

# Behavioural Biology (Ethology)

Peter Kabai (peter.kabai@gmail.com)

[www.behav.org](http://www.behav.org)

Interest: neural and genetic control of behaviour  
applied ethology  
evolution

Schrott A, Kabai P: ABCD: A functional database for the avian brain.

Zachar G, Schrott A, Kabai P: Context-dependent prey avoidance in chicks persists following complete telencephalectomy.

Nagy K, Schrott A, Kabai P: Possible influence of neighbours on stereotypic behaviour in horses.

Kabai P: Androgenic alopecia may have evolved to protect men from prostate cancer by increasing skin exposure to ultraviolet radiation.

# Ethology: topics

- 1) Roots of ethology: from Darwin to behaviourism
  - 2) Classical ethology: perception, elementary reactions, pre-wired learning
  - 3) Behavioural ecology approach: optimisation, game theory
  - 4) Neural and genetic control of behaviour (biological rhythms, CPG, simpler networks)
  - 5) Genetics and evolution of behaviour, evolution of communication
  - 6) Choosing the habitat and food
  - 7) Learning theories, cognition
  - 8) Parental investment
  - 9) Systems of reproduction
  - 10) Evolution of social behaviour, cooperation and conflict
- 20 hours at 7 x 3 session (1 hour for the test at last session)

# Course Requirements

- Lectures 7 times (3 hours each)
- Midterm test (timing negotiable)
- Those who passed form teams (cca. 4 teams) and work on some specific question relying on the primary literature.
  - Consultations: 3 times (students present talks)
  - Papers to be submitted by 26<sup>th</sup> November
- Oral exam: lecture material + discussion of paper (50 – 50 %)
- Grading: test (20%) + oral (80%)

# Paper

- Latest results form the primary literature: original research paper  
(introduction, methods, results, discussion)
- Review articles
- Books
- Example questions:
  - Causes and treatment of abnormal stereotypic behaviour
  - Extended phenotype of parasites
  - Function of infanticide
  - Behaviour therapy of whatever in dogs

# Course material

- Lecture notes by Péter Kabai at [www.behav.org](http://www.behav.org) (will be uploaded as we proceed)
- Chris Barnard: Animal Behaviour. Mechanism, Development, Function and Evolution. (available as e-book)



The screenshot shows a web browser window with the address bar displaying [www.behav.org/behav/pages/default.htm](http://www.behav.org/behav/pages/default.htm). The page features a navigation menu with links for [Google Hirdetések](#), [Matematika](#), [Pszichológia](#), [Ágy](#), and [Önismertel](#). Below the menu, there is a section titled **SALVE 1%** with a list of topics: [Behavioristák](#), [Klasszikus etológia](#), [Viselkedés ökológia szemlélete](#), [Etológiai módszerek](#), [Központi mintázat generátorok](#), [Etológiai ritmusok](#), [Egyszerűbb szabályozások](#), [Viselkedésgenetika](#), [Érzékelés](#), [Evolúció](#), [Tér tájékozódás](#), and [Tanulás, kogníció](#). To the right of this list, there is another column of topics: [Előhely](#), [Táplálkozás](#), [Ragadozók kivédése](#), [Bevándozás, Kotródás](#), [Kommunikáció](#), [Madárének](#), [Szociális viselkedés](#), [Szülői ráfordítás](#), [Reprodukciós viselkedés](#), [Szaporodási rendszerek](#), and [Emberszabványok](#). A small image of a person in a field is visible on the right side of the page. Below the topic lists, there is a note: "Könyvtár: ingyen elérhető források [itt](#)" and "Lecture notes in English will be available this September". A navigation bar contains the text [Viselkedés-biológia óravázlat](#) > [tartalom](#) > [előkészületben](#). Below this, there is a warning icon and the text "A viselkedéssel kapcsolatos oldalak tartalomjegyzéke". At the bottom of the page, there is a section for "Vizsga I. évfolyam, 2009-10 [tudnivalók](#)" and a link for "Etológiai módszerek (készülőben lévő [jegyzet](#))". A small image of a yellow chick and several black chicks is visible in the bottom right corner.

# Important

From next week on lecture starts at

15:00

# In the news

## Parasite-Infected Rodents Attracted to Cat Odor

Toxoplasma-infected male rats have altered activation in brain regions involved in fear and increased activation of brain regions involved in sexual attraction after exposure to cat odors.



# In the news

Premature baby brains can't tell pain from touch

Fetuses can tell the difference between pain and touch in only the last two weeks before birth, which could help to explain why babies born prematurely often have abnormal pain responses

Lorenzo Fabrizi from University College London and colleagues used EEG

Premature babies up to the age of 35 weeks had bursts of activity across the whole brain in response to both pain and touch, but a change happened around 35 weeks. Between 35 to 37 weeks – just before a fetus would normally be born – the brain seemed to become able to tell the two stimuli apart



# In the news

Scientists have discovered that female chickens have a remarkable ability to choose the father of their eggs. Working with feral fowl in Sweden, the scientists found that many matings were forced, as the roosters are twice the size of the hens.

Even when unforced, the females still exercised their right to choose by opting to eject the sperm of males they considered to be at the bottom of the pecking order.

With the reproductive odds stacked against them, these low-status roosters have fought back by developing larger ejaculates in the hope of increasing their chances of passing on their genes.

## Hens evolve secret sex strategy

By Matt McGrath

Science reporter, BBC World Service

Scientists have discovered that female chickens have a remarkable ability to choose the father of their eggs.

Wily hens have evolved the ability to eject the sperm of unsuitable mates say researchers working with Swedish birds.

Promiscuous roosters try to ensure that their genes are passed on by mating with as many females as possible.

But by removing the genetic material of males they consider socially inferior, the hens have managed to retain control of paternity.

Many species ranging from zebras to insects use the strategy of sperm ejection - but the evolutionary ideas behind it are often uncertain.

Among birds, male Dunnocks force females to eject the sperm of other suitors in order to protect their own genes.

But this research indicates that among



Chickens have evolved the ability to eject the sperm of unsuitable mates

# In the news

## Evolutionary mystery of female orgasm deepens

Some evolutionary biologists reckon the female orgasm is adaptive and possibly influences mate choice, strengthens pair bonds or indirectly helps to suck sperm into the uterus.

Others argue that women have orgasms for the same reason that men have nipples – being highly adaptive in one sex, the traits tag along for the ride in the other.

If female orgasm is a simple by-product of male orgasm, the duo argue, then similar genes would underlie orgasmic function in both men and women.

5000 sets of identical and non-identical twins and pairs of regular siblings. The questionnaire asked about the time to orgasm in men and the frequency and ease of orgasm in women.

genes do play a role, however, opposite-sex twins and siblings had virtually no correlation in orgasmability. Controversial...

### Evolutionary mystery of female orgasm deepens

› 18:00 09 September 2011 by [Aria Pearson](#)

---

Whence the female orgasm? After 40 years of debate evolutionary biologists are no closer to deciding whether it evolved to give women a reproductive boost, or whether it is simply a by-product of male orgasm evolution. The latest attempt to settle the dispute involves quizzing some 10,000 twins and pairs of siblings on their sexual habits.

Some evolutionary biologists reckon the female orgasm is adaptive and possibly influences mate choice, strengthens pair bonds or indirectly helps to suck sperm into the uterus. Others argue that women have orgasms for the same reason that [men have nipples](#) – being highly adaptive in one sex, the traits tag along for the ride in the other.

# Behavioural Biology

- What is its scope? Different levels of organisation.
- What are its methods?
- Where is it rooted? (outdated concepts surviving)
- Behaviourism (tabula rasa)
- Classical ethology (Lorenz, Tinbergen, von Frisch)
- Behavioural ecology (as an approach)
- Levels of organisation (from genes to memes)
- Behavioural systems (predation – antipredatory behaviour, sex, parental investment, sex, sex)

# Questions in ethology



- What do you see?

