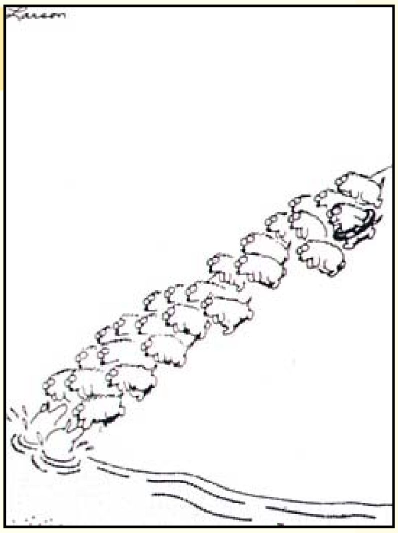
Cultural evolution, Gene-Culture coevolution and the evolution of Cooperation

Levels of Selection



Genes (Sociobiology)
Individuals (“basic” Neodarwinism)
Groups?
Multilevel selection?

Genetic Group Selection?

Wynne-Edwards:
“the good of the species” (...)

Intergroup effects weaker than intragroup, interindividual selection.
Intra x intergroup differences

Wilson DS & Wilson EO (2007)
Rethinking the theoretical foundation of sociobiology
Multi-level selection/ limits in kin selection theory/ “major transitions”
Eusociality: Kin Selection X Individual sel. + preadapts. (comm. nests etc)
Nowak, Tarnita & Wilson, *Nature* 2010
(X Abbot et **al** [+100!], *Nature* 2011)

Altruism and cooperation

How can altruism/cooperation evolve?
Kin Selection (Hamilton): Inclusive fitness
Unconditional altruism not viable:
adaptive value of "selfishness" in an "Altruist" population

COSTS and BENEFITS of RECIPROCAL ALTRUISM
(if costs are increased by "cheaters", how to reduce them?)

Iterated dyadic social relations:
Cooperation and reciprocity (Prisoner's Dilemma)
Small social groups:
Reputations
(Dunbar: "Grooming, Gossip and the Origin of Language")
Larger social groups, interactions with strangers: ?
Efficient cognitive mechanisms for cheaters' detection?
(Cosmides & Tooby: "Cognitive adaptations to social exchange")

The problem of altruistic punishment

Nowak 2006

Five Rules for the Evolution of Cooperation

Cooperation is needed for evolution to construct new levels of organization. Genomes, cells, multicellular organisms, social insects, and human society are all based on cooperation. Cooperation means that selfish replicators forgo some of their reproductive potential to help one another.
But natural selection implies competition and therefore opposes cooperation unless a specific mechanism is at work.

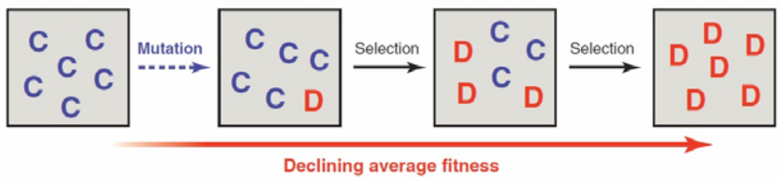
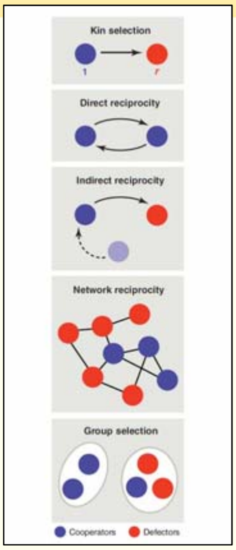


Fig. 1. Without any mechanism for the evolution of cooperation, natural selection favors defectors. In a mixed population, defectors, *D*, have a higher payoff (= fitness) than cooperators, *C*. Therefore, natural selection continuously reduces the abundance, *i*, of cooperators until they are extinct. The average fitness of the population also declines under natural selection. The total population size is given by *N*. If there are *i* cooperators and $N - i$ defectors, then the fitness of cooperators and defectors, respectively, is given by $f_C = [b(i-1)/(N-1)] - c$ and $f_D = bi/(N-1)$. The average fitness of the population is given by $\bar{f} = (b-c)i/N$.

Nowak 2006
Five Rules for the Evolution of Cooperation

- Kin selection
- Direct reciprocity
- Indirect reciprocity
- Network reciprocity
- Group selection



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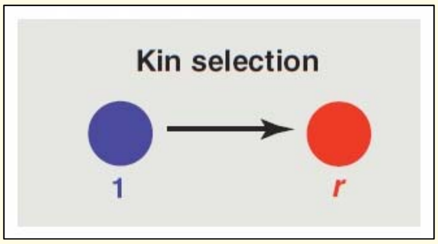

Kin Selection and indirect fitness

Hamilton Rule and the evolution of altruism:

Alleles that promote “altruistic” behavior towards non-descendants can spread (i.e., altruism can be *adaptive*) without resorting to “Group Selection” explanations if

$$b \times r > c \quad (\text{ou } r > b/c)$$

where

b = benefits to receivers
c = cost to direct fitness
r = coefficient of kinship (Wright 1922)

(J. Brown)
Direct Selection (Individual generates descendants) → N_1 descendants that survive without parental care; N_2 descendants that survive thanks to parental care

Indirect Selection (individual helps relatives) → N_3 relatives that survive thanks to the individual’s help

Kin Selection (J. Maynard Smith)

Direct Fitness → $(N_1\ r) + (N_2 \times r)$

Indirect Fitness → $(N_3 \times r)$

(-) Fitness derived from others’ help → $(N_4 \times r)$

Inclusive fitness (W. Hamilton)

N_4 = descendants that only survive to adult age thanks to the help of other individuals

r = coefficient of relatedness

Nowak 2006
Five Rules for the Evolution of Cooperation

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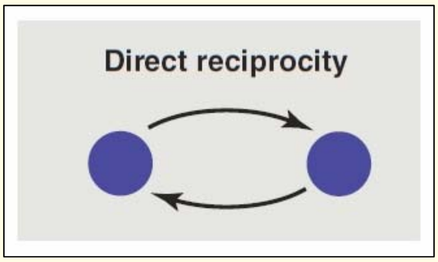
- Group selection



Cooperation: Social games

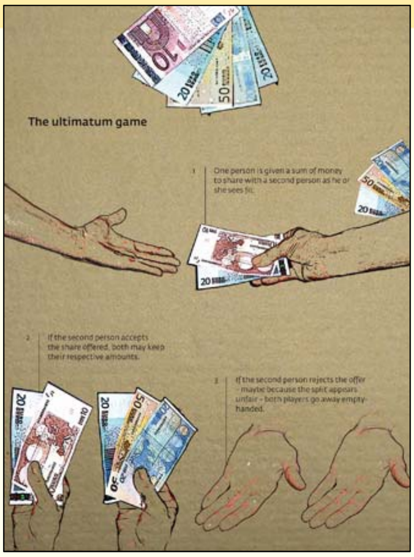
Prisoner's Dilemma

“Common Goods” game

Ultimatum Game

Dictator Game
(“Ultimatum” with no refusal)

variant: 3rd element
(altruistic punishment)



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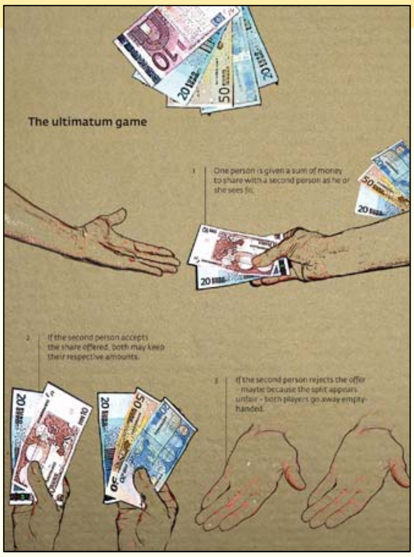


Nowak 2006
Five Rules for the Evolution of Cooperation

Direct Reciprocity

Trivers 1971: Cooperation between unrelated individuals
Repeated Prisoner's Dilemma: Axelrod & Hamilton 1981: **"tit-for-tat"**

