

Gene-Culture coevolution, group selection, and the evolution of Cooperation



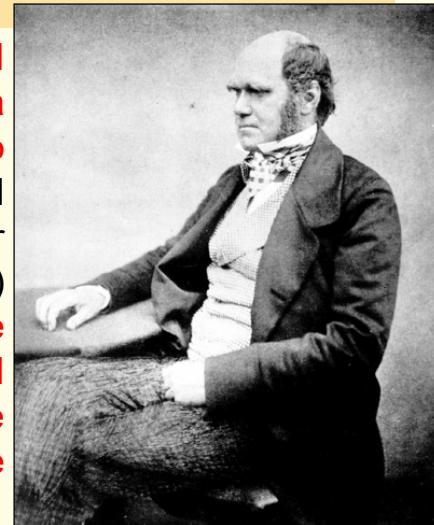
The Evolution of Cooperation

How can altruism / cooperation evolve?



Levels of Selection

"although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe (...) an advancement in the standard of morality will certainly give an immense advantage to one tribe over another."



(C. Darwin, *Descent of Man*, 1871)

Levels of Selection

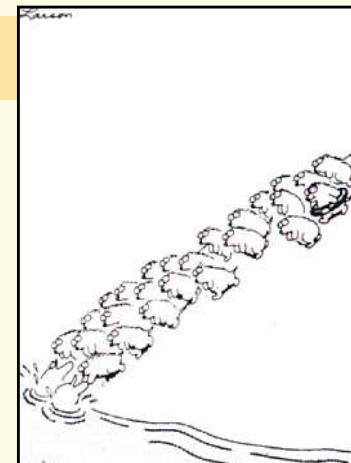
Individuals ("basic" [Neo]Darwinism)
Genes ("Selfish-gene" Sociobiology)
Groups?
Multilevel selection?
Higher-level adaptations?

Genetic Group Selection?

"Naïve group selectionism":

The probability of survival of individual living things, or of populations, increases with the degree with which they harmoniously adjust themselves to each other and to their environment. This principle is basic to the concept of the balance of nature, orders the subject matter of ecology and evolution, underlies organismic and developmental biology, and is the foundation for all sociology. (Allee et al. 1949)

"The good of the species" (Wynne-Edwards)



Levels of Selection

Migration, genetic drift, etc:

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

X

Wilson DS & Wilson EO (2007)

Rethinking the theoretical foundation of sociobiology

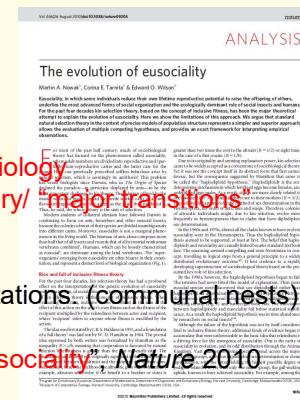
Multi-level selection/ limits in kin selection theory/ major transitions

Eusociality:

Kin Selection X Individual selection + preadaptations... (communal nests)

Nowak, Tarnita & Wilson, "The Evolution of Eusociality", *Nature* 2010

(X Abbot et al [+100!], *Nature* 2011)



"Major Transitions" in Evolution

Maynard Smith & Szathmáry 1997

Replicating molecules	→	Populations of molecules in compartments
Unlinked replicators	→	Chromosomes
RNA as gene and enzyme	→	DNA and protein (genetic code)
Prokaryotes	→	Eukaryotes
Asexual clones	→	Sexual populations
Single-celled organisms	→	Animals/plants/fungi (cell differentiation)
Solitary individuals	→	Social colonies (nonbreeding castes)
Primate societies	→	Human societies (language)

"Apart from the evolution of the genetic code, all these transitions involve the coming together of previously independent replicators, to cooperate in a higher-level assembly that reproduces as a single unit."

Natural selection & 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.

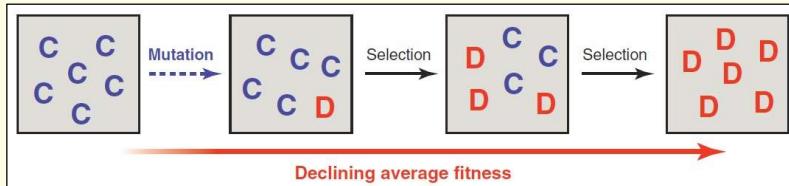


Fig. 1. Without any mechanism for the evolution of cooperation, natural selection favors defectors. In a mixed population, defectors, D , have a higher payoff (= fitness) than cooperators, C . Therefore, natural selection continuously reduces the abundance, i , of cooperators until they are extinct. 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

W. D. Hamilton (1964)

Inclusive fitness

Wright's coefficient of relationship, r

$$r \times b > c$$

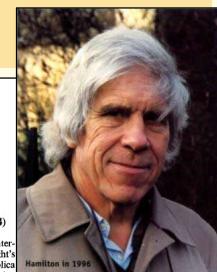
J. Theoret. Biol. (1964) 7, 1–16

The Genetical Evolution of Social Behaviour. I

W. D. HAMILTON

The Galton Laboratory, University College, London, W.C.2

(Received 13 May 1963, and in revised form 24 February 1964)



Hamilton in 1996

A general mathematical model is described which allows for interactions between relatives on one another's fitness. Making use of Wright's Coefficient of Relationship as the measure of the proportion of replacement genes in a relative, a quantity is found which indicates the maximizing property of Darwinian fitness. This quantity is called inclusive fitness. Species following the model show a tendency to evolve behaviour such that each organism appears to be attempting to maximize its inclusive fitness. This implies a limited restraint on selfish competitive behaviour and possibility of limited self-sacrifice.

Special cases of the model are used to show (a) that selection in the social situations newly covered tends to be slower than classical selection, (b) how in populations of rather non-dispersive organisms the model may apply to genes affecting dispersion, and (c) how it may apply approximately to competition between relatives, for example, within subspecies. Some artificialities of the model are discussed.

1. Introduction

With very few exceptions, the only parts of the theory of natural selection which have been supported by mathematical models admit no possibility of the evolution of any characters which are on average to the disadvantage of the individuals possessing them. If natural selection followed the classical models exclusively, species would not show any behaviour more positively social than the coming together of the sexes and parental care.

Sacrifices involved in parental care are a possibility implicit in any model in which the definition of fitness is based, as it should be, on the number of adult offspring. In certain cases, an individual may leave more adult offspring by spending care and materials on its offspring already born than by reserving them for its own survival and further fecundity. A gene causing its possessor to give parental care will then leave more replicas in the next generation than an allele having the opposite tendency. The selective advantage may be seen to lie through benefits conferred indirectly on a set of relatives each of which has a half chance of carrying the gene in question.

T.S.

