Social learning in animals

Objectives

- Differences and similarities between social learning and communication
- What are cues and how do they differ from signals?
- 4 different mechanisms of social learning
- Traditions and culture in animals

What is social learning?

Definition:

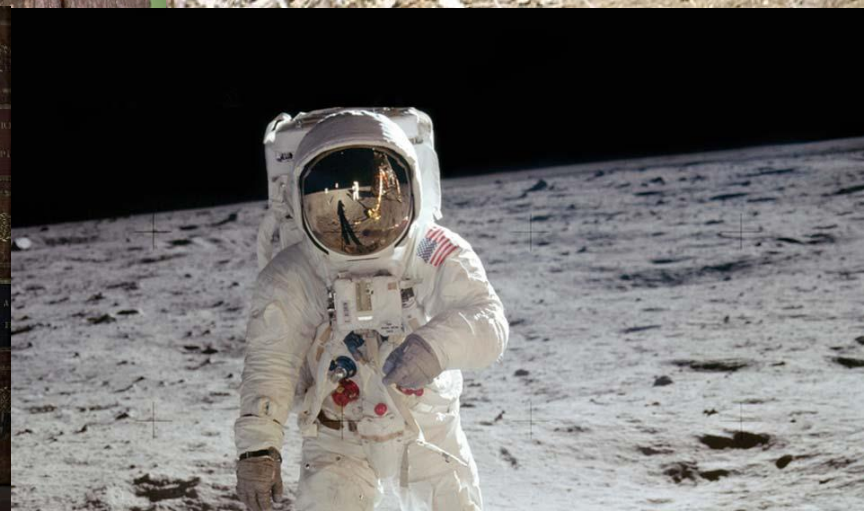
Learning that is influenced by observation of, or interaction with, another animal or its products (Heyes 1994)

Demonstrator or product

Observer


In many species
& many contexts


MEXICANA
A ROMA
86
144



How is SL different from communication?

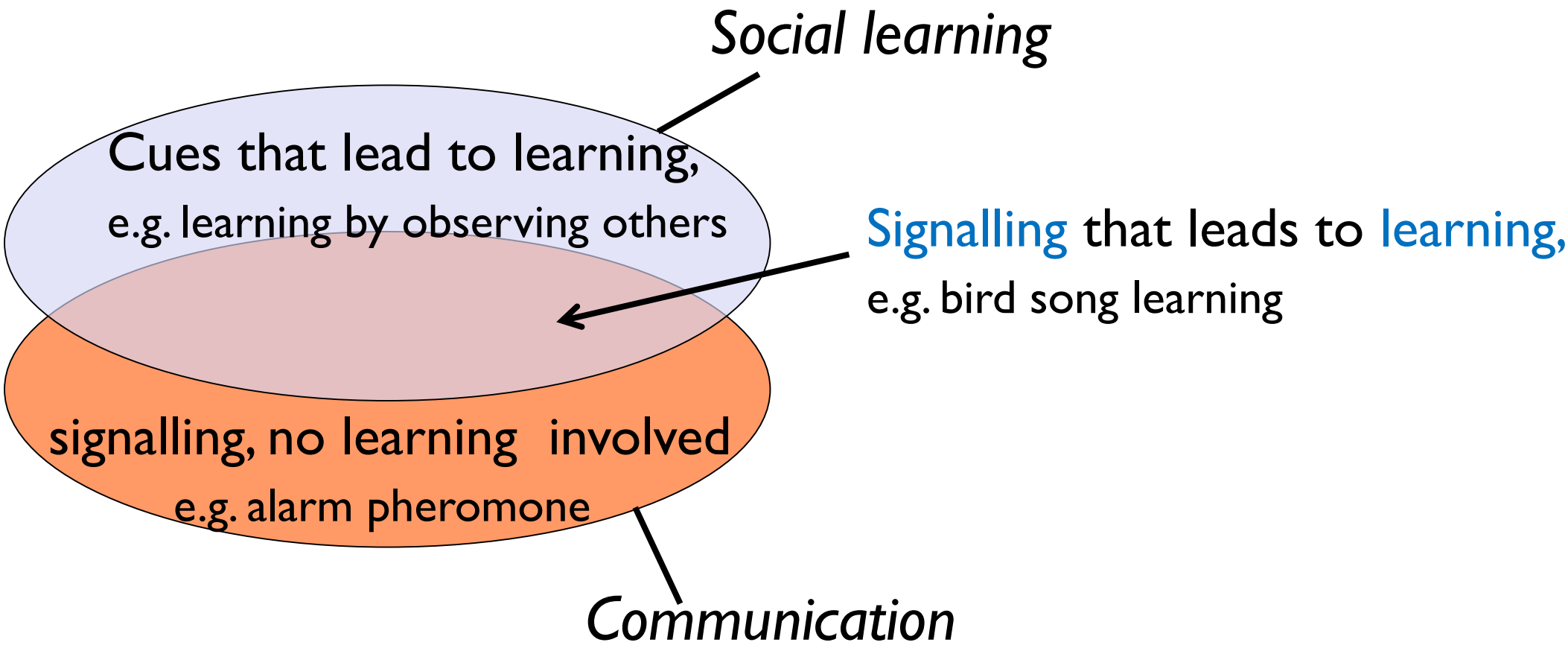
Communication

Information: signal

Social learning

Information:
- signal ***or*** cue,
- leads to learning

How is SL different from communication?



Common theme: **using social information**

What are information cues?

Cues: **inadvertent** social information
Signal: **intentional** social information

Examples of cues: nest-site selection in birds

Birds need to find a good breeding site, to raise as many offspring as possible

Difficult to anticipate where conditions are best...
...could check out the rearing success of other birds

Collared flycatcher
(*Ficedula albicollis*)

Cues for nest-site selection

Cues: number of offspring in nests
→ indicates habitat quality

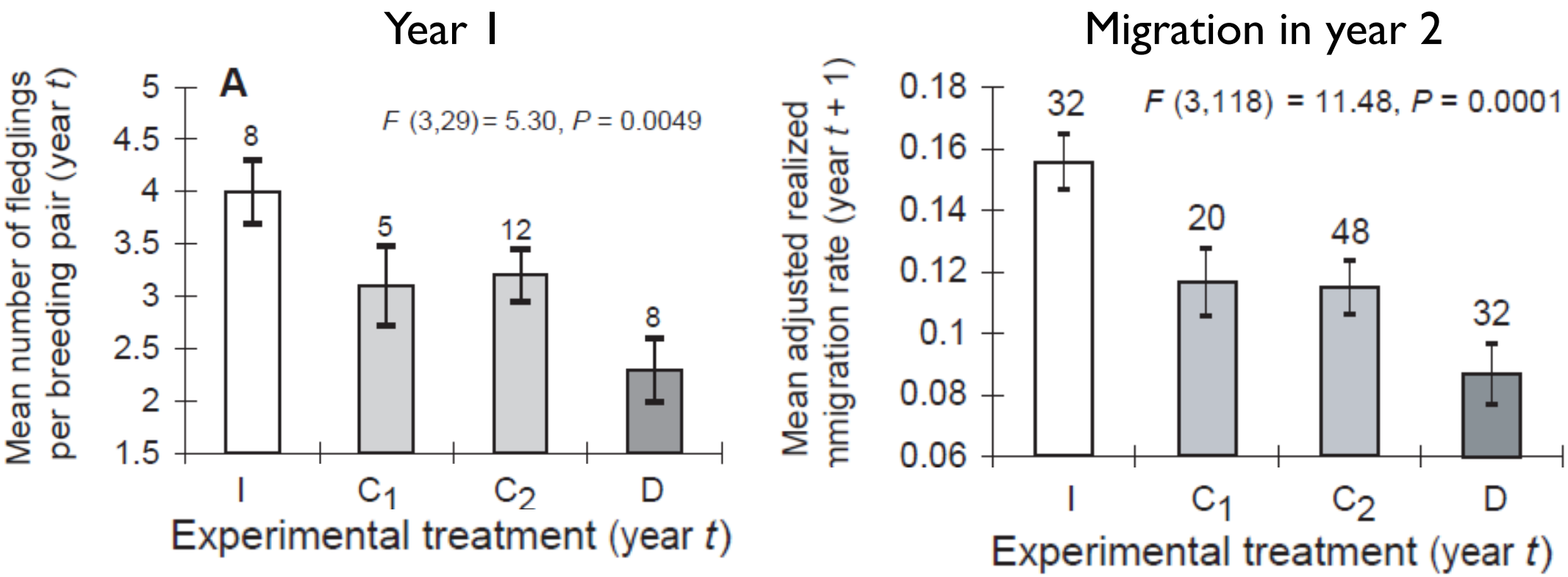
Year 1:

I: increased
Area 1

C: control
Area 2

D: decreased
Area 3

Birds migrate to areas with more fledglings



- Birds use "public information" (cues) to decide where to breed the following year
- Makes sense if number of fledglings indicates habitat quality

Doligez et al. (2002) *Science*

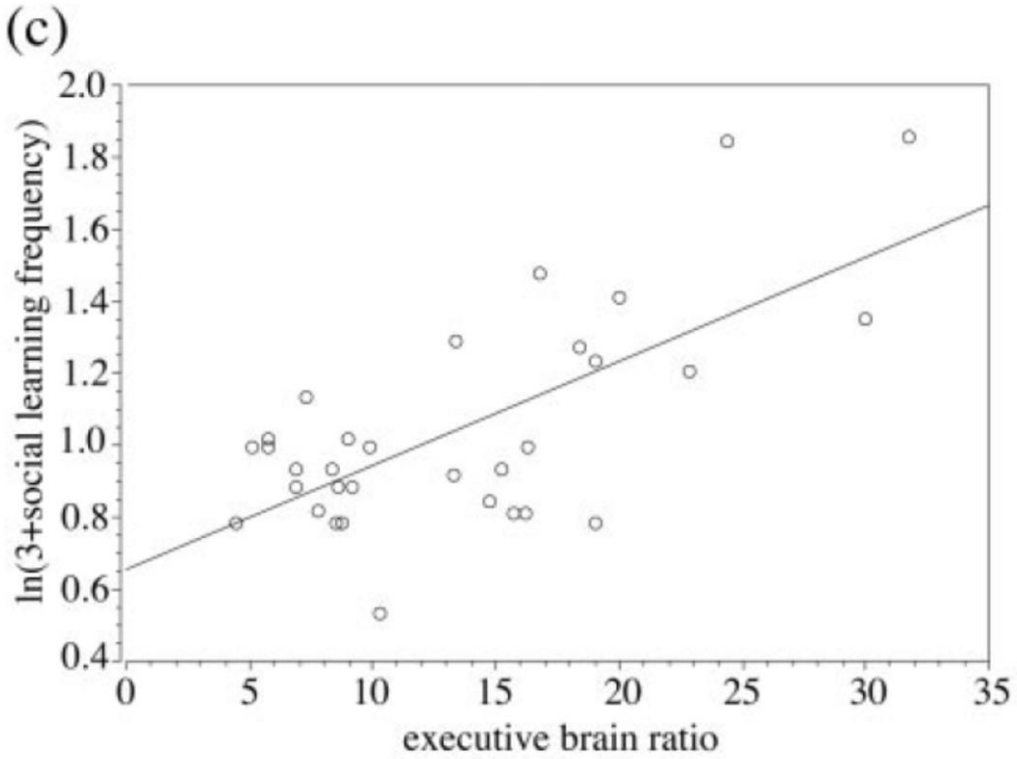
Do you have to be smart for social learning?

- Social learning has traditionally been studied in mammals and birds

- Researchers have often assumed that social learning is cognitively demanding…in other words, animals have to be smart to learn from others

Do you have to be smart for social learning?