Constraints:

$$T > R > P > S$$

$R > (T+S)/2$
(this avoids a strategy of “cooperating” by alternating cycles of T+S)

Player A \ Player B	Co-operation	Defection
Co-operation	R = 3 Reward for mutual Co-operation	S = 0 Sucker’s payoff
Defection	T = 5 Temptation to defect	P = 1 Punishment for mutual defection

Nowak 2006
Five Rules for the Evolution of Cooperation

Direct Reciprocity

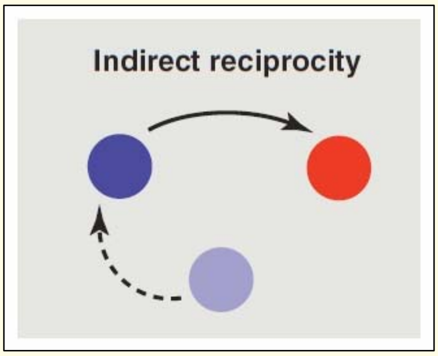
"Tit-for-tat" X erroneous moves: tit-for-tat cannot correct mistakes, because an accidental defection leads to a long sequence of retaliation.
Generous-tit-for-tat: a strategy that cooperates whenever you cooperate, but sometimes cooperates although you have defected [with probability 1 - (c/b)]. *(Natural selection can promote forgiveness)*.
Win-stay, lose-shift ("Pavlov" strategy) : repeating your previous move whenever you are doing well, but changing otherwise. Tit-for-tat is an efficient catalyst of cooperation in a society where nearly everybody is a defector, but once cooperation is established, win-stay, lose-shift is better able to maintain it. [Novak & Sigmund 1993].

Direct reciprocity can lead to the evolution of cooperation only if the probability, w, of another encounter between the same two individuals exceeds the cost-to-benefit ratio of the altruistic act:

$$w > c/b \text{ (or: } w \times b > c)$$

Nowak 2006
Five Rules for the Evolution of Cooperation

- Kin selection
- Direct reciprocity
- Indirect reciprocity
- Network reciprocity
- Group selection.



Nowak 2006
Five Rules for the Evolution of Cooperation

Indirect Reciprocity

Interactions among humans are often asymmetric and fleeting. One person is in a position to help another, but there is no possibility for a direct reciprocation. We help strangers who are in need.
The money that fuels the engines of indirect reciprocity is **reputation**.
Gossip (Dunbar 1996, etc)
Randomly chosen pairwise encounters (the same two individuals need not meet again). One individual acts as donor, the other as recipient.
The donor can decide whether or not to cooperate.
The interaction is observed by a subset of the population who might inform others. People who are more helpful are more likely to receive help.

Indirect reciprocity can only promote cooperation if the probability, *q*, of knowing someone's reputation exceeds the cost-to-benefit ratio of the altruistic act:

$$q > c/b \text{ (or } q \times b > c)$$

Nowak 2006
Five Rules for the Evolution of Cooperation

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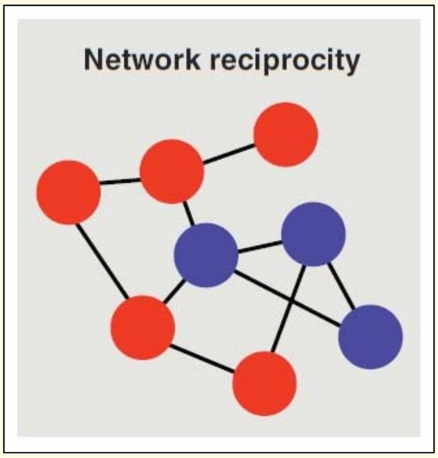
- Network reciprocity
- Group selection



Nowak 2006
Five Rules for the Evolution of Cooperation

Network Reciprocity

Spatial structures or social networks imply that some individuals interact more often than others.

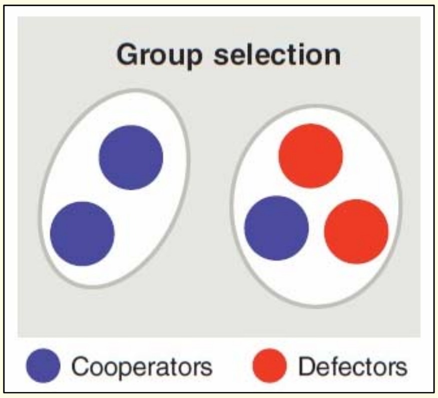
Cooperators can prevail by forming network clusters.

A simple rule determines whether network reciprocity can favor cooperation:
The benefit-to-cost ratio must exceed the average number of neighbors, k, per individual:

$$b/c > k$$

Nowak 2006
Five Rules for the Evolution of Cooperation

- Kin selection
- Direct reciprocity
- Indirect reciprocity
- Network reciprocity
- Group selection



Nowak 2006
Five Rules for the Evolution of Cooperation

Group Selection

Selection acts not only on individuals but also on groups. A group of cooperators might be more successful than a group of defectors.

There have been many theoretical and empirical studies of group selection, with some controversy, and recently there has been a renaissance of such ideas under the heading of “multilevel selection”.

Selection on the lower level (within groups) favors defectors, whereas selection on the higher level (between groups) favors cooperators.

In the mathematically convenient limit of weak selection and rare group splitting, we obtain a simple result: If *n* is the maximum group size and *m* is the number of groups, then group selection allows evolution of cooperation, provided that:

$$b/c > 1 + (n/m)$$

Nowak 2006
Five Rules for the Evolution of Cooperation

Other potential mechanisms for the evolution of cooperation

"Green beard” models: cooperators recognize each other via arbitrary labels;

Making the game voluntary rather than obligatory;

Punishment is an important factor that can promote cooperative behavior in some situations, but it is not a mechanism for the evolution of cooperation.
All evolutionary models of punishment so far are based on underlying mechanisms such as indirect reciprocity, group selection, or network reciprocity. Punishment can enhance the level of cooperation that is achieved in such models.

The two fundamental principles of evolution are mutation and natural selection. But evolution is constructive because of cooperation. New levels of organization evolve when the competing units on the lower level begin to cooperate.

Cooperation and punishment: the puzzle of costly punishment

"Direct" punishment in dyadic interactions is easily understandable, since its fitness consequences are clear (ex: a dominant chimpanzee attacks a subordinate trying to get a food item ahead of him).

Third-party punishment (non kin-related) or punishment of "defectors" in group cooperation are harder to explain, since "cooperators" that do not punish avoid the costs of punishing, so they have a higher fitness than "punishers".

Cooperation and punishment: the puzzle of costly punishment

In joint enterprises, free-riding individuals who do not contribute, but who exploit the efforts of others ("**Defectors**"), fare better than those who pay the cost of contributing ("**Cooperators**" and "**Punishers**"). If successful behavior spreads, for instance through imitation, these **Defectors** will eventually take over.

Punishment reduces the defectors' payoff, and thus may solve the social dilemma. However, because punishment is costly, it also reduces the **Punishers**' payoff. This raises a "second-order social dilemma": Costly punishment seems to be an altruistic act, given that individuals who contribute but do not punish ("**Cooperators**") are better off than the **Punishers**.

Cooperation and punishment: the puzzle of costly punishment

So, a population of "**Punishers**" (Cooperators that punish "Defectors") can be invaded by "**Cooperators**" (that don't punish, so don't pay the costs of punishing);

But then, once common, a population of "**Cooperators**" can be invaded by "**Defectors**" (who get the benefits but don't pay the costs of cooperation);

"**Punishers**" cannot invade a population of "**Defectors**", because they would be rare, at first, and the fitness costs of punishing many "**Defectors**" would be too high.

Hauert et al 2007
The Emergence of Costly Punishment

Four strategies:

Nonparticipants rely on some activity whose payoff is independent of the other players' behavior.

Those who participate include:
Defectors: do not contribute but exploit the contributions of the others;
Cooperators: contribute but do not punish;
Punishers: not only contribute to the commonwealth but also punish defectors.

In such a model, punishers will invade and predominate.

However, in the absence of the option to abstain from the joint enterprise, punishers are often unable to invade, and the population is dominated by defectors. This means that if participation in the joint enterprise is voluntary, cooperation-enforcing behavior emerges. If participation is obligatory, then the defectors are more likely to win.