- Open mouth
- Withdrawn lips
- Pulling the leash
- Ears back

# Questions in ethology



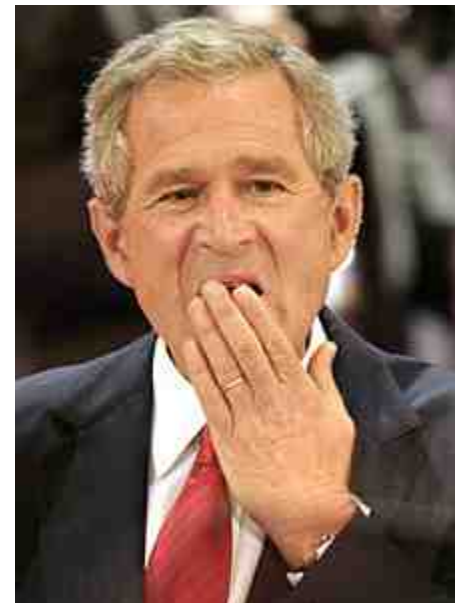
- Why?

- Trained to
- Bred to
- Angry
- Signaling attack
- All dogs display like this
- All canids display like this?

# Questions in ethology



# Questions in ethology



Why do we yawn?

# Questions in ethology



Anderson et al. (2004) Contagious yawning in chimpanzees

# In the news

Yawning is so contagious that chimpanzees can "catch" it from cartoons



Campbell et al. (2009) Roy Soc Proc

Physiological theory: heart rate increases

more oxygen? Giving people additional oxygen didn't decrease yawning, and decreasing the amount of carbon dioxide in a subject's environment also didn't prevent yawning.

Signal theory: while all vertebrates (including fish) yawn, only humans, chimps and possibly dogs find yawns contagious.

And people don't find them contagious until they're about 4 years old. Autistic children do not respond to yawning.

# What is behaviour?

- Movement of intact animals (Tinbergen 1955)
- Change of state of a single muscle fiber, or pigment cell

Problematic

Lack of movement?

Do plants behave?

Is cognition behaviour?

Antler fight of Red deer males is behaviour

Developing the antler is not?

# What is behaviour?

Levitis et al. (2009) Anim Behav:

Questionnaire to 174 researchers. Contradictory,  
sometimes self-contradictory responses

E.g. Plants do not behave, but swimming of algae is  
behaviour

Consensus:

- Ontogenetic changes are not
- Intact animal and not the parts of
- Always responds to external or internal stimuli

# What is behaviour?

Suggestion of Levitis et al.: behaviour is the internally coordinated responses (actions or inactions) of whole living organisms (individuals or groups) to internal and/or external stimuli, excluding responses more easily understood as developmental changes.

Received only 2 citations in 3 years!

# What is behaviour?

Problems:

- Interdisciplinary approach: behavioural biologists study the function of bird song together with neural, hormonal control.
- Behavioral ecology approach: way of fighting is individual strategy, however, size of antler is part of that.

Narrow sense: whatever you see from the outside

Broad sense: any individual trait

# Questions in ethology

What are the releasing stimuli?

How is it controlled by the nervous system?

**MECHANISM** (organisation, neural control)

Why is good for the animal?

What is the effect of the behaviour?

**FUNCTION** (the consequences of behaviour)

How does it change during life?

Interaction of learned and unlearned factors

**ONTOGENESIS** (learning and maturation)

How did it evolve?

Why did it evolve?

**EVOLUTION** (reconstruction and interpretation)



**Niko Tinbergen's  
four questions**

# Questions in ethology

Proximal questions:

- Mechanism
- Ontogenesis

Ultimate questions:

- Function
- Evolution



Niko Tinbergen's  
four questions

# Roots: Charles Darwin



Courtesy of the Wellcome Institute Library, London.  
Noncommercial, educational use only.

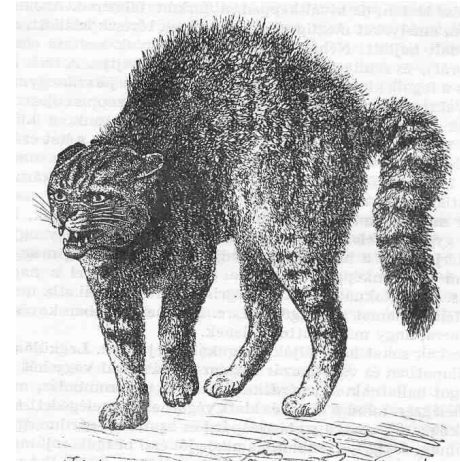
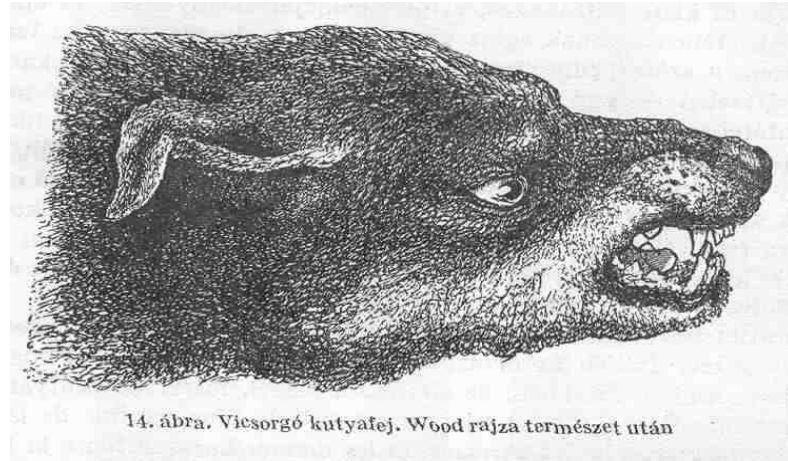
Charles Darwin (1889): *The Expression of the Emotions in Man and Animals*

Objective biological approach to behaviour

„Father of ethology”

Evolutionary process: Lamarckian....

# Roots of ethology



- Objective description of the pattern (how?)
- Interpretation of the pattern (why)
- Why in this form?
- Snarling: open mouth, withdrawn lips  
preparation to bite

Darwin's explanation: habits become inherited  
Today: **RITUALISATION**

# Roots of ethology

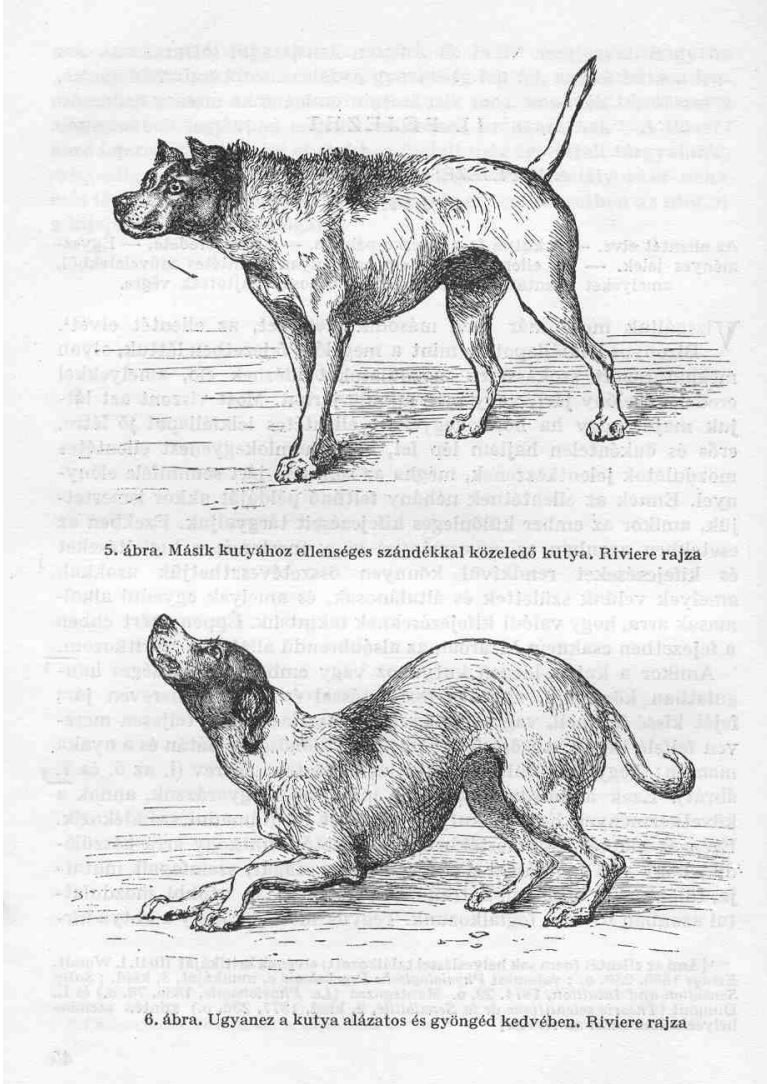


Fig. 5 „hostile frame of mind”

Fig. 6 „humble frame of mind”

Signal:

Expression of intention is adaptive

Signal must be unambiguous

Opposing intentions – opposing forms.