Literature search: 1000 articles in 4 primate journals, 32 species



Reader & Laland (2002) *PNAS*

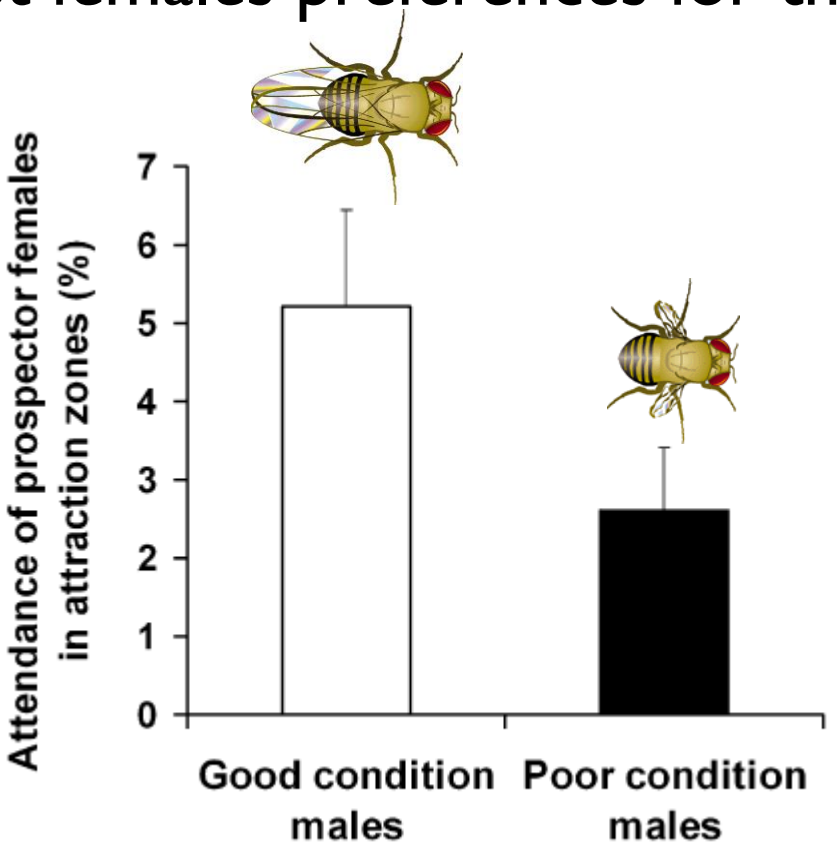
But: fruit flies can do it too

Step 1

Create good & bad condition males using a good *vs.* a poor diet

Step 2

Test females preferences for these 2 types of males

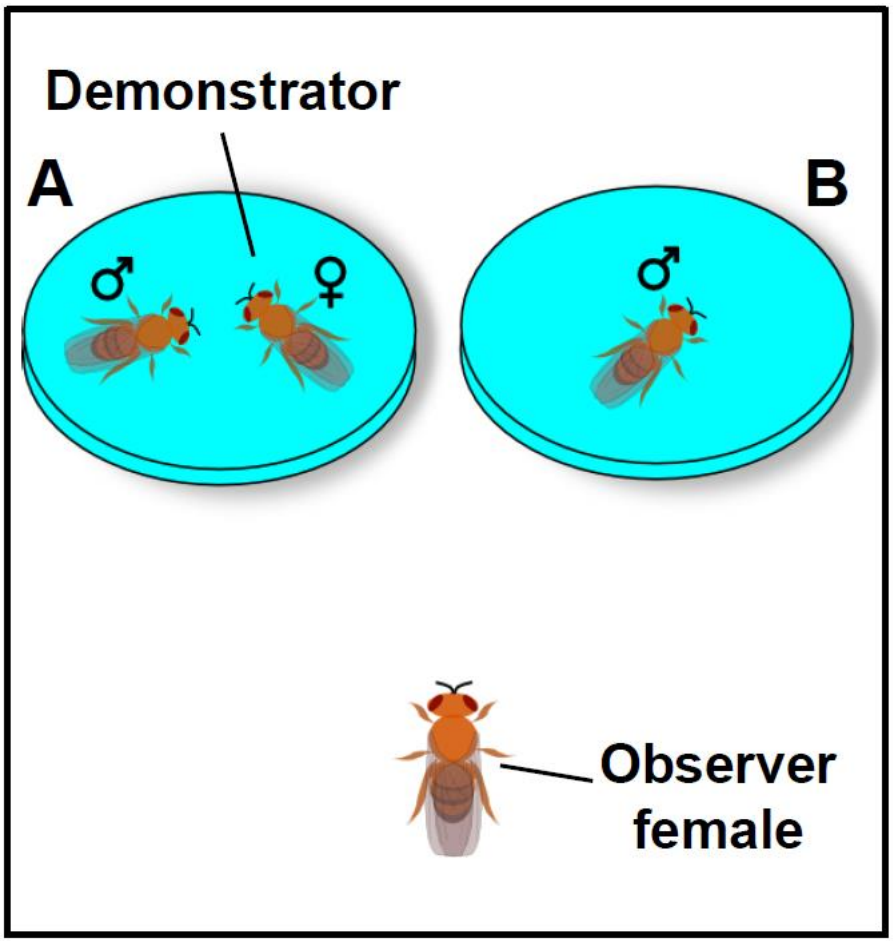


Mery et al. (2009) *Curr. Biol.*

Social learning in fruit flies

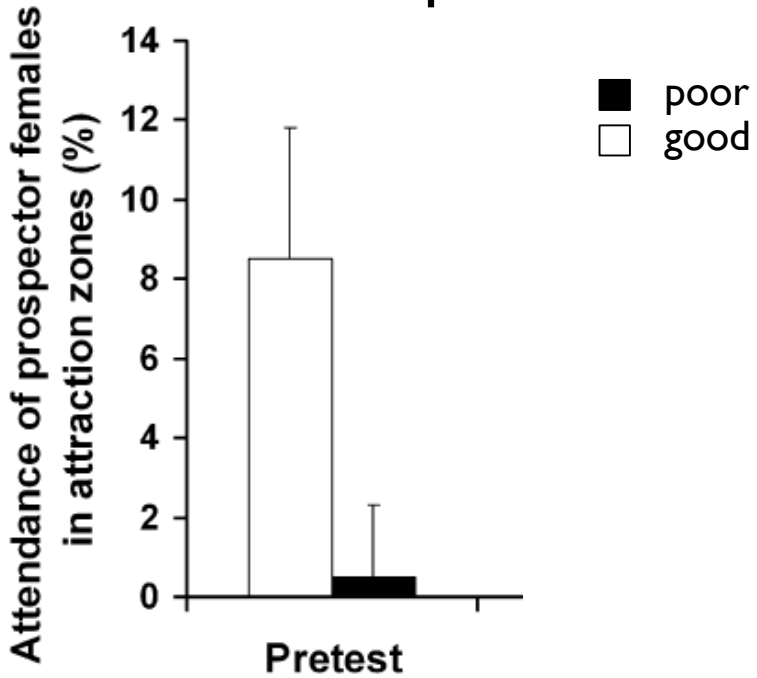
Step 3

Let ♀ observe males with another ♀



Step 4

Test ♀ again

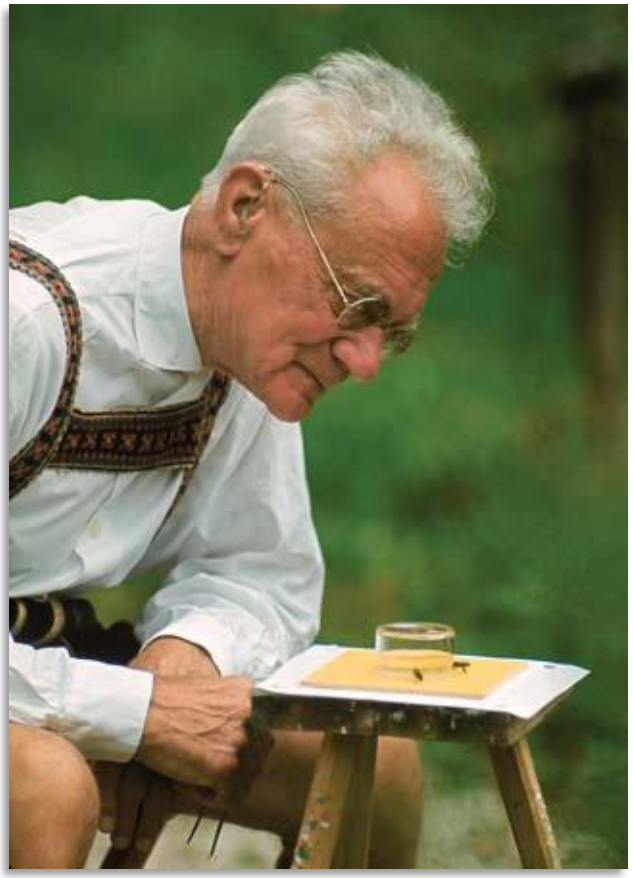


Poor quality ♂ became more attractive when observed with another ♀

Mery et al. (2009) *Curr. Biol.*

And honeybees even have a "language"

"Dance language":
sophisticated social learning



Karl von Frisch
Nobel Prize in 1973

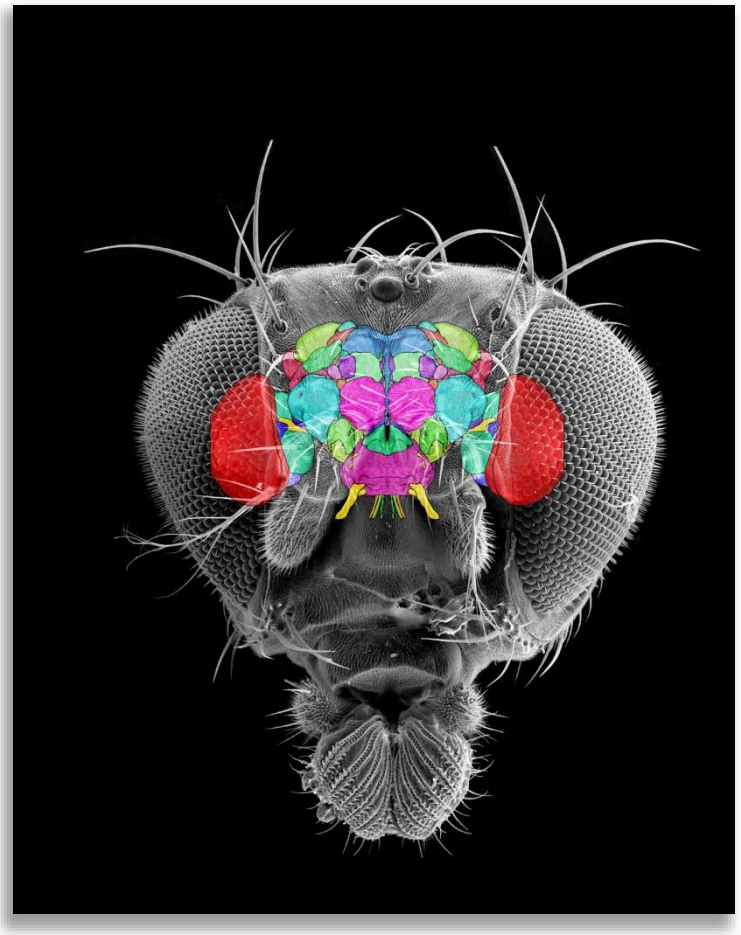
Do you have to be smart for social learning?

