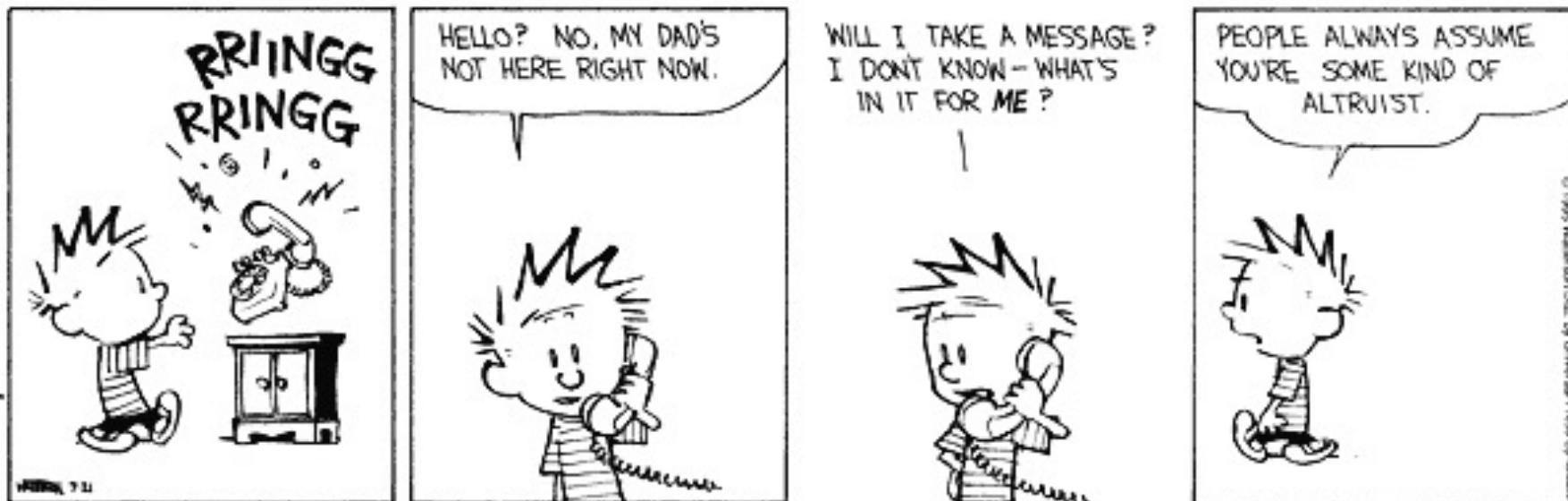


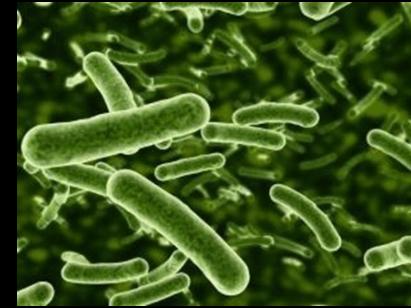
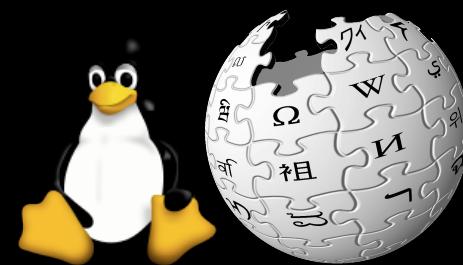


# The Calculus of Selfishness (cont.)





# cooperation at all scales



# Prisoner's dilemma or the *cost-benefit* dilemma

**Donor**

*Pays a cost  $c$*

**Receiver**

*Receives a benefit  $b > c$*

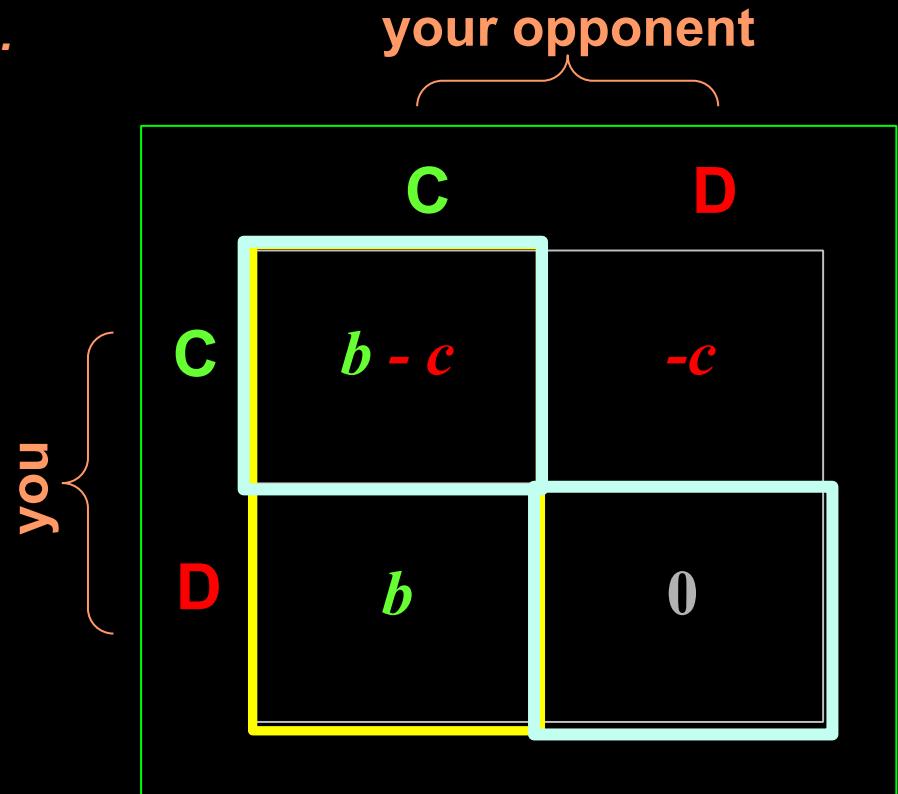
*If both play as a donor and as a receiver...*

**"RATIONAL" GOAL :**  
maximize your own payoff !

if your opponent plays C :  
you better play D.

if your opponent plays D :  
you better play D.

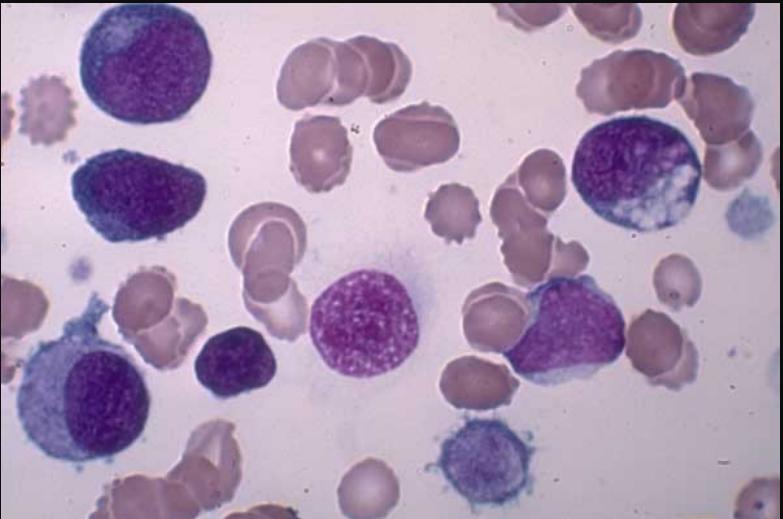
**BUT:**  
**CC** is better than **DD**.



**Dilemma :** despite mutual cooperation (CC) being better than mutual defection (DD), individual "rational choice" leads to DD