Hauert et al 2007

The Emergence of Costly Punishment

"**NonParticipants**": do not cooperate NOR get the benefits (ex.: forage alone)

IF NonParticipants' fitness **>** Defectors X Defectors:

NPs invade Ds ➡

Cs invade NPs ➡

Ds invade Cs ...➡

(In this case, Punishers **can** invade!)

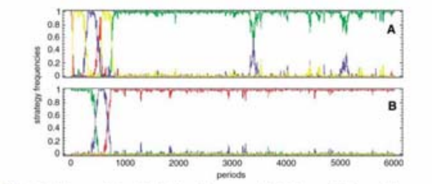


Fig. 1. Punishment and abstaining in joint-effort games. **(A)** Simulations of finite populations consisting of four types of players show that after some initial oscillations, punishers usually dominate the population. In longer runs, their regime can occasionally break down as a result of cooperators invading by neutral drift, but after another series of oscillations punishers will emerge again. The transient oscillations generally display a rock-paper-scissors–like succession of cooperators, defectors, and nonparticipants. When nonparticipants are frequent, groups are small, and punishing therefore is less costly, so that punishers have a chance to invade. **(B)** If participation is compulsory (no nonparticipants), defectors take over in the long run, even if the population consisted initially of punishers. Parameter values are $M = 100$, $N = 5$, $r = 3$, $\sigma = 1$, $\gamma = 0.3$, $\beta = 1$, $c = 1$, and $\mu = 0.001$.

Since Defectors are absent during part of each cycle of the oscillation, Punishers are not selected against during these periods and can invade rapidly. Once common, Punishers do better than other types, and it takes a long time for Cooperators and then Defectors to drift back in.

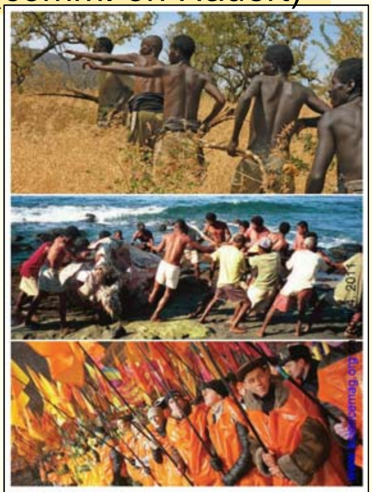
Boyd & Mathew 2007

A narrow road to cooperation (comm. on Hauert)

Hauert assumptions:
1. collective good must be excludable;
2. opting out is better than mutual defection;
3. there are no economies of scale.

Not always apply!

The model by Hauert et al. is an important contribution because it provides the first cogent mechanism that can jump-start the evolution of punishment. It can help us to understand the evolution of collective action in which benefits are excludable, opting out is preferable to mutual defection, and there are no economies of scale. The challenge is now to understand how punishment can arise in the remaining cases.



In or out? (Top) A group of Hadza men hunting cooperatively. Hadza hunter-gatherers living in Tanzania sometimes consume smaller kills in the bush, consistent with the Hauert *et al.* model. **(Center)** People from the village of Lamalera, Indonesia, hunt whales cooperatively. This form of cooperative hunting exhibits strong economies of scale not represented in the Hauert *et al.* model. **(Bottom)** Demonstrators in Kiev during the first anniversary of the Orange Revolution, November 2005. In the contemporary world people often participate in collective political action whose benefits are not excludable.

Boyd, Gintis & Bowles 2010
Coordinated punishment of defectors sustains cooperation and can proliferate when rare

Because mutually beneficial cooperation may unravel unless most members of a group contribute, people often gang up on free-riders, punishing them when this is cost-effective in sustaining cooperation. Current models of the evolution of cooperation assume that punishment is uncoordinated and unconditional and have difficulty explaining the evolutionary emergence of punishment because rare unconditional punishers bear substantial costs and hence are eliminated. Moreover, in human behavioral experiments in which punishment is uncoordinated, the sum of costs to punishers and their targets often exceeds the benefits of the increased cooperation that results from the punishment of free-riders.

BUT the total cost of punishing a free-rider declines as the number of punishers increases. We show that (coordinated) punishment can proliferate when rare, and when it does, it enhances group-average payoffs.

Riedl, Jensen, Call & Tomasello 2012
No third-party punishment in chimpanzees

Punishment can help maintain cooperation by deterring freeriding and cheating. Of particular importance in large-scale human societies is third-party punishment in which individuals punish a transgressor or norm violator even when they themselves are not affected.

Nonhuman primates and other animals aggress against conspecifics with some regularity, but it is unclear whether this is ever aimed at punishing others for noncooperation, and whether third-party punishment occurs at all.

Experimental study: Chimpanzees (*Pan troglodytes*), could punish an individual who stole food. Dominants retaliated when their own food was stolen, but they did not punish when the food of third-parties was stolen, even when the victim was related to them. **Third-party punishment as a means of enforcing cooperation, as humans do, might therefore be a derived trait in the human lineage.**

Genetic X Cultural Group Selection

The models proposed by Novak 2006, Nowak, Tarnita & Wilson 2010 (and other "group selectionists") do not convince the proponents of a Neodarwinian approach, because intergroup genetic selection is slower and weaker than intragroup (interindividual) selection:

More successful groups can grow more and split into new groups (i.e., "reproduce"), but the time intervals are slower than individuals' competition and reproduction.

The intergroup genetic selection is weaker because processes like individual selection, genetic drift and migration tend to decrease intergroup genetic variation in the population.

This may not be so in the case of *cultural* variation, selection and evolution.

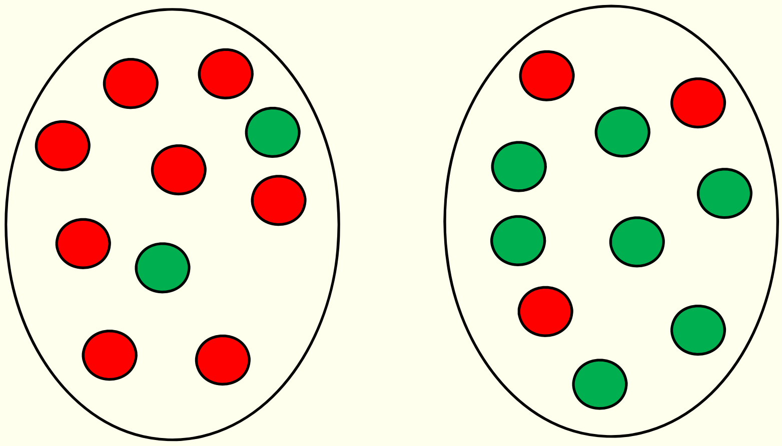
Cultural Group Selection

Feldman & Laland (1996): The theoretical argument against group selection is based on models that assume **genetic inheritance**, and the criticisms may not hold for **culturally transmitted traits**. When individuals adopt the behavior of the majority, a conformist transmission is generated. As a result of its frequency-dependence, conformist transmission can act to amplify differences in the frequency of cultural traits in different subpopulations.

Boyd & Richerson (1985): One of the by-products of a **conformist frequency-dependent bias** is an increase in the strength of the group selection of cultural variation so that it may be a strong force relative to forces acting within groups, such as natural selection.

Genetic X Cultural Group Selection

Genetic variation within/between groups



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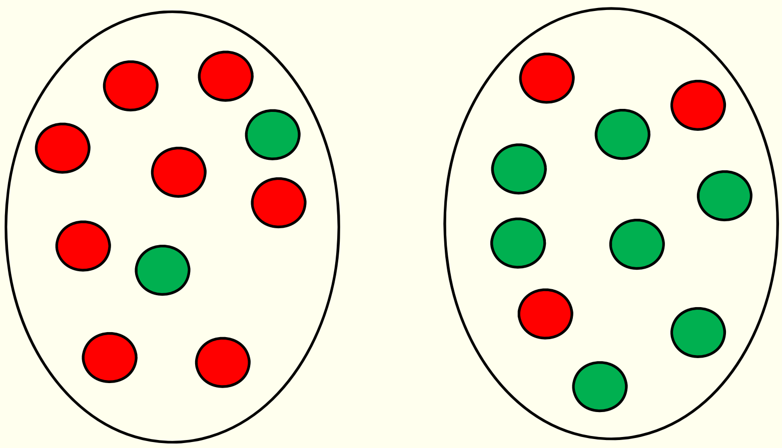


Cultural Group Selection
Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

Societies have many functional prerequisites. Social groups whose culturally transmitted values, beliefs, and institutions do not provide for these prerequisites become extinct. Cultural group selection is analogous to genetic group selection but acts on cultural rather than genetic differences between groups.