Social learning seems to require only a few neurons:

A **honeybee** brain contains less than 1 million neurons

A **fruit fly** brain contains has less than 100'000 neurons, a simple brain when compared to a primate brain

(**Humans** have ~90 billion neurons)



You don't have to be smart for social learning

- Very small brains can be very good at social learning
- Evolutionary need is more important than brain size
  → social learning is found when it benefits animals
- But: certain types of social learning might require more intelligence than others (e.g. imitation)

Chittka & Niven (2009) *Curr. Biol.*

Social learning mechanisms

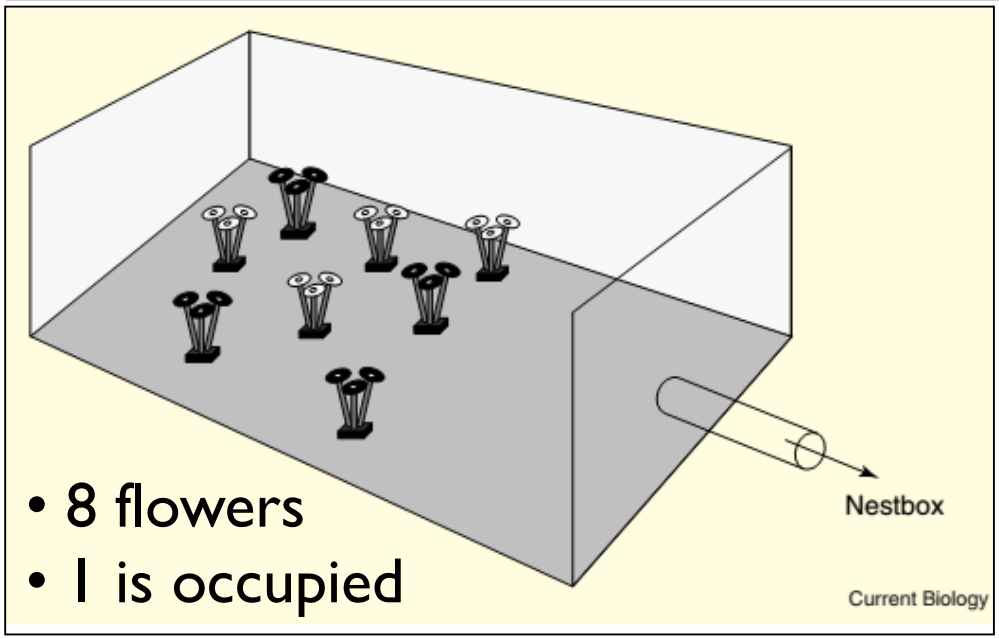
Mechanisms of social learning

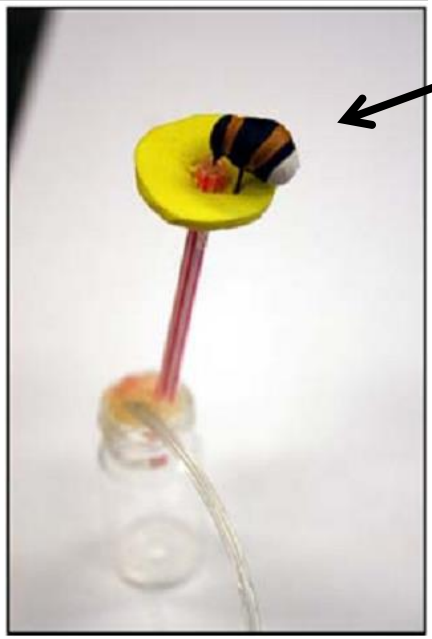
1. Local enhancement
2. Social facilitation
3. Imitation
4. Teaching

1. Local enhancement

- "simplest" mechanism
  1. A demonstrator attracts attention to a place **X**
  2. An observer interacts with objects at **X** and learns

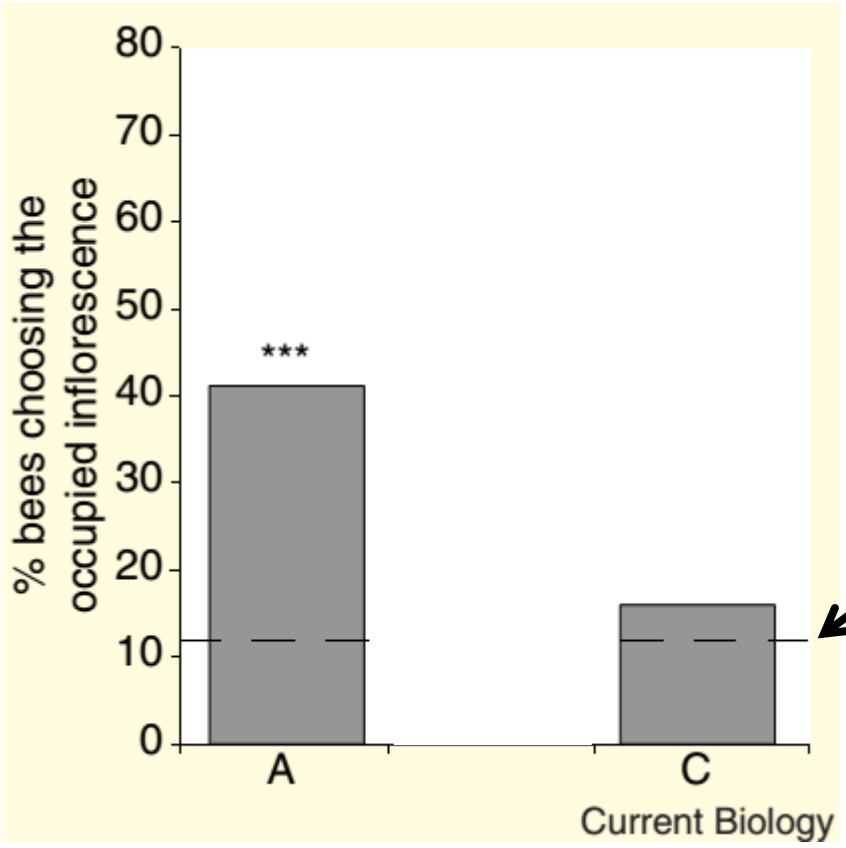
Local enhancement in bumblebees





Leadbeater & Chittka (2005) *Curr. Biol.*

1. Local enhancement



Random choice

A) Naïve observer bees on their first visit

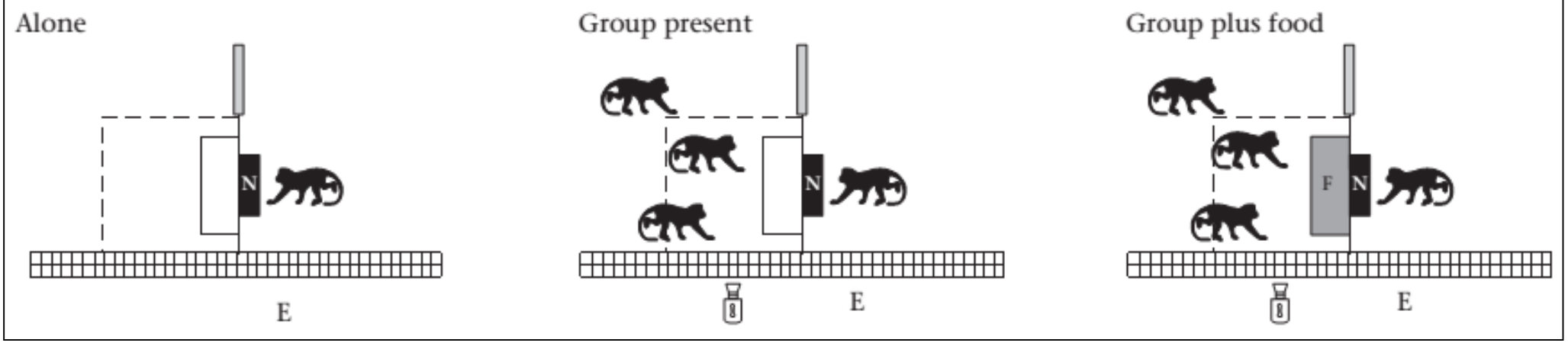
C) Experienced bees

Naïve bees chose the occupied flower more often than by chance

2. Social facilitation

- The presence of a demonstrator affects observer behaviour
- For example, an animal is more likely to explore its environment in the presence of others because:
  - it's safer (ultimate answer)
  - reduce individual stress of being alone (proximate answer)
  - reduce neophobic response (proximate answer)

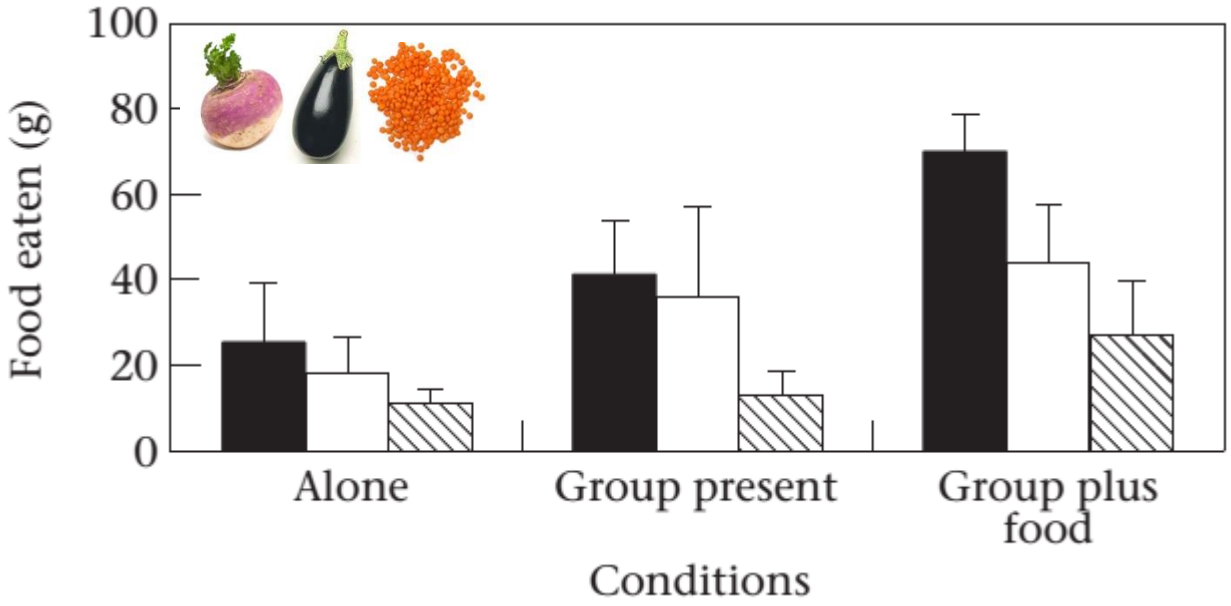
Social facilitation in capuchin monkeys: eating novel food



N = novel food

Visalberghi & Addessi (2000) *Anim. Behav.*

2. Social facilitation: eating novel food



1. In the presence of group members an observer ate more novel food
2. When group members ate food, there was an increase in accepting novel food
3. Trying food means learning about food

Visalberghi & Addessi (2000) *Anim. Behav.*

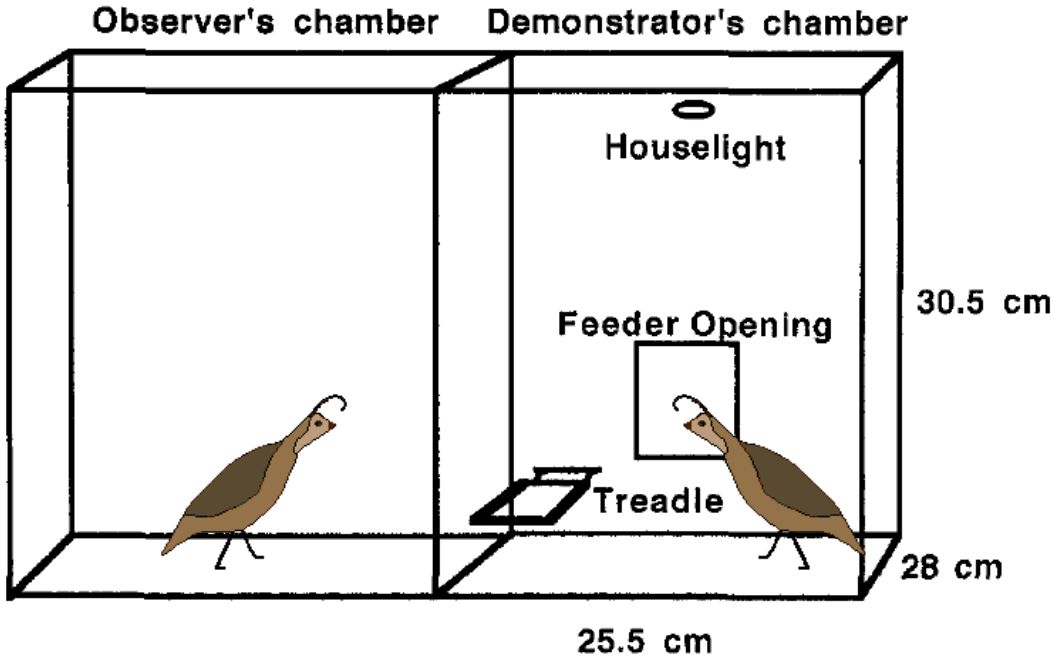
3. Imitation

Definition: learning of a new behaviour through observation of a demonstrator performing that behaviour