# evolutionary game theory

payoff → fitness → social success



genetic evolution



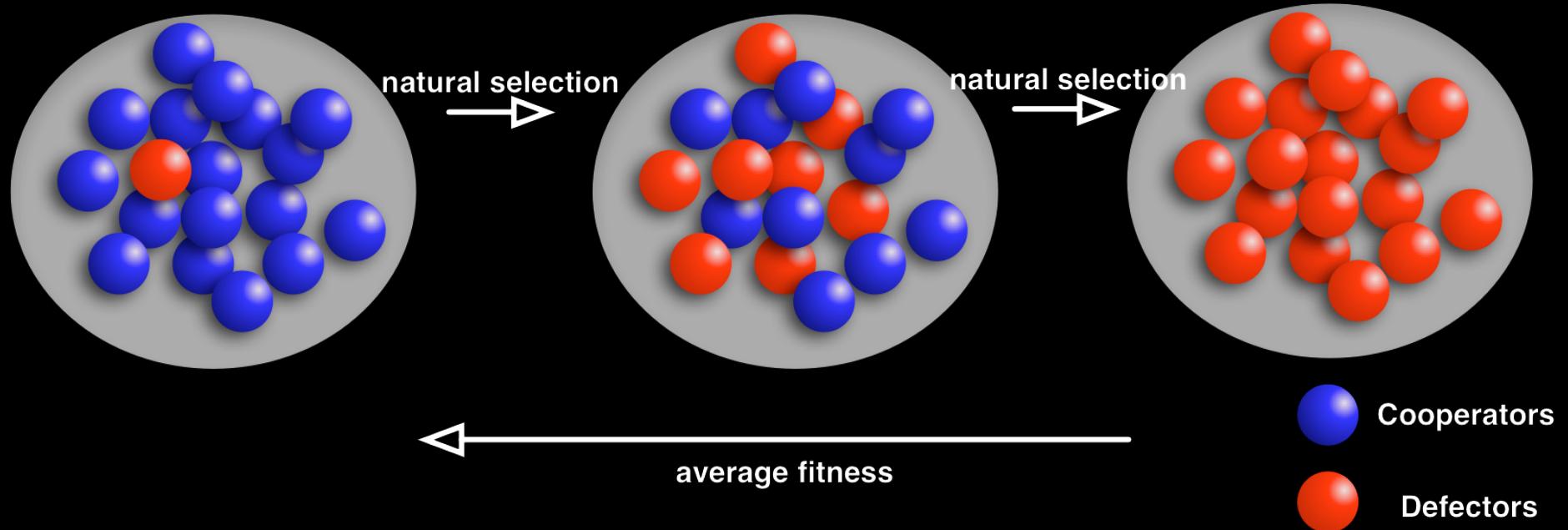
social/cultural evolution

**Individuals with higher fitness will *reproduce more***

**Or their behavior will be *imitated* more often  
(*social learning*)**

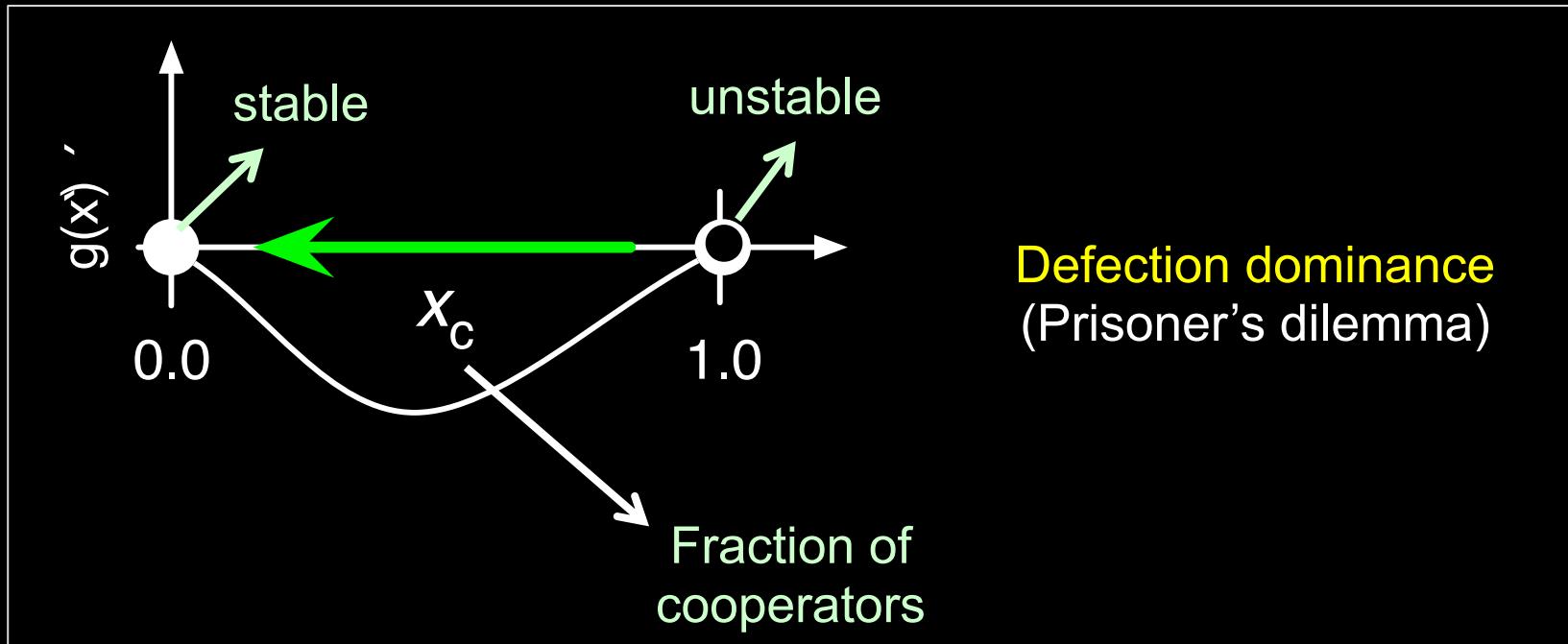
# evolutionary game theory

## cost-benefit dilemma (prisoner's dilemma)



Natural selection & self-organization  
leads to the **tragedy of the commons**

# The calculus of selfishness



Gradient of selection

$$\dot{x} = x(1-x)[f_C(x) - f_D(x)] = g(x)$$

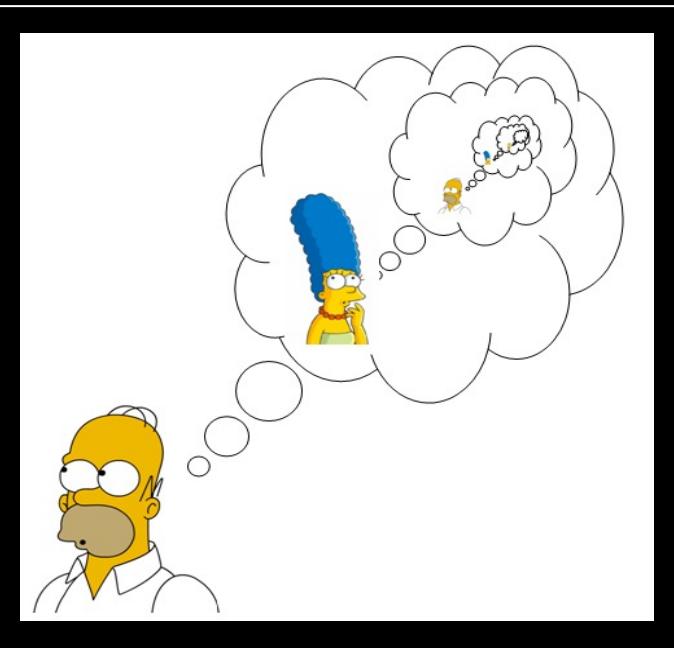
Replicator equation

# General stability concepts

## Game Theory

### Nash equilibrium

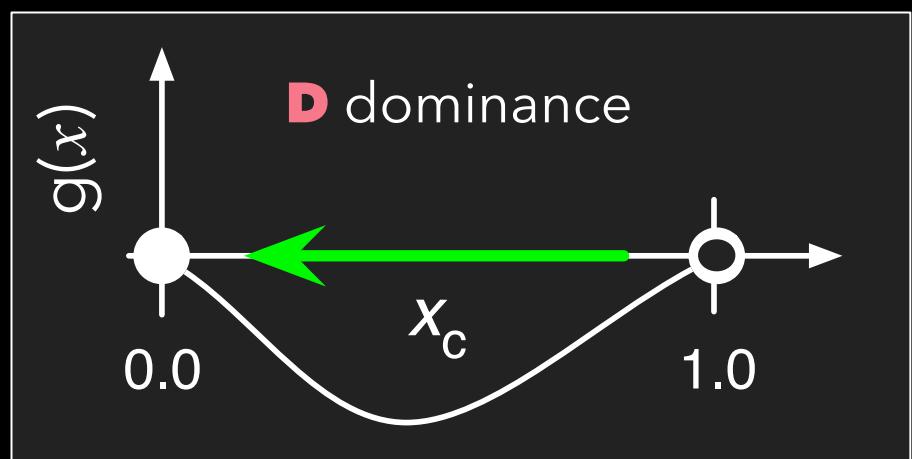
If a strategy is a Nash equilibrium, and if both players play that strategy, then neither person can deviate from that strategy and increase her payoff



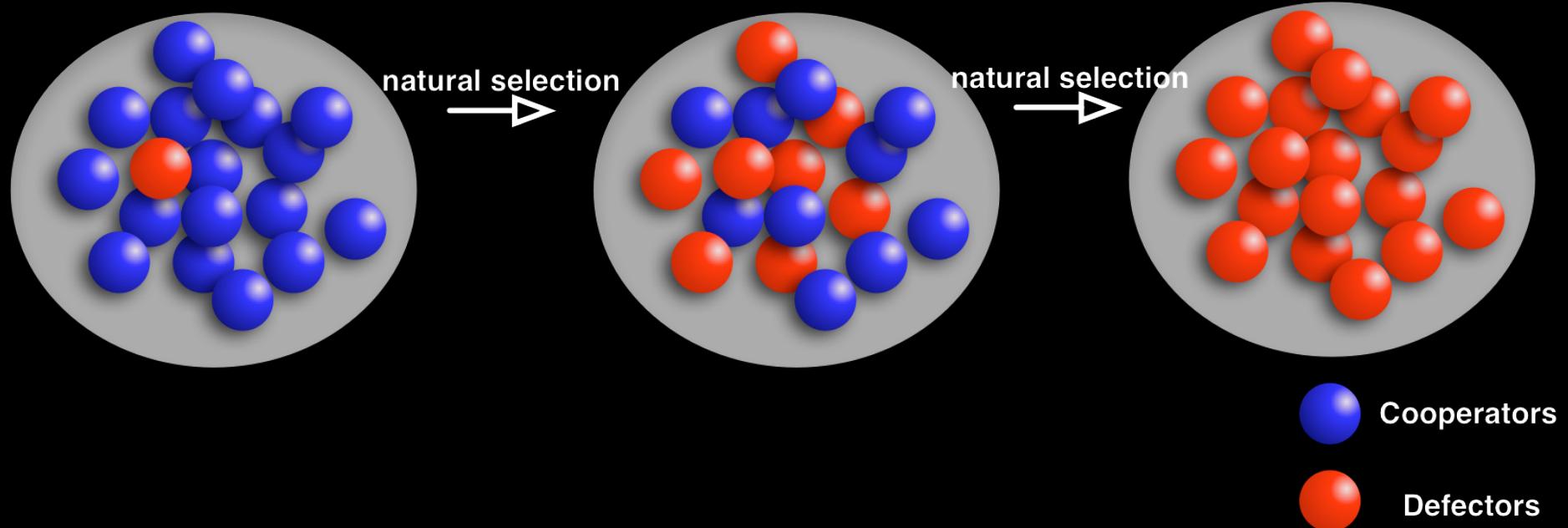
## Evolutionary Game Theory

### Evolutionarily Stable Strategy (ESS)

If a strategy is an ESS, then an infinitesimally small amount of players of the other strategy will never be able to invade (spread over the entire population)



# Dealing with an apparent paradox



but... cooperation surrounds us!!

What are we missing here ?

# mechanisms of cooperation

kin selection (Hamilton's rule)

multi-level selection (a.k.a., group selection)

