Toulouse School of Economics

TSE M1 – Semester 1

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Evolution of Economic Behavior
Week 7:
Natural, sexual and cultural selection

Natural, sexual and cultural selection: outline

- The basic features of natural selection: inheritance, variation and non-random survival
- The added ingredient of sexual selection
- Cultural selection – how group rivalry influences choices between multiple equilibria
- How cultural selection feeds back into natural selection
- How does this all help explain economic behavior?

Inheritance, variation and non-random survival

- Darwin's *Origin of Specie*s spent a long time showing how artificial selection could modify species characteristics

- For this there has to be

  - Variation - otherwise selection has nothing to work on

  - Inheritance – otherwise the selected characteristics do not transmit

  - Innovation (eg by mutation) – otherwise the selection process will converge to a limit

- Darwin's achievement was to show that selection did not require a conscious designer – any fitness gradient in nature could do as well

Since Darwin much has been learned about the mechanisms

- Darwin knew nothing about genes, the foundations of our knowledge of which were established by the work of Gregor Mendel (1882-1884)

- Since then the distinction between genotype and phenotype has become standard in biology – although our understanding of it has changed over time via

  - The notion of the "extended phenotype" (Dawkins)

  - Epigenetics and our understanding of gene regulation, particularly since the sequencing of the human and other genomes

Darwin, sexual selection and *The Descent of Man*

- Charles Darwin published *The Descent of Man* in 1871, 12 years after The Origin of Species
- In *The Origin* he had carefully avoided talking about human beings (though this did not avoid critics attributing views about human beings to him)
- It may seem puzzling that he talks about sexual selection in this book, a subject that doesn't seem intrinsically related to human beings more than to other species
- His biographers (Desmond & Moore 2009) explain this in terms of his wish to prove that human beings belong to the same species in spite of the superficial differences between races

What does sexual selection add to a general Darwinian perspective on economic behavior?

- The general Darwinian perspective (Darwin's *Origin of Species*) emphasizes rational decision-making as an adaptive response to scarcity of resources in an animal's environment

- Sexual selection (Darwin's *Descent of Man*) adds two features:
  - Organisms have not only to survive to adulthood but be able to mate
    - New constraints on phenotypes and behavior through competition for access to other sex – more generally, populations are *structured*
    - Force versus signaling as competitive strategies
  - Asymmetry in the scarcity of mating opportunities creates possible asymmetry in behavior between the sexes (eg risk aversion)

Why sexual reproduction? (I)

- Sexual reproduction evolved around 900 million years ago and for a long time its evolution was a puzzle: sexually reproducing individual transfers only half its genome to each offspring, and has to find replacement DNA for the remainder, at the cost of search and competition from others
- Cloning would seem more effective – but has a fatal disadvantage: clones accumulate harmful mutations (Muller, 1964), and are slow to develop beneficial ones in response to environmental change
- Kondrashov (1988) showed mutation would give an advantage to sexual reproduction only given strong assumptions about mutations
- However, experiments by McDonald et al (2016) suggest the empirical conditions for mutation advantage of sex are sometimes observed

Why sexual reproduction? (II)

- Adaptation to changing environments provides an alternative strength of sexual reproduction.
- Individuals are in an evolutionary arms race with their predators and parasites (Ridley 1993), and sexual reproduction adapts faster.
- However, random recombination of beneficial mutations seems unlikely to compensate for numerical disadvantage of sex
- Directed recombination of alleles in the Major Histocompatibility Complex provides a more plausible story (Milinski 2006)
- This implies that some sexual partners provide “better” DNA than others – selection matters!

Anisogamy and asymmetric parental investment (I)

- Researchers largely lost interest in sexual selection for about a century until Trivers (1972) located the origins of the phenomenon in asymmetric parental investment (but see Fisher, 1930)

- Most sexually reproducing species have two sexes with anisogamy - gametes of highly asymmetrical size (though some species have three or more sexes, and there is also hermaphroditism, conditional sex determination, etc…see Ainsworth 2015)

- Anisogamy is a more common solution than isogamy to trade-off gamete size/quantity (why? See Bulmer & Parker 2002)

- Larger gametes have higher survival rates; so do larger zygotes; but small male gametes may be able to free ride on larger female gametes

Anisogamy and asymmetric parental investment (II)

