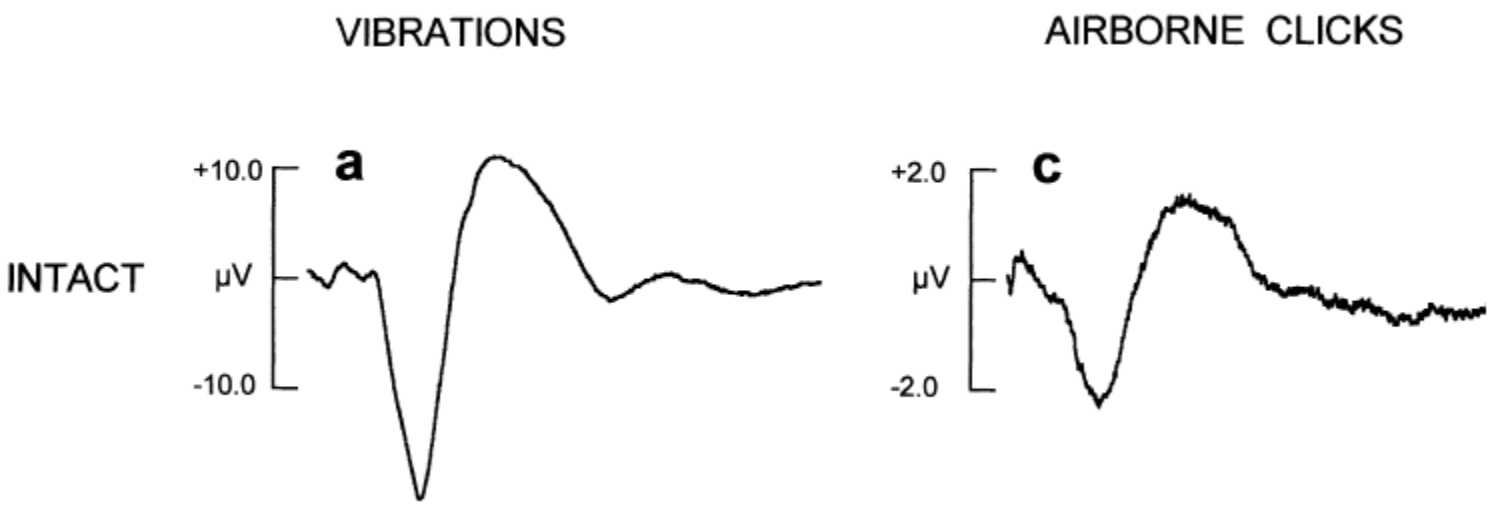
Hypothesis:

Mole rats communicate using soil-borne vibrations

Lab experiments

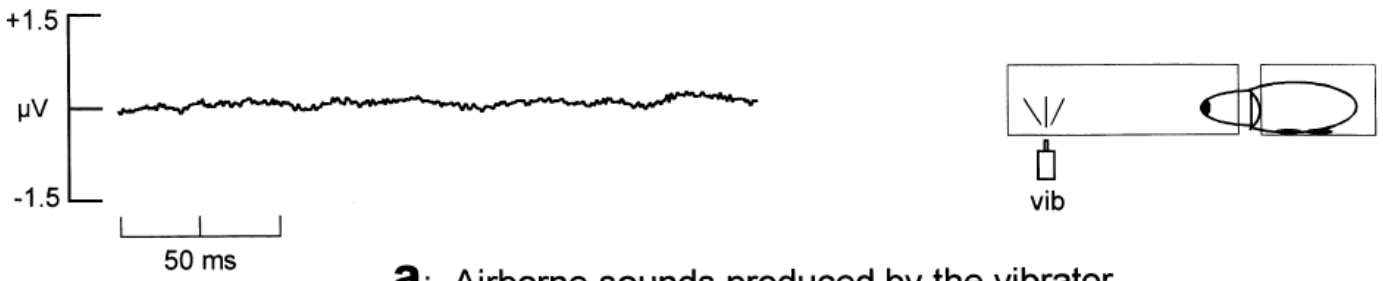


Rado, R (1998); J Comp Physiol

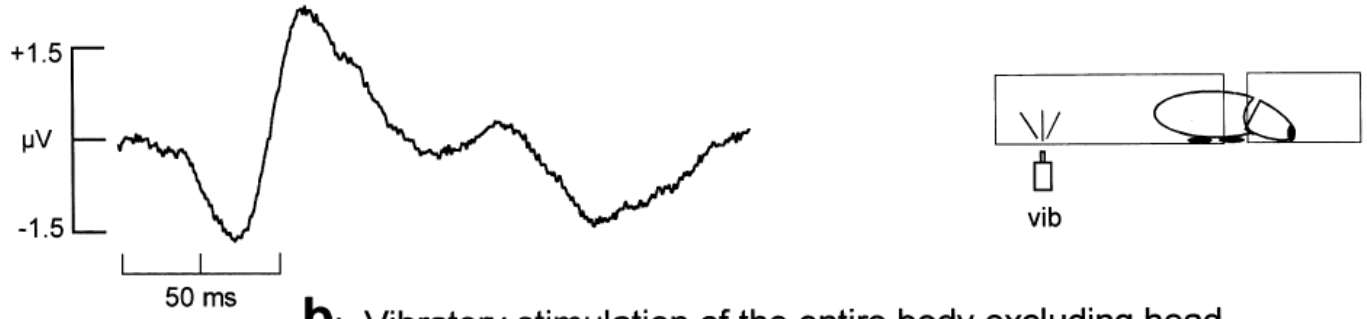


Middle latency response (MLR)