1

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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

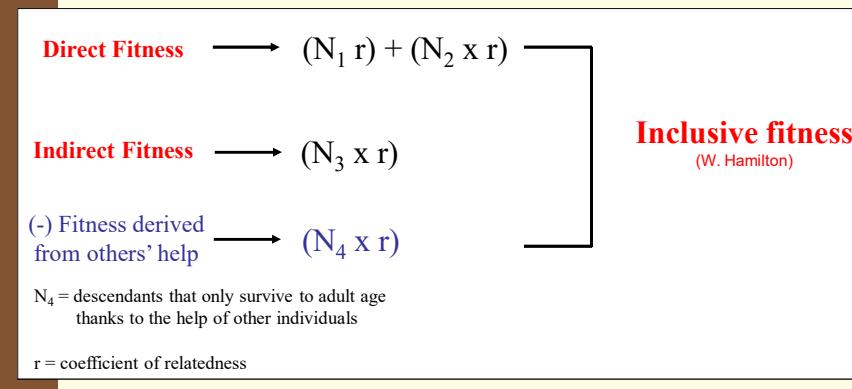
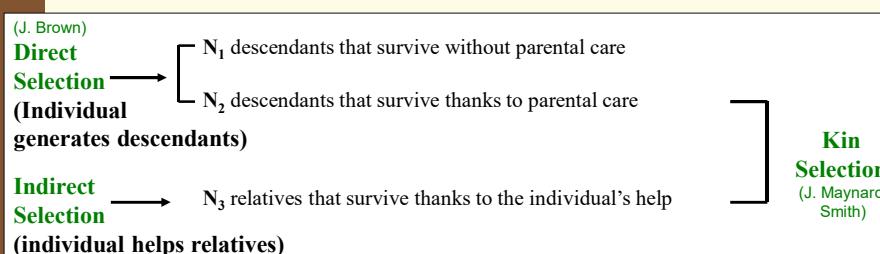
$$b \times r > c \text{ (ou } r > b/c\text{)}$$

where

b = benefits to receivers

c = cost to direct fitness

r = coefficient of relationship (Wright 1922)



The evolution of cooperation beyond kin



AllPosters

R.L. Trivers: *The evolution of reciprocal altruism* (1971)

Afogados e Salva-vidas: custos e benefícios, reciprocidade

Alelo "altruista"
 $W(a_2a_2) > W[a_1a_2 \text{ não inter}]$

(1) random choice
 $a_1 \text{ substitui } a_2$

(2) Nonrandom reference to individuals related (~ kin recognition)

If we assume that the entire population is sooner or later exposed to the same risk of drowning, the two individuals who risk their lives to save each other will be selected over those who face drowning on their own. Note that the benefits of reciprocity depend on the unequal cost/benefit ratio of the altruistic act, that is, the benefit of the altruistic act to the recipient is greater than the cost of the act to the performer, cost and benefit being defined here as the increase or decrease in chances of the relevant alleles propagating themselves in the population. Note also that, as defined, the benefits and costs depend on the age of the altruist and recipient (see *Age-dependent changes* below). (The odds assigned above may not be unrealistic if the drowning man is drowning because of a cramp or if the rescue can be executed by extending a branch from shore.)

THE EVOLUTION OF RECIPROCAL ALTRUISM
 By ROBERT L. TRIVERS
*Biological Laboratories, Harvard University,
 Cambridge, Mass. 02138*

ABSTRACT

A model is presented to account for the natural selection of what is termed reciprocal altruistic behavior. The model shows how selection can operate against the cheater (non-reciprocator) in the system. Three instances of altruistic behavior are discussed, the evolution of which the model can explain: (1) behavior involved in drowning accidents between humans and closely related animals; (2) behavior between members of the same species; and (3) behavior between members of different species.

Regarding human reciprocal altruism, it is shown that the details of the psychological system that regulates this altruism can be explained by the model. Specifically, the model predicts that the details of the psychology of human altruism, trueruthfulness, aspects of gullibility, and some forms of dishonesty and hypocrisy can be explained as important adaptations to regulate the altruistic system. Each individual has a set of genes that regulate his altruistic behavior, and the selection of these genes is sensitive to developmental variables that were selected to set the conditions at a balance appropriate to the local social and ecological environment.

INTRODUCTION

ALTRUISTIC behavior can be defined as behavior that increases the fitness of others at a cost to the performer, whether being apparently detrimental to the organism performing the behavior, beneficial and dominant being defined in terms of competition for limited resources. One human being leaping into water, at some danger to himself, to save another human being drowning is an instance of altruism. If he were to leap in to save his own child, the behavior would be called "altruistic" or an instance of "altruism"; he may merely be contributing to the survival of his own genes invested in the child.

Models that attempt to explain altruistic behavior in terms of natural selection have been designed to take the altruism out of altruism. For example, Hamilton (1964) has demonstrated that the rate of altruism can be a dominant parameter in predicting how selection will operate, and behavior which appears altruistic may, on knowledge of the genetic relationship between the organisms involved, be explicable in terms of natural selection: those genes being selected for that contribute to their own perpetuation, regardless of which individual they appear in. The term "kin selection" will be used here to denote models to cover instances of this type—that is, of organisms being selected to help their relatively close kin.

The present paper, however, needs to show how certain classes of behavior conveniently denoted as "altruistic" (or "reciprocally altruistic") can be selected for even when the genes being selected are not related to the organism performing the altruistic act that kin selection can be ruled out. The model will apply to cases where the altruistic behavior is between members of different species. It will be argued that under certain conditions natural selection can favor altruistic behavior, because in the long run they benefit the organism performing them.

THE MODEL

One human being saving another, who is not closely related and is about to drown, is an instance of altruism. Assume that the chance of the drowning man dying is negligible; no steps in to save him, but that the chance that his potential rescuer will drown if he leaps in to save him is much smaller, say, one in 35.

R.L. Trivers: *The evolution of reciprocal altruism* (1971)

(3) Nonrandom dispensation by reference to the altruistic tendencies of the recipient:

Altruista responde a atos não-altruístas (qdo custo p/ agente teria sido menor que benefício para receptor) suspendendo altruísmos futuros
(pode ser outro alelo altruísta > mesmo entre espécies diferentes!)

Chances dependem de :

- 1 – frequência das interações potencialmente altruísticas;
- 2 – repetição dentro de um subconjunto pequeno de indivíduos;
- 3 – "simetria" de custos e benefícios nas interações

Parâmetros biológicos:

Duração da vida /taxa de dispersão / grau de interdependência / cuidado parental / parentes: não só H24, reciprocidade tb! / (fraca) hierarquia de dominância / ajuda em combates

Exs:

simbioses de limpeza, chamados de alarme (aves etc)
altruísmo recíproco humano

R.L. Trivers: *The evolution of reciprocal altruism* (1971)

(3) Nonrandom dispensation by reference to the altruistic tendencies of the recipient:

“O sistema psicológico subjacente ao altruísmo recíproco humano”

- Sistema regulatório complexo
- Amizade e Emoções sociais (gratidão, culpa)
- Agressão moralista
- Disfarce e detecção de "cheaters"
- Reputações
- Altruísmo generalizado e regras de troca
[linguagem]
- Plasticidade ontogenética

The relationship between two individuals repeatedly exposed to symmetrical reciprocal situations is exactly analogous to what game theorists call the Prisoner's Dilemma (Luce and Raiffa, 1957; Rapoport and Chammah, 1965), a game that can be characterized by the payoff matrix

	A ₂	C ₂
A ₁	R, R	S, T
C ₁	T, S	P, P

where S < P < R < T and where A₁ and A₂ represent the altruistic choices possible for the two individuals, and C₁ and C₂, the cheating choices (the first letter in each box gives the payoff for the first individual, the second letter the payoff for the second individual). The other symbols can be given the following meanings: R stands for the reward each individual gets from an altruistic exchange if neither cheats; T stands for the temptation to cheat; S stands for the sucker's payoff that an altruist

O "Dilema do Prisioneiro"

[“Hamilton (pers. comm.)”: antecipa A&H 1981]

Axelrod & Hamilton 1981
Cooperation beyond kinship

The Evolution of Cooperation

Robert Axelrod and William D. Hamilton

To account for the manifest existence of cooperation and related group behavior, such as altruism and restraint in competition, evolutionary theory has recently acquired two kinds of extension. These extensions are, broadly, genetical kinship theory (3) and reciprocity theory (4, 5). Most of the recent activity, both in field work and in further develop-

Summary. Cooperation in organisms, whether bacteria or primates, has been a difficulty for evolutionary theory since Darwin. On the assumption that interactions between pairs of individuals occur on a probabilistic basis, a model is developed based on the concept of an evolutionarily stable strategy in the context of the Prisoner's Dilemma game. Deductions from the model, and the results of a computer tournament show how cooperation based on reciprocity can get started in an asocial world, can thrive while interacting with a wide range of other strategies, and can resist invasion once fully established. Potential applications include specific aspects of territoriality, mating, and disease.