direct reciprocity

indirect reciprocity

signaling & quorum sensing

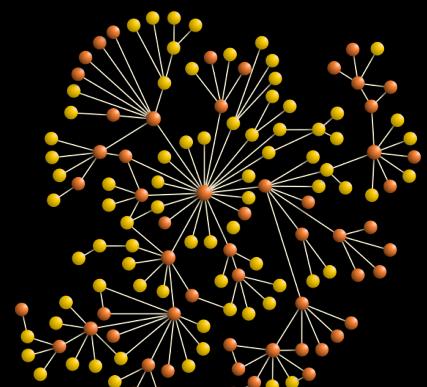
networked populations

commitments

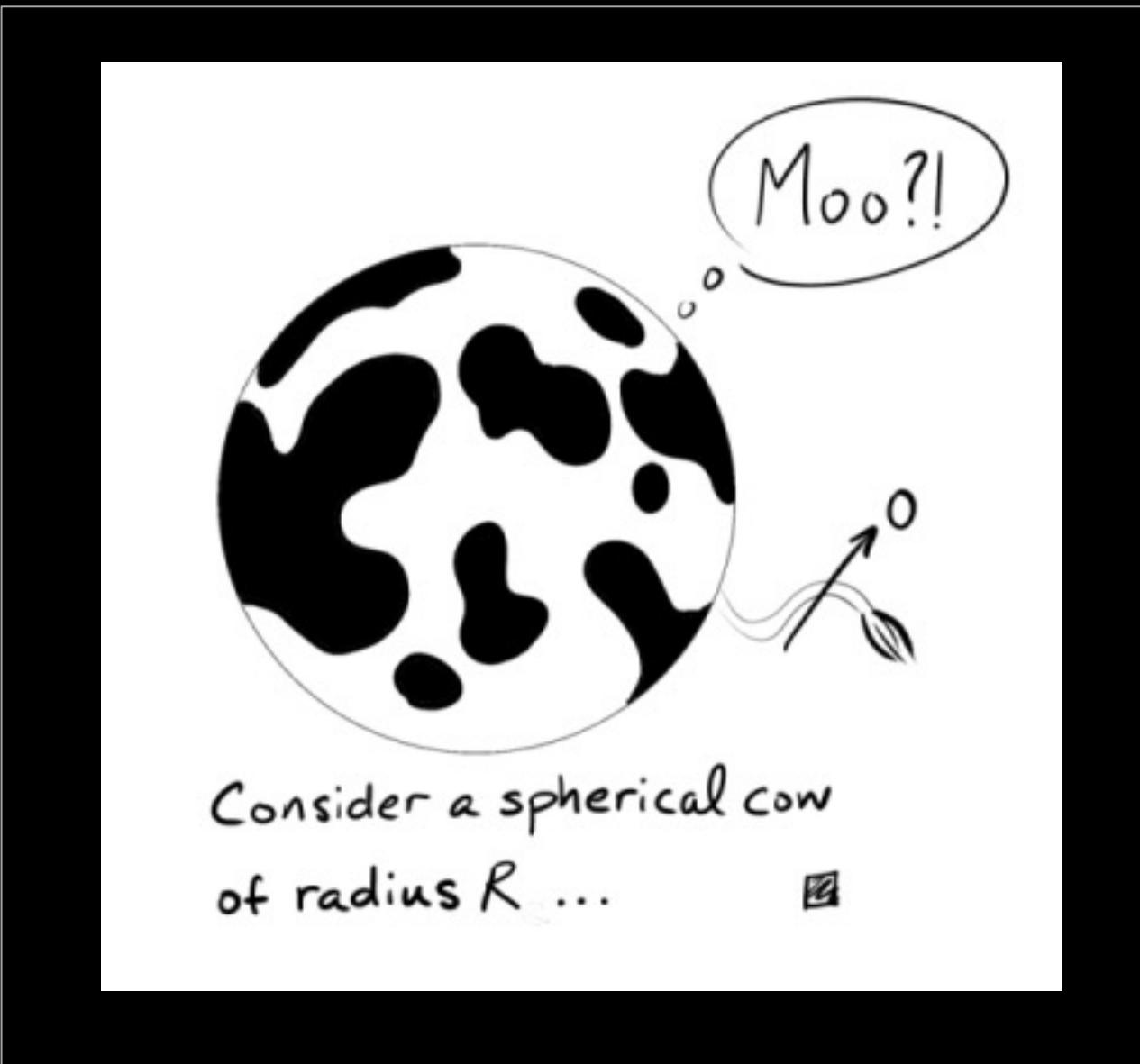
institutions, sanctions and rewards

social diversity

(...)



# The beauty of modelling core principles

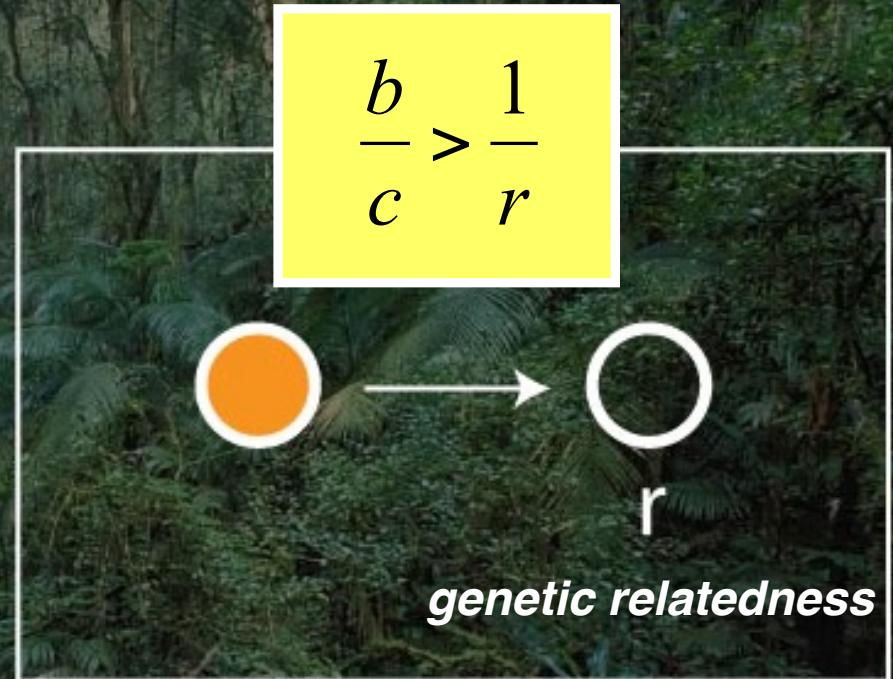
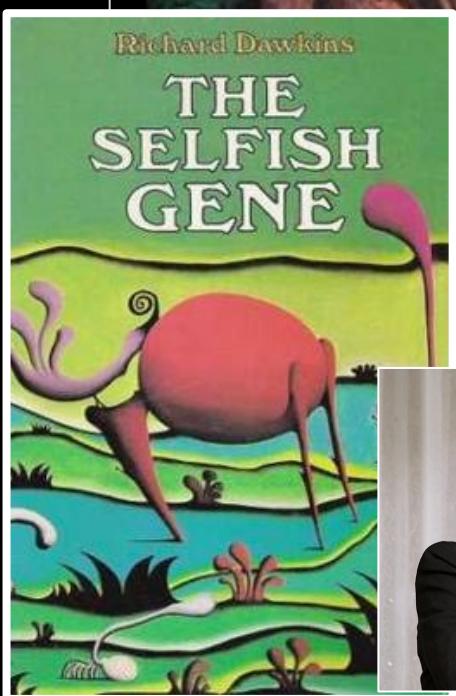


# Ways out of the dilemma

*all in the family . . .*

WD Hamilton, JTB (1964)  
G. Price, J Maynard-Smith, etc.

the more individuals are related, the more cooperation is feasible



The Genetical Evolution of Social Behaviour.

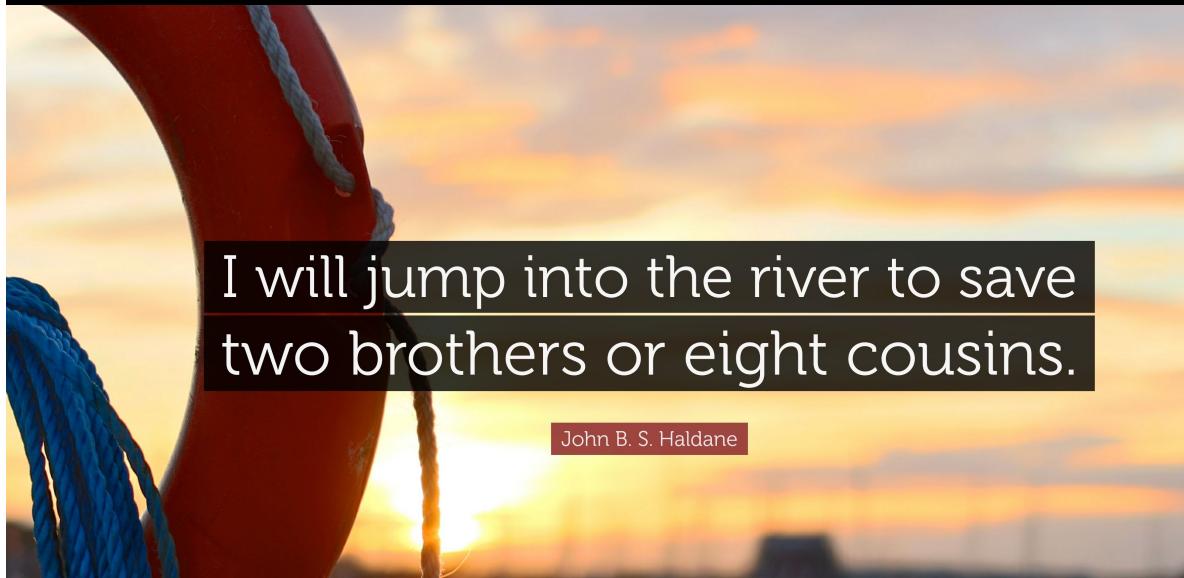
W. D. HAMILTON

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

*J. Theoret. Biol.* (1964)

# Ways out of the dilemma

*all in the family . . .*



I will jump into the river to save  
two brothers or eight cousins.

John B. S. Haldane



John B. S. Haldane (1892-1964)  
Evolutionary / Mathematical Biologist

# Kin selection

*all in the family . . .*

the more individuals *are related*, the more cooperation is feasible. **How ?**

*r* : (genetic) relatedness between individuals → *your action means r to me; hence, I also get r of what you get*; then

$$\begin{bmatrix} C & D \\ D & 0 \end{bmatrix} \quad \begin{bmatrix} C & -c + br \\ b - cr & 0 \end{bmatrix}$$

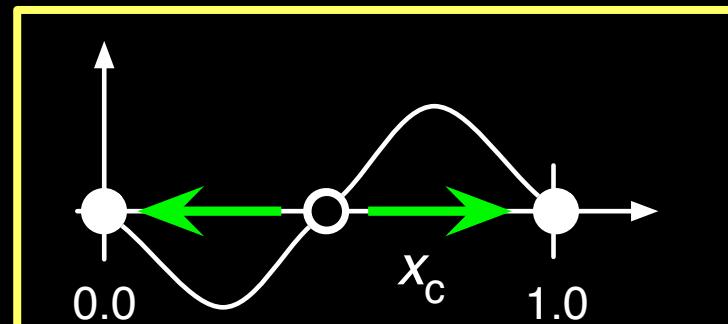
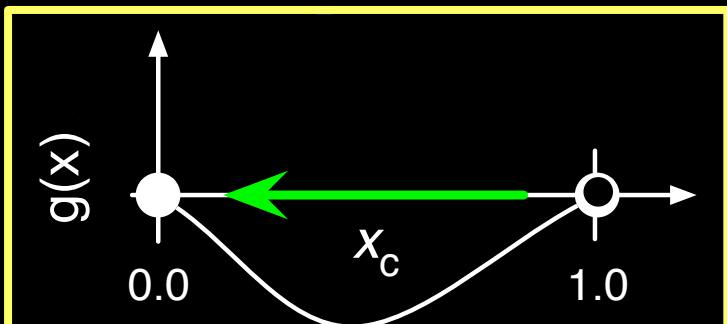
The matrix on the left is the payoff matrix for two individuals. The matrix on the right shows the effect of relatedness *r*. The diagonal elements are unchanged (C and 0). The off-diagonal elements are modified: the payoff to C from D is now  $(b - c)(1 + r)$ , and the payoff to D from C is now  $-c + br$ .