MLR is thought to represent the synchronous firing of neurons in the primary auditory cortex to an acoustic stimulus.



a: Airborne sounds produced by the vibrator

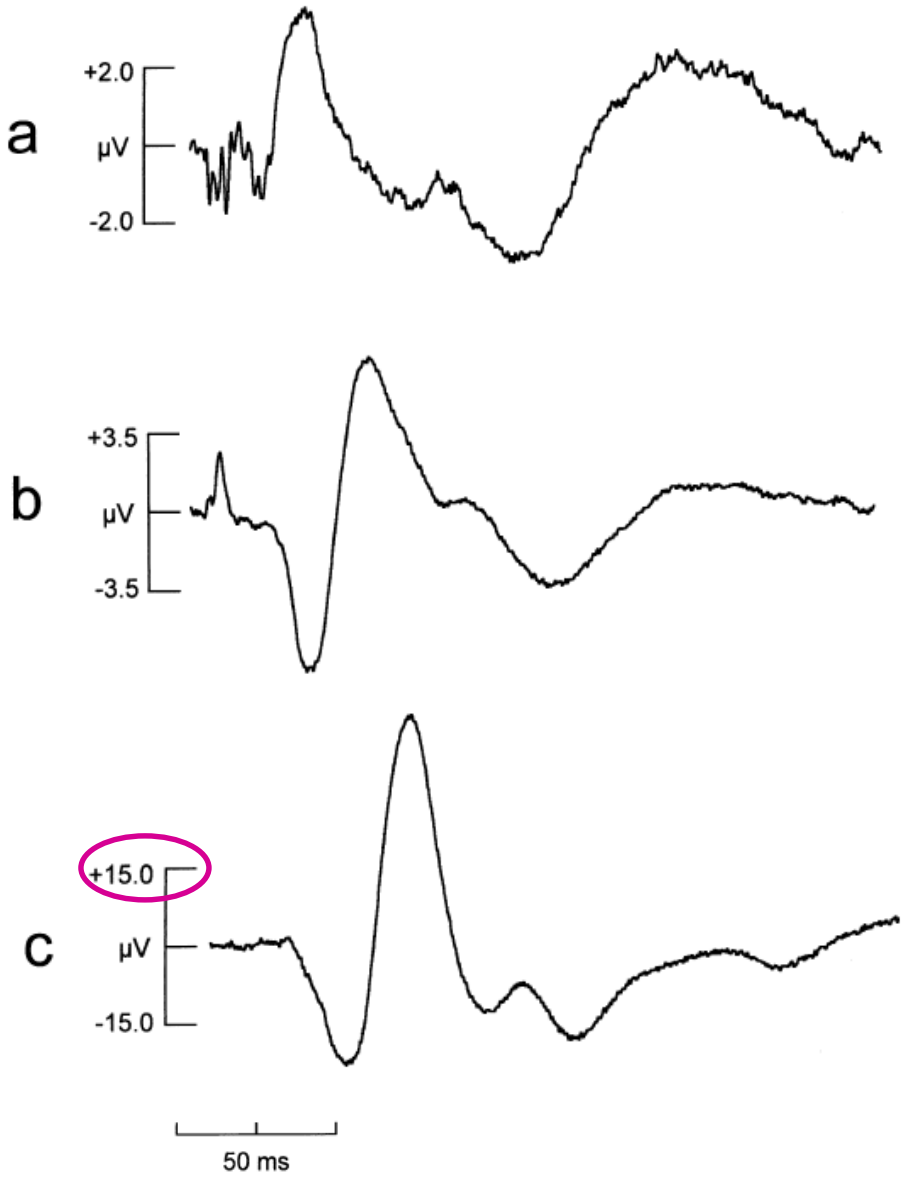


b: Vibratory stimulation of the entire body excluding head

c: Vibratory stimulation of the head - mainly the lower jaw

Middle latency response (MLR)

MLR is thought to represent the synchronous firing of neurones in the primary auditory cortex to an acoustic stimulus.