- The effect is "direct", not indirect as with local enhancement
- Many of the best examples include the learning of songs in birds and marine mammals

Testing imitation: the two-action method

- Observers watch demonstrators perform 1 of 2 different actions with the same outcome
- Observers then have to imitate this action to get outcome



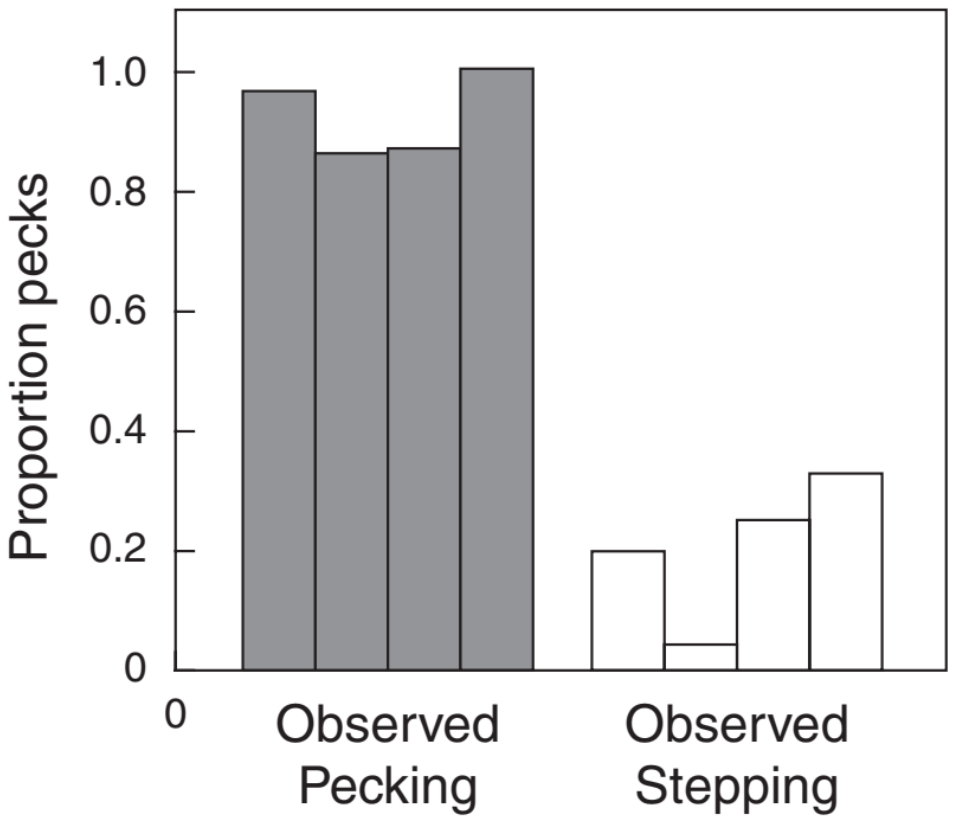
Japanese quail

- Demonstrators either *pecked* or *stepped* on treadle

Akins & Zentall (1996) *J. Comp. Psychol.*

3. Imitation

- Individuals that observed pecking were very likely to peck and *vice versa*



Evidence that quails imitate the actions of others

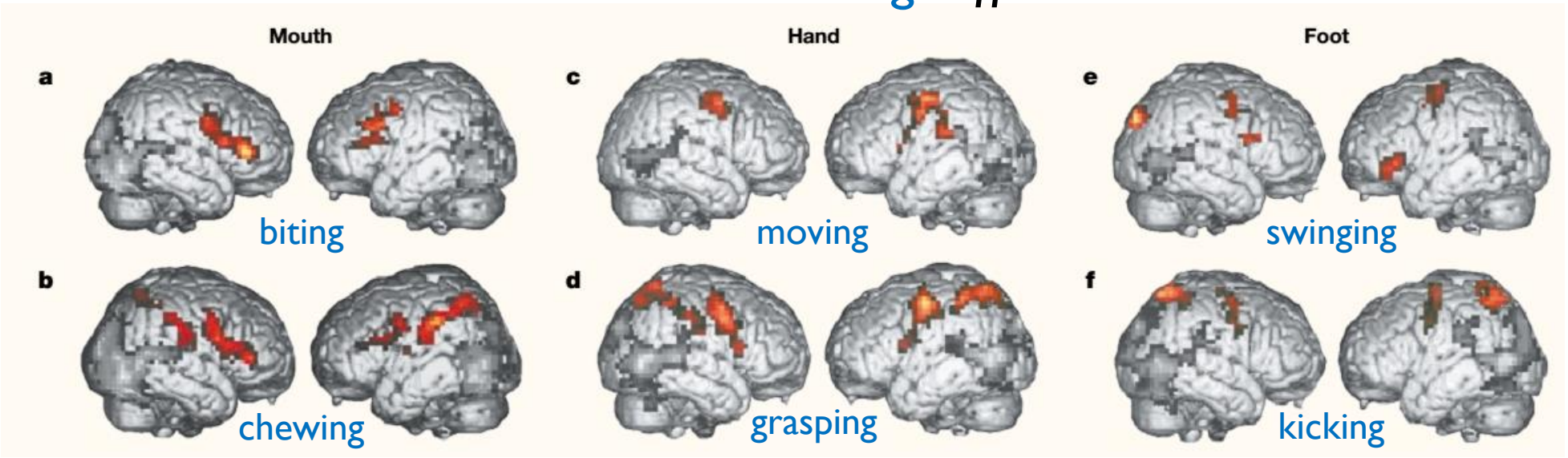
Akins & Zentall (1996) *J. Comp. Psychol.*

3. Imitation: neural basis

- What are the neural mechanisms of social learning: which brain regions, what kind of neurons etc.?

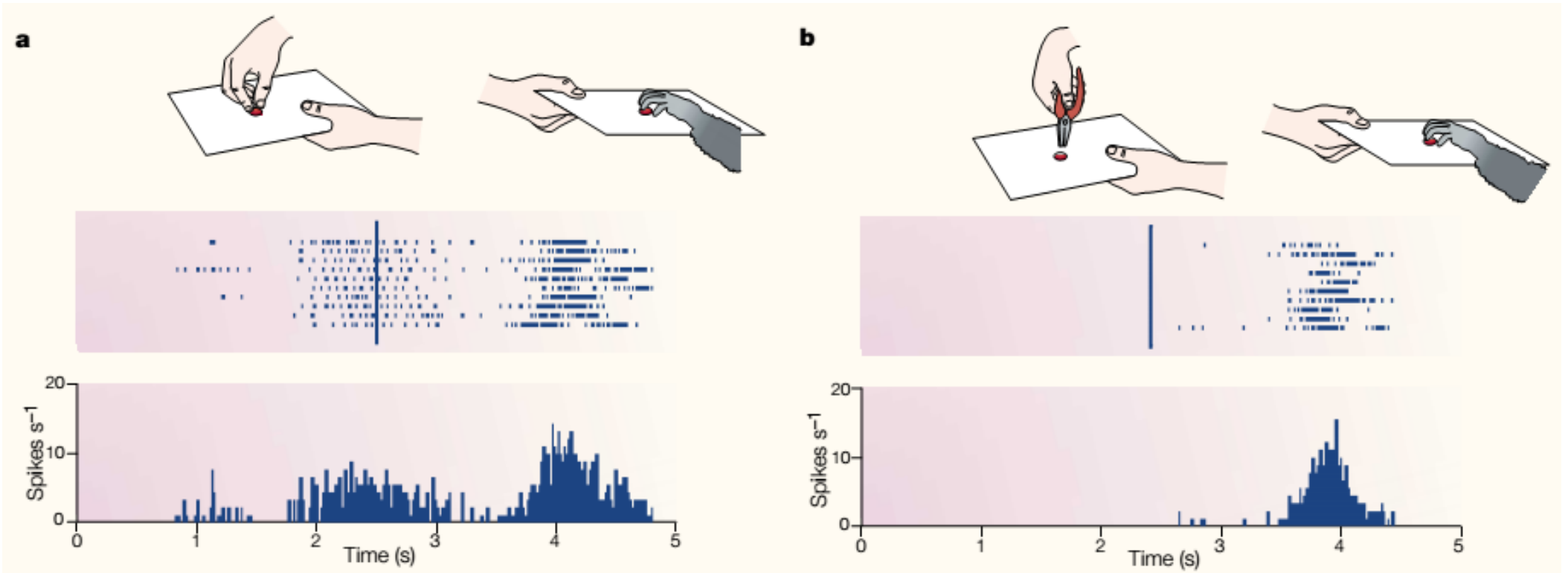
- Brain imaging studies have tried to identify the brain regions involved in social learning

Brain activation when observing different actions



3. Imitation: mirror neurons

- The discovery of "**mirror neurons**" provides a potential neural basis of imitation. They fire when:
    1. they see/hear a behaviour performed by others
    2. they perform the same behaviour themselves



Rizzolatti et al. (2001) *Nature Rev. Neurosci.*

3. Imitation: mirror neurons

- They function as a bridge between visual processing and the motor performance
- They might mediate action understanding, empathy

4. Teaching

- Experienced individuals actively facilitate learning in others

- For a long time thought to be unique to humans & the basis of our culture

Definition

Teaching has 3 criteria (Caro & Hauser 1992):

1. Individual **A** ("teacher") modifies its behaviour in the presence of a naïve individual **B**
2. Individual **A** has a **cost** or **no direct benefit**
3. Individual **B** learns the skill/behaviour **faster** or **more efficiently** than without **A**, or wouldn't have learned at all

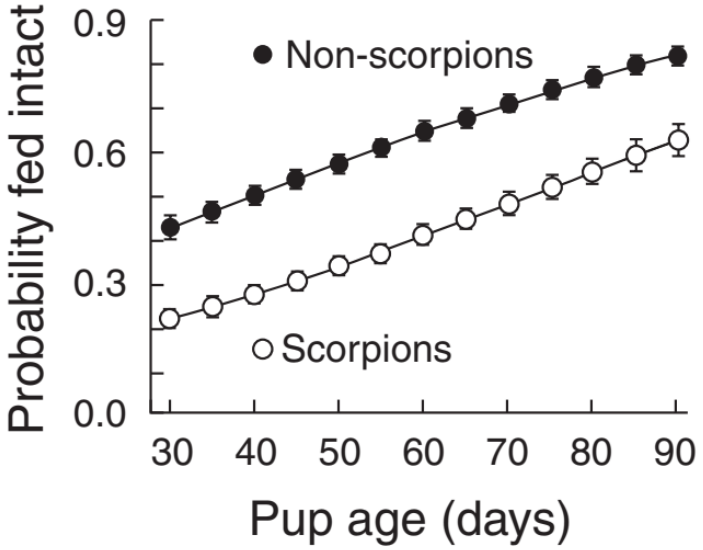
4. Teaching in meerkats

- Does teaching exist in animals in natural circumstances?