**ESS condition :**

$$\frac{b}{c} > \frac{1}{r}$$

this is the famous **Hamilton's rule of kin-selection**

[W. D. Hamilton, J. Theor. Biol. 7, 1 (1964)]



# Ways out of the dilemma

*pick the right team...*

*Wynne-Edwards (1962),  
DS Wilson & EO Wilson, Am Sci (2008)  
Traulsen & Nowak, PNAS (2006), etc.*

Cooperative groups tend to be more successful than groups of defectors



# Multi-level selection

*pick the right team...*



**Even if the unity of selection is solely the individual, selection may occur at different levels**

- selection inside groups
- competition between groups

***Hence, if I'm a defector and cheat someone, this has a direct impact on my own success whenever conflicts raise between groups (creating a kind of "kin" relation).***

# Multi-level selection

*pick the right team...*

## Evolution of cooperation by multilevel selection

Arne Traulsen and Martin A. Nowak\*

Program for Evolutionary Dynamics, Departments of Organismic and Evolutionary Biology and Mathematics, Harvard University, Cambridge, MA 02138

Edited by Simon A. Levin, Princeton University, Princeton, NJ, and approved May 25, 2006 (received for review March 28, 2006)

We propose a minimalist stochastic model of multilevel (or group) selection. A population is subdivided into groups. Individuals interact with other members of the group in an evolutionary game that determines their fitness. Individuals reproduce, and offspring are added to the same group. If a group reaches a certain size, it can split into two. Faster reproducing individuals lead to larger groups that split more often. In our model, higher-level selection emerges as a byproduct of individual reproduction and population structure. We derive a fundamental condition for the evolution of cooperation by group selection: if  $b/c > 1 + n/m$ , then group selection favors cooperation. The parameters  $b$  and  $c$  denote the benefit and cost of the altruistic act, whereas  $n$  and  $m$  denote the maximum group size and the number of groups. The model can be extended to more than two levels of selection and to include migration.

finite populations | prisoner's dilemma | group selection |  
fixation probability | stochastic process

Our simple model has some interesting features. Evolutionary dynamics are driven by individual individuals are assigned payoff values. Only individuals induce. Groups can stay together or split (divide) a certain size. Groups that contain fitter individuals critical size faster and, therefore, split more often leads to selection among groups, although only one group reproduces. The higher-level selection emerges from the competition between groups that split more often. Remarkably, the two levels of selection pose each other.

Any evolutionary game can be analyzed in our model. Here, we focus on the interaction between cooperators and defectors. Cooperators pay a cost,  $c$ , which ensures that they receive no benefit. Defectors benefit from the presence of cooperators in the same group. In an all-cooperator group, both cooperators and defectors have a higher payoff than cooperators in a mixed group. Defectors benefit from the presence of cooperators in the same group. In an all-defector group, defectors have a higher payoff than cooperators. This is because defectors do not pay the cost of cooperation, but still receive the benefit of cooperation.

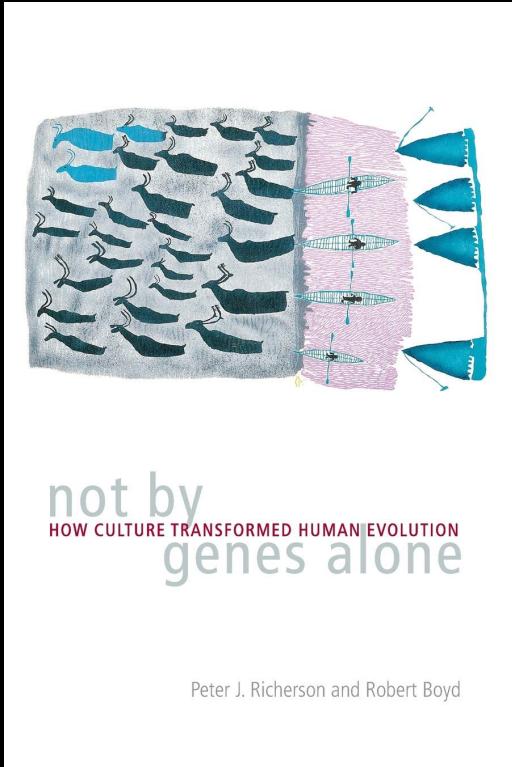
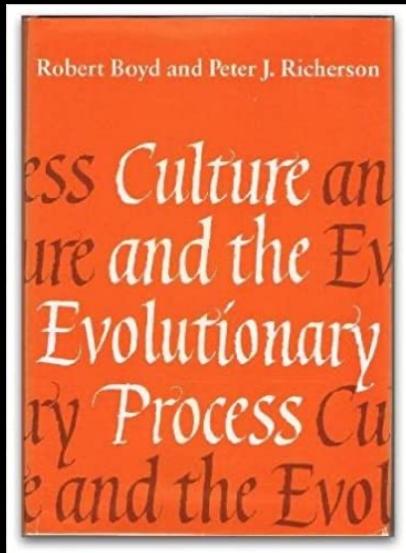
Even in  
different

- select  
- compete



**Hence, if I'm a defector and cheat someone, this has a direct impact on my own success whenever conflicts raise between groups (creating a kind of "kin" relation).**

# Gene & culture evolution



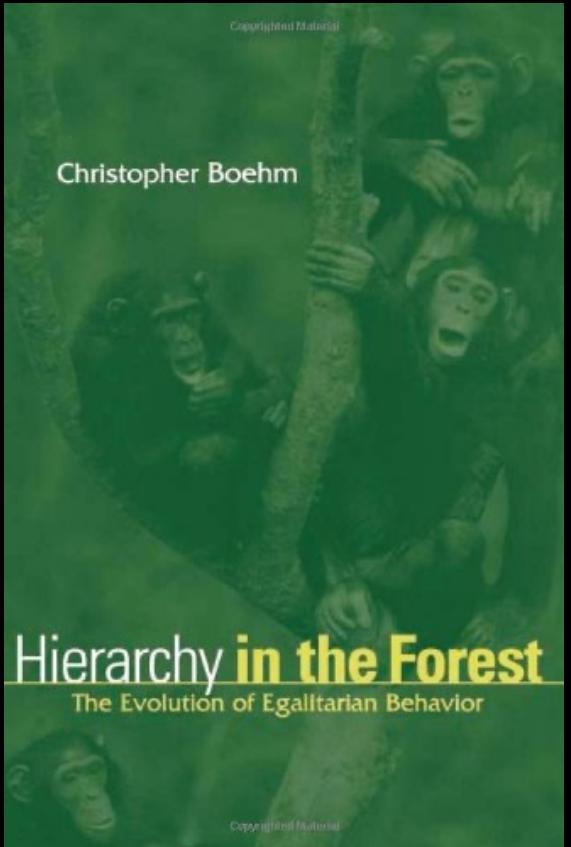
Peter J. Richerson and Robert Boyd

## A Cooperative Species

HUMAN RECIPROCITY AND ITS EVOLUTION



SAMUEL BOWLES & HERBERT GINTIS



Copyrighted Material

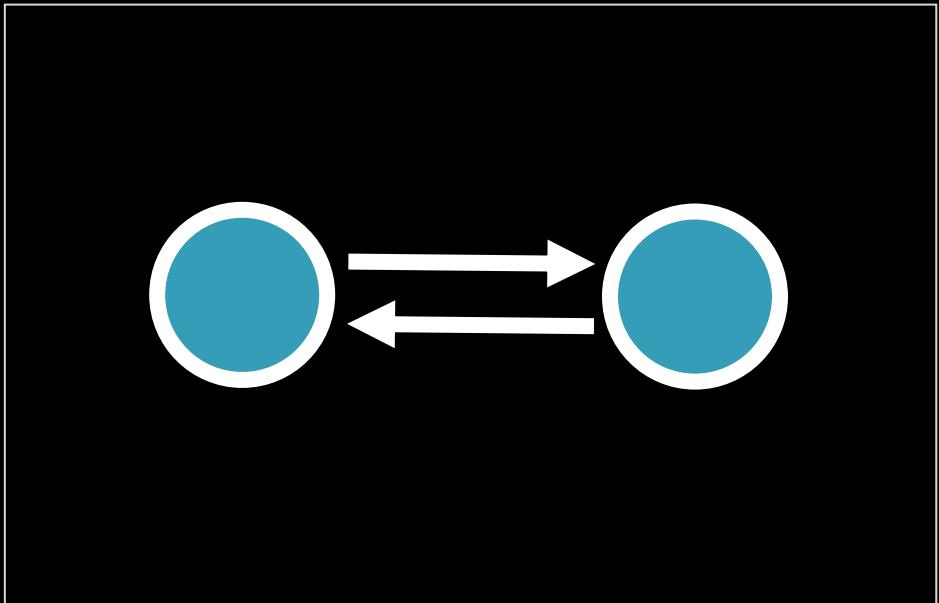
Copyrighted Material

Boyd, Richerson, Bowles, Gintis and others show how the act of social learning and cooperation within groups, have been essential for survival, and may allow human populations to accrue information over many generations.

# Direct reciprocity

R. Trivers, Q. Rev. Biol. 46, 35 (1971)

*repeated interactions, memory, complex strategies, ...*



*I scratch your back & you scratch mine . . .*

direct reciprocity  
relies on individuals' experience & memory

# Direct reciprocity

*I scratch your back & you scratch mine . . .*

## Axelrod's tournaments

**1<sup>st</sup> tournament : 14 players ; winner : *tit-for-tat***

*Anatol RAPOPORT:*

*Start by cooperating, and repeat the strategy of your opponent in the previous move*