Cultural variation is more prone to group selection than genetic variation and that this may explain why human societies, in contrast to those of other animals, are frequently cooperative on scales far larger than kin groups.

CGS requires that
(1) there be cultural differences among groups
(2) these differences affect persistence or proliferation of groups
(3) these differences be transmitted through time.
If these three conditions hold, then cultural attributes that enhance the persistence or proliferation of social groups will tend to spread.

Cultural Group Selection
Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

Unlike many genetic models, this form of group selection does not require that the people who make up groups die during group extinction. All that is required is the disruption of the group as a social unit and the dispersal of its members throughout the metapopulation.

Such dispersal has the effect of cultural extinction, because dispersing individuals have little effect on the frequency of alternative behaviors in the future; in any one host subpopulation, they will be too few to tip it from one equilibrium maintained by convention or conformity to another.

Cultural group selection is very sensitive to the way in which new groups are formed. If new groups are mainly formed by individuals from a single preexisting group, then the behavior with the lower rate of extinction or higher level of contribution to the pool of colonists can spread even when it is rare in the metapopulation. If, instead, new groups result from the association of individuals from many other groups, group selection cannot act to increase the frequency of rare strategies.

Cultural Group Selection
Aoki et al 1996

The spread of agriculture

Since farming allows human populations to attain a higher density than hunter-gathering, a population that adopts farming may increase in number and expand geographically. But farming may also spread through the conversion of hunter-gatherers by social learning. In Aoki et al. (1996) model, there are no genes influencing which behavior (farming or hunting and gathering) is adopted. However, there are two kinds of selection operating, Darwinian selection and cultural selection, the latter representing the conversion of hunter-gatherers to farmers. The model monitors the dynamics of initial farmers, converted farmers and hunter-gatherers, and yields the conditions under which wave fronts of initial or converted farmers' advance.

Cultural Group Selection
Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

Cultural evolution by cultural group selection:
Empirical Evidence

Ethnographic literature of Irian Jaya and Papua New Guinea

To justify using this model of cultural group selection we need data that allow us to answer three questions:

1. **Group extinction**: do groups suffer disruption and dispersal at a rate high enough to account for the evolution of any important attributes of human societies?

2. **New group formation**: are new groups formed mainly by fission in groups that avoid extinction?

3. **Cultural variation among groups**: are there transmissible cultural differences among groups that affect their growth and survival, and do these differences persist long enough for group selection to operate?

Cultural Group Selection
Soltis, Boyd & Richerson 1995
Boyd & Richerson 2005

Table 11.1. Summary of group extinction rates for five regions of Papua New Guinea and Irian Jaya

Region	Groups	Extinctions	Years	Percentage of groups extinct every 25 years	Source
Mae Enga	14	5	50	17.9	Meggitt (1977)
Maring	32	1–3	50	1.6–4.7	Vayda (1971)
Mendi	9	3	50	16.7	Ryan (1959)
Fore/Usufura	8–24	1	10	31.3–10.4	Berndt (1962)
Tor	26	4	40	9.6	Oosterwal (1961)

Cultural Group Selection
Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

The data from New Guinea provide some qualified support for the model of group selection described.

1. **Group disruption and dispersal are common**. Extinction rates per generation range from 2 percent to 31 percent, with a median of 10.4 percent in the five areas for which quantitative data are available, and the frequent mention of extinction elsewhere suggests that these rates are representative.

2. **New groups are usually formed by fission of existing groups**. The detailed picture from the Mae Enga and the Mendi is supported by anecdotal evidence from other ethnographies. We are not aware of any ethnographic report from New Guinea in which colonists of new land are drawn from multiple groups.

3. There is variation among local groups, but it is unknown whether this variation persists long enough to be subject to group selection and whether this variation is responsible for the differential extinction or proliferation of groups.

Cultural Group Selection

Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

Rates of Change

By assuming that all extinctions result from a single heritable cultural difference (or a tightly linked complex of differences) between groups, we can calculate the maximum rate of cultural change.

Such an estimate suggests that **group selection is unlikely to lead to significant cultural change in less than 500 to 1 ,000 years.**

Cultural Group Selection

Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

Rates of Change

If the rates of group extinction estimated for New Guinea are representative of small-scale societies, cultural changes such as these cannot be explained in group-functional terms. There has not been enough time for group selection to have driven a single cultural attribute to fixation, even if that attribute had a strong effect on group survival.

Processes based on **individual decisions** are likely to account for such episodes of rapid evolution.

Cultural Group Selection
Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

Rates of Change

These results also suggest that group selection cannot justify the practice of interpreting many different aspects of a culture as group-beneficial. If group selection can cause the substitution of a single trait in 500 to 1,000 years, the rate for many traits will be substantially longer.

It is important to understand that slow does not necessarily mean weak. Thus, it follows that these results do not preclude interpreting some aspects of contemporary cultures in terms of their benefit to the group.

Cultural Group Selection
Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

CGS provides a potentially acceptable explanation for the increase in scale of sociopolitical organization in human prehistory and history precisely because it is so slow.

Scholars convinced of the overwhelming power of individual-level processes have real difficulty in explaining slow, long term historical change.
Anatomically modern humans appear in the fossil record about 90,000 years ago, yet there is no evidence for symbolically marked boundaries (perhaps indicative of a significant sociopolitical unit encompassing an "ethnic" group of some hundreds to a few thousand individuals) before about 35,000 years ago.
The evolution of simple states from food-producing tribal societies took about 5,000 years, and that of the modern industrial state took another 5,000. Evolutionary processes that lead to change on 10- or 100-year time scales cannot explain such slow change unless they are driven by some environmental factor that changes on longer time scales.

Cultural Group Selection
Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

In contrast, the more or less steadily progressive trajectory of increasing scale of sociopolitical complexity over the past few tens of thousands of years indeed is consistent with adaptation by a relatively slow process of group selection.

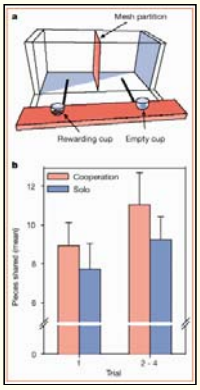
Cultural Group Selection and the Evolution of Cooperation

Feldman & Laland 1996
Since selection between groups may favor beliefs and attitudes that benefit the group at the expense of the individual, this provides a new explanation for human cooperation.
Conformist transmission may be favored by natural selection even though it has this deleterious effect for individuals, because it increases the chances of acquiring locally adaptive variants in a heterogeneous environment.

Non-human primates:
Cooperative use of tools in the laboratory

Chimpanzees (*Pan troglodytes*) Savage-Rumbaugh *et al* 1978
Baboons (*Papio hamadryas*) Beck 1973
Capuchin monkeys (*Sapajus apella*) de Waal 2000

Sherman & Austin - S.-Rumbaugh *et al* (1978)

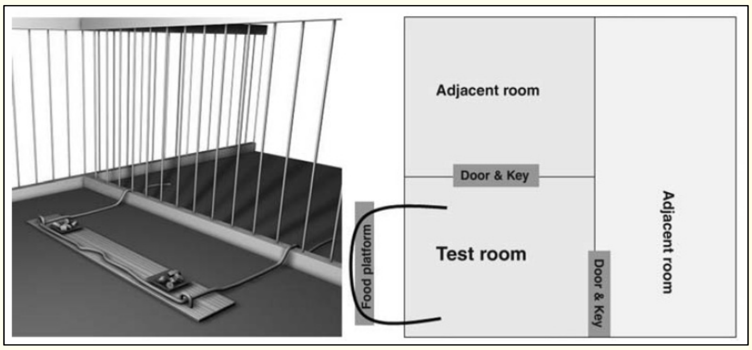


de Waal (2000)