**THE PRINCIPLE OF ANTITHESIS**



# George Romanes



Darwin's follower: Romanes

Animal intelligence: evolutionary ladder

Relied heavily on anecdote and an anthropomorphic projection of human capacities onto other species

„But that some species of ants display marked signs of what we may call sympathy even towards healthy companions in distress, is proved by the following observation of Mr. Belt.”

Romanes was heavily criticised

# Roots: psychology



Morgan, Conwy Lloyd  
1852-1936

Criticised Romanes

Urged for empirical studies



Lloyd Morgan's Canon: "In no case is an animal activity to be interpreted in terms of higher psychological processes, if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development" (Morgan 1903).

Ochram's razor, Morgan's Canon, parsimony

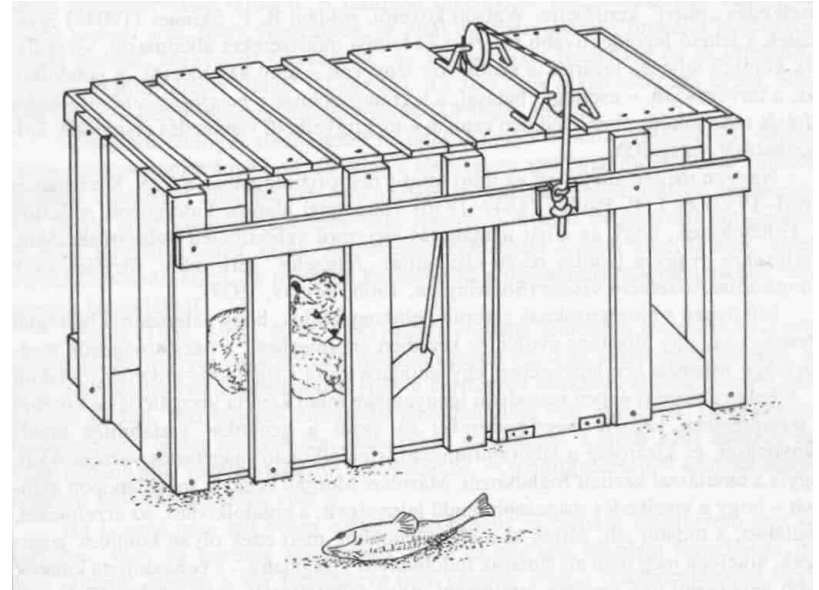
# Roots: psychology



Thorndike  
(1874-1949)

Experiments  
instead of  
anecdotes

Problem box

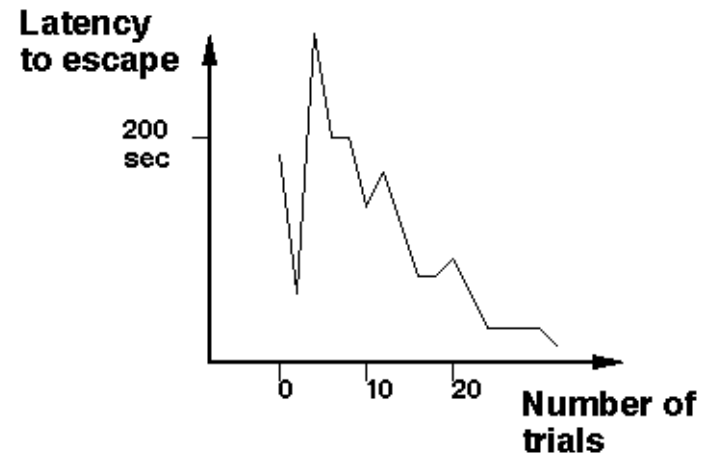


Task: defined by the experimenter

Solution: found by the animal by trial and error

# Roots: psychology

The **law of effect**: responses closely followed by satisfaction will become firmly attached to the situation and therefore more likely to reoccur when the situation is repeated.



Conversely, if the situation is followed by discomfort, the connections to the situation will become weaker and the behavior of response is less likely to occur when the situation is repeated.

# Behaviourism

Watson, John (1878-1958)



## PSYCHOLOGY AS THE BEHAVIORIST VIEWS IT

BY JOHN B. WATSON

*The Johns Hopkins University*

Psychology as the behaviorist views it is a purely objective experimental branch of natural science. Its theoretical goal is the prediction and control of behavior. Introspection forms no essential part of its methods, nor is the scientific value of its data dependent upon the readiness with which they lend themselves to interpretation in terms of consciousness. The behaviorist, in his efforts to get a unitary scheme of animal response, recognizes no dividing line between man and brute.

Controlled experiments.

Model animals, data, statistics

What cannot be observed does not exist

# Behaviorizmus



Skinner, Burrhus  
Frederic

1904 - 1990

Operant conditioning

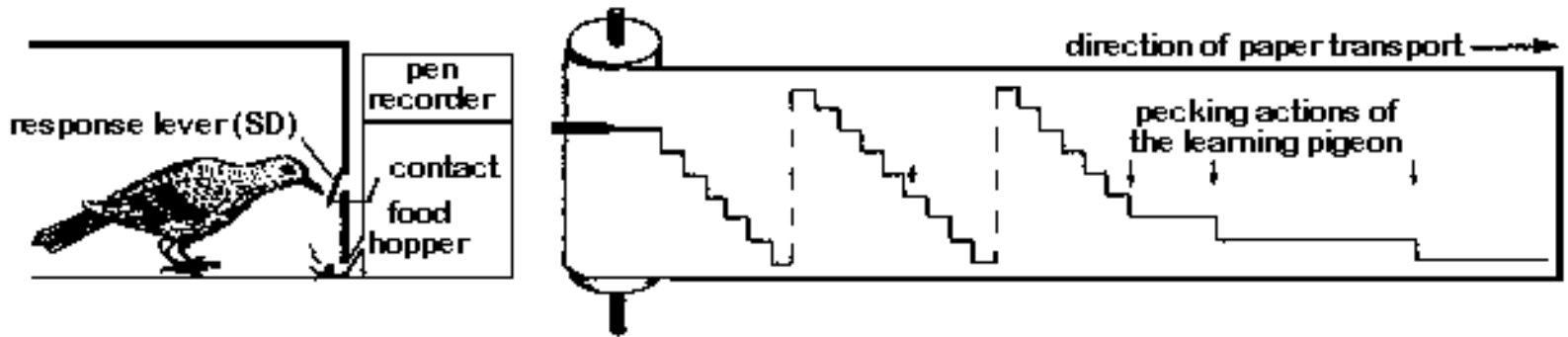
Behaviour can be  
manipulated

Correct response: defined by the experimenter  
(e.g. Pecking at a key)

Trial and error

Untold secret: shaping (corn glued on the key)