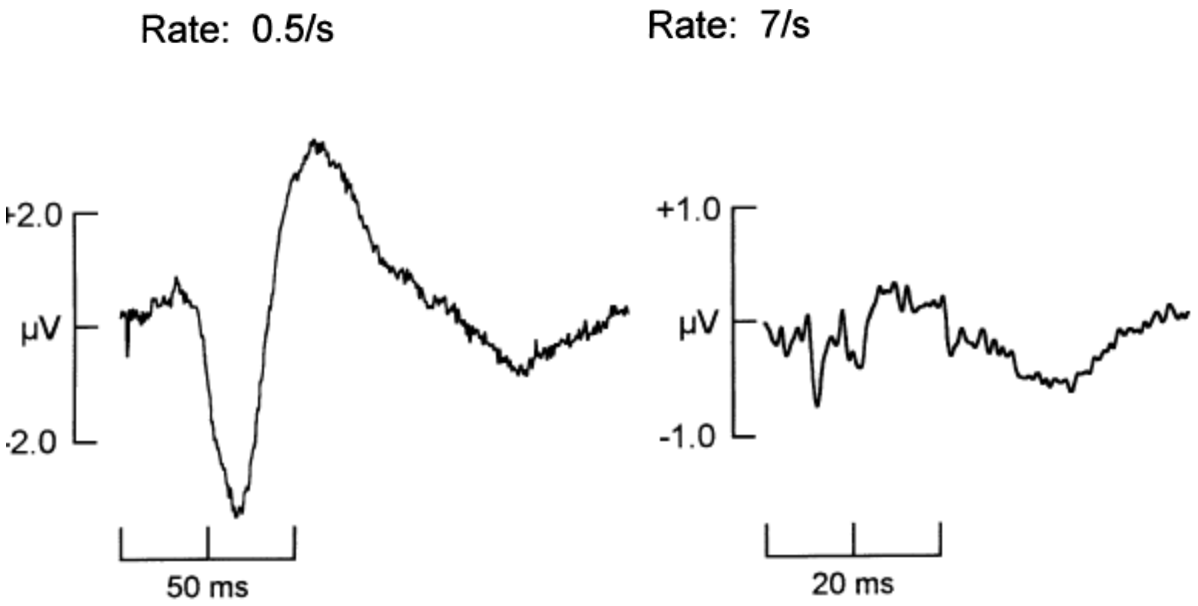


Jaw is barely touching the tube

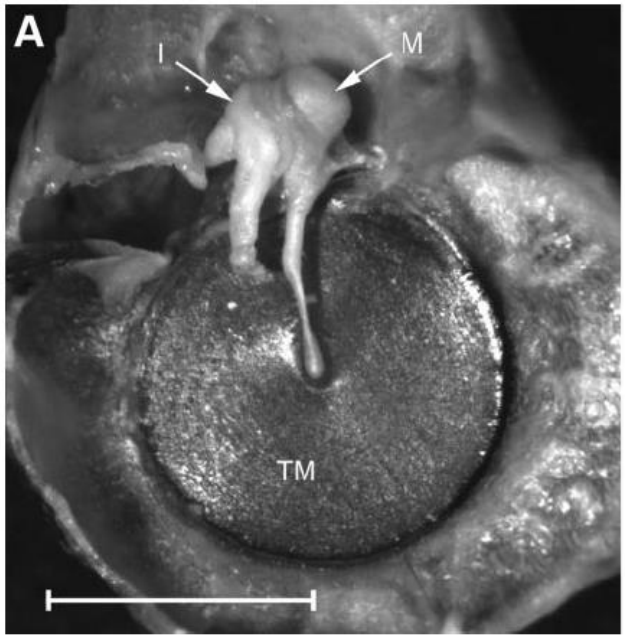
Jaw is laying on the tube

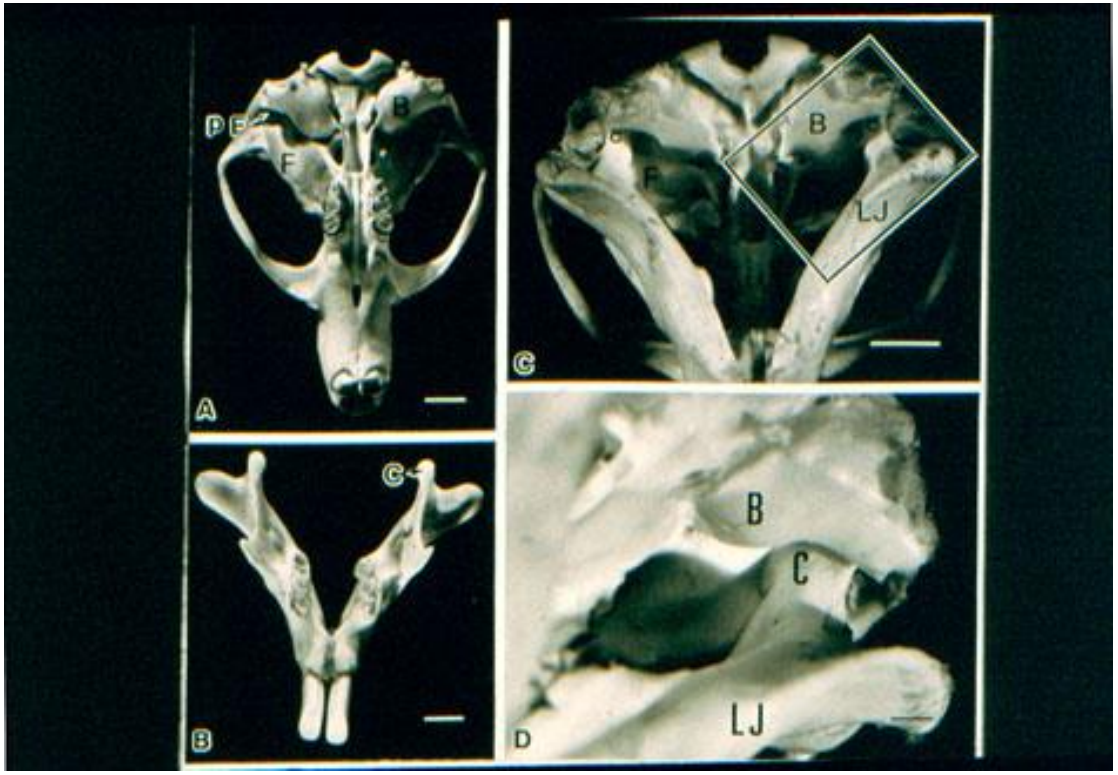
Jaw is firmly pressed against the tube surface