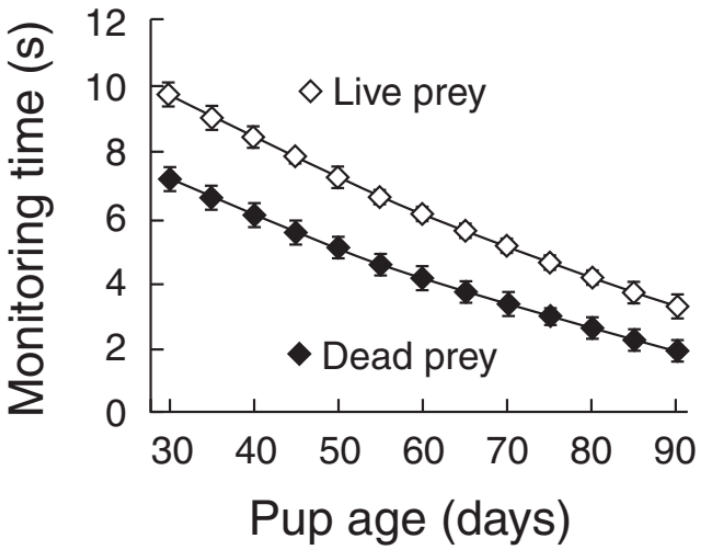
- Meerkats are cooperative breeders, up to 40 individuals/group
- Dominant ♂ + ♀ are parents of 80% of pups (young offspring)
- Helpers feed pups until 90 days
- Dangerous food: scorpions
- Helpers disable them before feeding them to pups

Thornton & McAuliffe (2006) *Science*

4. Teaching in meerkats



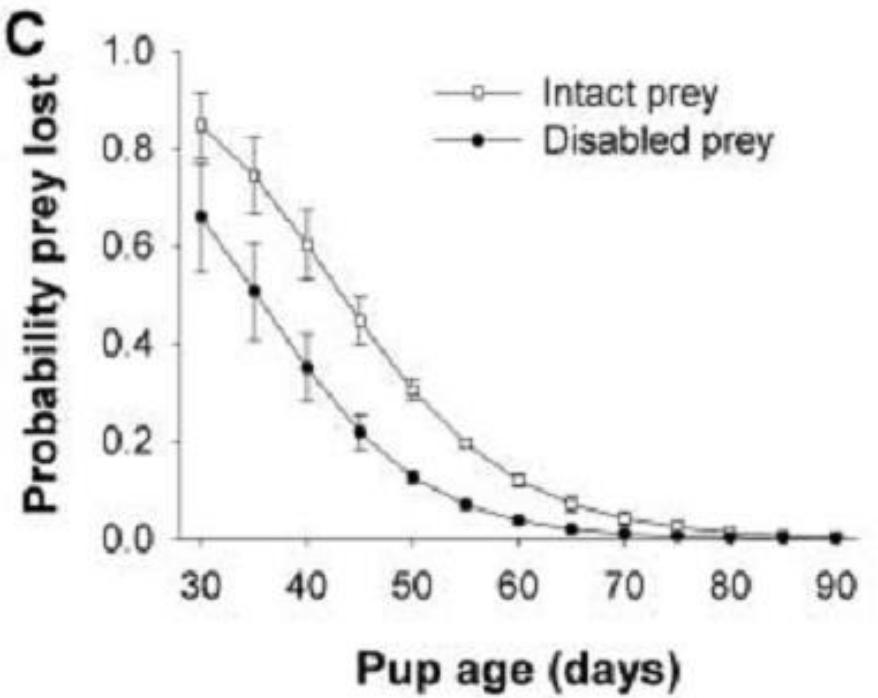
- Helpers give more dangerous food as pups become older
- Helpers modify their behaviour in response to pup competence



Helpers seem to be teaching the pups how to eat food

Thornton & McAuliffe (2006) *Science*

4. Teaching in meerkats



- Pups become better with age

Thornton & McAuliffe (2006) *Science*

4. Teaching in meerkats

3 teaching criteria (Caro & Hauser 1992):

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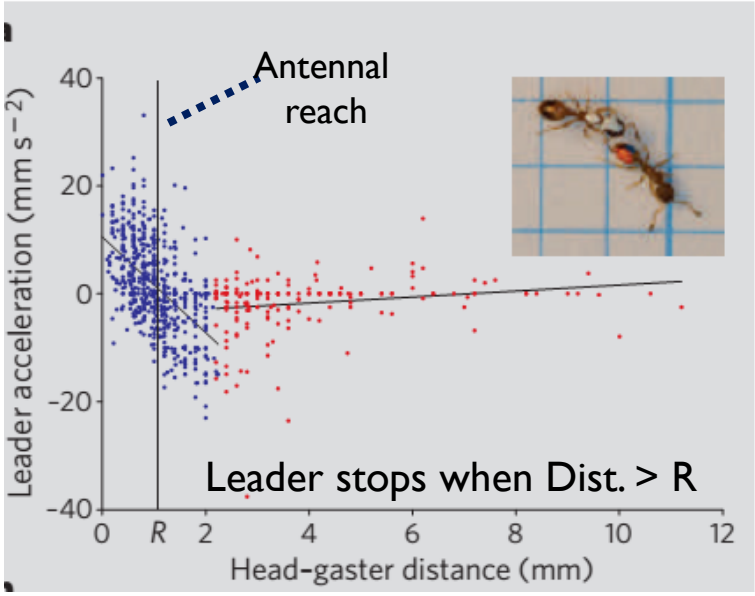
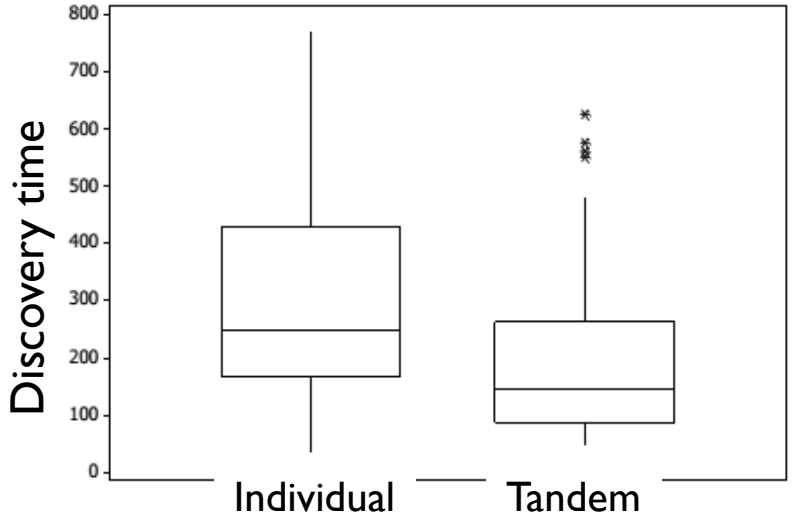
4. Teaching in ants

1. Leaders modify behaviour to maintain contact

2. Leaders are 4x slower than when walking normally → costly

3. Followers discover food source faster → learns more quickly





Franks & Richardson (2006) *Nature*

4. Teaching

- Teaching doesn't require ants to be smart ("understanding", "intentionality"), it can rely on genetically determined behaviours
- But because teaching is costly for the teacher, we expect teaching more frequently in social groups:
  - In ants teachers get indirect benefits *via* kin selection
  - In meerkats it's less clear: delayed direct benefits?

Animal traditions and culture

Animal tradition & culture

Definition of tradition

A behaviour shared by members of a social group that persists over time and is learned socially

Definition of **culture** is controversial, dozens of different definitions have been proposed

Culture ≈ multiple behavioural traditions

At the beginning of a tradition is often an **innovation**, which is then spread socially

Animal tradition & culture

- Identification of tradition often starts by documenting behavioural differences between populations

- Identifying animal tradition/culture is difficult, because of alternative & simpler explanations:

    - genetic differences and genetic adaptation
    - habitat differences that could explain behavioural differences *via* individual learning

Suspected traditions: hunting in Orcas

- Orcas (*Orcinus orca*) are found in all oceans
- Orcas hunt cooperatively for a wide range of prey, including seals & sea lions

Suspected traditions: hunting in Orcas

Intentional stranding

- 568 hunting attempts
  - 35.7% in open water → 20.7% successful
  - 64.3% with stranding → 34.4% successful

+ 13.7%
P < 0.05

Lopez & Lopez (1985) *J. Mamm.*

Suspected traditions: hunting in Orcas

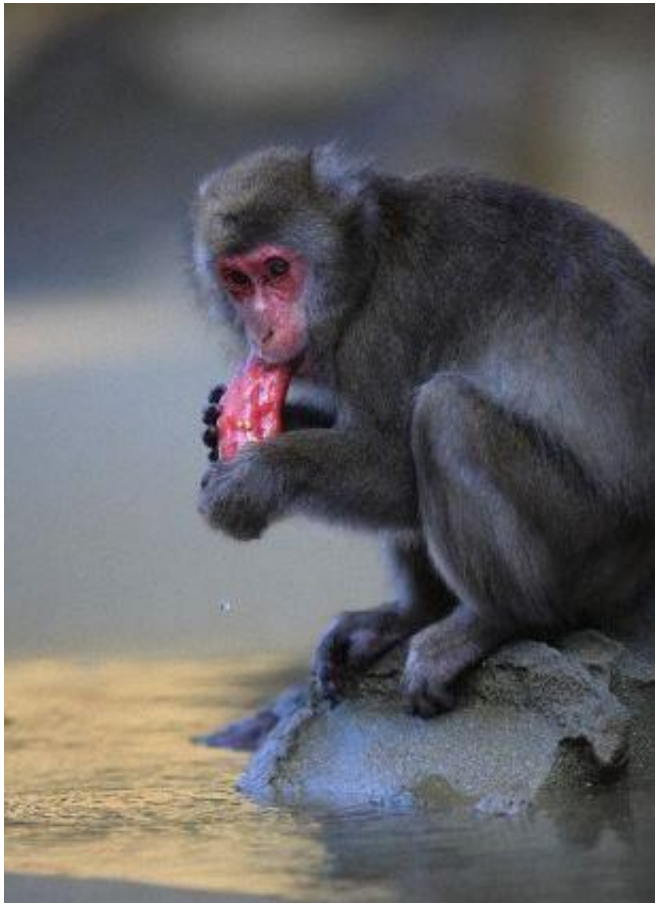
- Behavioural pattern, shared by members of a local population
- But how is it learned?
- Observations suggest teaching by the mother

1. Young are pushed up the beach by mother
2. Adults are more successful when hunting without young
3. Some evidence that training with mother improves skill

Rendell & Whitehead (2001)

Suspected traditions: potato washing

- A well-known case of an animal tradition was started in 1953 by an 18 month old, female Japanese macaque called "Imo"



Potato washing

- Researchers studying a population on Koshima island gave them sweet potatoes to attract them
- "Imo" started to wash the potatoes before eating them
- Within 10 years the behaviour spread from her closest family members to all under middle-aged monkeys (older monkeys did not wash potatoes)