1390 0036-8075/81/0327-1390\$01.50/0 Copyright © 1981 AAAS SCIENCE, VOL. 211, 27 MARCH 1981

Cooperation: Social games

- Prisoner's Dilemma
- "Common Goods" game
- Ultimatum Game
- Dictator Game
(“Ultimatum” with no refusal)
- variant: 3rd element
(altruistic punishment)

The illustration shows a hand holding a stack of banknotes (20, 50, 100) above another hand. The top hand is labeled "The ultimatum game". Below, a box contains text: "One person is given a sum of money to share with a second person. If he or she accepts the offer, both may keep their respective amounts. If the second person rejects the offer, maybe because the offer is unfair, both players go away empty-handed."

Cooperation: Social games

Prisoner's Dilemma

"Common Goods" game

Ultimatum Game

Dictator Game
("Ultimatum" with no refusal)

variant: 3rd element
(altruistic punishment)

		Henry	
		Not Guilty	Guilty
		Dave	
	Not Guilty		
	Guilty		

The Evolution of Cooperation

Direct Reciprocity

Trivers 1971:

Cooperation between unrelated individuals: **Reciprocal Altruism**

Axelrod & Hamilton 1981: Repeated Prisoner's Dilemma: "**tit-for-tat**"

Constraints:

$$T > R > P > S$$

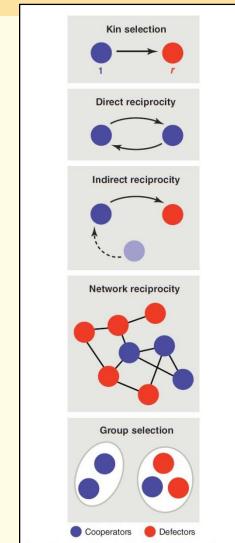
$$R > (T+S)/2$$

(this avoids a strategy of "cooperating" by alternating cycles of $T+S$)

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

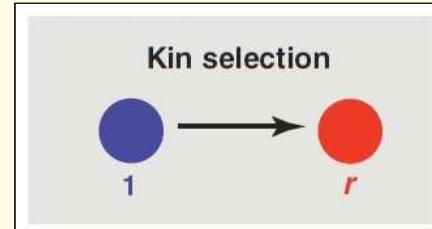
Nowak 2006 Five Rules for the Evolution of Cooperation

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



Nowak 2006 Five Rules for the Evolution of Cooperation

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Nowak 2006 Five Rules for the Evolution of Cooperation

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- Group selection

Direct reciprocity



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*).

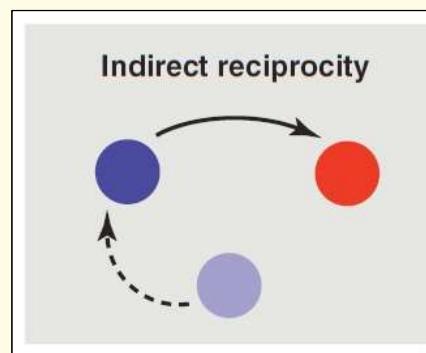
Win-stay, lose-shift ("Pavlov" strategy) : repeating your previous move whenever you are doing well, but changing otherwise. Tit-for-tat is an efficient catalyst of cooperation in a society where nearly everybody is a defector, but once cooperation is established, win-stay, lose-shift is better able to maintain it. [Nowak & Sigmund 1993].

Nowak 2006: 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.



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.**

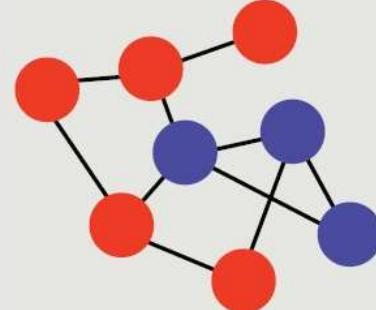
Nowak 2006: Indirect reciprocity can only promote cooperation if the probability, ***q***, of knowing someone's reputation exceeds the cost-to-benefit ratio of the altruistic act:

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

Nowak 2006
Five Rules for the Evolution of Cooperation

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

Network reciprocity



The Evolution of Cooperation

Network Reciprocity

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

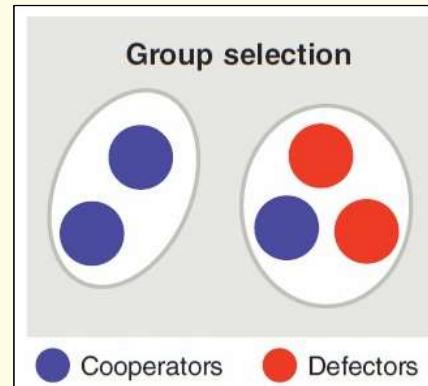
Cooperators can prevail by forming network clusters.

Nowak 2006: 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**



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.

Nowak 2006: 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.

Non-human primates:

Cooperative use of tools in the laboratory

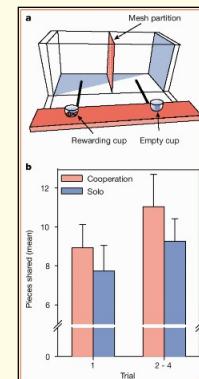
Chimpanzees (*Pan troglodytes*) Savage-Rumbaugh et al 1978

Baboons (*Papio hamadryas*) Beck 1973

Capuchin monkeys (*Sapajus*) de Waal 2000



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

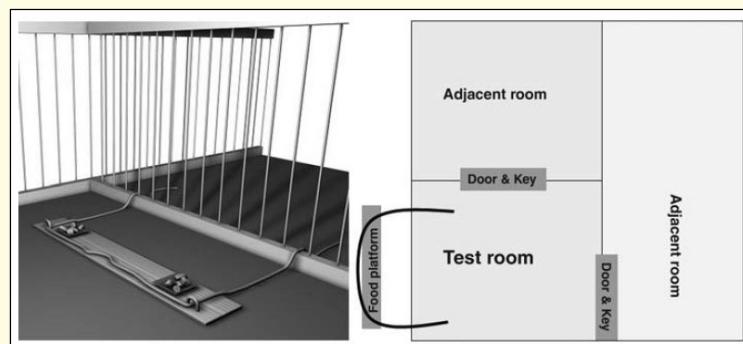


de Waal (2000)

Melis, Hare & Tomasello 2006

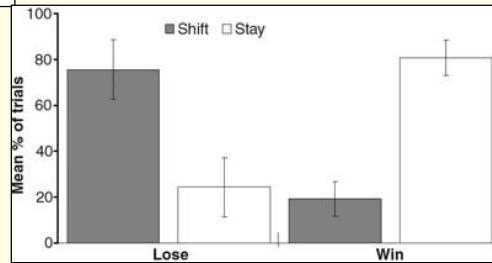
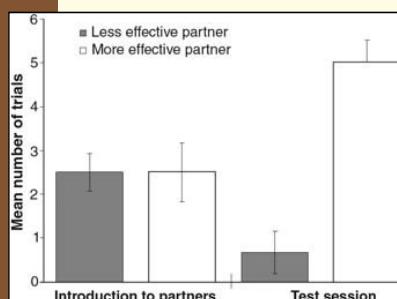
Chimpanzees recruit the best collaborators

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



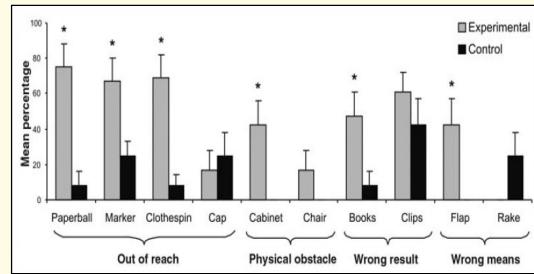
Warneken & Tomasello 2006 Altruistic helping in human infants and young chimpanzees

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.