# Behaviourism



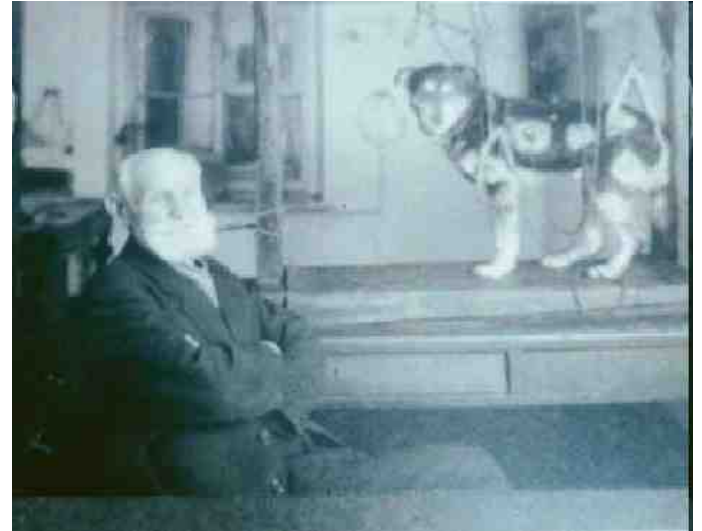
- Skinner box: automated
- Presentation of stimuli
- Data on response (pressing lever, pecking at key)
- Reward (or punishment) given automatically



# Classical conditioning



Pavlov  
(1849 - 1936 )



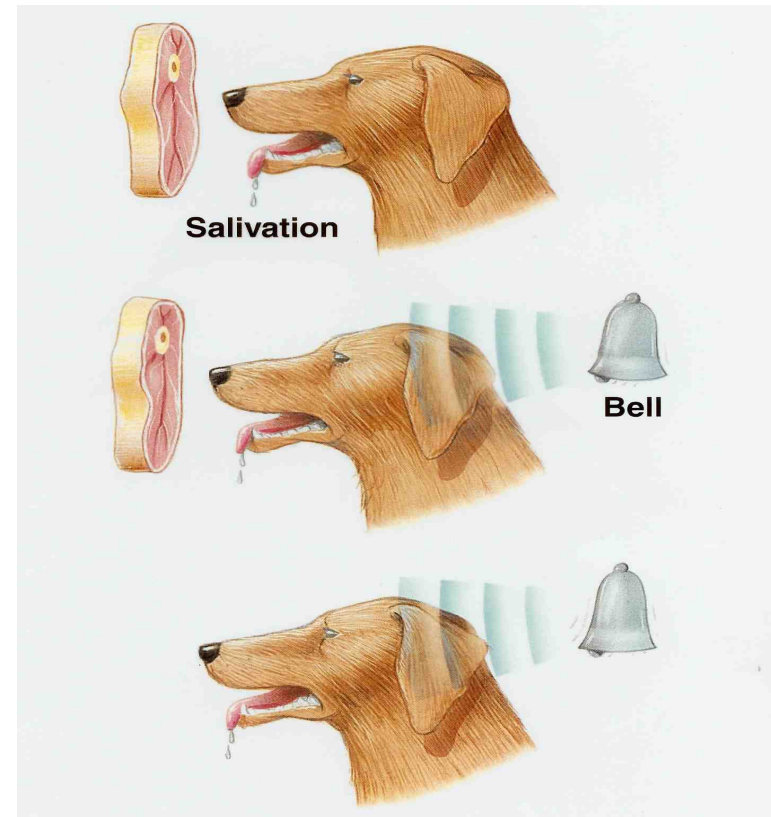
Nobel prize in 1904: „ "in recognition of his work on the physiology of digestion”

Learning theory: he observed that dogs salivate when hearing the approach of the caretaker.

# Classical conditioning



bell	→	orientation
food	→	salivation
Bell +food	→	salivation
Food: US	→	salivation: US
Bell: CS	→	salivation: CR



# Associative learning

Classical and operant conditioning

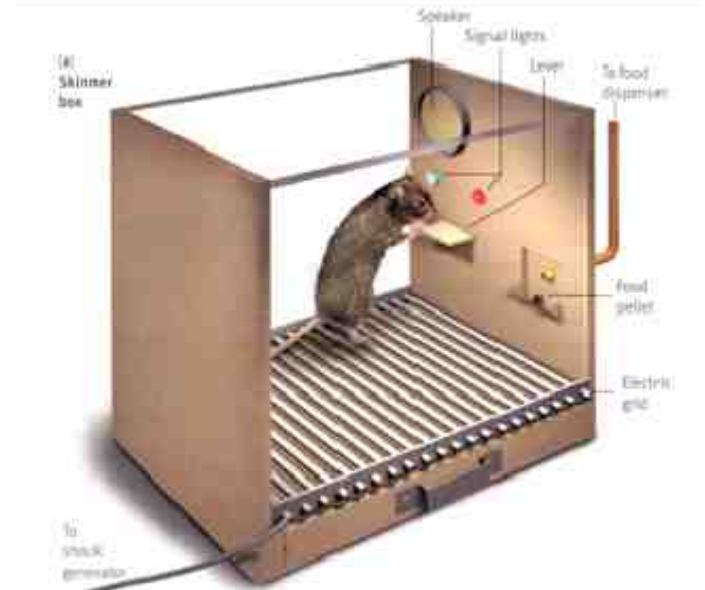
Reinforcement

positive: reward - negative: punishment

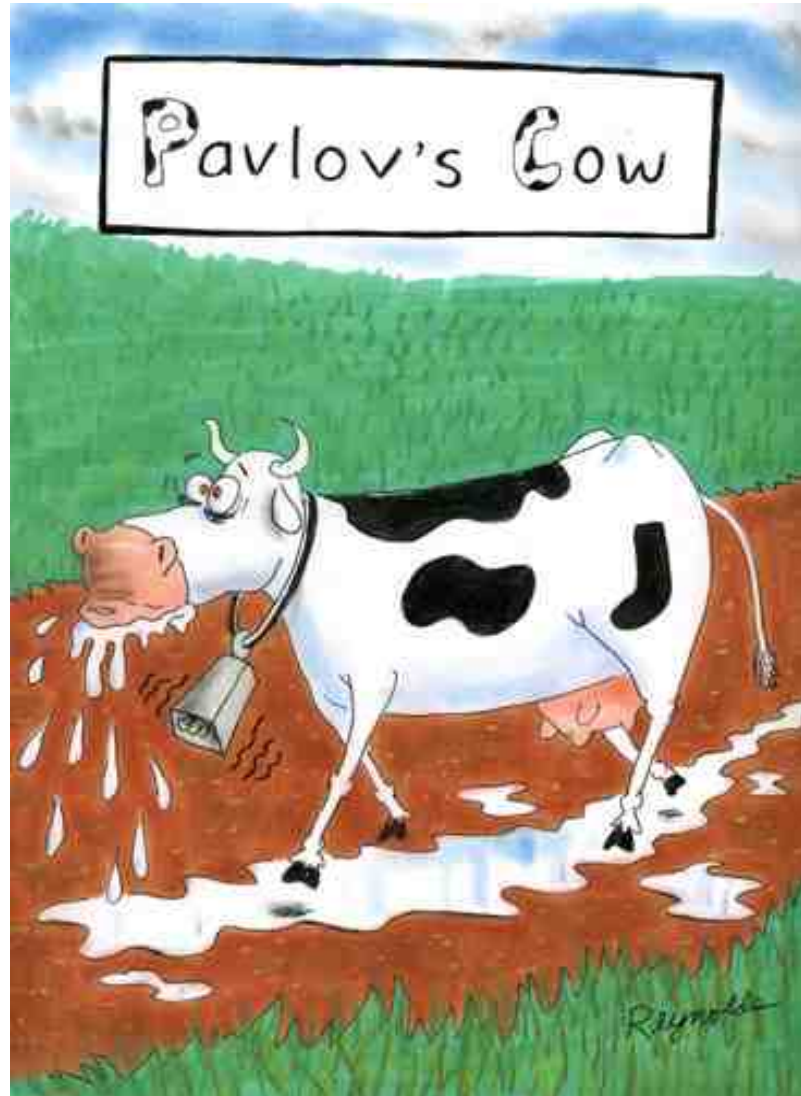
Behaviour

active: does something - passive: does nothing

e.g. One-trial passive avoidance learning



# Classical learning theory



# Habituation

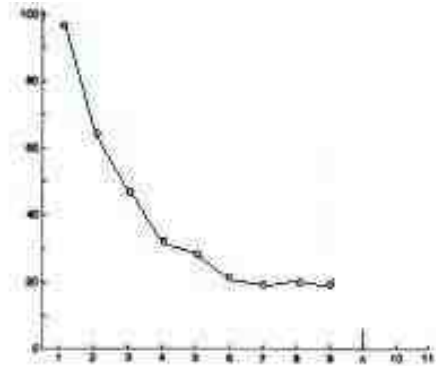
Stimulus – response  
(e.g. orientation, escape etc.)