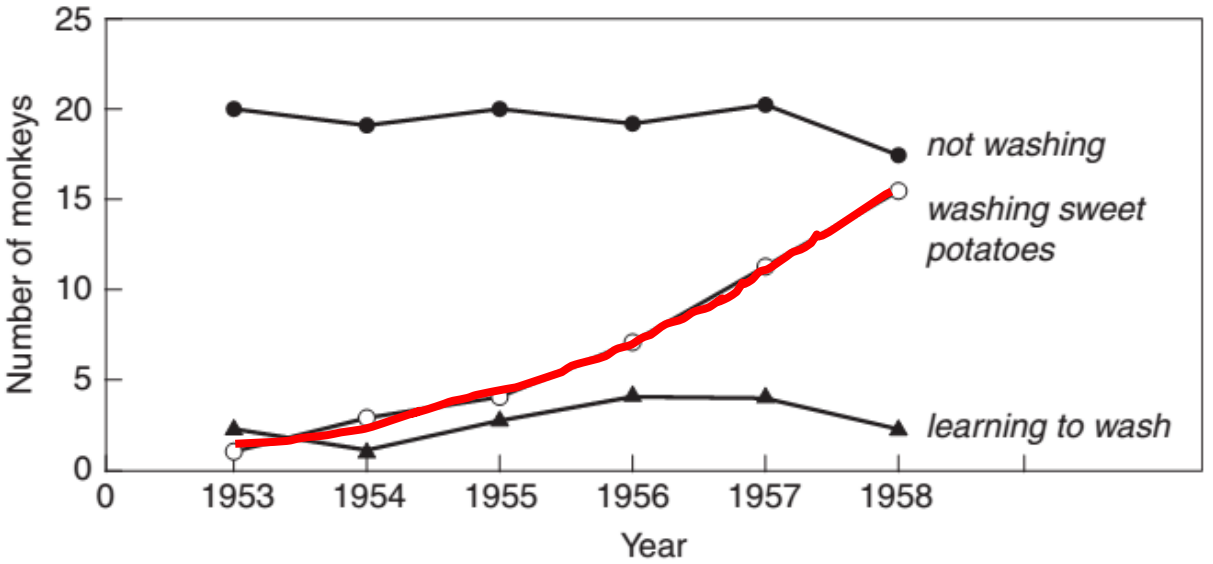
https://www.youtube.com/watch?v=uZ8HCdgEwCs

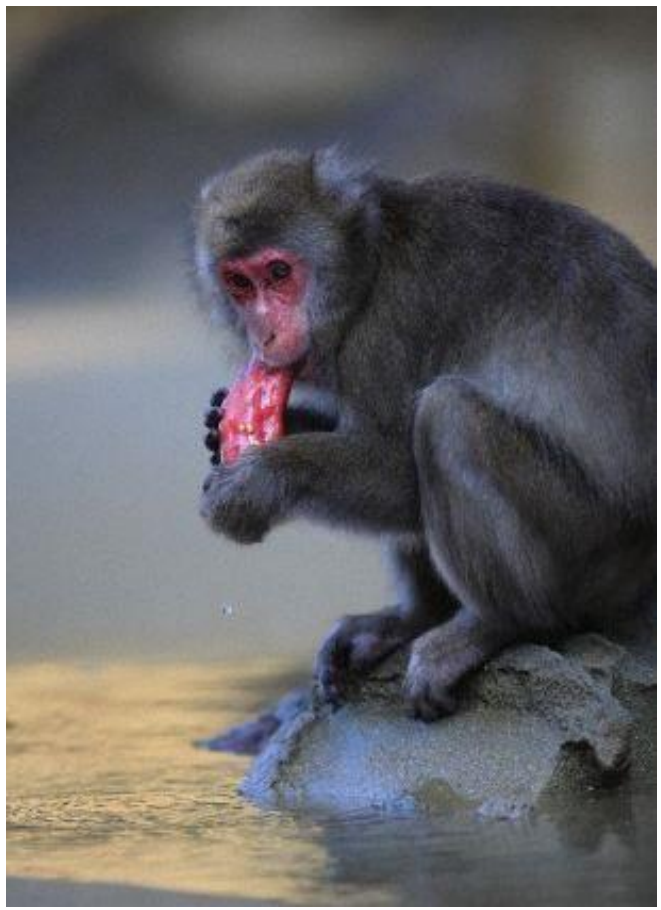
✓ Behavioural innovation

✓ Change in behaviour too fast to be explained by genetic adaptation

Potato washing

- But can we really be sure that the spreading of the behaviour happened through social transmission? What about individual learning?





- The shape of the curve:
  - Linear increase: individual learning
  - Accelerating increase: social learning

Culture in animals

- Animal culture: a combination of many behavioural traditions, that differ between populations and cannot be explained by genetic differences, individual learning or habitat differences

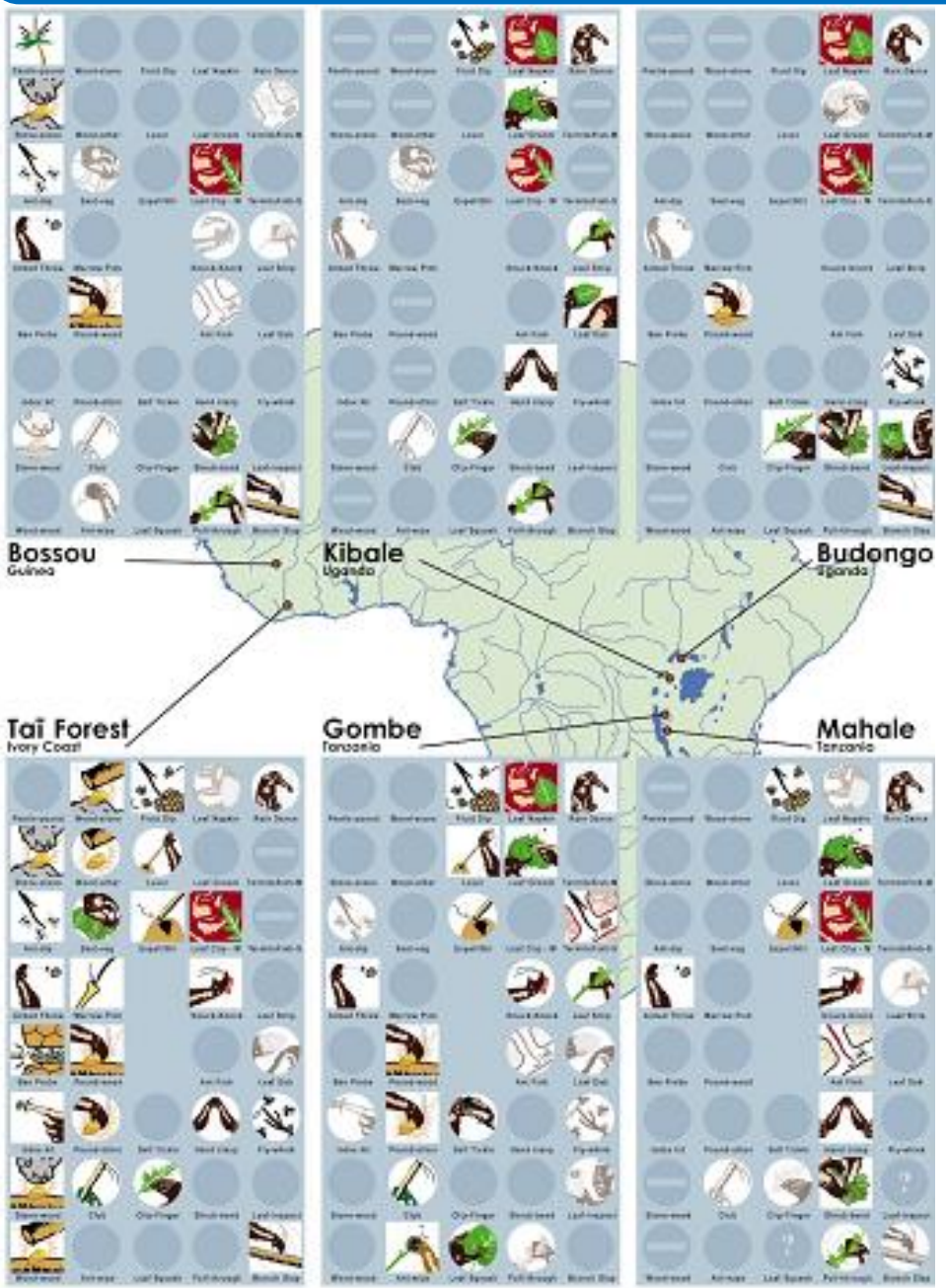
- Studies on chimpanzee behaviour in Africa suggested various behavioural differences between populations

- Results of 7 long-term projects were combined

→ Extensive differences in behaviour between populations

Whiten et al. (1999) *Nature*

Cultures in chimpanzees



- 39 behaviours differed between populations, including tool use, grooming or courtship
- Researchers exclude ecological and genetic explanations
- First study to document extensive variation in multiple socially learned behaviours in animals

⇒ Different cultures

Whiten et al. (1999) *Nature*

Animal tradition/culture, is it adaptive?

- Many cases of animal traditions seem to be adaptive:
  - Intentional stranding of orcas is a more successful hunting strategy
  - Potato washing might reduce exposure to parasites/pathogens

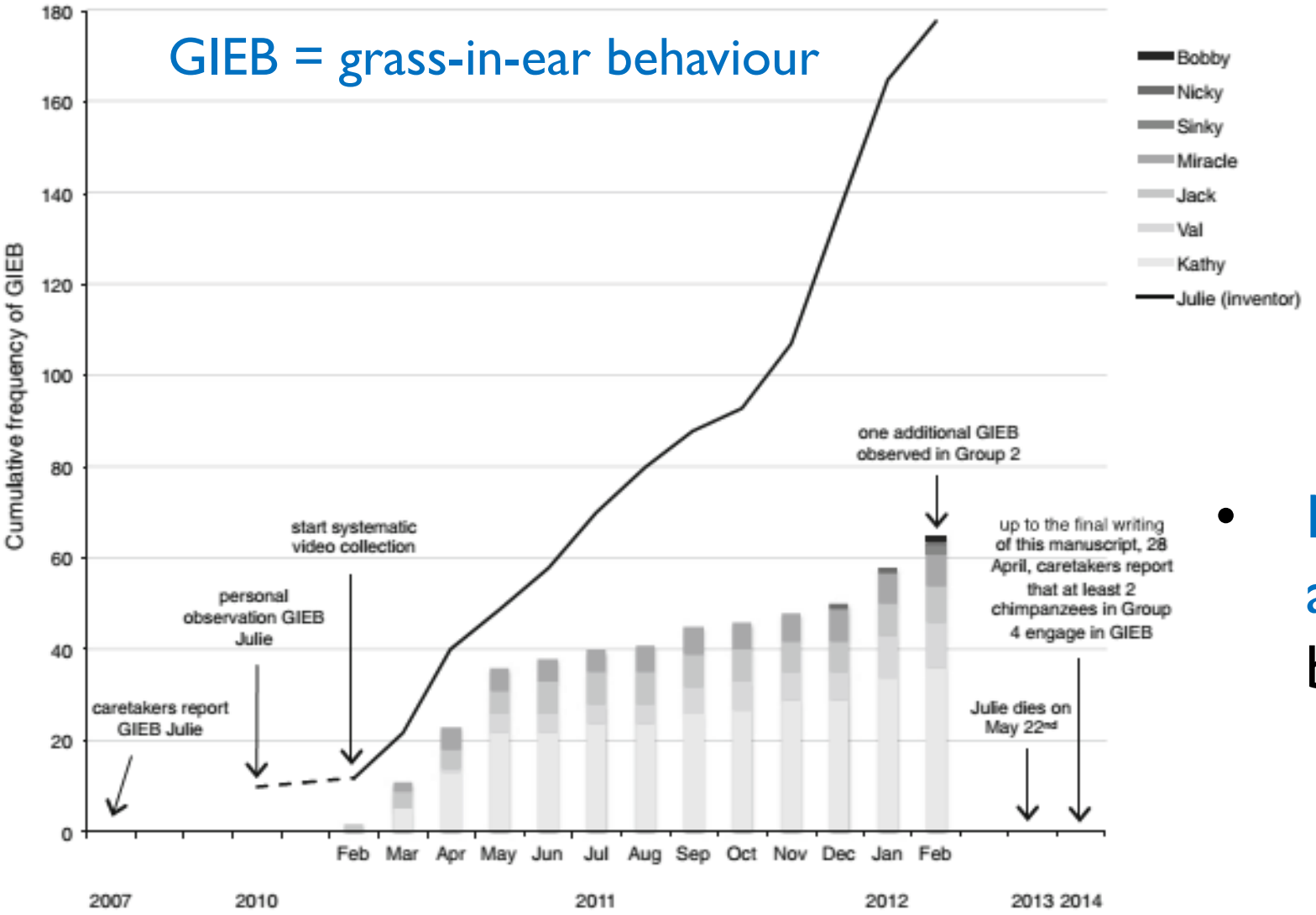
- But are cultural differences in tools and signs in chimps adaptive?
- Could social transmission lead to arbitrary "fashions" that are selectively neutral or even non-adaptive?