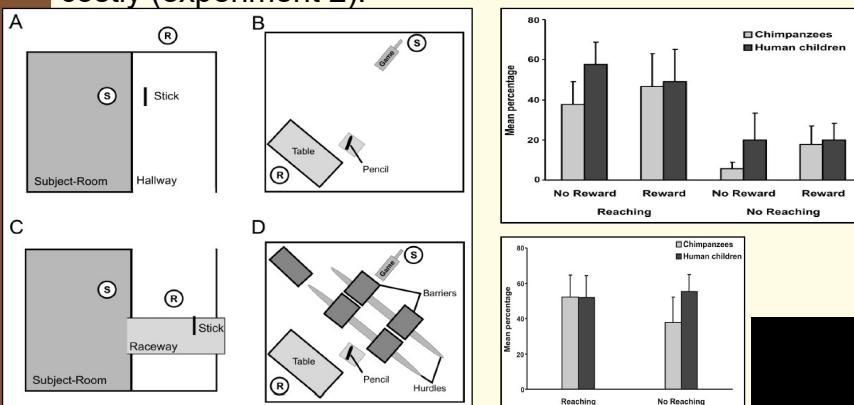
Similar though less robust skills and motivations in three young chimpanzees (for reaching tasks only).

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).



Warneken et al 2007

Spontaneous altruism by chimpanzees and young children

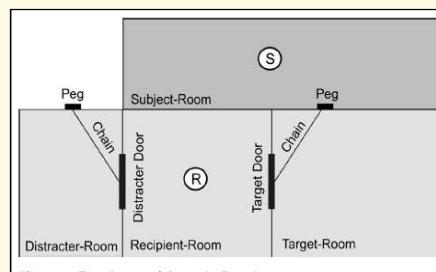
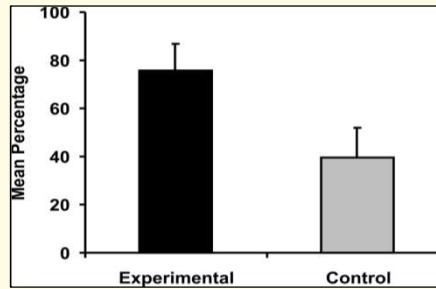


Figure 4. Test Area and Setup in Experiment 3

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.



Cooperation: Social games

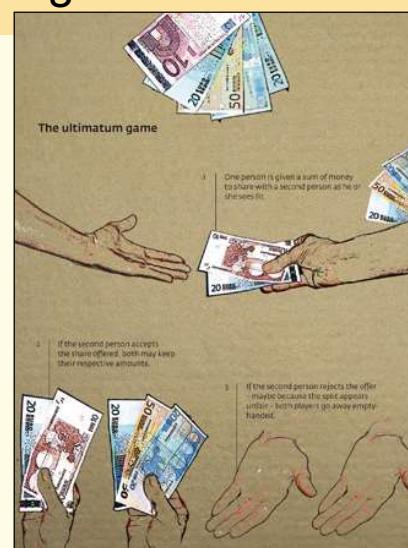
Prisoner's Dilemma

“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. 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)].

Game	Proposer Offers	Payoffs	Responder Rejections
5/5	39 (75%) 13 (25%)	8 (1) 5 (1)	2 (5%) 0 (0%)
2/8	45 (87%) 7 (13%)	8 (1) 2 (1)	3 (7%) 0 (0%)
8/2	53 (100%)	8 (1) 8 (1)	6 (11%)
10/0	29 (54%) 25 (46%)	8 (1) 10 (1)	4 (14%) 11 (44%)

Jensen et al (2007)

Cooperation in chimpanzees?

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 (5). 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.

(BUT: no refusals by the respondents)

Chimpanzees return favors at a personal cost

Schmelz et al. 2017

Chimpanzees are willing to incur a material cost to themselves to deliver a material reward to a conspecific, but they do this only if that conspecific previously incurred a risk to assist them.

Exp.1: Partner's "risky assistance" x No assistance.

Exp.2: Prosocial option costly to subject.

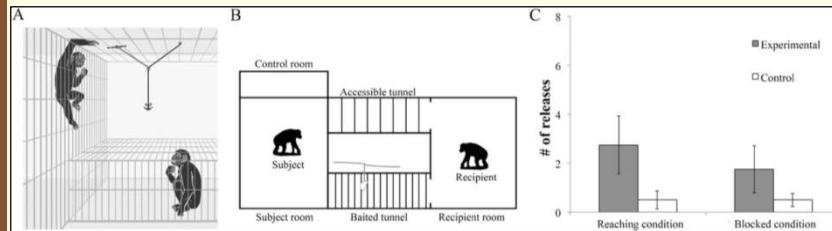
Exp.3: Non-Risky Assistance Condition: no food in option A.

Experiment/Condition	Option	Subject's payoff	Partner's payoff
Experiment 1	A	•	•
	B	••	••
	C	•••	•••
Experiment 2	A	••••	••••
	B	•••••	•••••
	C	••••••	••••••
Experiment 3 RA and NA	A	••	••
	B	•••	•••
	C	••••	••••
Experiment 3 NRA	A	••	••
	B	•••	•••
	C	••••	••••

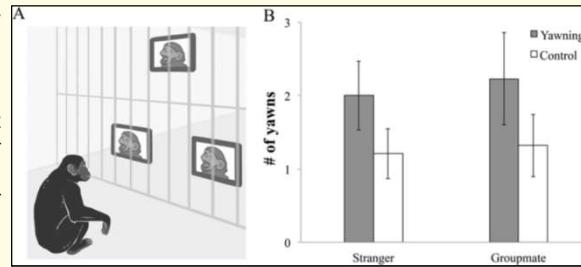
Dots represent pieces of food.

Cooperation (& xenophilia*) in bonobos

Tan, Ariely & Hare 2017



Bonobos voluntarily aided an unfamiliar, non-group member in obtaining food even when he/she did not make overt requests for help. Bonobos also showed evidence for involuntary, contagious yawning in response to videos of yawning conspecifics who were complete strangers.



(* prosociality toward unfamiliar people)

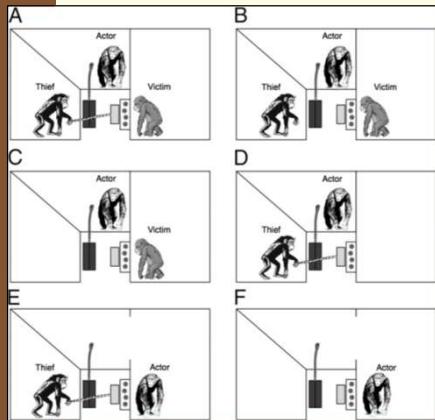
Riedl, Jensen, Call & Tomasello 2012 No third-party punishment in chimpanzees

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.**

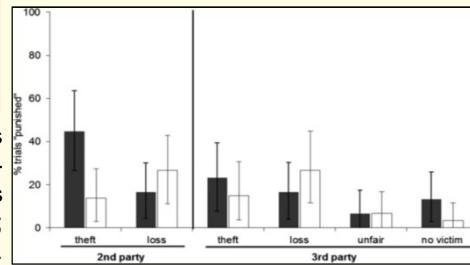
Riedl, Jensen, Call & Tomasello 2012 No third-party punishment in chimpanzees



(A) third-party theft (thief could pull food tray away from victim), (B) third-party unfair (experimenter moved food tray away from victim and toward thief), (C) third-party loss (experimenter moved food tray from victim to empty cage), and (D) third-party no-victim (thief could pull food tray away from empty victim's cage).