**2<sup>nd</sup> tournament : 63 players ; many of the new strategies would have won the 1<sup>st</sup> tournament**

**winner : *RAPOPORT & TIT for TAT***

**It's very hard to predict the outcome against an unknown set of strategies!**

# Ecology of direct reciprocity

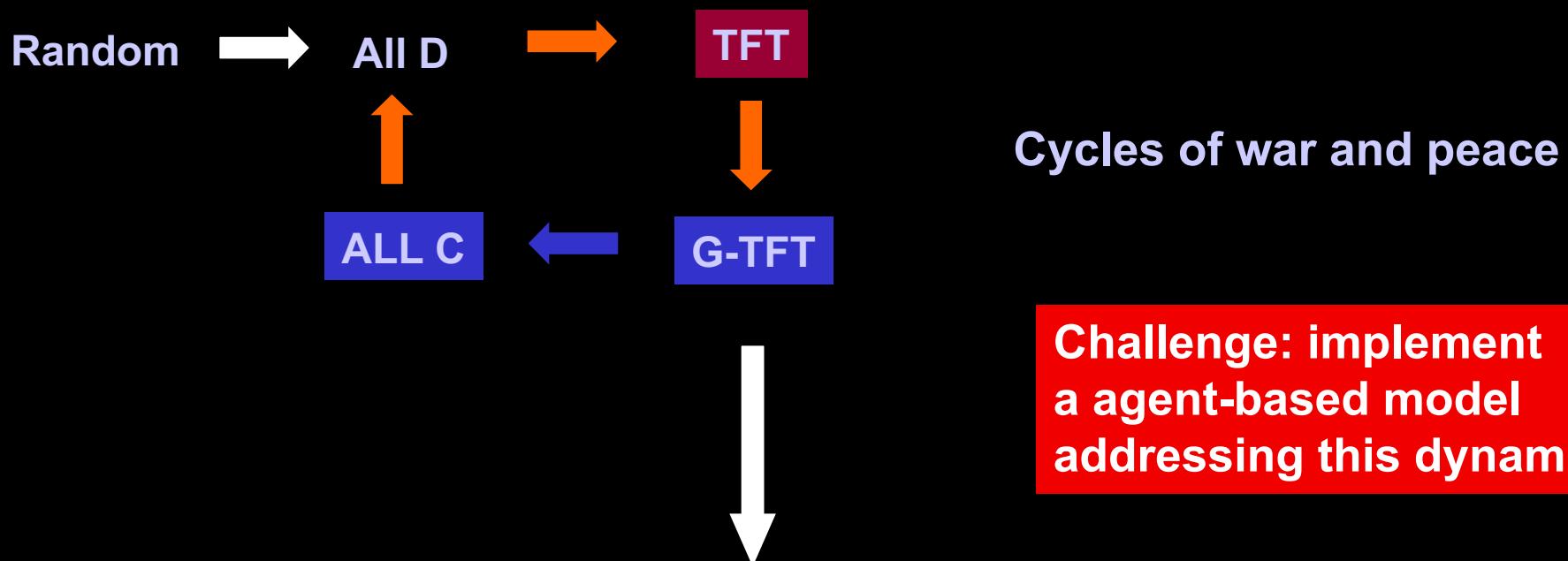
*I scratch your back & you scratch mine . . .*

is **tit-for-tat** the final word ? **NO !**

**tit-for-tat** is **BAD** at correcting errors ( *trembling hand effect . . .* )

Generous TFT: *Never forget a good move, sometimes forget a bad one*

Let evolution decide:



Challenge: implement  
a agent-based model  
addressing this dynamics

**win-stay, lose-shift** : if in the previous move I got ( $b-c$ ) or ( $b$ ), I stick to the “winning strategy”; if not, I change to the other strategy.

# Ecology of direct reciprocity

*I scratch your back & you scratch mine . . .*

PD: T>R>P>S

What's the trick?

**WSLS vs WSLs:** takes a couple of moves to correct an error

WSLS : C C C C C C C D C C C ...

WSLS : C C C C C C D D C C C ...  
error

...creating a positive feedback

Public enemy: dumb AllCs

ALLC : C C C C C C C C C C C C ...

WSLS : C C C C C D D D D D D ...

ALLC : C C C C C C C C C C C C ...

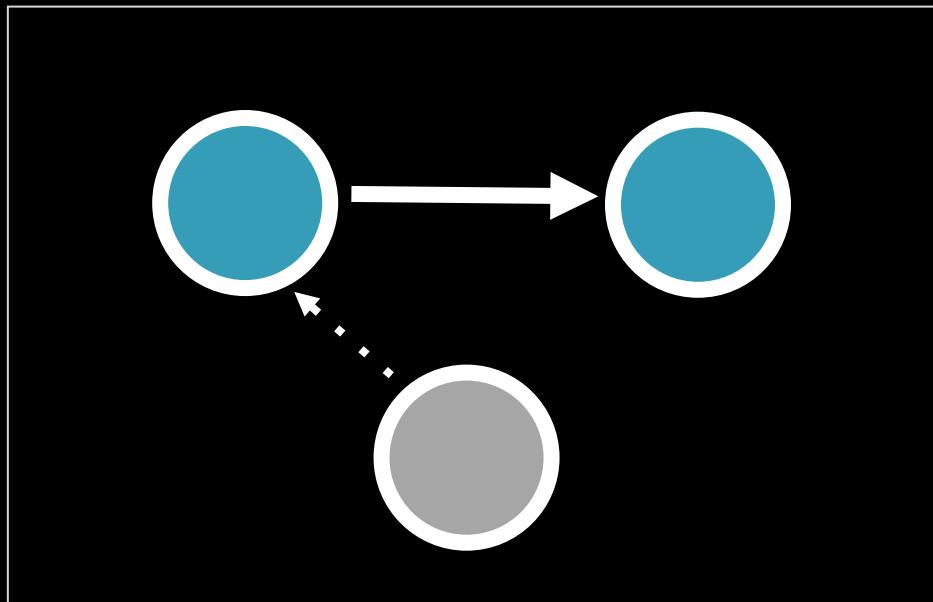
TFT : C C C C C D C C C C C ...

... contrary to TFTs, WSLS will  
shamelessly exploit AllCs

# Indirect reciprocity

*RD Alexander, The Biology of Moral Systems, 1987*

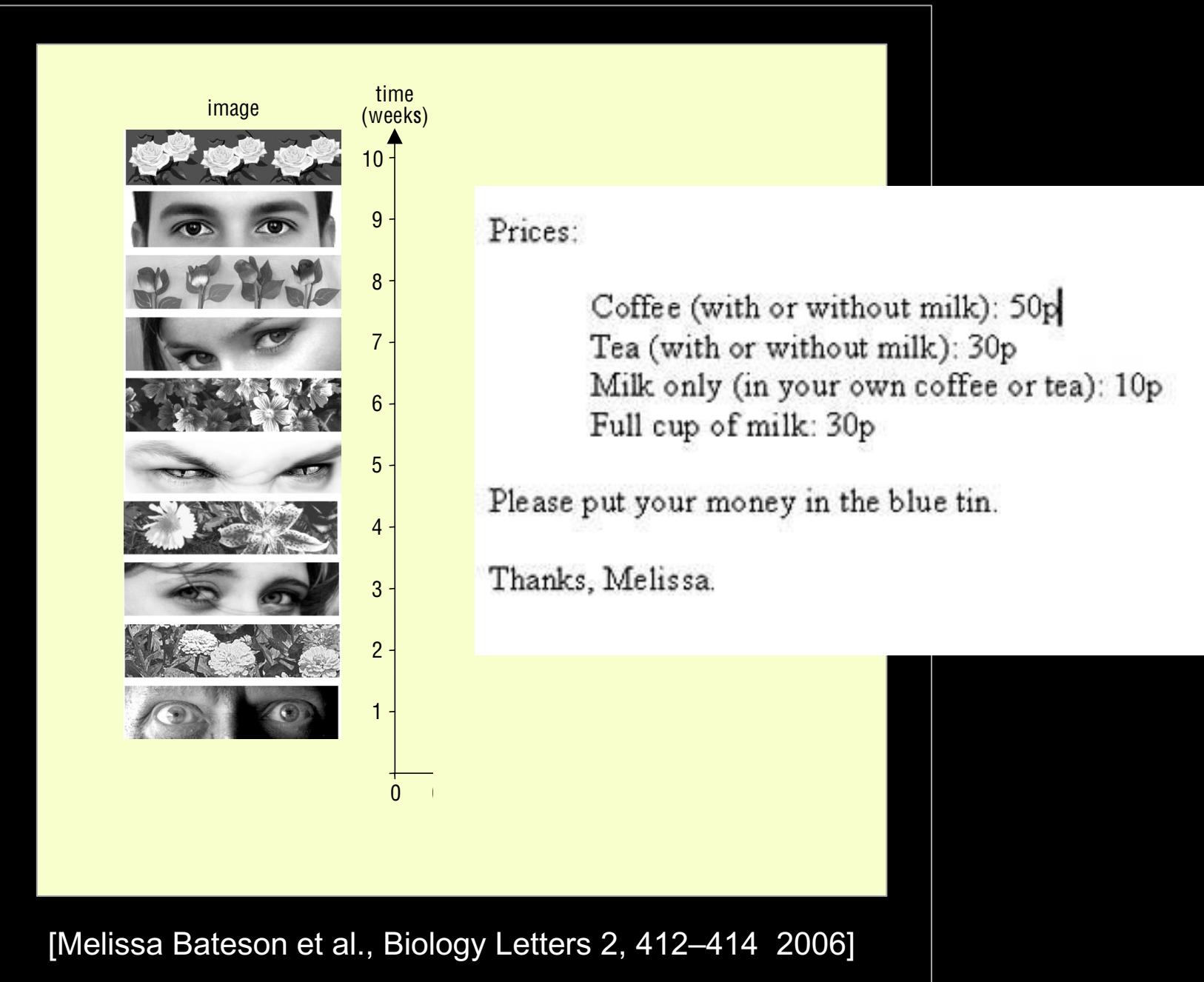
One shot interactions with reputation based strategies



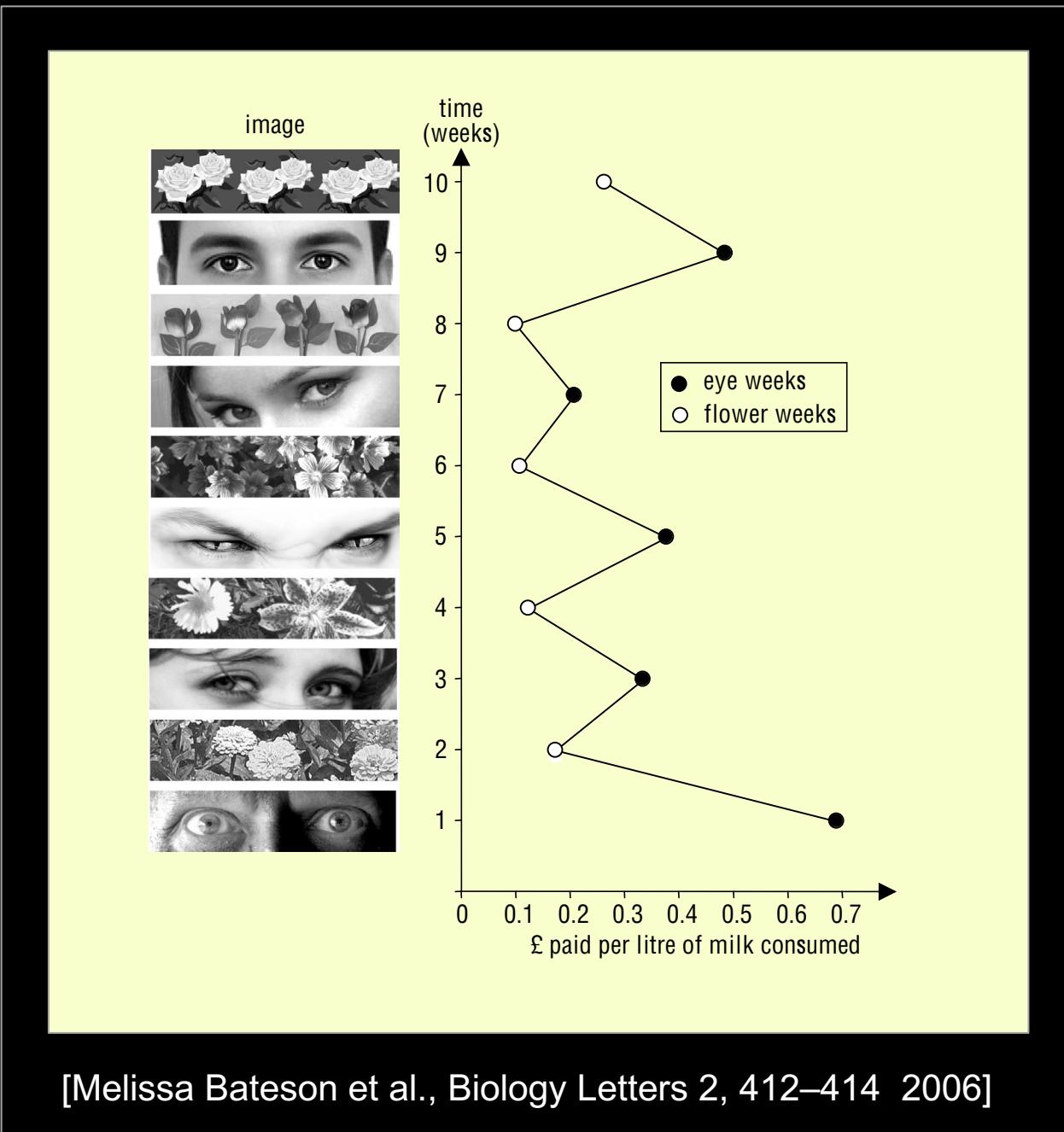
*I scratch your back & someone else scratches mine . . .*