Fashion in chimpanzees

- Behaviour was discovered in 2007 in a sanctuary in Zambia

van Leeuwen et al. (2014) *Anim. Cogn.*

Fashion in chimpanzees



- No purpose or adaptive value has been discovered

Chimpanzees have fashions (short-term traditions)

Van Leeuwen et al. (2014) *Anim. Cogn.*

Culture/tradition for local adaptation

- Are traditions adaptive? No general answer
- Having a neural systems that is able to use cultural information is likely to be adaptive
- However, the details of a culture or a tradition (e.g. fashions) might often not improve fitness or even reduce it

Example: cooking & language

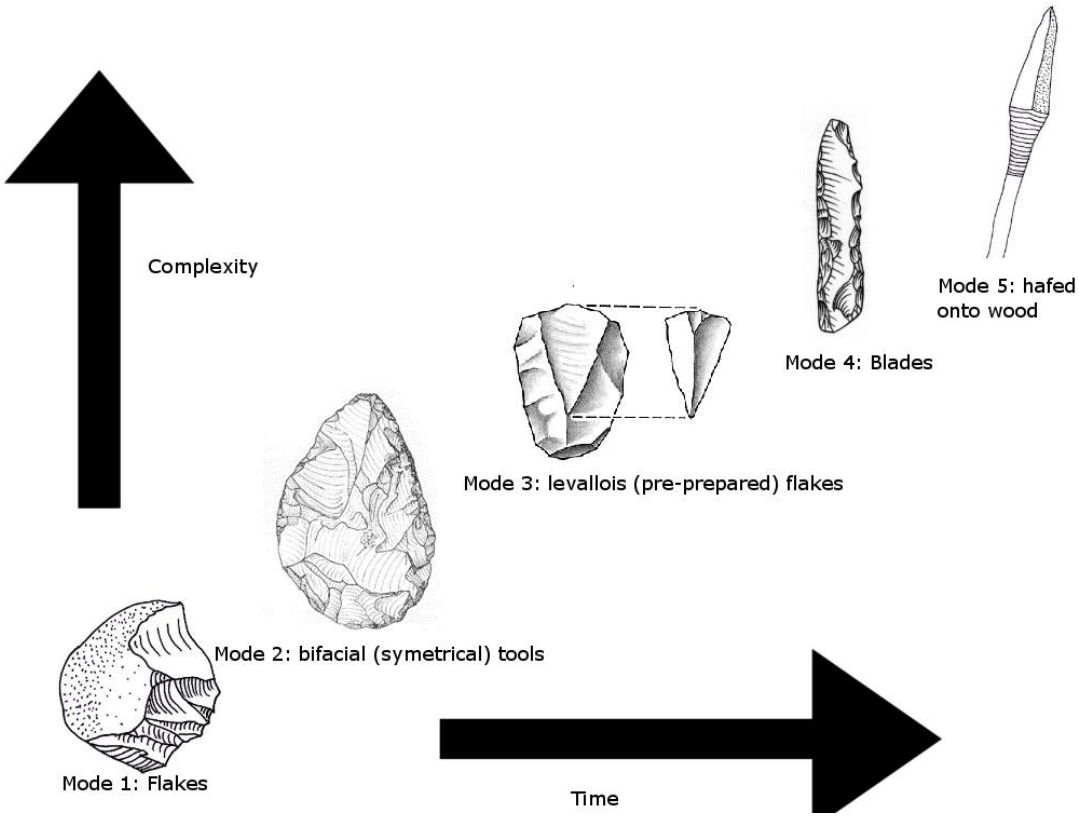
- It may not matter whether you cook Italian or Indian or whether you call this animal a:
  - Yaguar (in Tupí)
  - Jaguareté (in Guaraní)

Important is the **ability** to socially learn how to prepare food or use a language to name important things

Cumulative culture in humans

- Animals have culture, what is different about human culture?

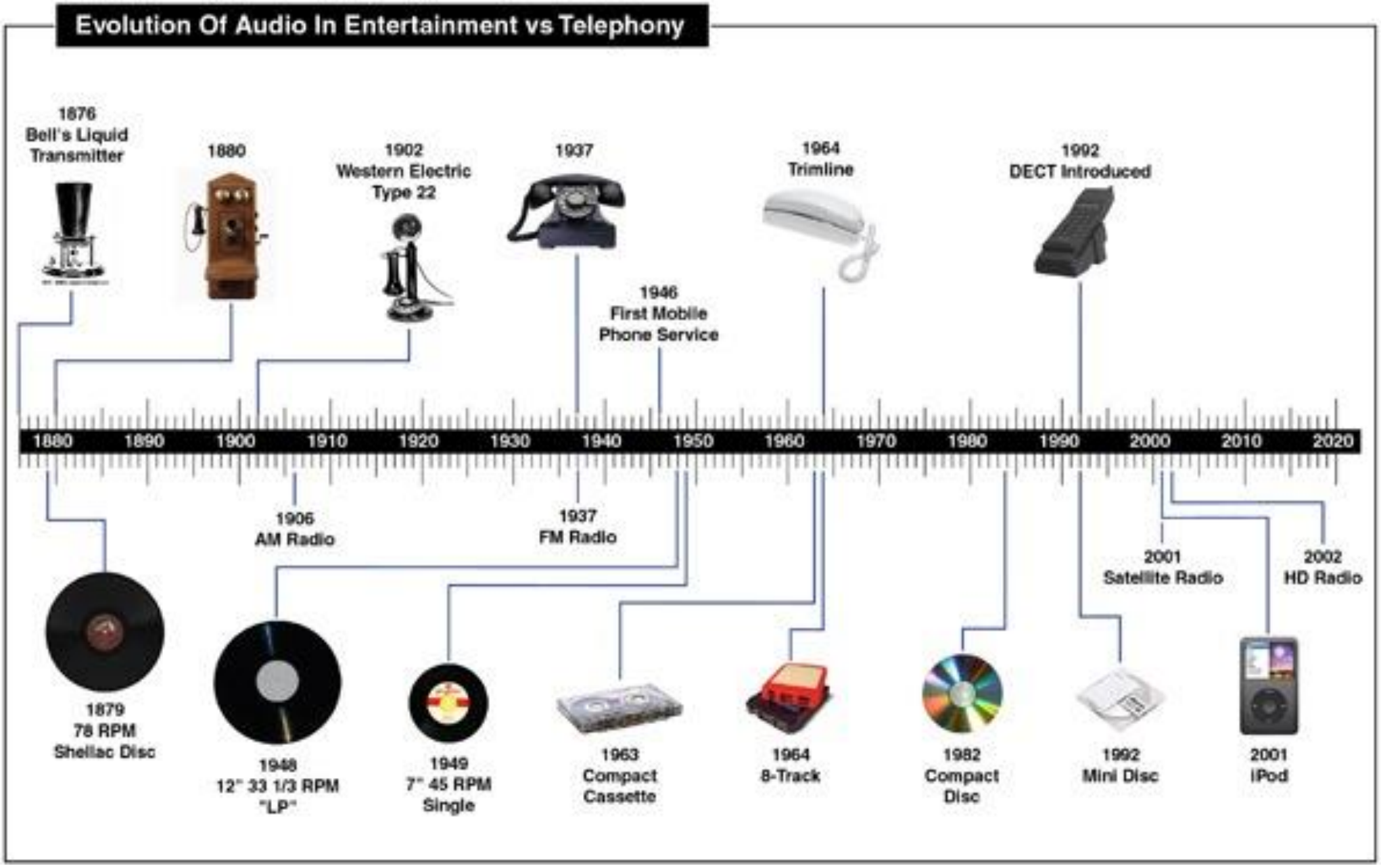
Humans have cumulative culture



- Is it evidence for cumulative culture?
- Or did we simply get smarter as nutrition inproved?

Culture or genetic adaptation or improved diet?

Cumulative culture in humans



Cumulative culture in humans

- Changes in our artefacts happen too fast to be genetic. Rather, its mainly based on social transmission *via* language & writing
- Social learning mechanisms: teaching & imitation
- Some argue that cumulative culture is the key to modern society, not intelligence

No matter how smart you are, you couldn't invent the iPhone from scratch

Hypothetical you: Yes, but culture is the result of our intelligence?!

Boyd & Richerson (2009) *Phil. T. R. Soc.*

Human vs. animal social intelligence

- Researchers have suggested that humans are special in their reliance on social learning
- …and this might have driven the evolution of cognitive abilities

→ "cultural intelligence (CI) hypothesis"

- Human cognitive skills are an adaptation to our highly social life-style, the need to be part of and exchange knowledge in cultural groups

Herrmann et al. (2007) *Science*

Human vs. animal social intelligence

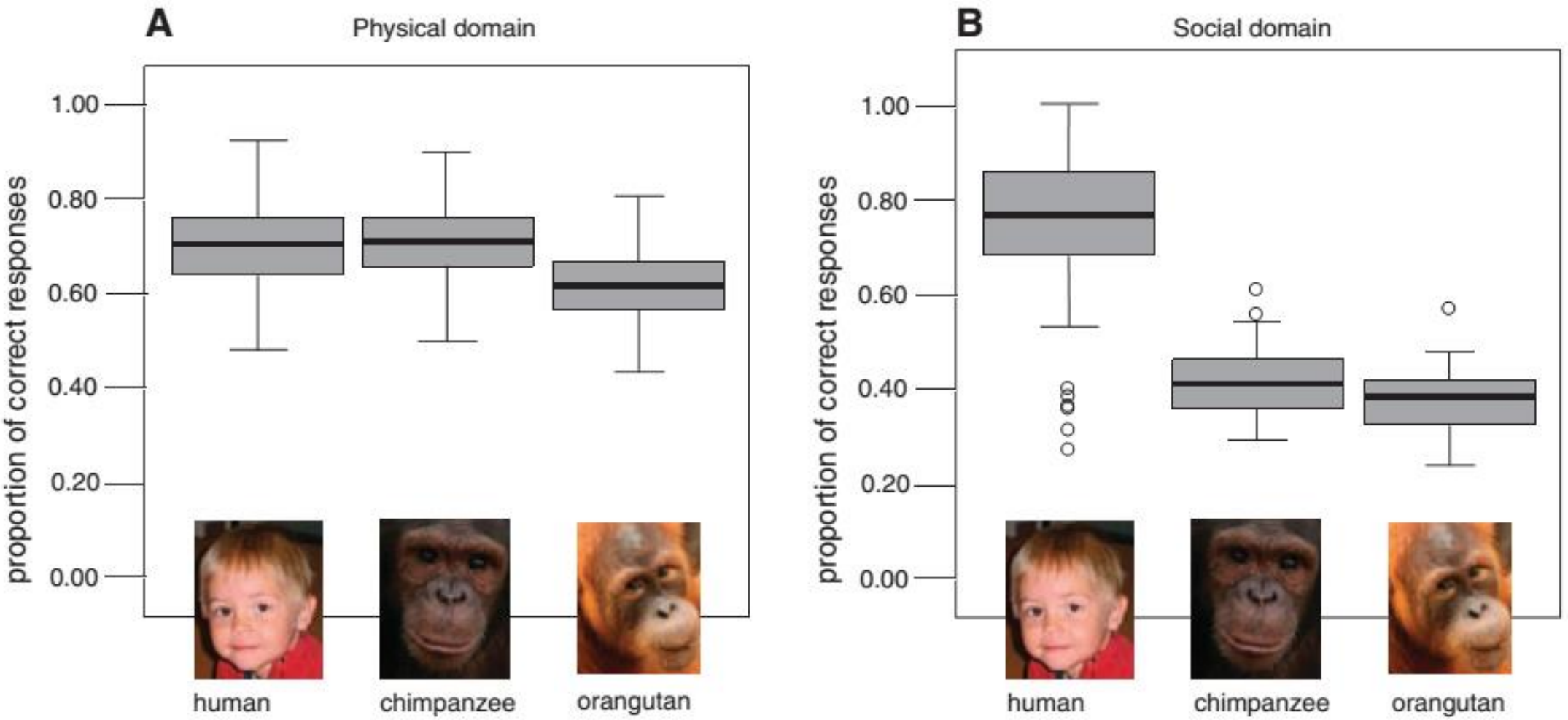
- To test predictions, Herrmann et al. (2007) did cognitive tests with chimpanzees, orangutans and 2.5 year old children

- Cognitive tests in two domains: 1. physical world & 2. social world:

    1. Spatial memory, quantity discrimination, causality, tool use, etc.
    2. Social learning, communication, gaze following etc.