Melis, Hare & Tomasello 2006

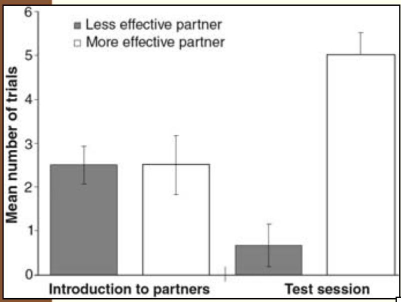
Chimpanzees recruit the best collaborators

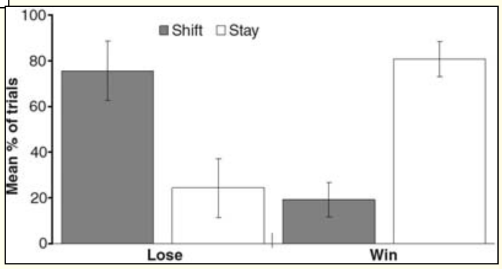
We presented chimpanzees with collaboration problems in which they had to decide when to recruit a partner and which potential partner to recruit. In an initial study, individuals recruited a collaborator only when solving the problem required collaboration. In a second study, individuals recruited the more effective of two partners on the basis of their experience with each of them on a previous day.



Melis, Hare & Tomasello 2006

Chimpanzees recruit the best collaborators





Warneken & Tomasello 2006

Altruistic helping in human infants and young chimpanzees

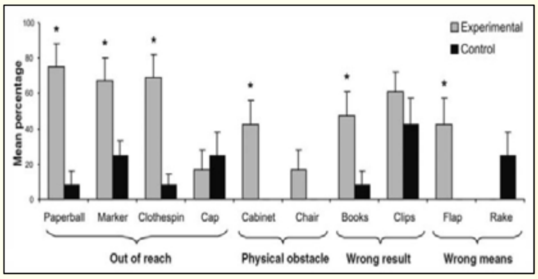
Human children as young as 18 months of age (prelinguistic or just-linguistic) quite readily help others to achieve their goals in a variety of different situations.

This requires both an understanding of others' goals and an altruistic motivation to help.

In addition, we demonstrate similar though less robust skills and motivations in three young chimpanzees.

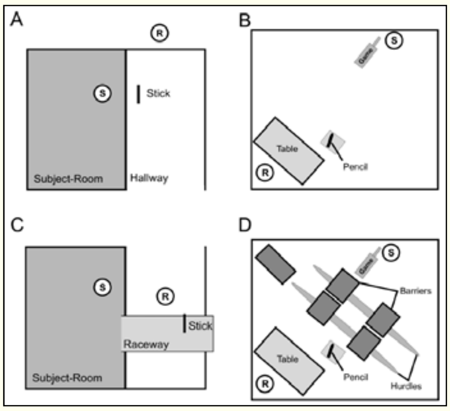
Table 1. Examples of problems used in child study.

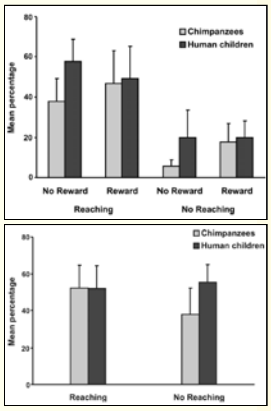
Category	Task	Problem
Out-of-reach	Marker	The adult accidentally drops a marker on the floor and unsuccessfully reaches for it (experimental) or intentionally throws a marker on the floor (control).
Physical obstacle	Cabinet	The adult wants to put magazines into a cabinet, but the doors are closed so that he bumps into it (experimental) versus bumping into the doors as he tries to lift the magazines onto the cabinet (control).
Wrong result	Book	A book slips from a stack as the adult attempts to place it on top of the stack (experimental) or he places it next to the stack (control).
Wrong means	Flap	A spoon drops through a hole and the adult unsuccessfully tries to grasp it through the small hole, ignorant of a flap on the side of the box (experimental). Alternatively, he throws the spoon in the box on purpose (control).



Warneken et al 2007
Spontaneous altruism by chimpanzees and young children

In two comparative studies, semi–free ranging chimpanzees helped an unfamiliar human to the same degree as did human infants, irrespective of being rewarded (experiment 1) or whether the helping was costly (experiment 2). In a third study, chimpanzees helped an unrelated conspecific gain access to food in a novel situation that required subjects to use a newly acquired skill on behalf of another individual.





Warneken et al 2007
Spontaneous altruism by chimpanzees and young children

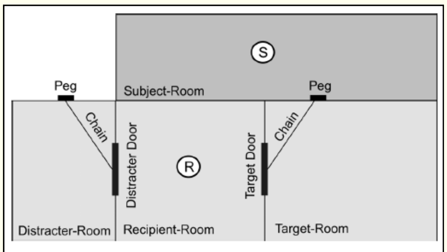
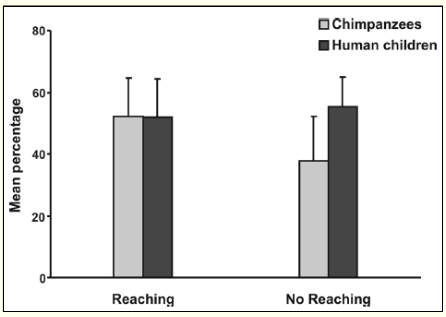


Figure 4. Test Area and Setup in Experiment 3



Cooperation: Social games

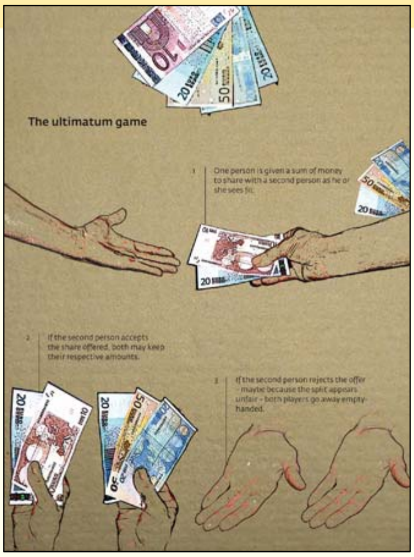
Prisoner's Dilemma

"Common Goods" game

Ultimatum Game

Dictator Game
("Ultimatum" with no refusal)

variant: 3rd element
(altruistic punishment)



Cooperation in chimpanzees?

Jensen, Call & Tomasello (2007)

Chimpanzees Are Rational Maximizers in an Ultimatum Game

Keith Jensen,* Josep Call, Michael Tomasello

Traditional models of economic decision-making assume that people are self-interested rational maximizers. Empirical research has demonstrated, however, that people will take into account the interests of others and are sensitive to norms of cooperation and fairness. In one of the most robust tests of this finding, the ultimatum game, individuals will reject a proposed division of a monetary windfall, at a cost to themselves, if they perceive it as unfair. Here we show that in an ultimatum game, humans' closest living relatives, chimpanzees (*Pan troglodytes*), are rational maximizers and are not sensitive to fairness. These results support the hypothesis that other-regarding preferences and aversion to inequitable outcomes, which play key roles in human social organization, distinguish us from our closest living relatives.

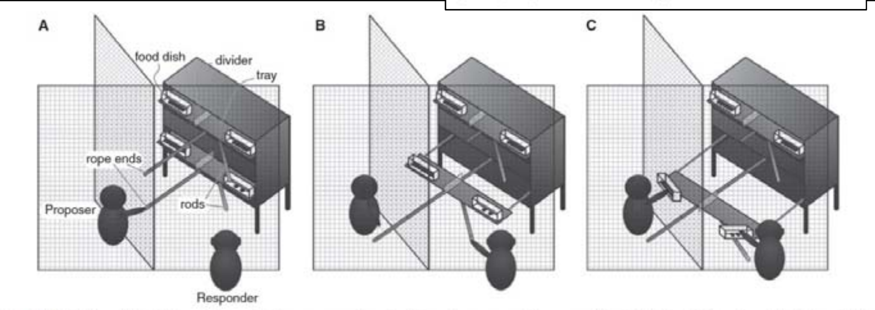


Fig. 1. Illustration of the testing environment. The proposer, who makes the first choice, sits to the responder's left. The apparatus, which has two sliding trays connected by a single rope, is outside of the cages. (**A**) By first sliding a Plexiglas panel (not shown) to access one rope end and by then pulling it, the proposer draws one of the baited trays halfway toward the two subjects. (**B**) The responder can then pull the attached rod, now within reach, to bring the proposed food tray to the cage mesh so that (**C**) both subjects can eat from their respective food dishes (clearly separated by a translucent divider).