Vibration frequency

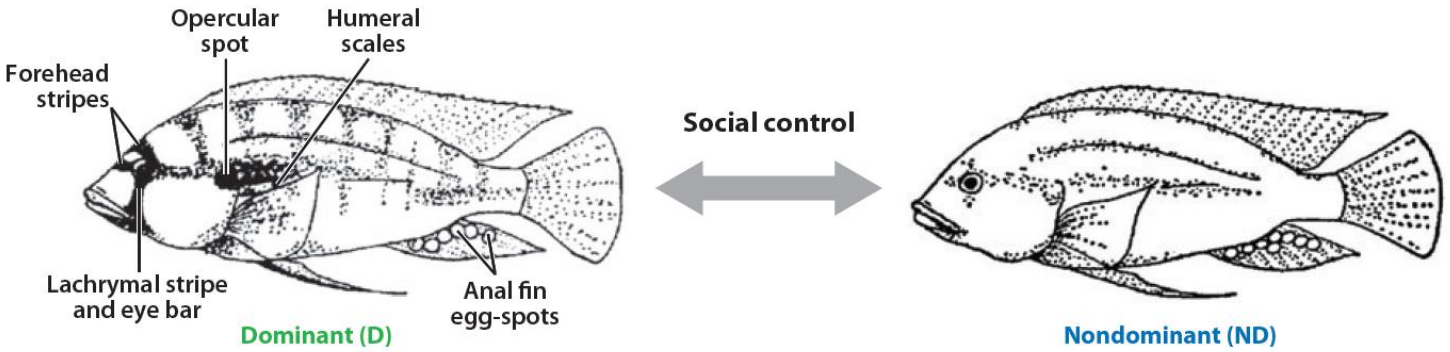


Vibration signals detection via bone conduction



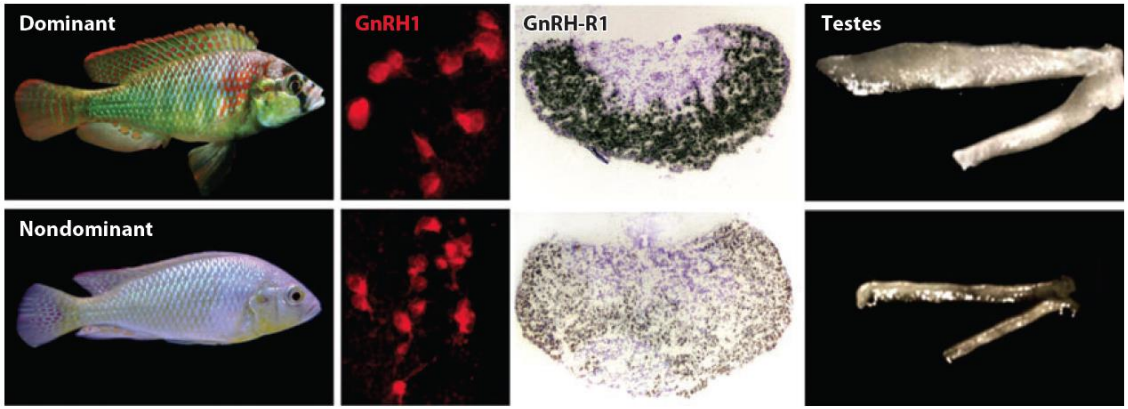


Example 2: Social control of the brain in the African cichlid fish model



- 10–20% of males
- Bright coloration/eyebar
- Complex behavior (17 distinct behaviors)
- Large GnRH neurons; large testes
- Reproductive

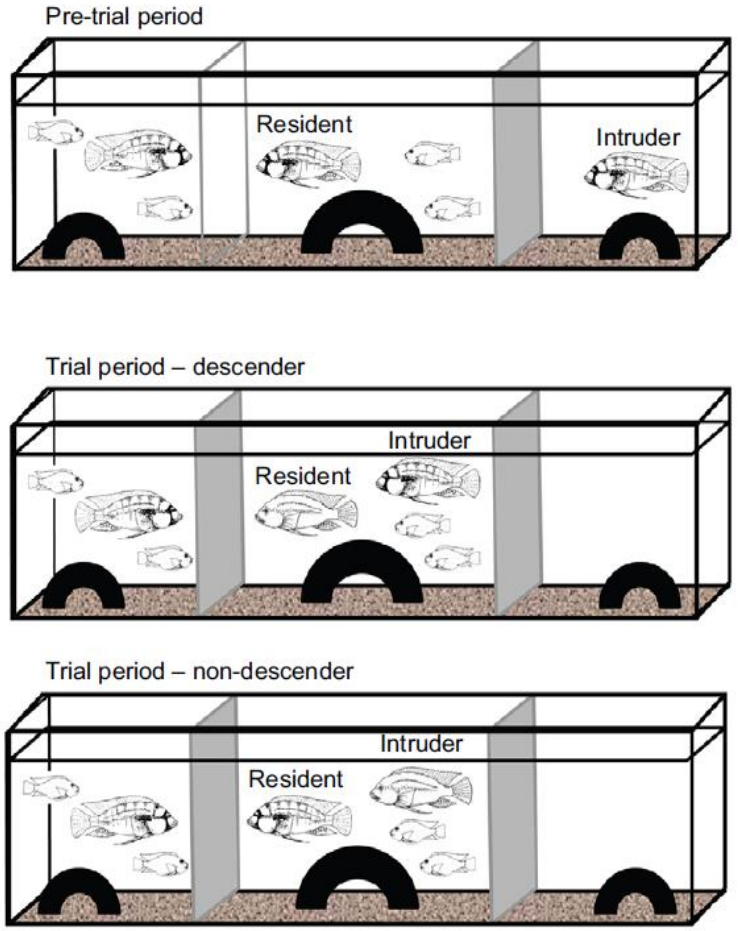
- 80–90% of males
- Dull coloration/no eyebar
- Simple behaviors (schooling/fleeing)
- Small GnRH neurons; small testes
- Nonreproductive