- Trivers argued that anisogamy created an asymmetry in costs and benefits of alternative mating opportunities between the male and female partners
- For Trivers the fact that male gametes outnumber female ones directly creates the asymmetry in costs and benefits of alternative mating opportunities, and therefore in incentives for parental investment
- Males have higher Operational Sex Ratio (OSR) and therefore higher higher Potential Reproduction Rates (PRRs)
- Sexual selection therefore leads males to provide even less parental care than females, thereby amplifying the initial asymmetry in investment due to anisogamy

Anisogamy and asymmetric parental investment (III)

- However, Queller (1977) pointed out that if all offspring have one male and one female parent, then the average unconditional benefits of alternative mating opportunities must be the same for males and females
- Nevertheless, *conditional* benefits of alternative mating opportunities may differ, because males who are currently mating will have higher than average alternative mating opportunities
- And benefits of parental investment are affected by paternity uncertainty

Anisogamy and asymmetric parental investment (IV)

The equilibrium parental investment by parent $i \in (m, f)$ in mating j occurs where

$$(1) \quad \frac{\partial \mathrm{E}\left(F_{ij} \middle| E_{ij}\right)}{\partial E_{ij}} = -\sum_{k \neq j}^{N} \frac{\partial \mathrm{E}\left(F_{ik} \middle| E_{ij}\right)}{\partial E_{ij}}$$

where

F_{ij} is the fitness of parent i via mating j

E_{ij} is the investment by parent i in offspring j

k are other matings undertaken by parent i

Anisogamy and asymmetric parental investment (V)

- Given concavity of the fitness function, equation (1) may be satisfied at higher levels of investment for women than men if

$$\frac{\partial \mathrm{E}\left(F_{fj} \middle| E_{fj}\right)}{\partial E_{fj}} > \frac{\partial \mathrm{E}\left(F_{mj} \middle| E_{mj}\right)}{\partial E_{mj}} \text{ for } E_{fj} = E_{mj}$$

- or if

$$-\sum_{k \neq j}^{N} \frac{\partial \mathrm{E}\left(F_{mk} \middle| E_{mj}\right)}{\partial E_{mj}} > -\sum_{k \neq j}^{N} \frac{\partial \mathrm{E}\left(F_{fk} \middle| E_{fj}\right)}{\partial E_{fj}} \text{ for } E_{fj} = E_{mj}$$

- Note that the latter may hold even if

$$\sum_{k \neq j}^{N} \mathrm{E}\left(F_{mk}\right) = \sum_{k \neq j}^{N} \mathrm{E}\left(F_{fk}\right)$$

Implications of anisogamy for male-female relations

- Conflict is at the heart of cooperation: strategies that increase male fitness may decrease female fitness and vice versa – *even though fitness from current mating is by definition identical*
- Natural selection has selected for selectivity in females and persistence in males, in an evolutionary spiral
- Male persistence sometimes expresses itself through force, sometimes through signaling
- The wastefulness of force is obvious….

Conflict: omnipresent in sexual reproduction

- Conflict occurs even over where and how to mate
- Female selectivity creates an adaptive advantage for strategies of male persistence – which in turn favors the evolution of female selectivity still more
- This can lead to violent mating conflicts in
  - Elephant seals
  - Water striders
  - Tunnel-web spiders
  - Scorpions
  - Bed-bugs