Second-party conditions: the victim could enter the actor's cage: (E) second-party theft (thief could pull food tray away from the actor) and (F) second-party loss (experimenter moved food tray away from actor to the empty thief's cage).

Relative frequency of actors collapsing the trapdoor in second-party and third-party conditions (dominants to the thief, solid bars; subordinates, open bars).



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**.

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. Coordinated punishment can proliferate when rare, and when it does, it enhances group-average payoffs.

Cooperation and Punishment
reducing the costs of punishment

Institutional punishment (law enforcement)



Imaginary punishment (religion)



Innate or learned internalized punishment (moral emotions)



Prosociality and punitive gods

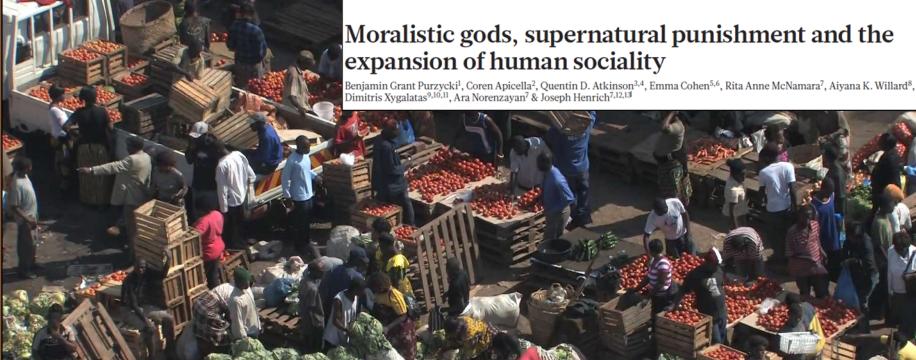
Purzycki & al 2016

LETTER

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Moralistic gods, supernatural punishment and the expansion of human sociality

Benjamin Grant Purzycki¹, Coren Apicella², Quentin D. Atkinson^{3,4}, Emma Cohen^{5,6}, Rita Anne McNamara⁷, Aiyana K. Willard⁸, Dimitris Xygalatas^{9,10,11}, Ara Norenzayan⁷ & Joseph Henrich^{7,12,13}



Since the **origins of agriculture**, the scale of human cooperation and societal complexity has dramatically expanded. This fact challenges standard evolutionary explanations of prosociality because well-studied mechanisms of cooperation based on genetic relatedness, reciprocity and partner choice falter as people increasingly engage in **fleeting transactions** with **genetically unrelated strangers** in large anonymous groups.

Prosociality and punitive gods
Purzycki & al 2016

LETTER

Moralistic gods, supernatural punishment and the expansion of human sociality

Hypothesis:
cognitive representations of gods as increasingly knowledgeable and punitive, and who sanction violators of interpersonal social norms, foster and sustain the expansion of cooperation, trust and fairness towards co-religionist strangers.

Table 1 | Site descriptive statistics

Site	Researcher	Economy	Moralistic god	Local god or spirit	n	Females	Age	Material insecurity
Coastal Tanna ⁵	Atkinson	Horticulture	Christian god	Garden spirit (<i>Tupunus</i>)	44	23	35.02 (14.13)	0.22 (0.36)
Hadza	Apicella	Hunting	Celestial figure (<i>Haire</i>) ⁶	Sun (<i>Ishoko</i>) ⁶	68	31	39.82 (12.08)	0.82 ⁷ (0.36)
Inland Tanna ⁸	Atkinson	Horticulture	Kalapan (traditional)	Garden spirit (<i>Tupunus</i>)	76	38	37.00 (16.17)	0.26 (0.38)
Lovi	Willard	Wage labour	Hindu Bhagwan	None available	76	52	44.56 (16.94)	0.83 (0.33)
Mauritius	Xygalatas	Wage labour and farming	Hindu Shiva	Spirit/soul/ghost (<i>Nam</i>)	94	27	36.56 (15.05)	0.39 (0.35)
Pesqueiro	Cohen	Wage labour	Christian god	Virgin Mary	77	40	34.12 (13.08)	0.86 (0.24)
Tyva Republic	Purzycki	Wage labour and herding	Budha Burgan	Spirit-masters (<i>Cher eezi</i>)	81	58	33.53 (12.52)	0.47 (0.28)
Yasawa	McNamara	Fishing and farming	Christian god	Ancestor spirits (<i>Kalou-vu</i>)	75	41	38.04 (15.91)	0.50 (0.40)
				Grand mean	73.88	—	37.34	0.55

Means indicated (standard deviations in parentheses). See Extended Data Fig. 1 for a map of field sites.
§One individual was removed from the local co-religionist game due to coin visibility.
#These two gods closely overlap in conception.
‡Answer options were “Yes”, “no” or “I don’t know”.

Ethnographic interviews to identify the most moralistic deities. We verified the degree to which gods care about morality with a free-list task asking about gods' concerns and scales created to measure **how important participants claim punishing theft, murder and deceit are to these supernatural beings**.

Prosociality and punitive gods
Purzycki & al 2016

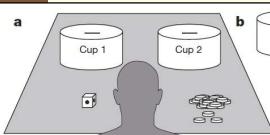
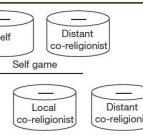
a 
b 

Figure 1 | The random allocation game. a, b, Generic game setup (a) and variants used in present work (b).

Participants play in private with 30 coins, two cups and a fair die with three sides of one colour and three sides of another colour. Their job is to allocate each coin to one of the two cups. First, they mentally choose one of the cups and then roll the die. If one coloured side comes up > put the coin into the cup they mentally chose. If the die comes up the other colour > put the coin into the opposite cup from the one they chose. As cup selection occurs only mentally, participants can overrule the die in favour of one of the cups without anyone else observing their decision. If people play by the rules and thereby allocate the coins impartially, the mean number of coins in each cup should be 15, and the distribution around this average will be binomial.

Figure 2 | Allocations to distant co-religionists increase as a function of moralistic gods' punishment. Punishment indices are mean values of a two-item scale (see Supplementary Information section S2.3.2). Error bars represent bootstrapped (1,000 replications) 95% confidence intervals of the mean. Histogram labels are sample sizes per category. Note that among the 32 individuals who responded “I don't know” to the questions pertaining to moralistic gods' punishment, 17 were Hadza and 15 were inland Tannese.

Self game: Self x Distant Co-religionist
LC game: Local x Distant Co-religionists

“Beliefs in moralistic, punitive and knowing gods increase impartial behaviour towards distant co-religionists, and therefore can contribute to the expansion of prosociality.”

Genetic X Cultural Group Selection



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.