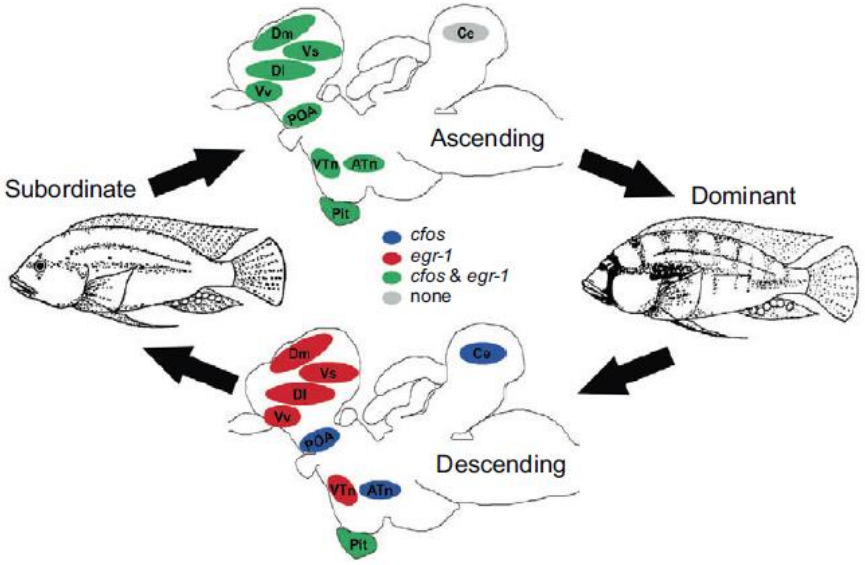


*Social information has a profound influence on the function of the reproductive (HPA) axis

Fernald 2012, Ann Rev Neuroscience

Example 2: Social control of the brain in the African cichlid fish model





Immediate early gene expression (indication of neuronal activity)

This study shows that dropping in social rank rapidly activates specific socially relevant brain nuclei in a pattern that differs from when males rise to a higher status position.

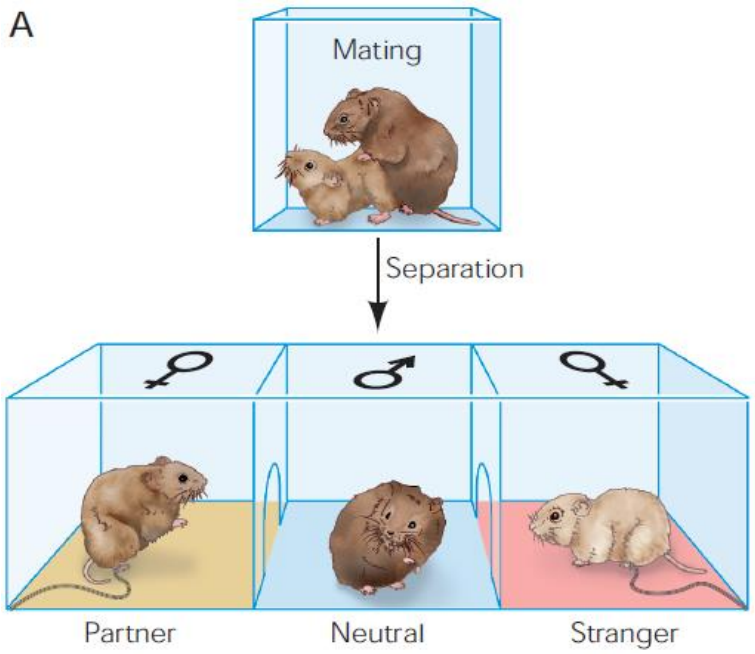
Maruska et al 2013, J Exp Biol

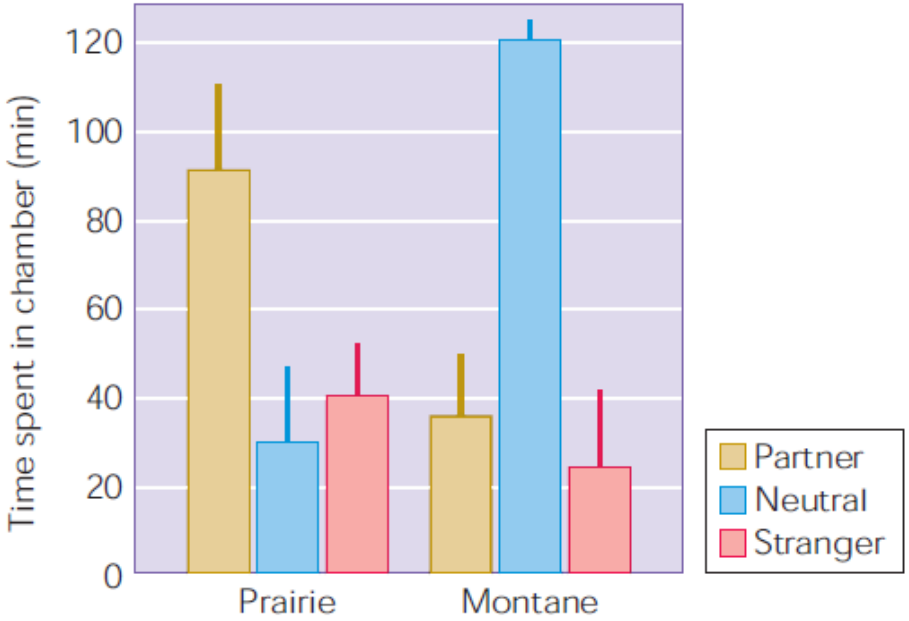
Example 3: The neuronal basis of pair bonding in voles