Cooperation in chimpanzees?

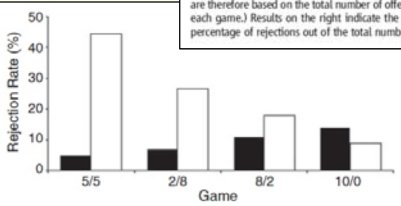
Responders did not reject unfair offers when the proposer had the option of making a fair offer; they accepted almost all nonzero offers; and they reliably rejected only offers of zero.

Low emotional arousal
(x food removal, x humans)

Fig. 2. Offers made by proposers and rejections by responders in the four games. In each game, the proposer could choose between two payoff options: 8/2 (8 raisins for the proposer and 2 for the responder) and an alternate [2/8 (2 for the proposer and 8 for the responder), 5/5 (5 for the proposer and 5 for the responder), 8/2 (8 for the proposer and 2 for the responder), and 10/0 (10 for the proposer and 0 for the responder)]. Results on the left show the total number and corresponding percentage of offers for each option made by proposers in each game. (Trials in which the proposer did not participate are not included, therefore the total number of offers varies across the games; percentages are therefore based on the total number of offers for each option out of the total number of trials played for each game.) Results on the right indicate the total number of each offer rejected and the corresponding percentage of rejections out of the total number of offers for each game.

Game	Proposer Offers	Payoffs Proposer	Payoffs Responder	Responder Rejections
5/5	39 (75%)	8	2	2 (5%)
	13 (25%)	5	5	0 (0%)
2/8	45 (87%)	8	2	3 (7%)
	7 (13%)	2	8	0 (0%)
8/2	53 (100%)	8	2	6 (11%)
		8	2	
10/0	29 (54%)	8	2	4 (14%)
	25 (46%)	10	0	11 (44%)

Fig. 3. Rejection rates (% of trials) of 8/2 offers in the four games for chimpanzees in this study (black bars) and for human participants (white bars) [data are from (*23*)].



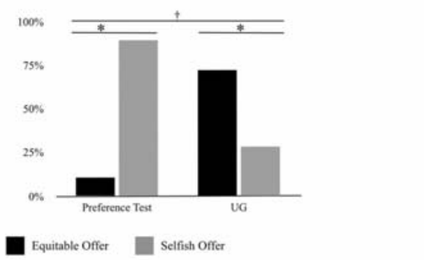
Jensen et al (2007)

Cooperation in chimpanzés?

X Proctor, Williamson, de Waal & Brosnan (2013)

Chimpanzees play the ultimatum game

Both apes and children responded like humans typically do. If their partner's cooperation was required, they split the rewards equally. However, with passive partners (situation akin to the "dictator game") they preferred the selfish option.



* Denotes significant difference between equitable and selfish offer; Binomial Test $p<0.05$
† Denotes significant change from Preference Test to UG; McNemar's Test $p<0.05$

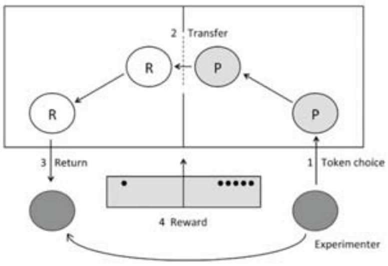
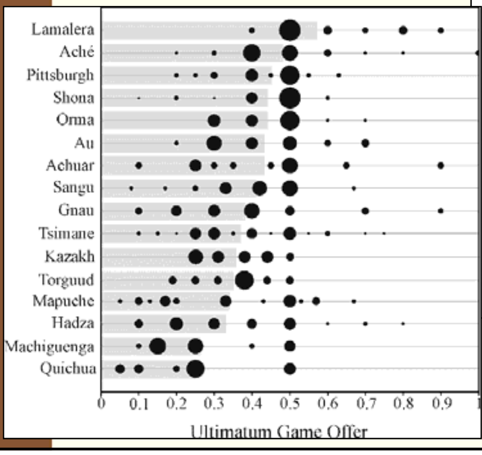


Fig. 1. Experimental setup for pairs of chimpanzees following a four-step sequence. Step 1: The proposer (P) is presented with a choice of two tokens, one representing an equal split of the rewards and the other representing an unequal split favoring the proposer. The proposer is free to select either token. Step 2: The proposer passes the selected token to the respondent (R) through a mesh panel. Step 3: The respondent either returns the token to the experimenter to accept the offer, drops the token, or does not return it for 30 s. Step 4: Six banana rewards are visibly divided on a tray in front of the chimpanzees according to the token selected. Here the dots represent an unequal 5:1 distribution of rewards in favor of the proposer. The tray is then pushed within reach of the chimpanzees so that each can collect its reward (s). Note that the experimental setup for children was similar, except that a commercially available baby gate was used to separate the participants and the experimenter.

Cooperation: cross-cultural comparison
Henrich et al (2005)



BEHAVIORAL AND BRAIN SCIENCES (2005) 28, 795–855
Printed in the United States of America

"Economic man" in cross-cultural perspective: Behavioral experiments in 15 small-scale societies

Joseph Henrich
Robert Boyd
Samuel Bowles
Colin Camerer
Ernst Fehr
Herbert Gintis
Richard McElreath
Michael Alvard
Abigail Barr
Jean Ensminger
Natalie Smith Henrich
Kim Hill
Francisco Gil-White
Michael Gurven
Frank W. Marlowe
John Q. Patton
David Tracer

Cooperation: cross-cultural comparison
Henrich et al (2005)

Group-level differences in economic organization and the structure of social interactions explain a substantial portion of the behavioral variation across societies: the higher the degree of market integration and the higher the payoffs to cooperation in everyday life, the greater the level of prosociality expressed in experimental games.

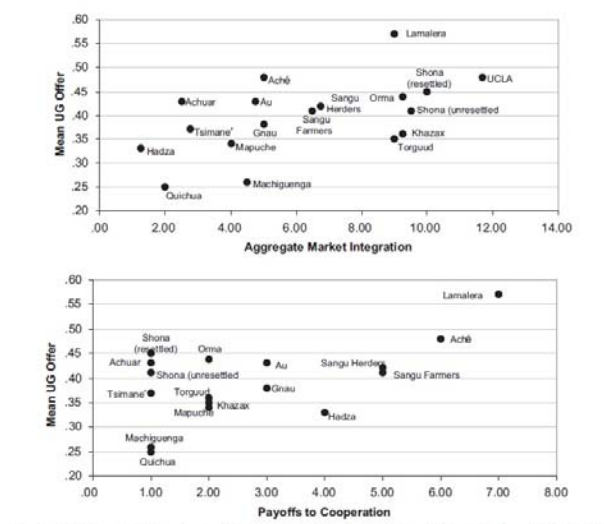


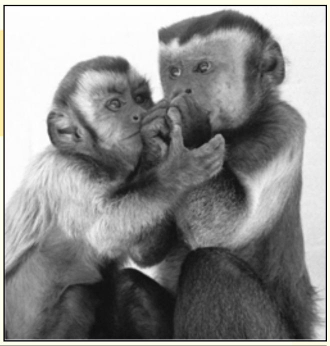
Figure 5. Plots Mean UG offers as a function of the PC and AMI indices. Because AMI and PC are almost uncorrelated (r = .09), these bivariate plots give a useful picture of their effects.

A sense of "fairness" in capuchin monkeys?