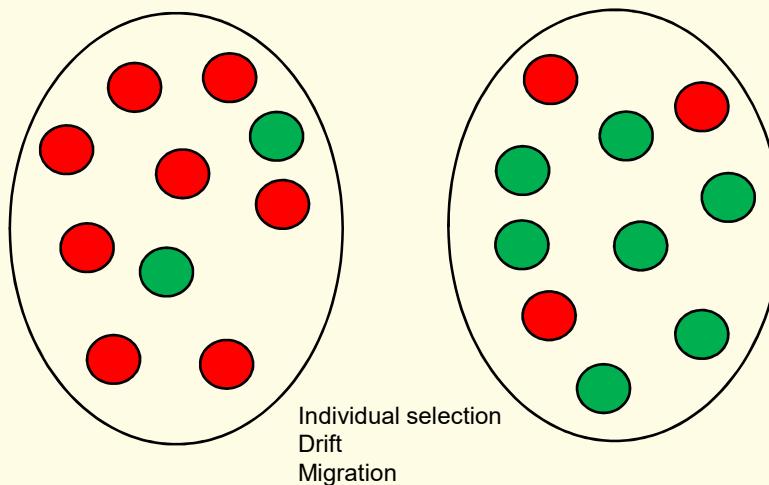
Cultural Group Selection

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.

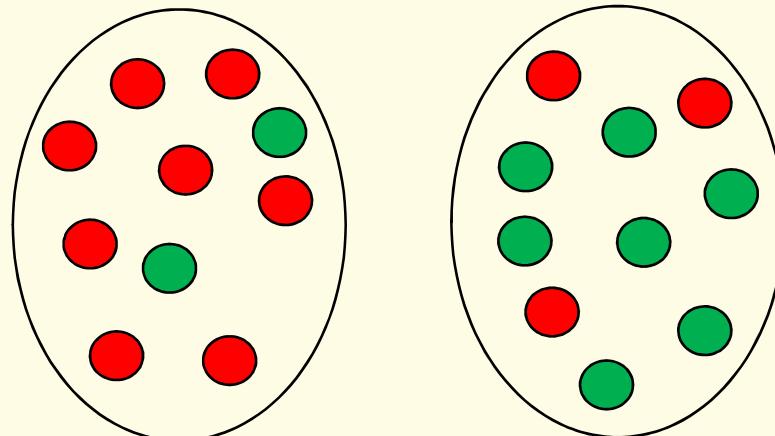
Genetic X Cultural Group Selection

Genetic variation within/between groups



Genetic X Cultural Group Selection

Cultural variation within/between groups

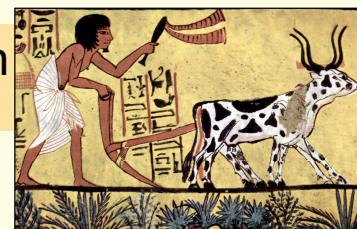


Conformist transmission

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 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.

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.

Modelling 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 evolution by cultural group selection

Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

Group selection works by eliminating those societies that have deleterious practices or institutions. If it takes a particular number of extinctions to eliminate a deleterious ritual form, then it will take a greater number to eliminate the deleterious ritual form and a deleterious marriage practice. Still further extinctions will be required to cause other aspects of the society to become adaptive.

Hallpike (1986) argues that **human societies do not have high enough extinction rates for group selection to cause many different attributes to be adaptive at the group level simultaneously**.

Cultural evolution by cultural group selection

Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

Here we describe a theoretical model and present supporting data which show that a role for cultural group selection should not be ruled out. Boyd and Richerson (1985, 1990) have analyzed mathematical models of group selection acting on culturally transmitted variation and have shown that **cultural group selection will work if certain key assumptions are met.**

Ethnographic data from Papua New Guinea and Irian Jaya give credence to some of the assumptions that underpin the group-selection model. These data also allow us to **estimate an upper bound on the rate of adaptation that could result from group selection.** We argue that these data suggest that **group selection is too slow to be used to justify the common practice of interpreting as group-beneficial the detailed aspects of particular cultures.** However, the data do not exclude the possibility that **group selection may account for the gradual evolution of some group-level adaptations, such as complex social institutions,** over many millennia.

Cultural evolution by cultural group selection

Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

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

Empirical Evidence:
Ethnographic literature of Irian Jaya
and Papua New Guinea



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.

Table 11.3. Minimum number of generations necessary to change the fraction of groups in which a favorable trait is common assuming a particular extinction rate

Initial fraction favorable trait	Final fraction favorable trait	1.6%	10.4%	17.9%	31%
0.1	0.9	192	40.0	22.3	11.8
0.01	0.99	570	83.7	46.6	24.8

Note: Extinction rates were chosen as follows: 1.6 percent (for the Maring) is the lowest estimate, 10.4 percent is the median extinction rate, 17.9 percent (for the Mae Enga) is the estimate based on the best data, and 31 percent (for the Fore/Usufura) is the highest estimate.

Such an estimate suggests that **group selection is unlikely to lead to significant cultural change in less than 500 to 1000 years.**

Cultural Group Selection

Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

The arrival of the sweet potato to in the highlands of New Guinea (...) in the XVIII century led to many important cultural changes. The introduction of the horse to the Great Plains of N. America led to the evolution of the culture complex of the Plain Indians in less than 300 years. 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 cultural 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 1000 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

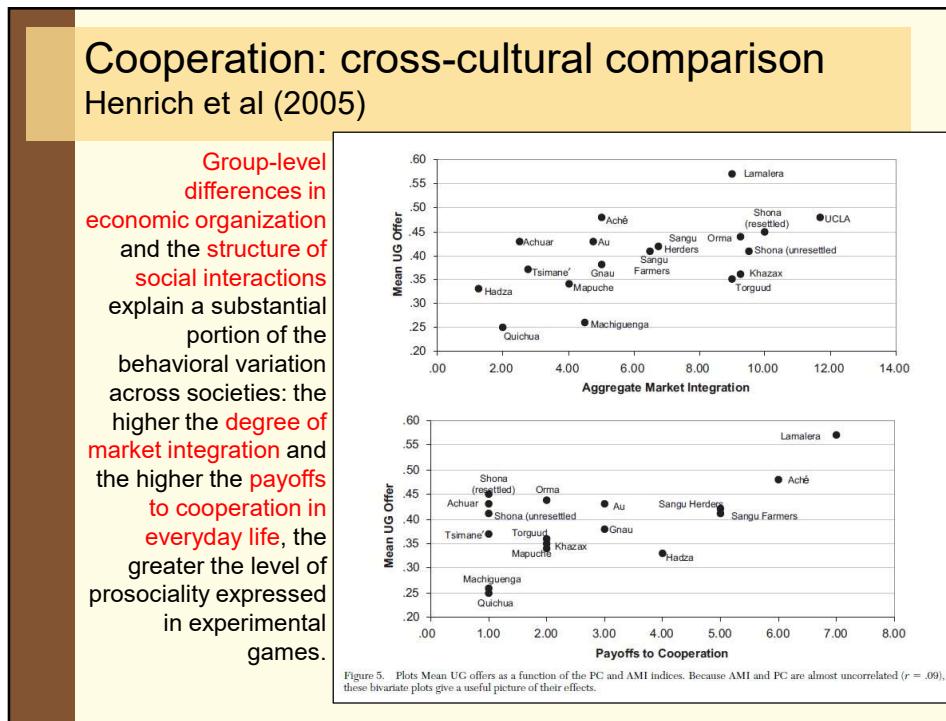
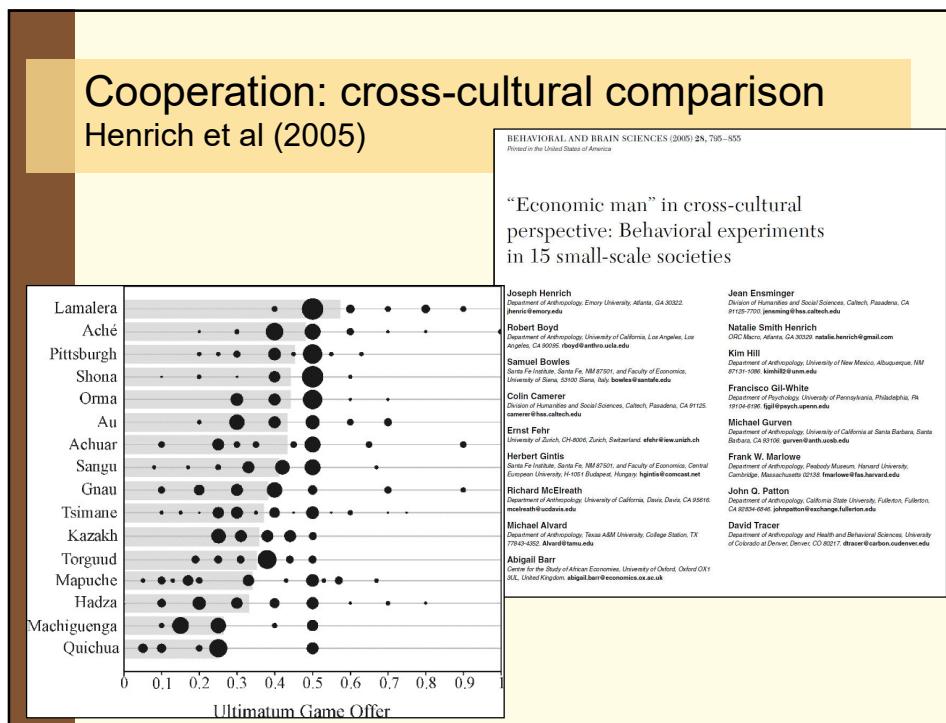
Soltis, Boyd & Richerson 1995 / Boyd & Richerson 2005