Pair bonding and social behavior in voles

- **Prairie voles**
- Highly social
- Monogamous
- Spend more than 50% of their time interacting with other prairie voles

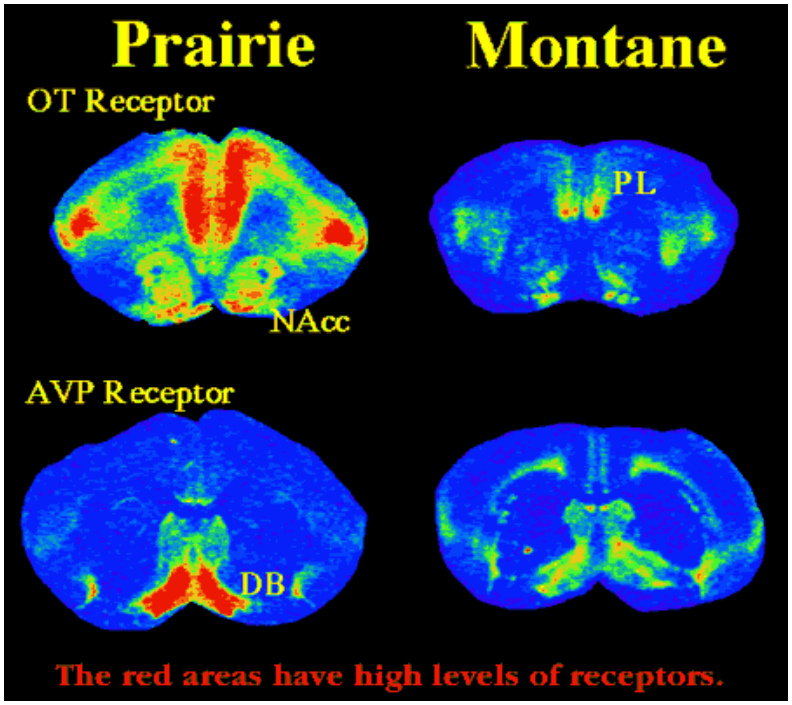
- **Montane voles**
- Avoid social contact except for the purpose of mating
- Polygamous
- Spend only around 5% of their time socially interacting.





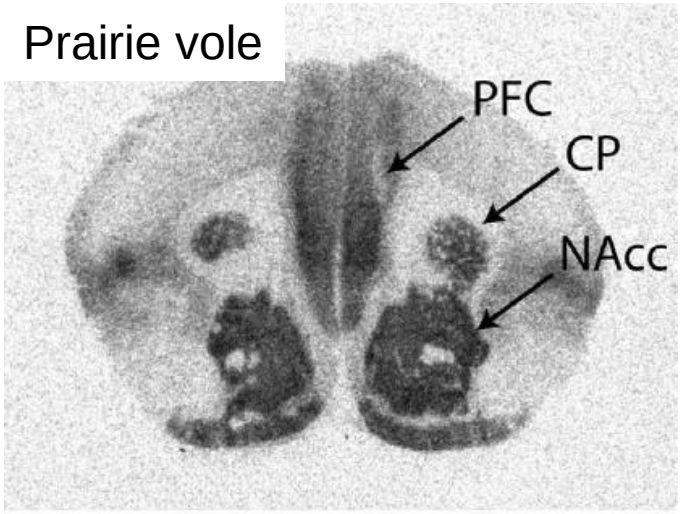
Hemanth et al 2006 *Physiology*

- Prairie voles have high levels of OT receptor in the nucleus accumbens and the basolateral amygdala relative to montane voles
- Prairie voles have high densities of the V1a subtype of the AVP receptor in the ventral pallidum and the medial amygdala compared with montane voles.
- Montane voles have much higher levels of V1a receptors in the lateral septum than do prairie voles.