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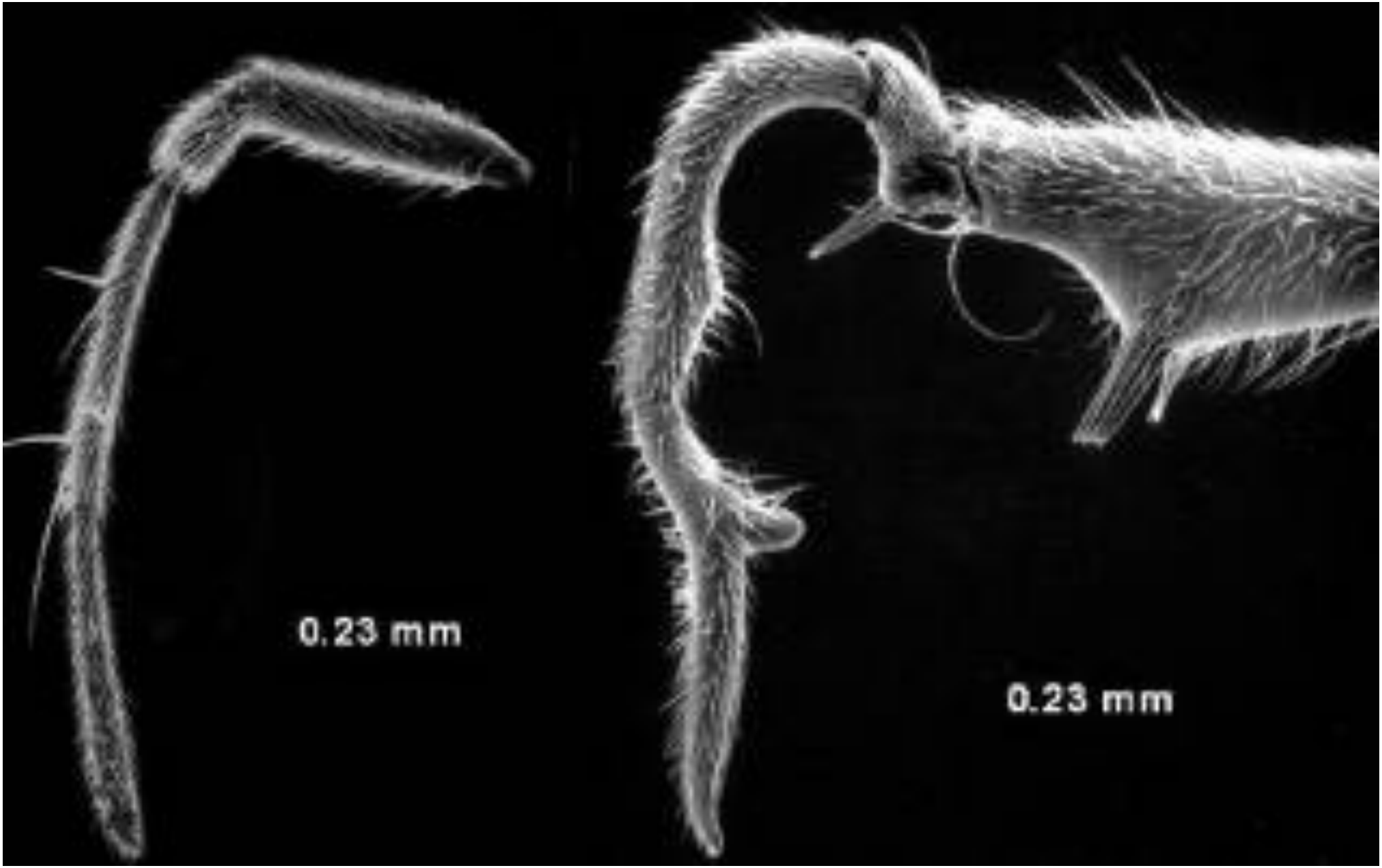