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 Niche Construction and Cooperation





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**.

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

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

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 favored 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 **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 favored 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.

“Moral Emotions”, Evolutionary Psychology and Gene-Culture Coevolution: convergences



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 it is correct to obey to legitimate authority and respect individuals in high positions.
- Exaltation of purity, cleanliness and sanity, contempt for decay, for contamination and for carnality.

J. Haidt: five “themes”:

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

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

A sense of “fairness” in non-human primates?

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

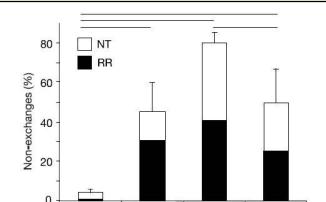
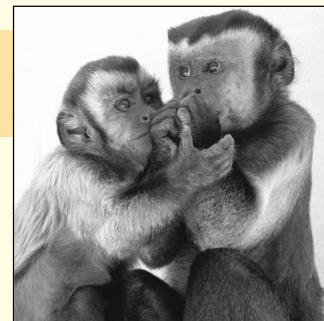


Figure 1 Mean percentage \pm s.e.m. of failures to exchange for females across the four test types. Black bars (RR) represent the proportion of non-exchanges due to refusals to accept the reward; white bars (NT) represent those due to refusals to return the token. s.e.m. is for combined non-exchanges.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

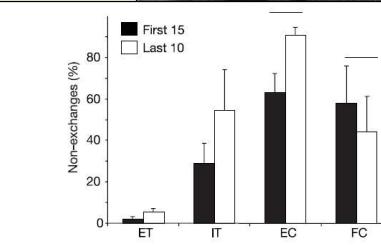


Figure 2 Mean percentage \pm s.e.m. of failures to exchange in the first 15 trials (black bars) versus the last 10 trials per test (white bars). Lines indicate differences at $P = 0.06$ (exact Wilcoxon signed ranks test). ET, equality test; IT, inequality test; EC, effort control; FC, food control.

Brosnan & de Waal (2003)

X Henrich (2004): humans will not reject unless this affects the other's pay-off

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”

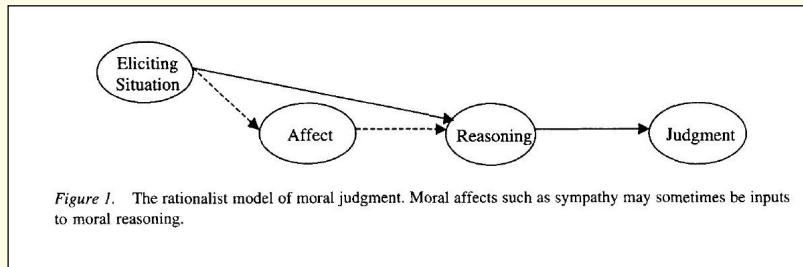
Julie and Mark are brother and sister. They are traveling together in France on summer vacation from college. One night they are staying alone in a cabin near the beach. They decide that it would be interesting and fun if they tried making love. At the very least it would be a new experience for each 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:

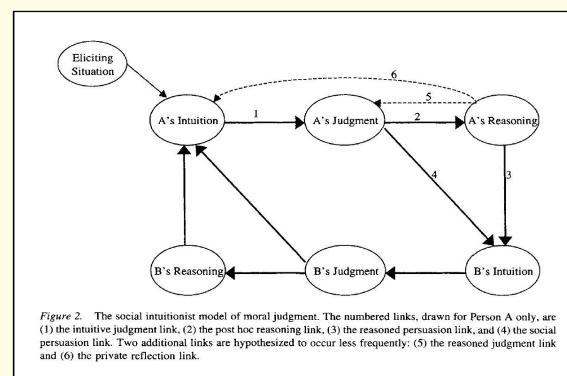


A Social-Intuitionist approach to Moral Judgement

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 encultured**".

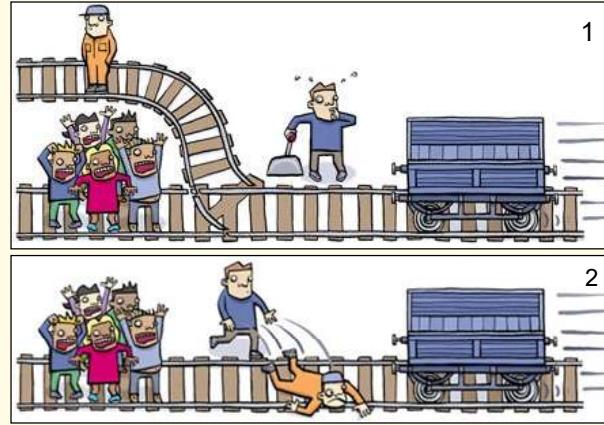
The "Social-Intuitionist" Model:



Moral emotions: Utilitarianism and the “Trolley Problem”

Phillipa Foot (1967)

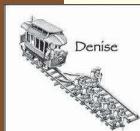
The “double effect” principle: Planned/instrumental harm
X predicted collateral consequence



“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 is 1 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.

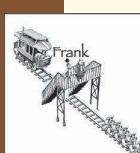
Is it morally permissible for Denise to turn the train?

89%

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.