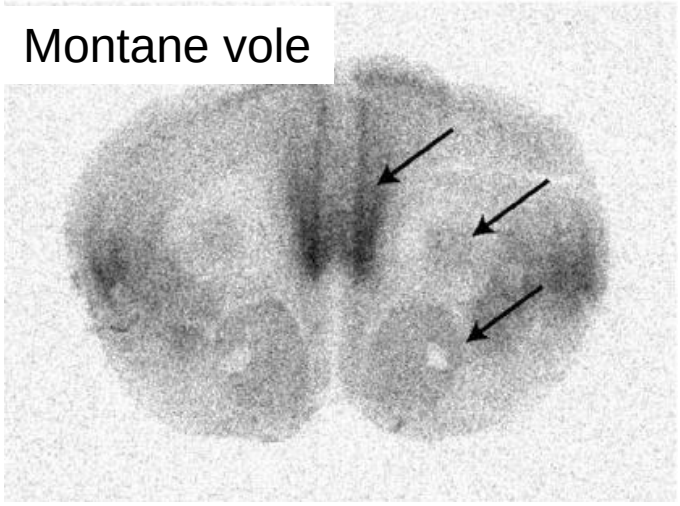


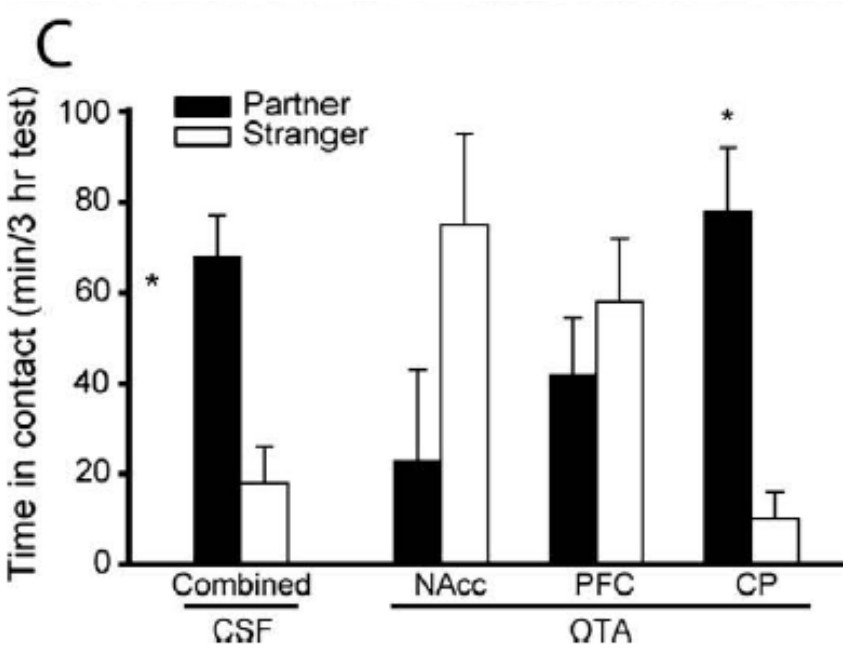
Oxytocin and partner preference in Prairie voles

Prairie vole



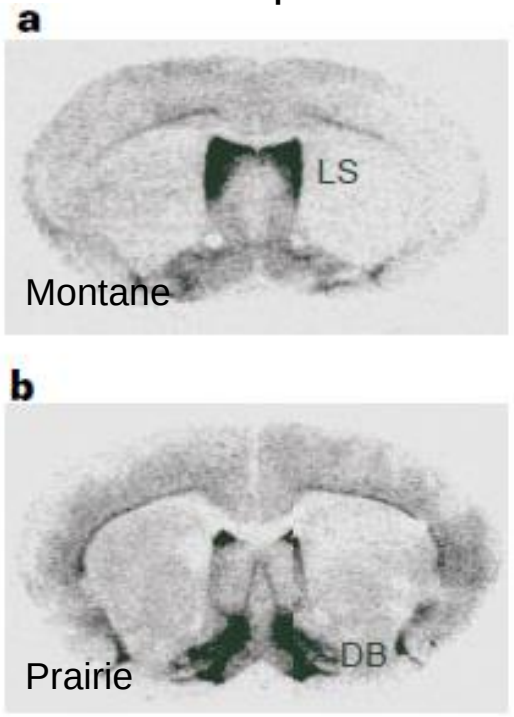
Montane vole

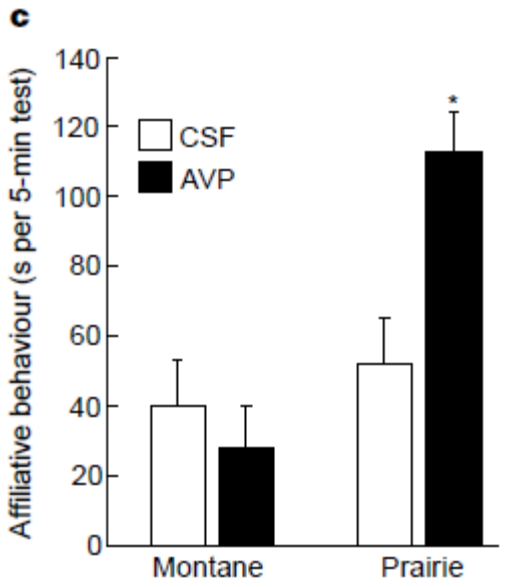




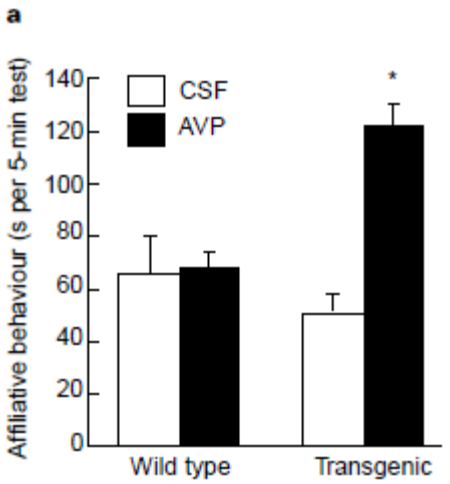
Vasopressin receptor and pair bonding in Prairie voles and Montane voles