indirect reciprocity  
relies on reputations, gossip, **social control**, moral systems, etc.

# The strength of third parties & social control



# The strength of third parties & social control



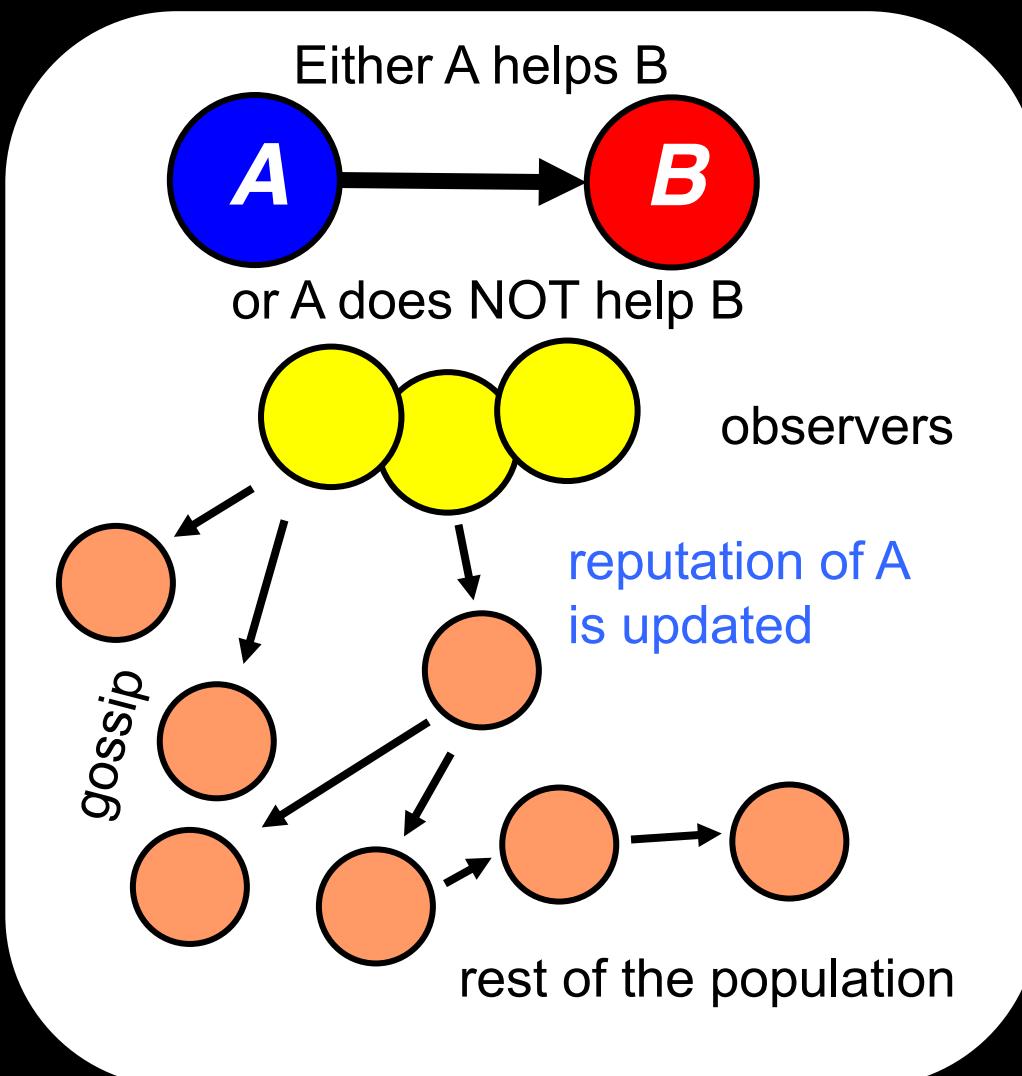
[Melissa Bateson et al., Biology Letters 2, 412–414 2006]

# Indirect reciprocity

RD Alexander, The Biology of Moral Systems, 1987  
Nowak & Sigmund, Nature 1998, Nature 2005  
Ohtsuki & Iwasa, J Theor Biol 2004, 2006, etc.

*I scratch your back & someone else scratches mine . . .*

**I help you and somebody else will help me**



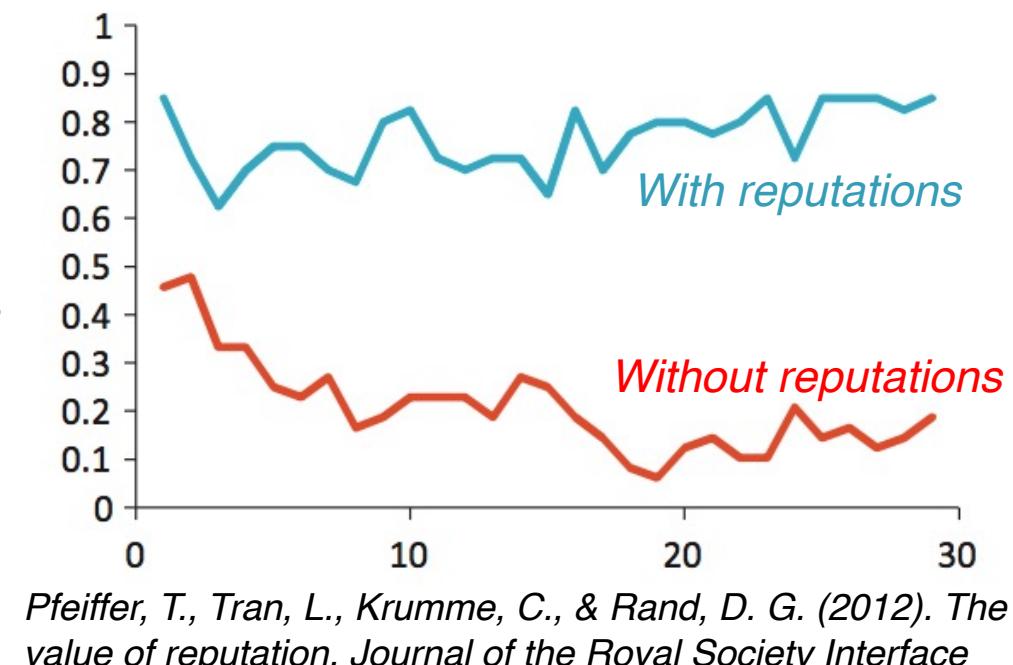
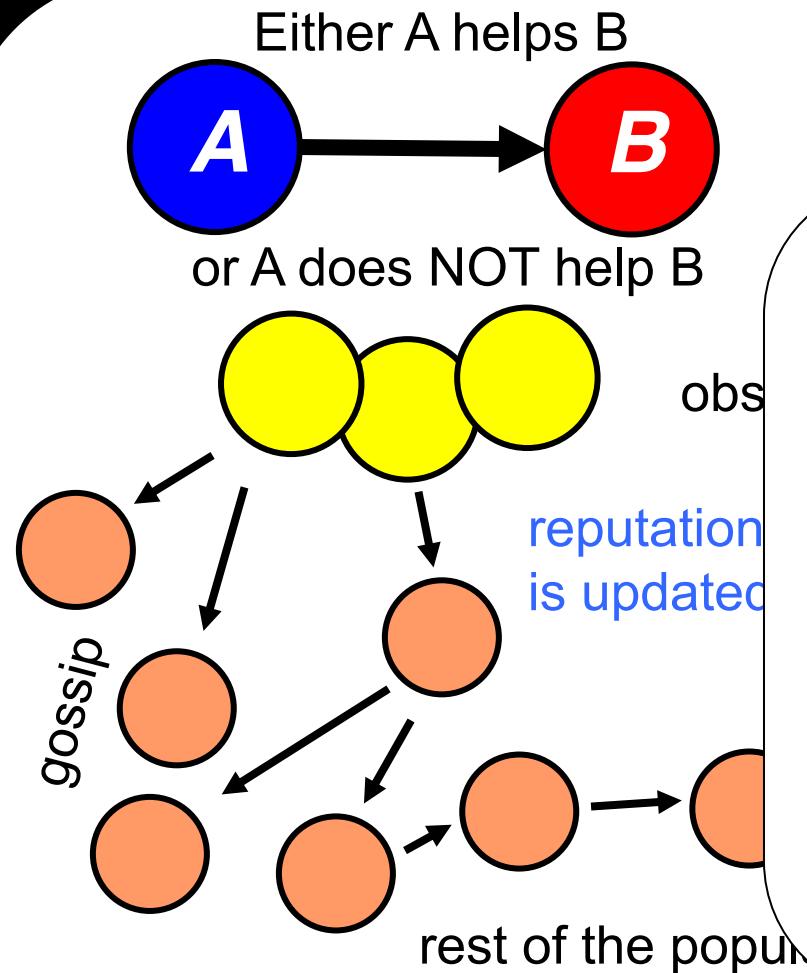
By helping someone, individuals may increase their reputation, which may change the predisposition of others to help them in the future