2

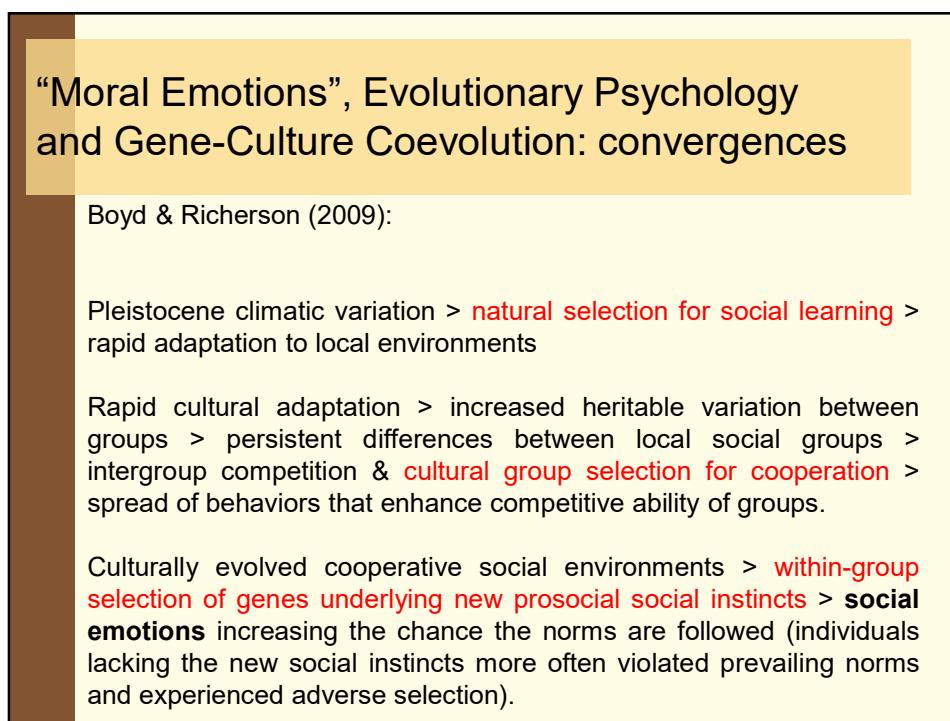
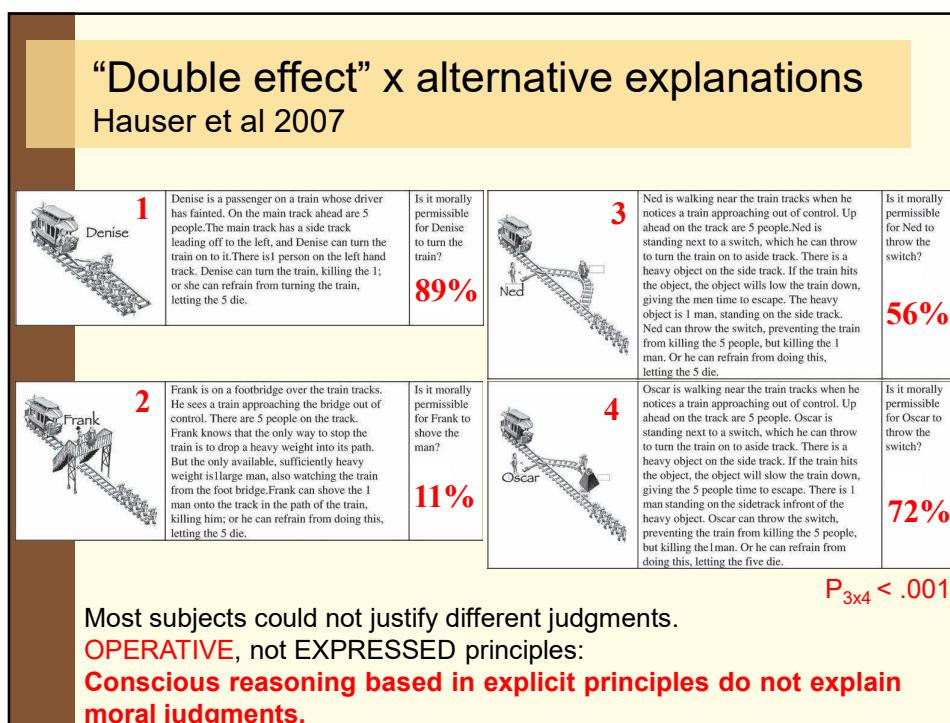


Frank is on a footbridge over the train tracks. He sees a train approaching the bridge out of control. There are 5 people on the track. Frank knows that the only way to stop the train is to drop a heavy weight into its path. But the only available, sufficiently heavy weight is large man, also watching 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%

$P_{1x2} < .001$



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 a strict analogy between genes and “memes” and pay the due attention to the underlying psychological and social processes.

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

Final considerations: On Darwinian Models of Cultural Evolution

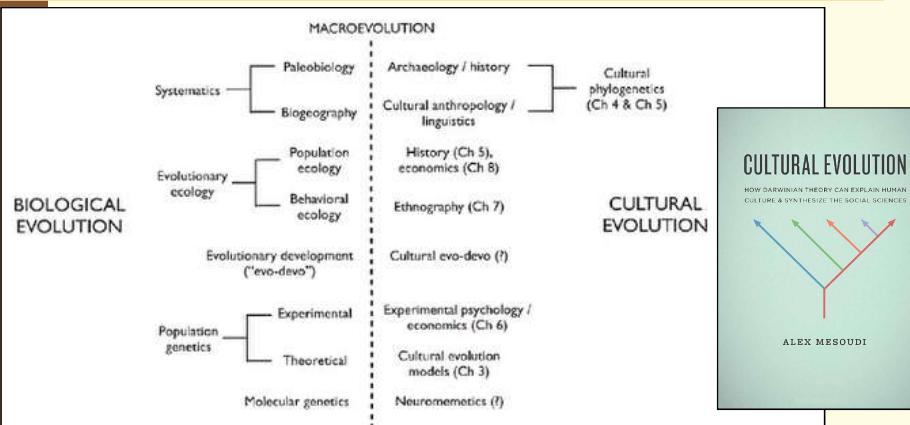
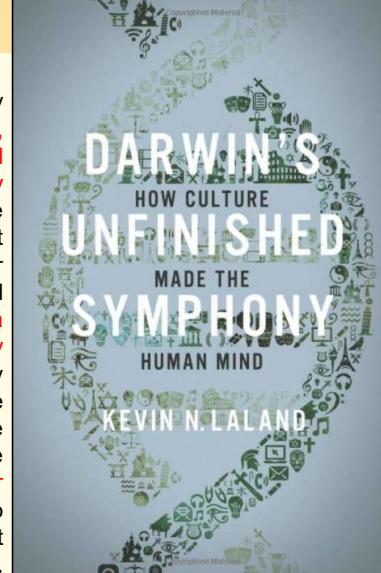


FIGURE 10.1 The structure of a potential science of cultural evolution (righthand side), as mapped on to the existing structure of evolutionary biology (lefthand side).

Mesoudi 2011

Laland (2017)

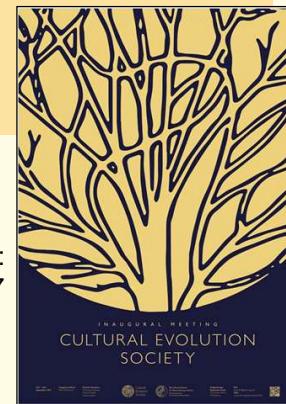
"All species are unique, but we are uniquely unique. To account for the rise of our species, we must recognize what is genuinely special about us, and explain it using evolutionary principles. Doing so requires analysis of the evolution of culture, because it turns out that culture is far more than just another component, or an outgrowth, of human mental abilities. Human culture is not just a magnificent end product of the evolutionary process (...) The learned and socially transmitted activities of our ancestors, far more than climate, predators, or disease, created the conditions under which our intelligence evolved. Human minds are not just built for culture; they are built by culture. In order to understand the evolution of cognition, we must first comprehend the evolution of culture, because for our ancestors and perhaps our ancestors alone, culture transformed the evolutionary process".



Cultural Evolution Society

<https://culturalevolutionsociety.org/>

CES Inaugural Meeting:
Jena, Germany, September 2017



<https://www.eiseverywhere.com/ehome/ces18>