V1aR expression

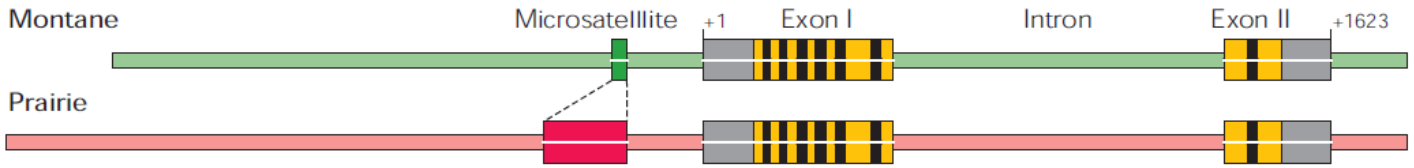


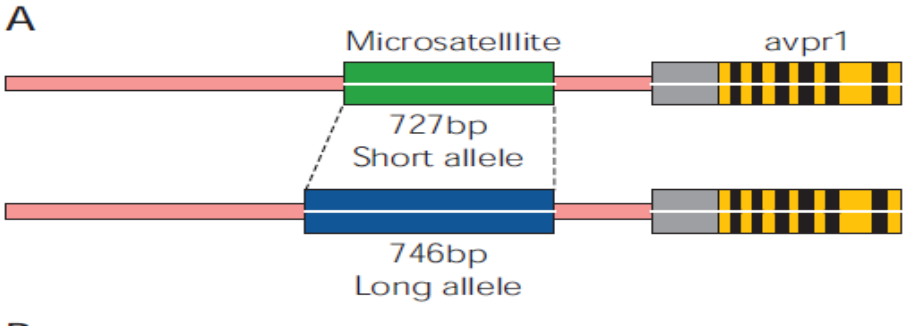


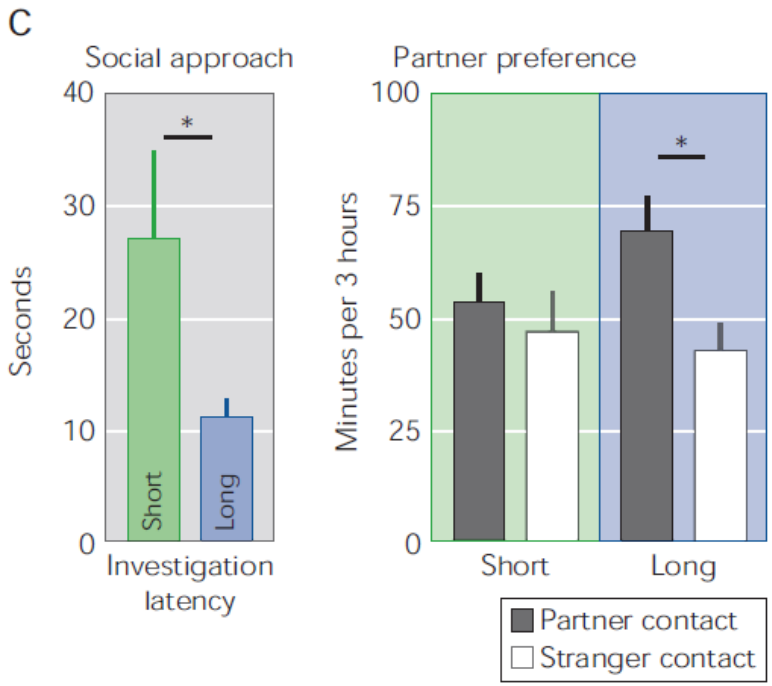
Transgenic mice expressing the V1aR of the prairie vole

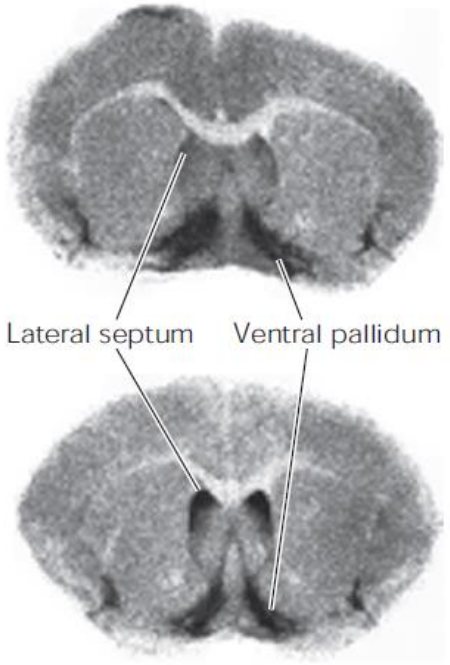


Young et al 1999; *Nature*









Hammock & Young, 2005 *Science*

The "Fidelity gene"

"A single gene can turn the Don Juan of voles into an attentive home-loving husband". BBC news

Meadow voles (*Microtus pennsylvanicus*)

Promiscuous social behavior

Prairie voles (*Microtus ochrogaster*)

Monogamous social behavior

Young et al. 1999 *Nature*

The genetic basis for pair bounding

Vasopressin R1a

?

Genetic variation in the vasopressin receptor 1a gene (*AVPR1A*) associates with pair-bonding behavior in humans

Pair-bonding has been suggested to be a critical factor in the evolutionary development of the social brain. The brain neuropeptide arginine vasopressin (AVP) exerts an important influence on pair-bonding behavior in voles. There is a strong association between a polymorphic repeat sequence in the 5′ flanking region of the gene (*avpr1a*) encoding one of the AVP receptor subtypes (V1aR), and proneness for monogamous behavior in males of this species. It is not yet known whether similar mechanisms are important also for human pair-bonding. Here, we report an association between one of the human *AVPR1A* repeat polymorphisms (RS3) and traits reflecting pair-bonding behavior in men, including partner bonding, perceived marital problems, and marital status, and show that the RS3 genotype of the males also affects marital quality as perceived by their spouses. These results suggest an association between a single gene and pair-bonding behavior in humans, and indicate that the well characterized influence of AVP on pair-bonding in voles may be of relevance also for humans.

Walum et al 2008, *PNAS*