-> *social control, gossip, assessment of actions (social norms)*

# Indirect reciprocity

*I scratch your back & someone else scratches mine . . .*

**I help you and somebody else will help me**



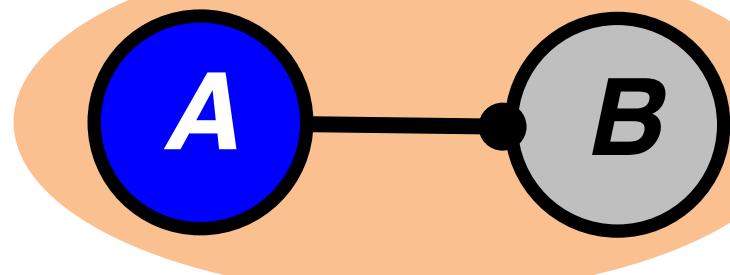
# Indirect reciprocity and the evolution of moral systems

*I scratch your back & someone else scratches mine . . .*

**After each interaction a new reputation is assigned...**

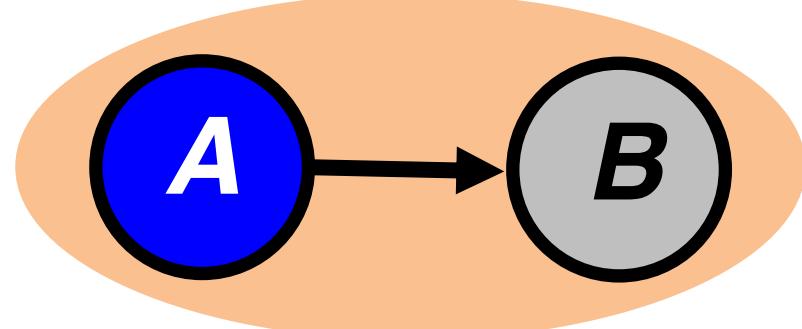
**How do we define a *social norm*?**

A does not help B



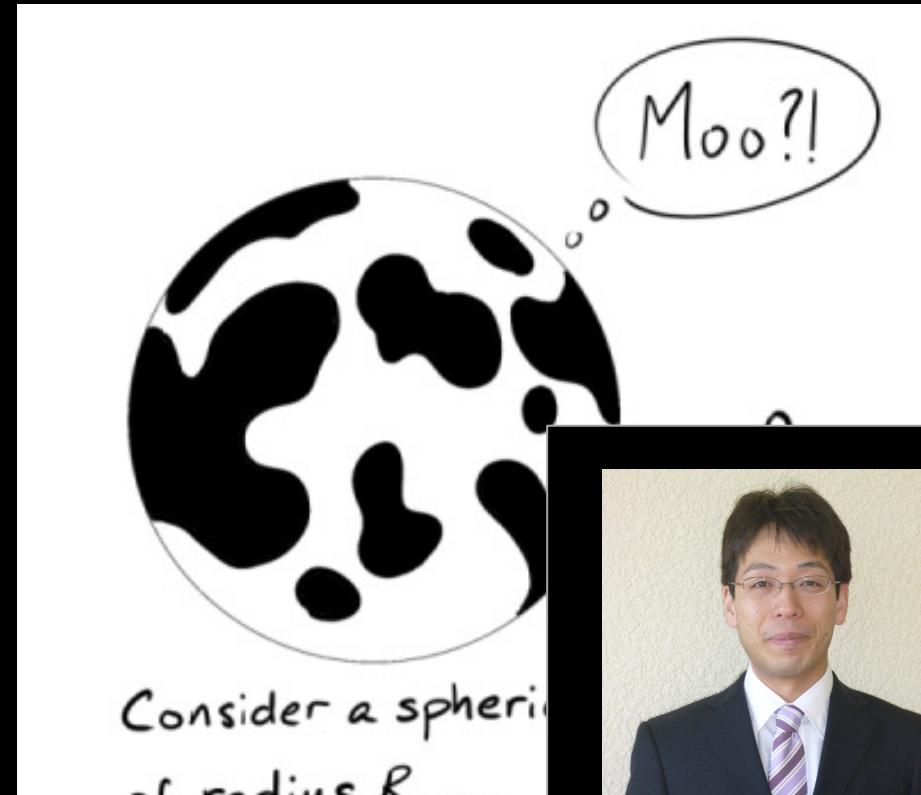
Should the reputation of A **decrease**?

A helps B



Should the reputation of A **increase**?

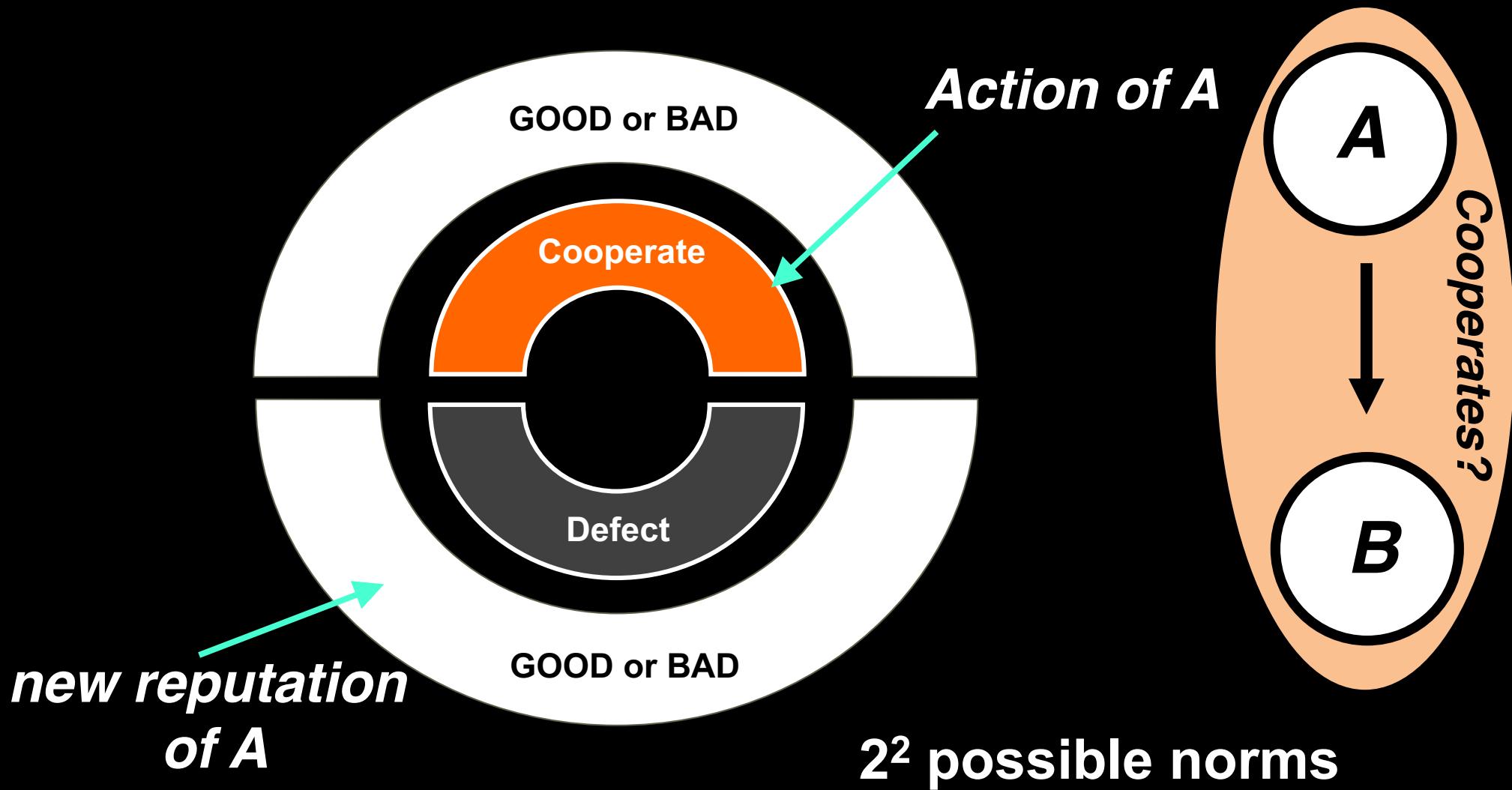
# The beauty of modelling core principles



**Otsuki, H., & Iwasa, Y.,**  
J Theor. Biol. (2004), J Theor Biol. (2006),  
J Theor Biol. (2007)

# 1<sup>st</sup> order norms in a black & white world

The simplest assessment rule (2 bits)... 1<sup>st</sup> order norm ('98)

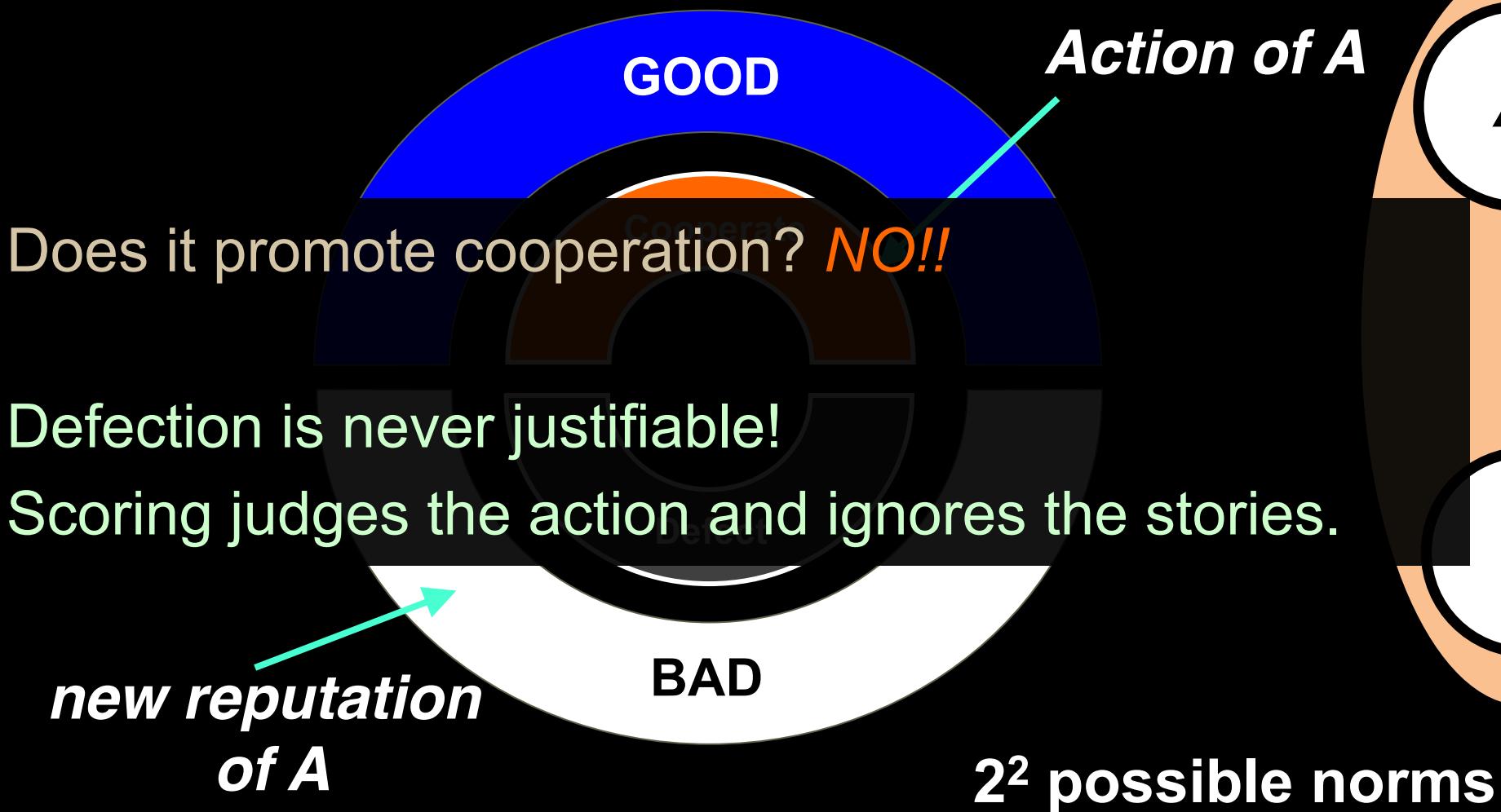


## 1<sup>st</sup> order norms: Image scoring ('98)

The simplest assessment rule (2 bits)... 1<sup>st</sup> order norm ('98)