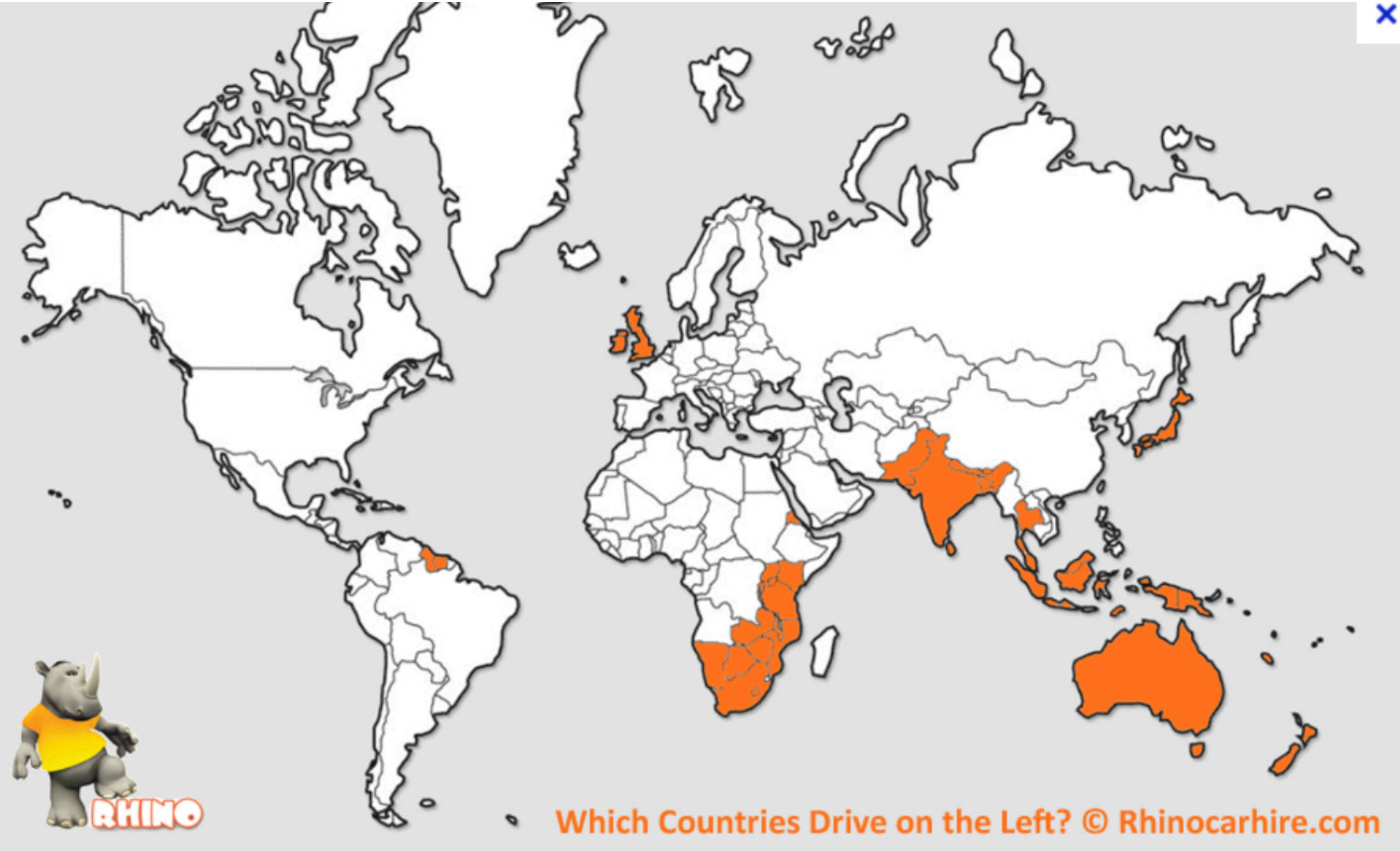
Female antennae ***Rheumatobates rileyi*** Male antennae

The male anaesthetizes the female with a powerful toxin and mates with her while she Is unconscious

Cimex lectarius punctures the female's abdomen with a dagger-like projection and injects sperm directly into the body. The costs to the female (infection, blood loss, organ repair) can be high

How does cultural evolution fit into all this?

- Genetic inheritance radically underdetermines phenotypes, including behavioral phenotypes, because of (inter alia)
  - Gene regulation
  - Learning
  - Social interactions
- Cultural behaviors are often equilbria of social processes which have multiple equilibria
- Consider diriving on the left and on the right


RHINO
Which Countries Drive on the Left? © Rhinocarhire.com

How does cultural evolution fit into all this? (II)

- Consider two groups with identical distributions of genes, facing identical environments, but who have adopted different equilibrium behaviors

- Rivalry between the groups may cause the more successful group's behavior to spread, because

  - The more successful population physically replaces the less successful population

  - The members of the less successful population begin to adopt the behaviors of the members of the more successful population

Cultural evolution also feeds back into genetic evolution

- Consider cooking….
- It has substituted external digestion for part of the process of internal digestion of food
- As a result we have smaller teeth, stomachs and intestines than the other great apes

How does cultural evolution fit into all this? (III)

- In principle, behavior could spread from one individual to another for reasons unrelated to either individual's fitness
- Dawkins (1976) called units of cultural evolution "memes" and speculated that they might spread for reasons unrelated to fitness of the organisms that adopt them
- Think of "catchy" tunes or memorable anecdotes
- Tomasello (1999) has shown that human beings are very good at imitation compared to other primates, and that we often engage in "over-imitation", adoption of features of behavior that are unrelated to its adaptive value