Monkeys reject unequal pay

Sarah F. Brosnan & Frans B. M. de Waal

Living Links, Yerkes National Primate Research Center, Emory University, Atlanta, Georgia 30329, USA



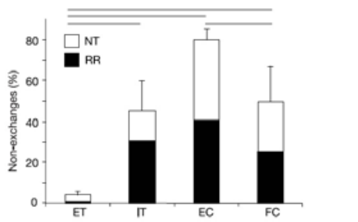


Figure 1 Mean percentage ± s.e.m. of failures to exchange for females across the four test types. Black bars (RR) represent the proportion of non-exchanges due to refusals to accept the reward; white bars (NT) represent those due to refusals to return the token. s.e.m. is for combined non-exchanges. Lines indicate significant differences between conditions (Tukey's multiple comparisons). ET, equality test; IT, inequality test; EC, effort control; FC, food control.

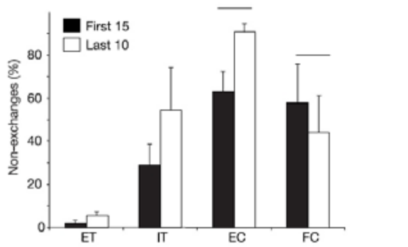


Figure 2 Mean percentage ± s.e.m. of failures to exchange in the first 15 trials (black bars) versus the last 10 trials per test (white bars). Lines indicate differences at $P = 0.06$ (exact Wilcoxon signed ranks test). ET, equality test; IT, inequality test; EC, effort control; FC, food control.

Boyd & Richerson 2009
Culture and the evolution of human cooperation

The **scale** of human cooperation is an evolutionary puzzle.

Something makes our species different: **cultural adaptation**:

1. Cumulative cultural evolution allows humans to culturally evolve highly refined adaptations to local environments relatively quickly compared with genetic evolution;

2. Rapid cultural adaptation also vastly increased heritable variation between groups;

3. In such culturally evolved cooperative social environments, **social selection within groups favored genes that gave rise to new, more prosocial motives**. Moral systems enforced by systems of sanctions and rewards increased the reproductive success of individuals who functioned well in such environments, and this in turn led to the evolution of other regarding motives like **empathy** and **social emotions** like shame.

Boyd & Richerson 2009
Culture and the evolution of human cooperation

CULTURE ALLOWS RAPID LOCAL ADAPTATION

The human species occupies a wider range of habitats, uses a much greater range of resources, and lives in more diverse social systems than any other animal species. We constitute a veritable adaptive radiation, albeit one without any true speciation.
Ecological success = superior cognitive abilities?
Cultural complexity: While we are rather clever animals, we cannot do this because we are not close to clever enough [no kayak module...]
Combining even limited, imperfect **learning mechanisms** with **cultural transmission** can lead to relatively rapid, cumulative adaptation.
Culture leverages individual creativity in just the way Darwin imagined.
Hypothesis: the psychological capacities that allow humans to learn from others evolved during the Middle Pleistocene in response to increased rapid, high amplitude climate variation.

Boyd & Richerson 2009
Culture and the evolution of human cooperation

RAPID CULTURAL ADAPTATION POTENTIATES GROUP SELECTION

Larger more cooperative groups defeat smaller less cooperative groups.
However, in all but the simplest transactions, individuals experience a cost now in return for a benefit later and thus are vulnerable to defectors who take the benefit but do not produce the return. Imperfect monitoring or effort and quality also give rise to opportunities for free riding.

Aside from humans, only a few other taxa, most notably social insects, make cooperation a cornerstone of their adaptation. Those that do are spectacular evolutionary successes.

Nonetheless, cooperative behavior does not usually evolve because it is vulnerable to exploitation.

Boyd & Richerson 2009
Culture and the evolution of human cooperation

SELECTION IN CULTURALLY EVOLVED SOCIAL ENVIRONMENTS MAY HAVE FAVOURED NEW TRIBAL SOCIAL INSTINCTS

We hypothesize that this new social world, created by rapid cultural adaptation, led to the genetic evolution of new, derived social instincts. Cultural evolution created cooperative groups.

Such environments favored the evolution of a suite of new social instincts suited to life in such groups including a psychology which 'expects' life to be structured by moral norms, and that is designed to learn and internalize such norms.

New emotions evolved, like shame and guilt, which increase the chance the norms are followed. Individuals lacking the new social instincts more often violated prevailing norms and experienced adverse selection.

Cooperation and group identification in inter-group conflict set up an arms race that drove social evolution to ever-greater extremes of in-group cooperation.

Boyd & Richerson 2009
Culture and the evolution of human cooperation

SELECTION IN CULTURALLY EVOLVED SOCIAL ENVIRONMENTS MAY HAVE FAVOURED NEW TRIBAL SOCIAL INSTINCTS (2)

~ 100.000 years ago: tribal-scale societies: egalitarian, diffuse political power.

People are quite ready to punish others for transgressions of social norms, even when personal interests are not directly at stake.

The tribal instincts that support identification and cooperation in large groups are often at odds with selfishness, nepotism and face-to-face reciprocity.

We think that human social instincts constrain and bias the kind of societies that we construct, but the details are filled in by the local cultural input. When cultural parameters are set, the combination of instincts and culture produces operational social institutions.

Social Motives, Morality & Emotions

Moral "Universals"?

Richard Shweder & Alan Fiske (anthropologists):

•Sense of justice, loyalty to a group, exchange and solidarity between its members and conformity to its rules.
•Belief that its is correct to obey to legitimate authority and respect individuals in high positions.
•Exaltation of purity, cleanliness and santity, contempt for decay, for contamination and for carnality.

Haidt: five "themes":

Agression / Justice / Comunity Sense (group loyalty) / Autority / Purity

Moral Emotions as **adaptations** for social living?

Moral Judgement: rational construction x intuition & emotion

Jonathan Haidt (2001, 2003):
the "intuitionist" approach to moral judgement

(X Piaget, Kohlberg: "construction" of moral rationality)

Judgment [followed by justification] of certain "episodes":

> A woman is cleaning out her closet and she finds her old American flag. She doesn't want the flag anymore, so she cuts it up into pieces and uses the rags to clean her bathroom.

> A family's dog is killed by a car in front of their house. They heard that dog meat was delicious, so they cut up the dog's body and cook it and eat it for dinner.

Moral Judgement: rational construction x intuition & emotion

Jonathan Haidt (2001, 2003)

The "catch": all narratives already incorporate "counter-arguments" to typical "justifications". In the end, subjects answered that "they knew it was wrong – if if they didn't know *why*"

Julie and Mark are brother and sister. They are traveling together in France on summer vacation from college. One night they are staying alone in a cabin near the beach. They decide that it would be interesting and fun if they tried making love. At the very least it would be a new experience for each of them. Julie was already taking birth control pills, but Mark uses a condom too, just to be safe. They both enjoy making love, but they decide not to do it again. They keep that night as a special secret, which makes them feel even closer to each other. What do you think about that? Was it OK for them to make love?

A Social-Intuitionist approach to Moral Judgement

Haidt (2001)

"Perhaps because moral norms vary by culture, class, and historical era, psychologists have generally assumed that morality is learned in childhood, and they have set out to discover how morality gets from outside the child to inside."

The "Rationalist" Model:

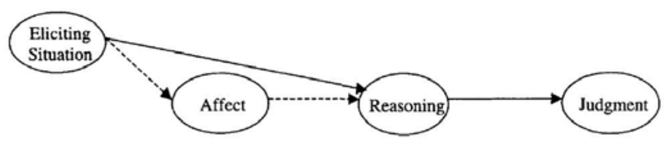


Figure 1. The rationalist model of moral judgment. Moral affects such as sympathy may sometimes be inputs to moral reasoning.

A Social-Intuitionist approach to Moral Judgement
Haidt (2001)

"The social intuitionist model takes a different view. It proposes that **morality, like language, is a major evolutionary adaptation for an intensely social species**, built into multiple regions of the brain and body, that is better described as emergent than as learned - yet that requires input and shaping from a particular culture. **Moral intuitions are therefore both innate and enculturated**".