Repeated presentation – response attenuates

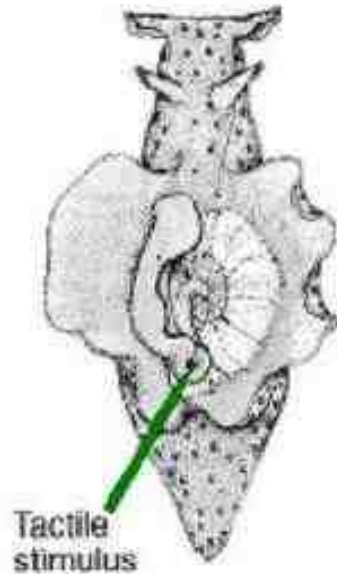
# Habituation

Aplysia: response diminishes following repeated stimulation

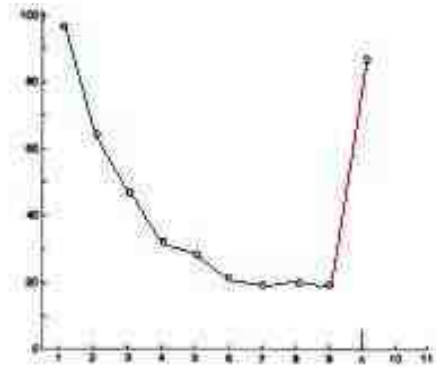
Active, adaptive learning



Sensitization

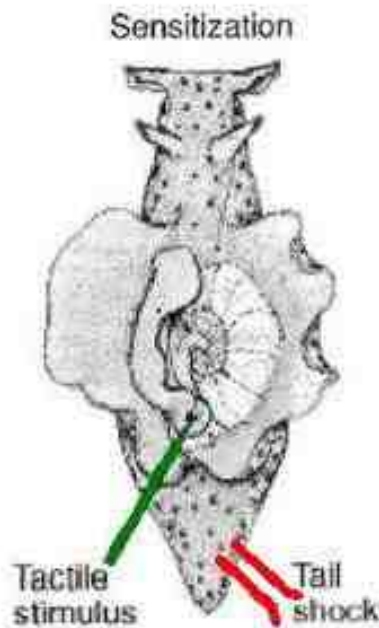


# Sensitisation



Habituation followed by mild shock  
Same stimulus – huge response

## Non-associative learning



# Behaviorism: theory

„laws of association”

Method of conditioning – strength of memory trace

Random positive reinforcement – better learning

Transfer of learned behaviour to new tasks

Stimulus generalisation

# Behaviorism: practice

„training of animals”:

Breaking complicated tasks  
into small steps

Conditioning every step

Chain the steps together

# Behaviorism: human applications

Psychology: behaviour therapy

Learning new behaviour patterns, counter-conditioning against the old ones

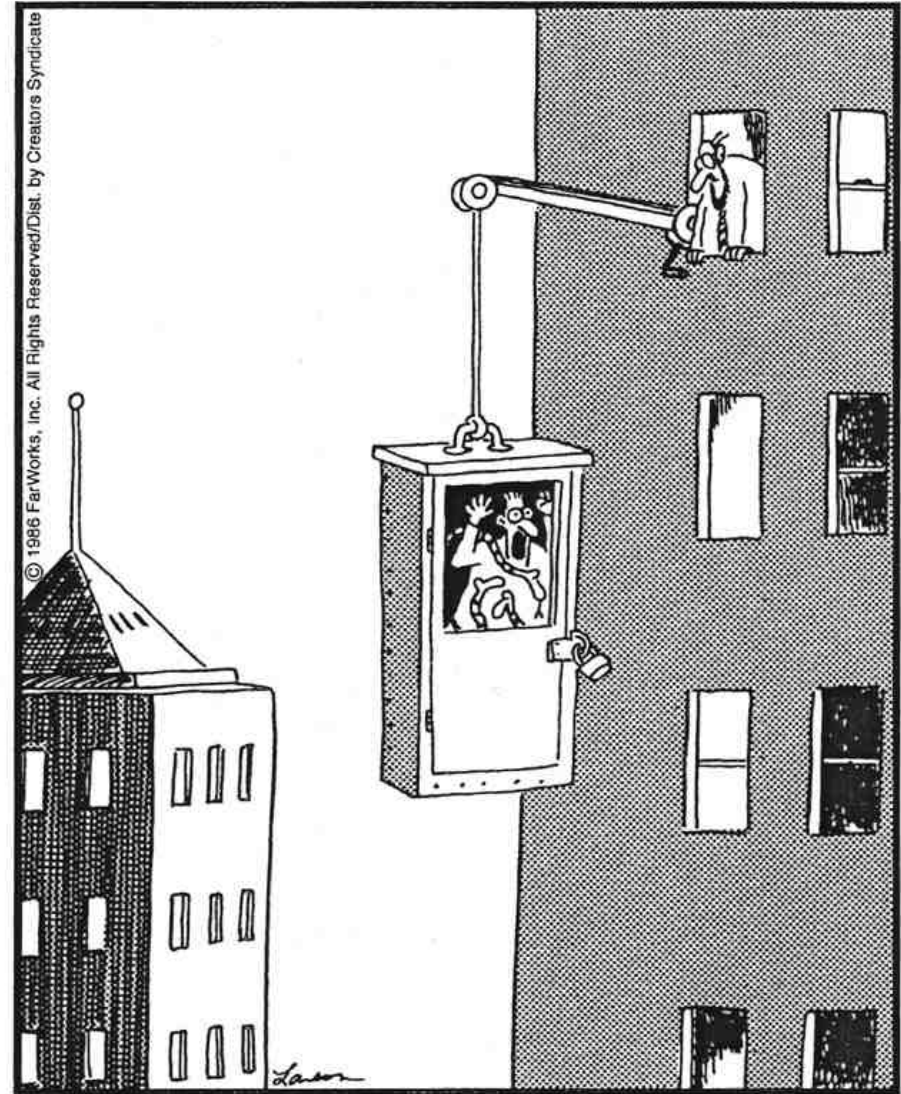
Desensitisation: treatment of fobias

Association: treating alcoholism by associating alcohol with disgust ☹️

Pedagogy: teaching strategies, positive reinforcement

# Behaviorism

Behaviour therapy:  
Flooding technique



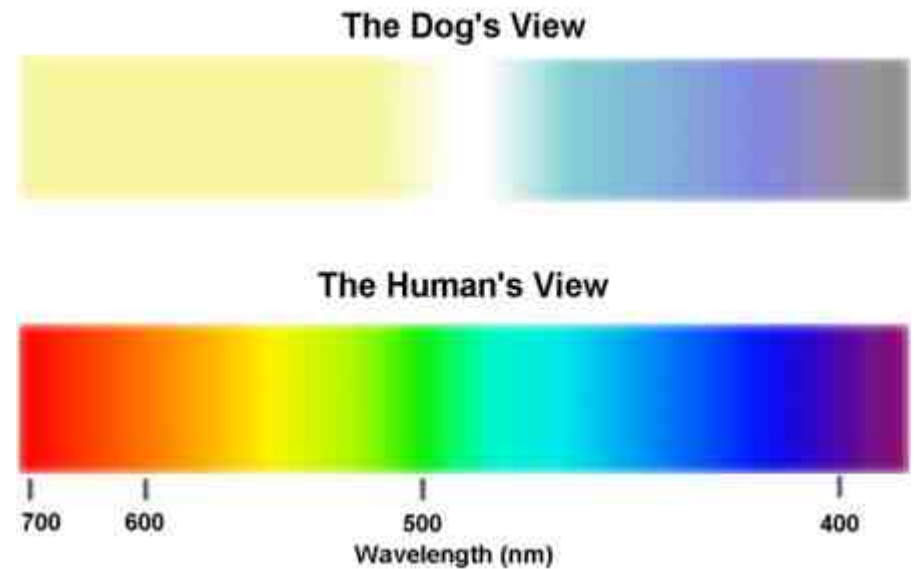
Professor Gallagher and his controversial technique of simultaneously confronting the fear of heights, snakes, and the dark.