Prediction of the CI-hypothesis: humans perform better in these tests only in the social domain

Human vs. animal social intelligence



Children were not more intelligent *per se*, but only in the social domain → consistent with the CI hypothesis

Herrmann et al. (2007) *Science*

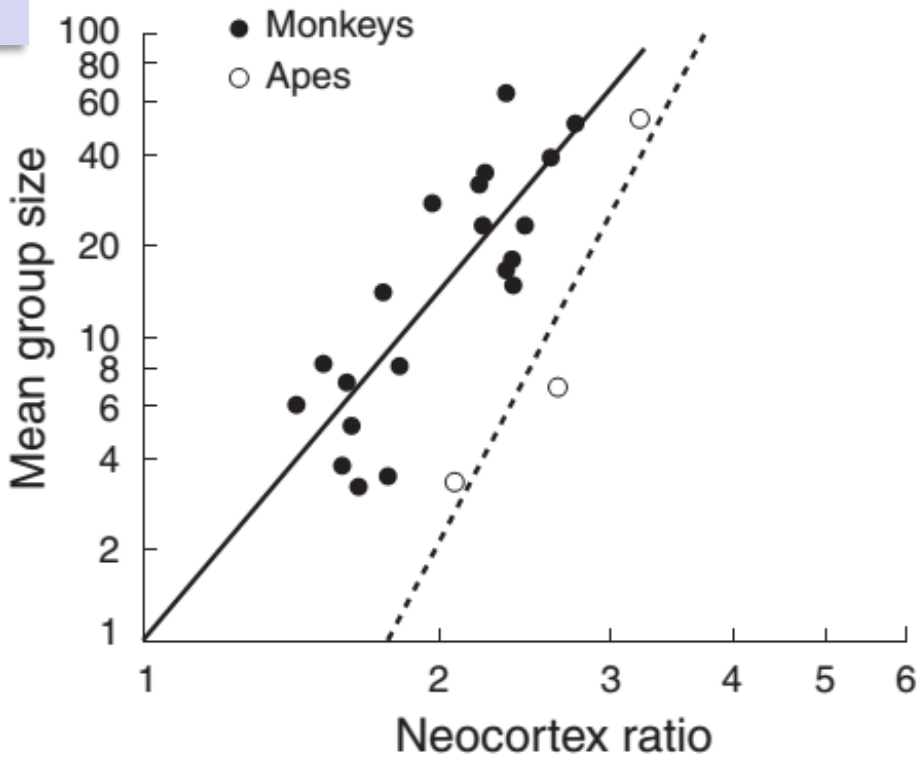
Relationship between group size and brain

- The "cultural intelligence hypothesis" is related to the more general "social intelligence hypothesis":

Brain size/intelligence are the result of the demands of living in a group

- More challenging to follow the social dynamics in large groups

- But: difficult to interpret because we don't know what different brain regions do

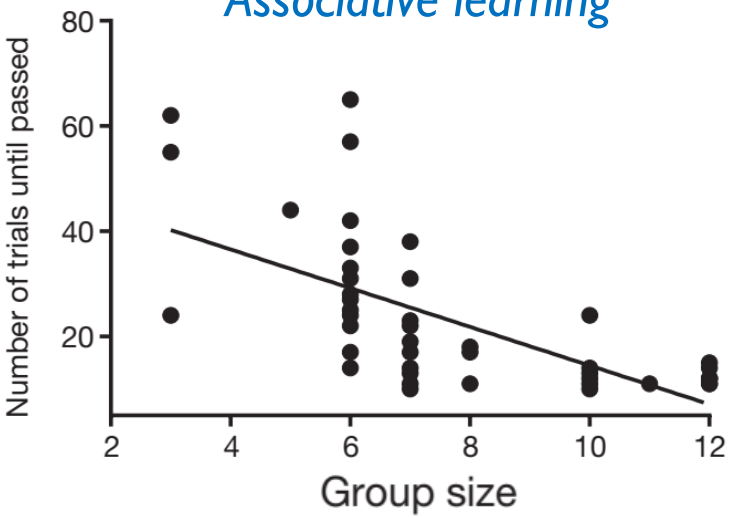


Shettleworth (2010)

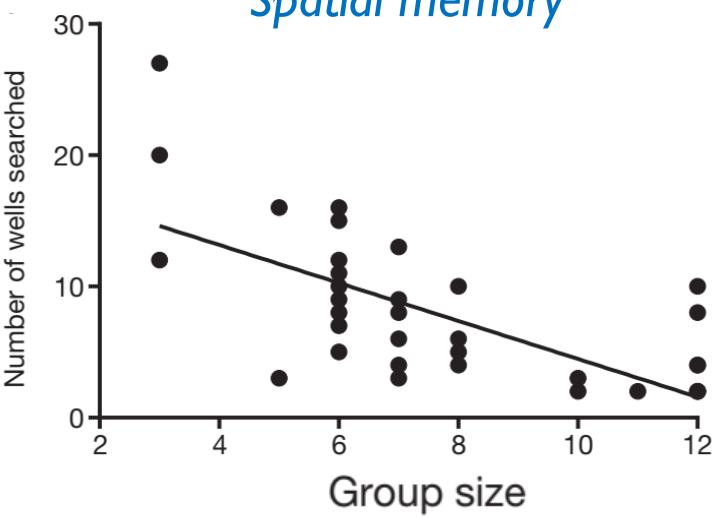
Social intelligence hypothesis: intraspecific test

- What about intraspecific links between group size and cognitive abilities?
- Australian magpies are cooperative breeders that live in groups of variable size

Associative learning



Spatial memory

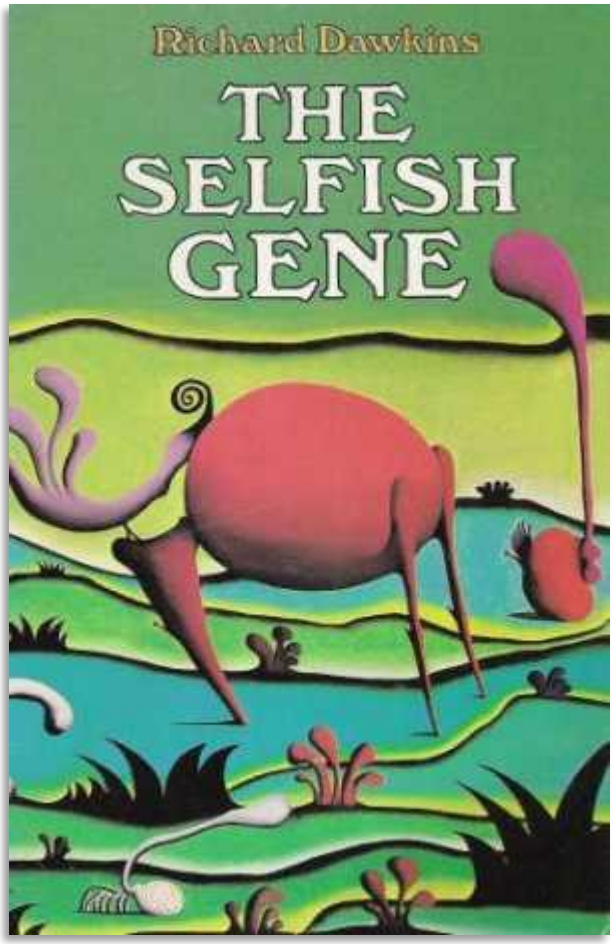


Ashton et al. (2018) *Nature*

Memes and cultural evolution

Memes

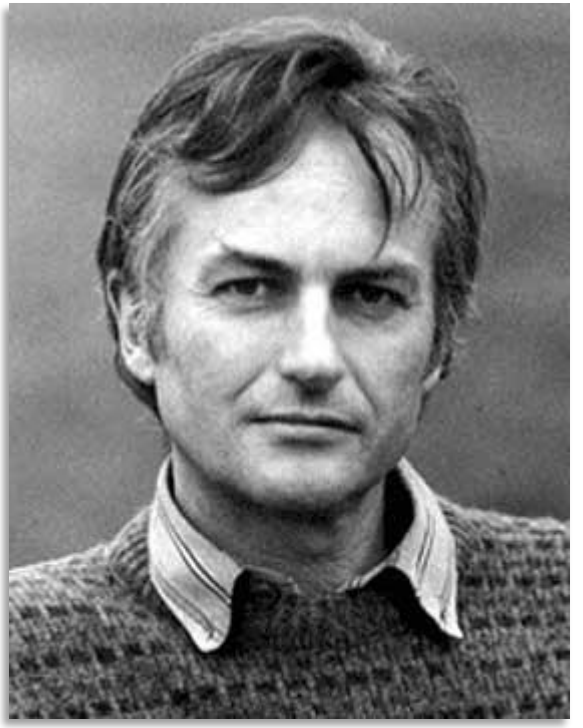
- If culture and behavioural traditions can be non-adaptive, how do they evolve?



Richard Dawkins (1976)

Memes

"We need a name for a new replicator, a noun that conveys the idea of a unit of cultural transmission, or a unit of *imitation*". 1976, p. 206



Gene = unit of genetic transmission

Meme = unit of cultural transmission

- Once cultural transmission has evolved, "ideas" (memes) can spread like genes:
  - Variation
  - Heredity
  - Differential fitness

Defining memes

Definition
Meme ~ neural representation of an idea

- Memes specify:
  - Fashions
  - Diets & recipes
  - Language & symbols
  - Songs & melodies
  - Political & religious ideas (memeplex)

Mechanism of transmission
Dawkins proposed "imitation", but he used it in a sense of "social learning" → any mechanism of social learning

Defining memes

- Memes are stored in brains, but there are extra-neural storage locations, e.g. books, hard-drives, internet etc.

- Memes evolve by natural selection: they compete against each other for our attention and acceptance and "jump" from brain to brain:
  → Some memes are more successful, that is better at spreading, than others

Hypothetical successful meme:
You will be happy if you spread the meme, but terrible things will happen to you if you don't spread it!

Example: fondue meme

- Variation (different varieties)
- Heredity (recipe spreads via social learning)
- Differential fitness (*moitié-moitié* is most popular)
- Meme stored in brains, but also books and the internet
- It is successful because of it's psychological appeal: pleasant experience

The "fondue" meme has evolved in the way it has because it is *advantageous to itself*, not to the individual that carries it → "selfish"

Memes are "selfish"

- Because memes are "selfish" in the sense that genes are "selfish" (Dawkins 1976), successful memes can spread in a population even if they provide no fitness benefits to the individuals that carry the meme

Memes in animals

- The concept of memes can be applied to animals:
    - Local dialects in bird songs
    - Behavioural fashions
    - Culturally transmitted tool use

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