The "Social-Intuitionist" Model:

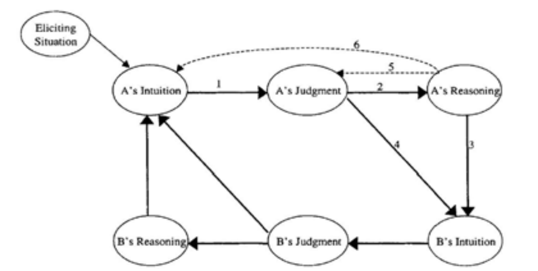
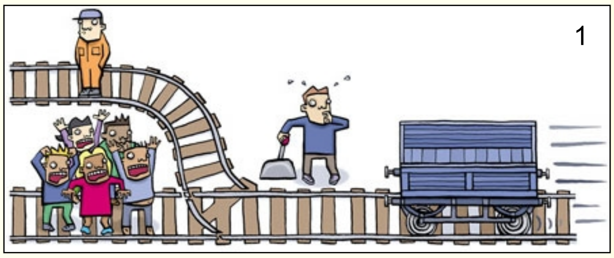
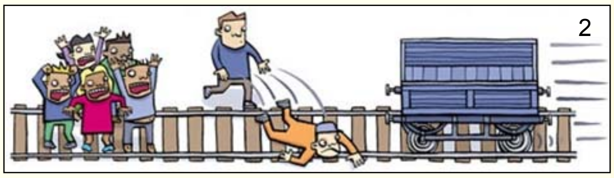


Figure 2. The social intuitionist model of moral judgment. The numbered links, drawn for Person A only, are (1) the intuitive judgment link, (2) the post hoc reasoning link, (3) the reasoned persuasion link, and (4) the social persuasion link. Two additional links are hypothesized to occur less frequently: (5) the reasoned judgment link and (6) the private reflection link.

Moral emotions:
Utilitarism and the "Trolley Problem"

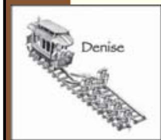
Phillipa Foot (1967)
The "double effect" principle: Planned/instrumental harm X predicted collateral consequence



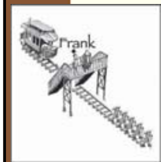


“Double effect” x alternative explanations
Hauser et al 2007

1

	Denise is a passenger on a train whose driver has fainted. On the main track ahead are 5 people.The main track has a side track leading off to the left, and Denise can turn the train on to it.There is1 person on the left hand track. Denise can turn the train, killing the 1; or she can refrain from turning the train, letting the 5 die.	Is it morally permissible for Denise to turn the train? **89%**

2

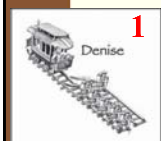
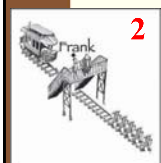
	Frank is on a footbridge over the train tracks. He sees a train approaching the bridge out of control. There are 5 people on the track. Frank knows that the only way to stop the train is to drop a heavy weight into its path. But the only available, sufficiently heavy weight is1large man, also watching the train from the foot bridge.Frank can shove the 1 man onto the track in the path of the train, killing him; or he can refrain from doing this, letting the 5 die.	Is it morally permissible for Frank to shove the man? **11%**

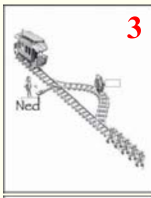
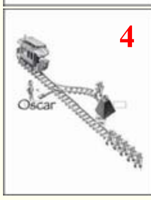
$P_{1x2} < .001$

Possible underlying “principles”:

1. **“Double effect”**: It is more permissible to cause harm as an unintended consequence (albeit predictable) than as a means to an end;
2. **Redirecting x Introduction of a new threat** (less permissible);
3. **Personal x Impersonal**: it is less permissible to cause harm by direct physical **contact** than by indirect means.

“Double effect” x alternative explanations
Hauser et al 2007

1 	Denise is a passenger on a train whose driver has fainted. On the main track ahead are 5 people.The main track has a side track leading off to the left, and Denise can turn the train on to it.There is1 person on the left hand track. Denise can turn the train, killing the 1; or she can refrain from turning the train, letting the 5 die.	Is it morally permissible for Denise to turn the train? **89%**
2 	Frank is on a footbridge over the train tracks. He sees a train approaching the bridge out of control. There are 5 people on the track. Frank knows that the only way to stop the train is to drop a heavy weight into its path. But the only available, sufficiently heavy weight is1large man, also watching the train from the foot bridge.Frank can shove the 1 man onto the track in the path of the train, killing him; or he can refrain from doing this, letting the 5 die.	Is it morally permissible for Frank to shove the man? **11%**

3 	Ned is walking near the train tracks when he notices a train approaching out of control. Up ahead on the track are 5 people.Ned is standing next to a switch, which he can throw to turn the train on to aside track. There is a heavy object on the side track. If the train hits the object, the object wills low the train down, giving the men time to escape. The heavy object is 1 man, standing on the side track. Ned can throw the switch, preventing the train from killing the 5 people, but killing the 1 man. Or he can refrain from doing this, letting the 5 die.	Is it morally permissible for Ned to throw the switch? **56%**
4 	Oscar is walking near the train tracks when he notices a train approaching out of control. Up ahead on the track are 5 people. Oscar is standing next to a switch, which he can throw to turn the train on to aside track. There is a heavy object on the side track. If the train hits the object, the object will slow the train down, giving the 5 people time to escape. There is 1 man standing on the sidetrack infront of the heavy object. Oscar can throw the switch, preventing the train from killing the 5 people, but killing the1man. Or he can refrain from doing this, letting the five die.	Is it morally permissible for Oscar to throw the switch? **72%**

$P_{3x4} < .001$

Most subjects could not justify different judgments.
OPERATIVE, not EXPRESSED principles:
Conscious reasoning based in explicit principles do not explain moral judgments.

"Moral Emotions", Evolutionary Psychology, Cultural Evolution and Gene-Cultural Coevolution: convergences

Boyd & Richerson (2009): We hypothesize that this new social world, created by rapid cultural adaptation, led to the genetic evolution of new, derived social instincts. Cultural evolution created cooperative groups.

Such environments favored the evolution of a suite of new social instincts suited to life in such groups including a psychology which 'expects' life to be structured by moral norms, and that is designed to learn and internalize such norms.

New emotions evolved, like shame and guilt, which increase the chance the norms are followed. Individuals lacking the new social instincts more often violated prevailing norms and experienced adverse selection.

Final considerations:
On Darwinian Models of Cultural Evolution

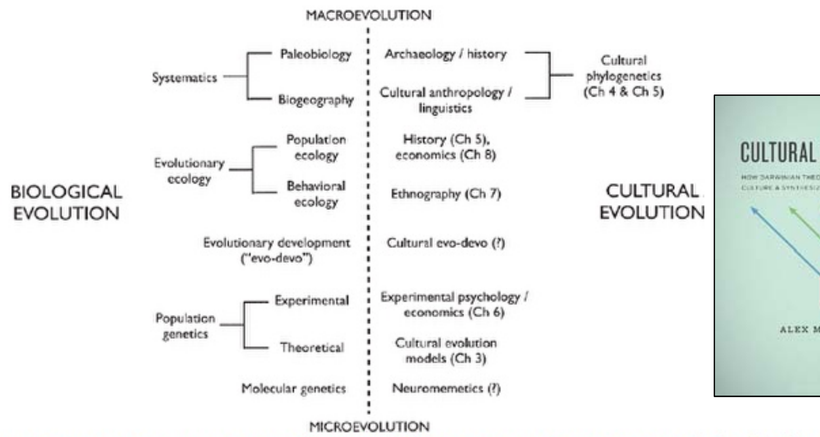
Cultural evolution can be Darwinian, though not "Neo-Darwinian"

Variation: not random: Content and Context biases - frequency (Conformity) or model-based (Prestige etc)…
Inheritance: Vertical + Oblique + Horizontal; no "Replicators".

Darwinian evolutionary models and concepts from population dynamics can be very useful to understand the evolution of culture, if we are not bound to an strict analogy between genes and "memes" and pay the due attention to the underlying psychological and social processes.

A Darwinian paradigm can be an useful tool to unify the social and biological sciences.

Final considerations:
On Darwinian Models of Cultural Evolution



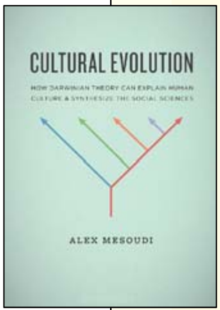


FIGURE 10.1 The structure of a potential science of cultural evolution (*righthand side*), as mapped on to the existing structure of evolutionary biology (*lefthand side*).

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