# Behaviorism: tool

Ask the animal!

Sensory discrimination

Cognitive capacity



# Modification of behaviour

Habituation: active conditioning to aversive stimuli

Systematic desensitisation: structured habituation to low then to high intensity stimulus

Classical conditioning: e.g. clicker training

Operant conditioning: unintentional leads to unwanted behaviour (jumping at people)

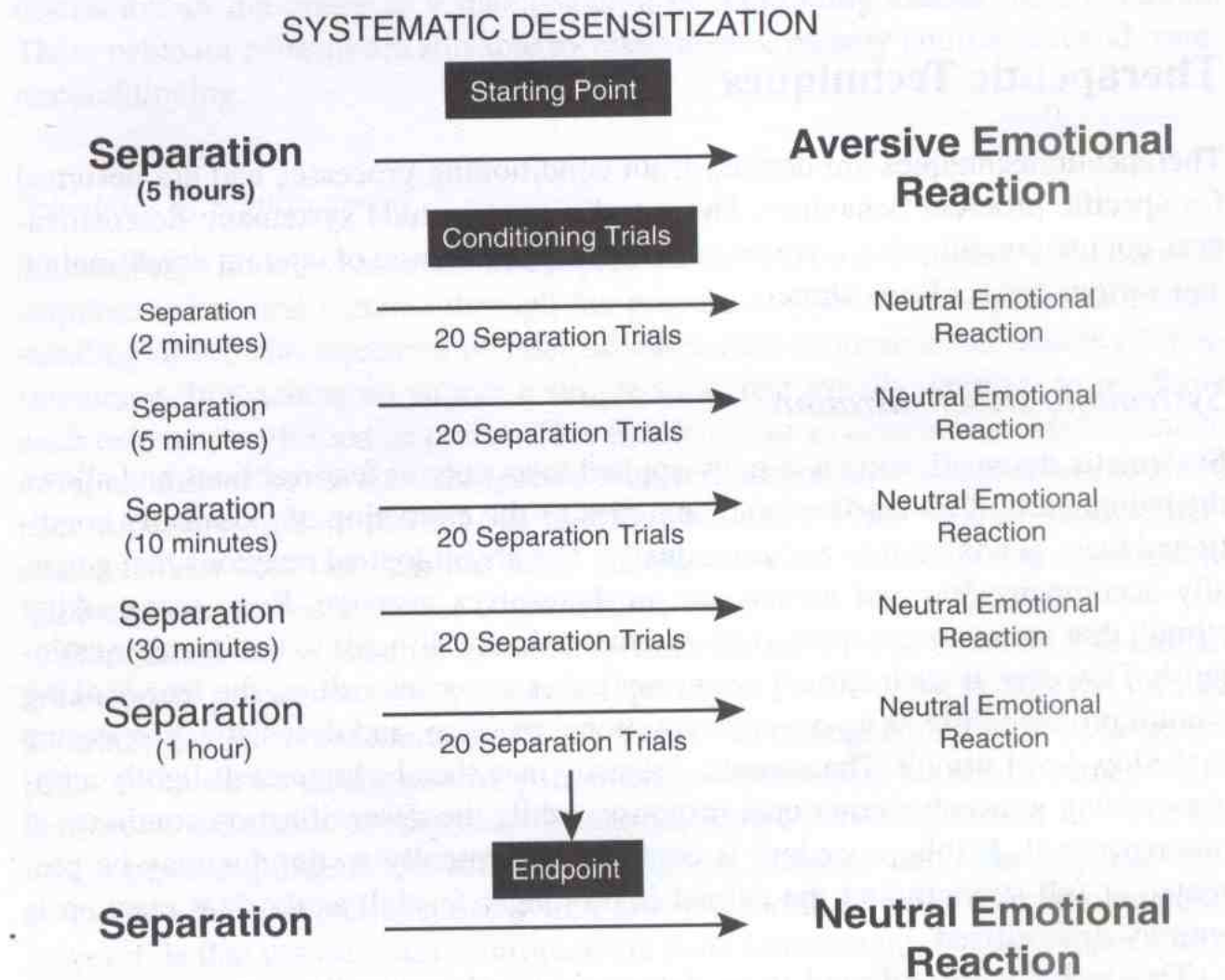
Successive proximation: built up of simple elements

Schedules of reinforcement:

positive: rare and random

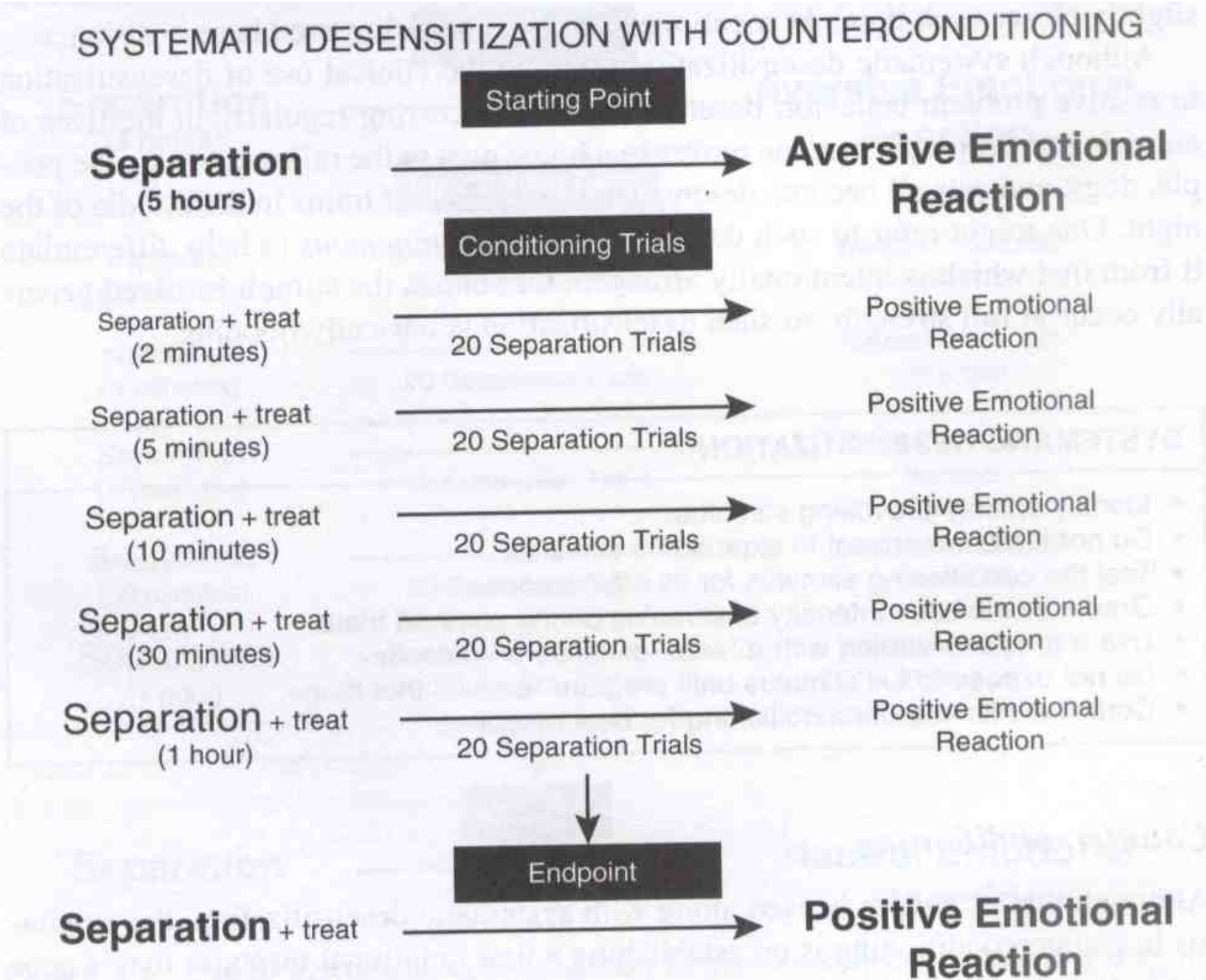
negative: without delay

# Example



**Figure 3-1** Use of systematic desensitization to treat separation anxiety in a dog. In this example, the initial problem is an aversive emotional reaction, manifested by extreme anxiety, when the dog is left alone for more than 15 minutes. The starting point of treatment is short departures (2 minutes), representing a weak separation stimulus. The weak separation stimulus should evoke a neutral emotional reaction, and with multiple separations the dog will become desensitized to short separations. The dog is continuously desensitized to longer periods of separation.

# Example



**Figure 3-2** Use of a combination of systematic desensitization and counterconditioning to treat separation anxiety in a dog. The systematic desensitization aspect is the same as in Figure 3-1 except that by adding counterconditioning with a food treat paired with the departure, a positive emotional reaction is associated with separation.

# Negative reinforcement

Punishment:

- Interactive: physical, grabbing, yelling
- Remote: shock collar, electric fence
- Social: withdrawal of attention

# Interactive punishment

Hitting, yelling, grabbing:

- Not recommended in therapy
- May lower motivation
- Can elicit aggression
- Enhances fear related problems
- Undermines trust



# Remote punishment

## Controversial

- If correctly applied should help
- Dog does not associate punishment with owner but with behaviour
- One-trial learning
- Good results in place avoidance

# Shock collar

Citronella spray, electric shock.

Controversial: abuse, false conditioning, stress

No elevation of stress hormones

Improvement of behaviour is expected soon. If problematic behaviour remains following the first few sessions, conditioning should be stopped (excessive barking)



# Latent learning



Edward Tolman (1886-1959)

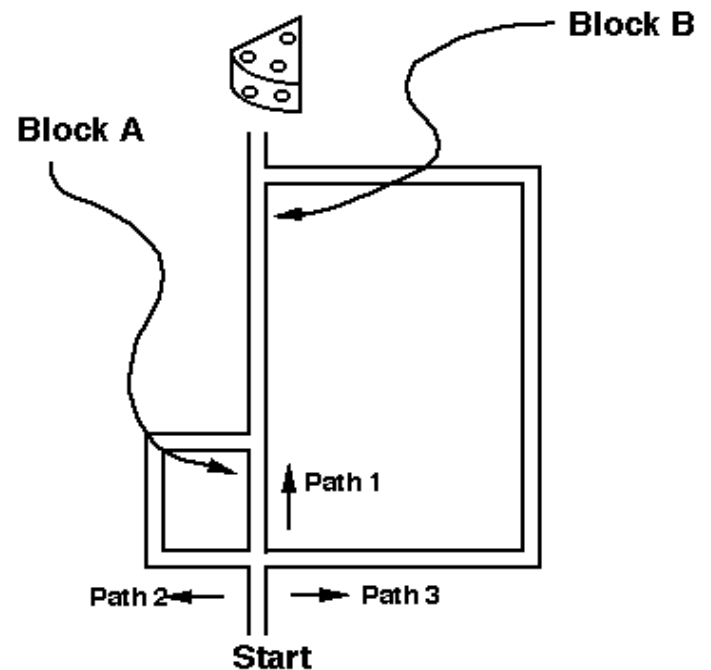
Rat walking in the maze learns about the maze without and reinforcement.

Chooses the shortest path (Path 1)

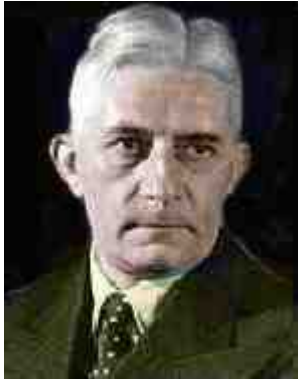
Block A: Path 2

Block B: Path 3

Cognitive map



# Belátásos tanulás



Wolfgang Köhler

Solution without trial and error

Mental manipulation

Chimps presented with unreachabile  
banana + boxes

Chimp Grande solves the task without  
trials



# Insight learning



# Social learning

Albert Bandura

Social learning theory

Humans learn a lot from  
observation and imitation of  
others



# Social learning

Bobo doll experiment 1961

3-6 year old children in 2 groups.

1. Adult attacked the doll
2. Adult ignored the doll

Test: children were frustrated (they were not allowed to play with toys)  
38% of boys, 13% of girls in the „agressive” group attacked the doll.



# Social learning

Young banded mongoos is escorted by an adult (brother, uncle)

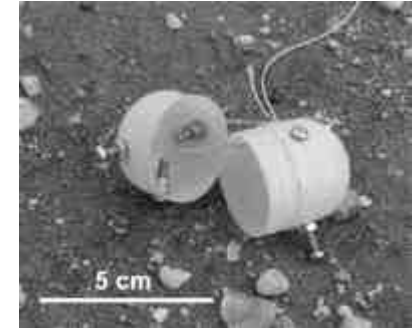
They walk, play and eat together.

Müller and Cant (2010) presented modified Kinder eggs filled with food.

Some adult opened the egg by biting, others by hitting to the ground.

Young mongooses followed the technique of the escort.

Culture of traditions.



# Imitation

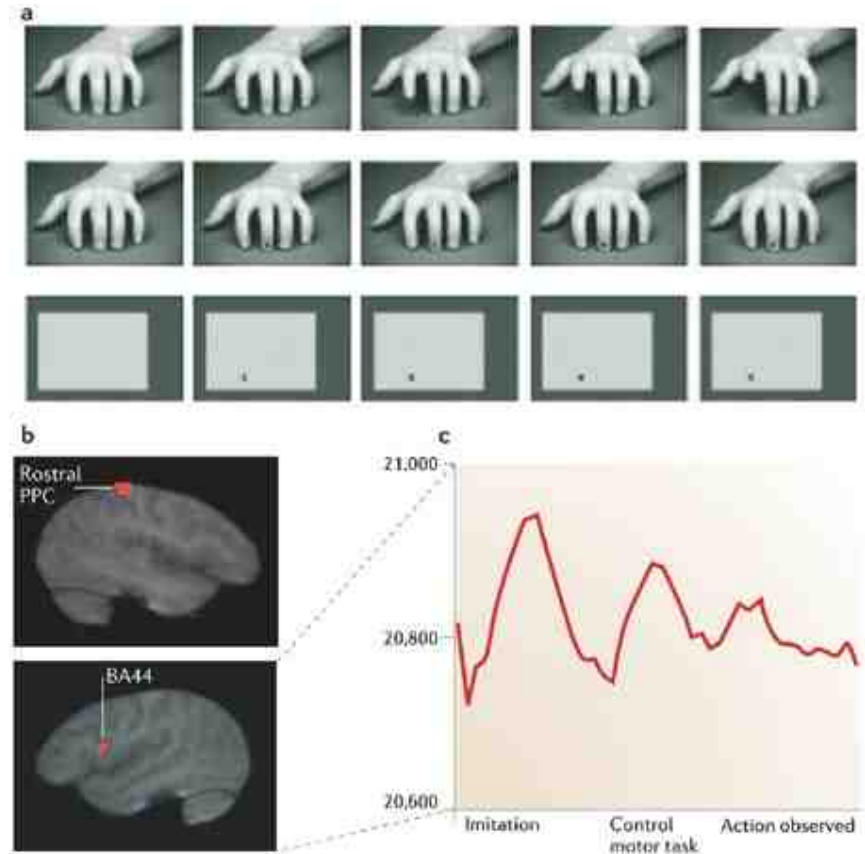
Mechanism: mirror neuron system

fMRI: activity of brain areas

3 treatments:

- 1) Observed and imitated lifting of finger
- 2) Visual control: no movement of stimulus, finger marked with X
- 3) Motor control: at the appearance of the cross, they lifted finger

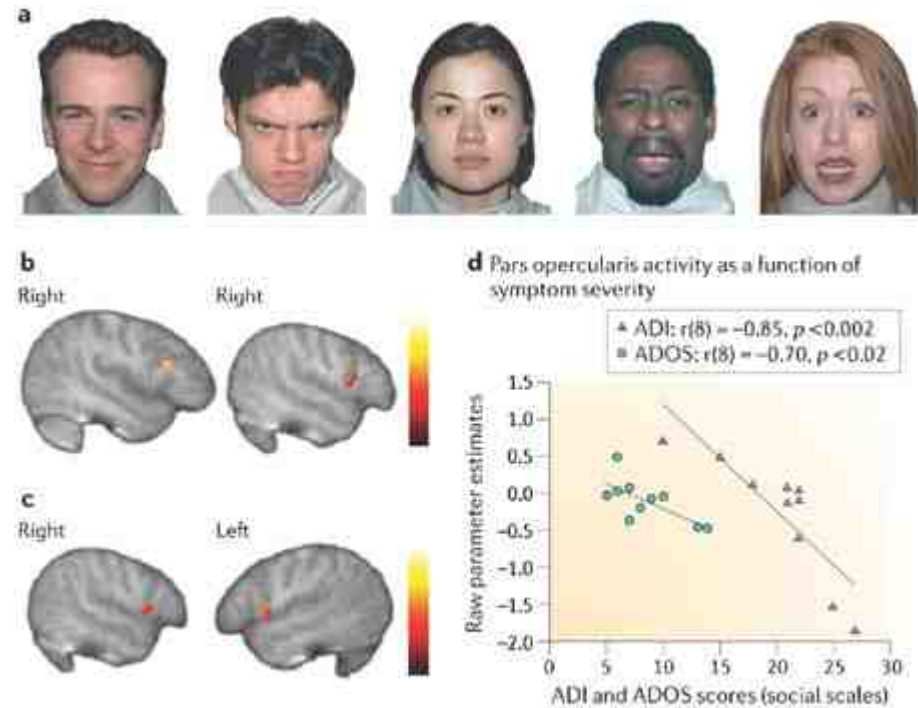
Mirror neuron system was activated in two areas



Copyright © 2006 Nature Publishing Group  
Nature Reviews | Neuroscience

# Mirror neurons and autism

Autistic and control children imitated facial gestures (a)  
Children with more severe symptoms had lower activity of the mirror neuron system (d).



Copyright © 2006 Nature Publishing Group  
Nature Reviews | Neuroscience

# Behaviorism: dogma

Tabula rasa: anything can be learned

No emotions, no reasoning

Humans and animals are responding robots

Speech and thinking are reflex chains

All people are born with equal capacities

USA: behaviorism

Soviet-union: „pavlovian” psychology

# Behaviorism: dogma

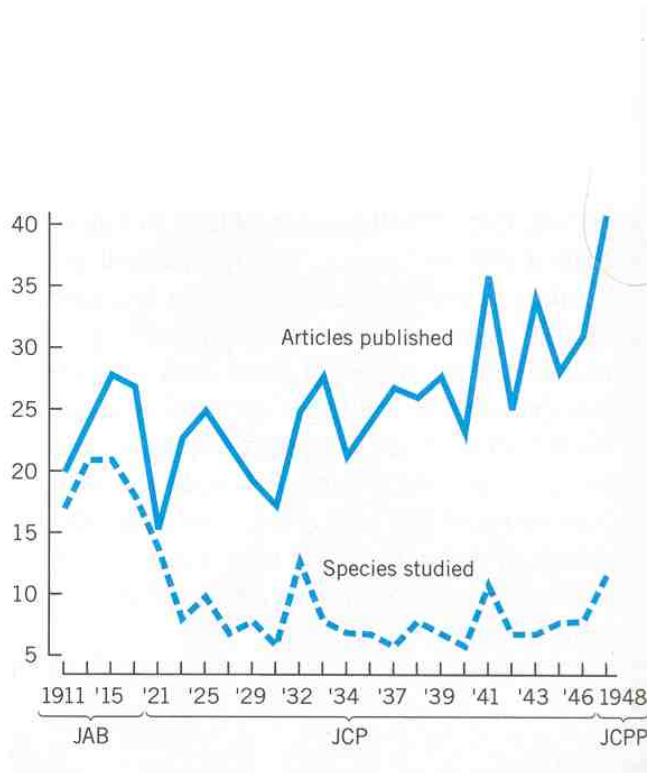


Skinner's  
daughter in  
Skinner box



"Give me a dozen healthy infants, well-formed, and my own specified world to bring them up in, and I'll guarantee to take any one at random and train him to become any type of specialist I might select--doctor, lawyer, artist merchant-chief, and, yes, even beggarman and thief, regardless of his talents, penchants, tendencies, abilities, vocations, and race of its ancestors." (Watson, 1930)

# Behaviorism: problems



Mouse, rat, pigeon, human

Insight learning: no trial and error

Latent learning, social learning:  
no reinforcement

Validity of behaviourist research  
is limited (few species in similar  
environments)

Techniques: good in simple cases

Do not force a dyslexic child to  
practice reading extensively

# Behaviorism: problems

	Phase 1	Phase 2	Test
Exp. 1	$A \rightarrow +$	$AX \rightarrow +$	X
Exp. 2	$B \rightarrow 0$	$BY \rightarrow +$	Y

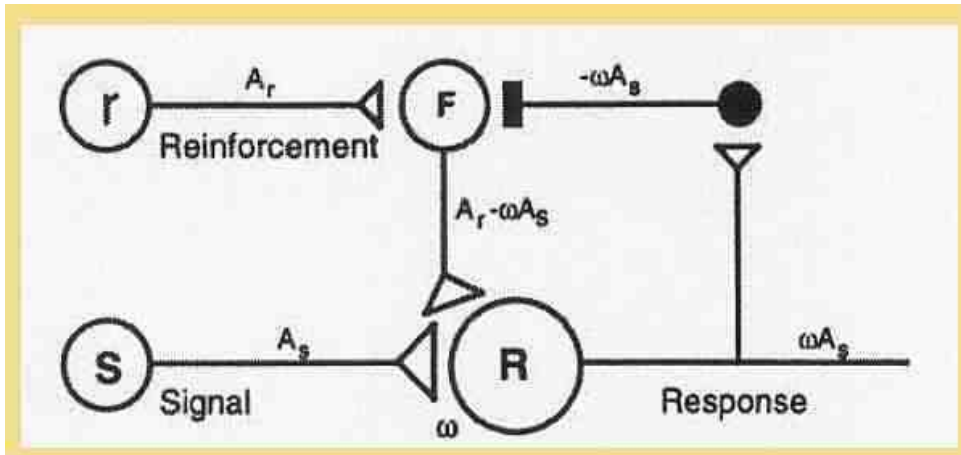
Theory of association:

A and X reinforced together, reinforcement  
→ animal reacts to X

No reaction to X, Reaction to Y

What's going on?

# Prediction error



Schultz:

prediction error

No surprise – no learning

# Behaviorism: problems



Zoologists:

adaptive responses are learned quicker

much of behaviour is species specific

inner state is important

they had no explanation

Do it by instinct!