Only one makes sense (*Image scoring*):

Good when C, Bad when D



## 2<sup>nd</sup> order norms (4 bits):

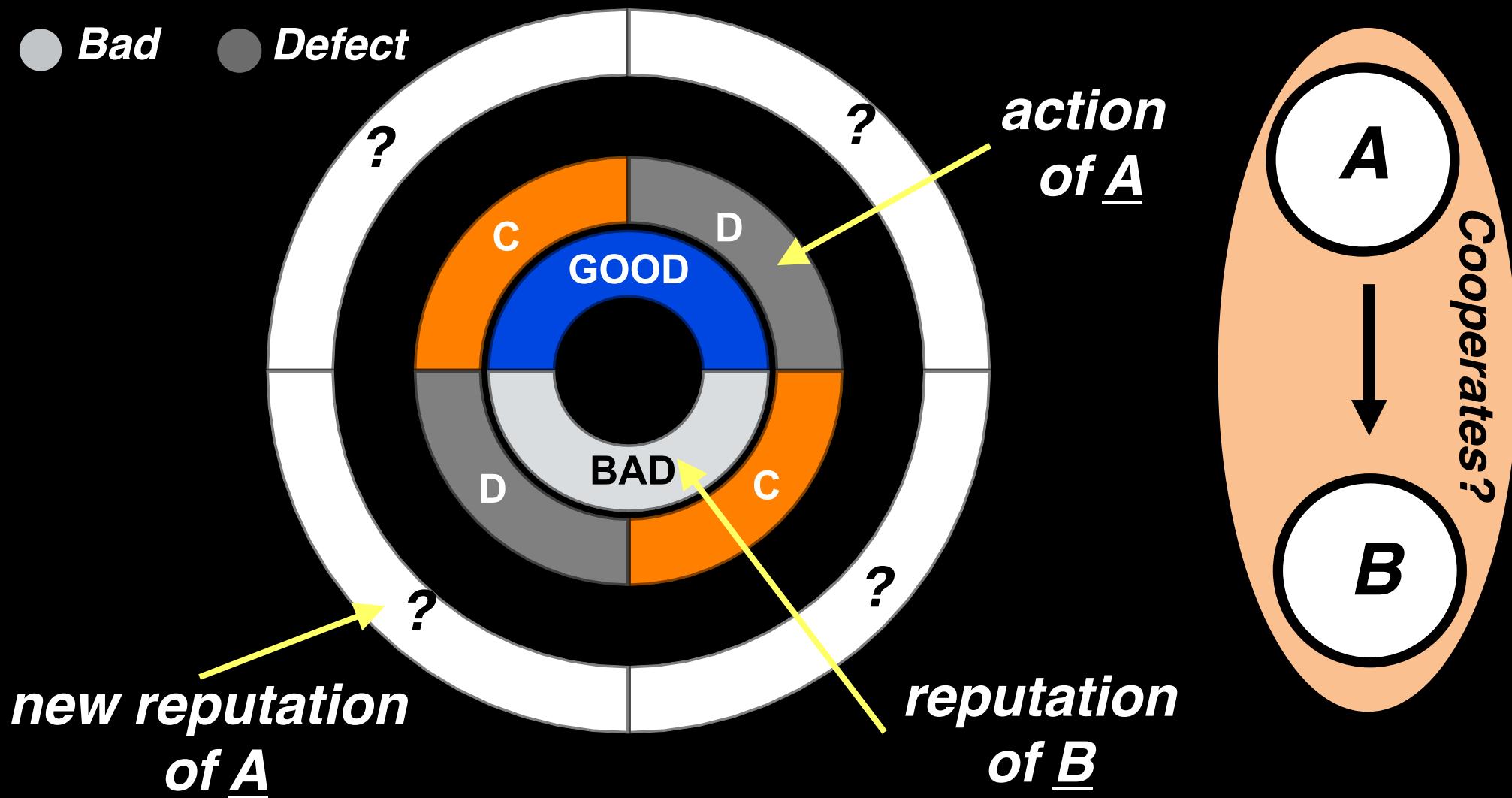
adding the recipient's reputation

Leimar, Hammerstein, PRSB 2001  
Ohtsuki, Iwasa, JTB, 2004, JTB 2006

***2<sup>4</sup> norms***

● *Good* ● *Cooperate*

● *Bad* ● *Defect*



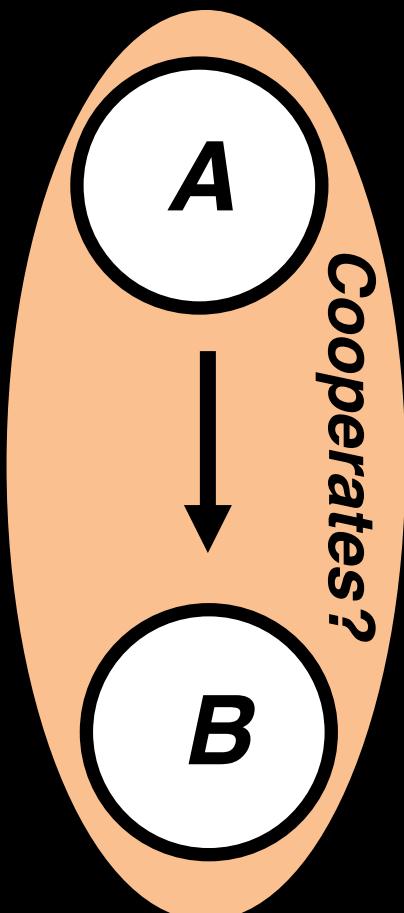
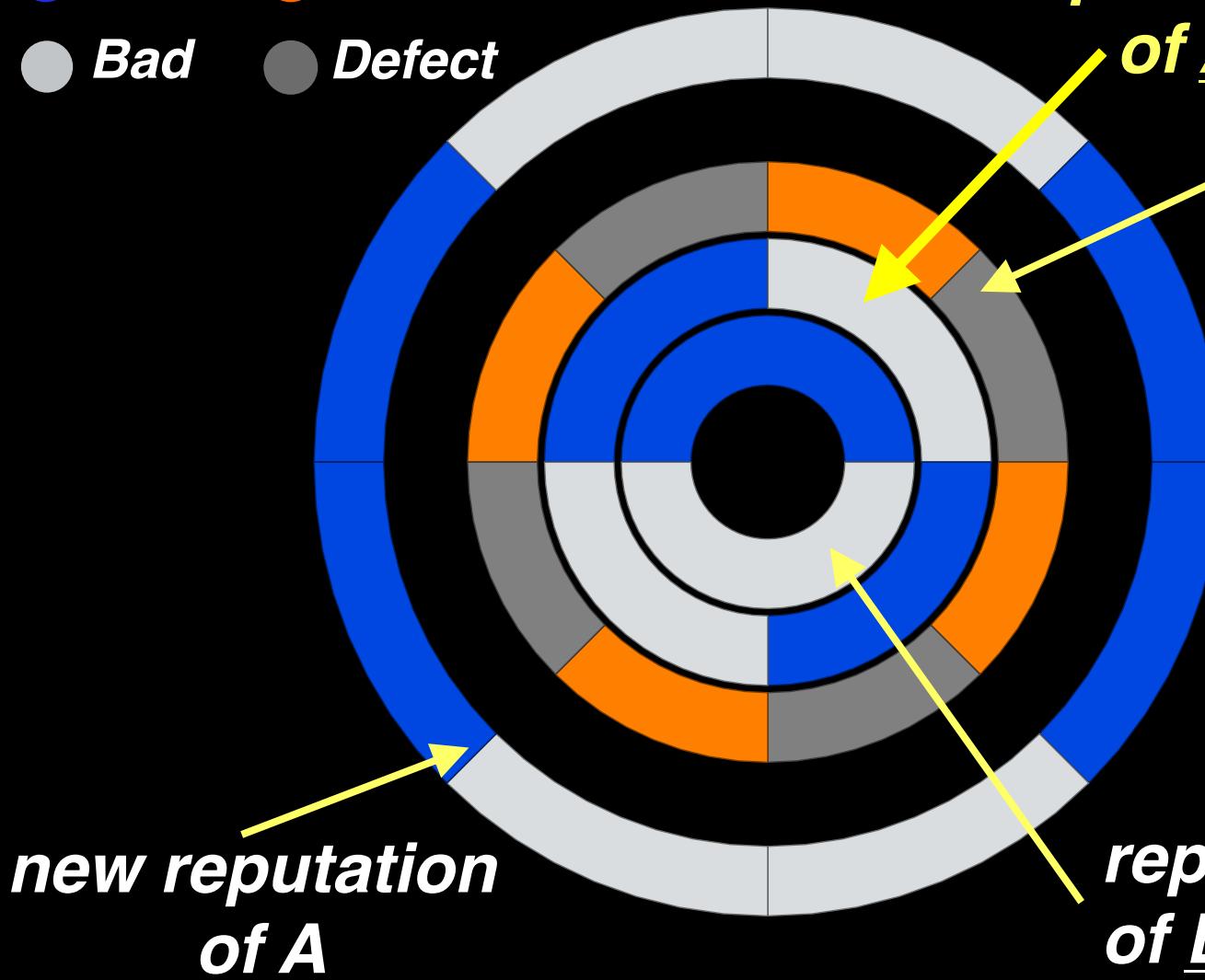
## 3<sup>rd</sup> order norms (8 bits): adding the donor's reputation

- *Good*
- *Bad*
- *Cooperate*
- *Defect*

*2<sup>8</sup> norms*

*reputation  
of A*

*action  
of A*

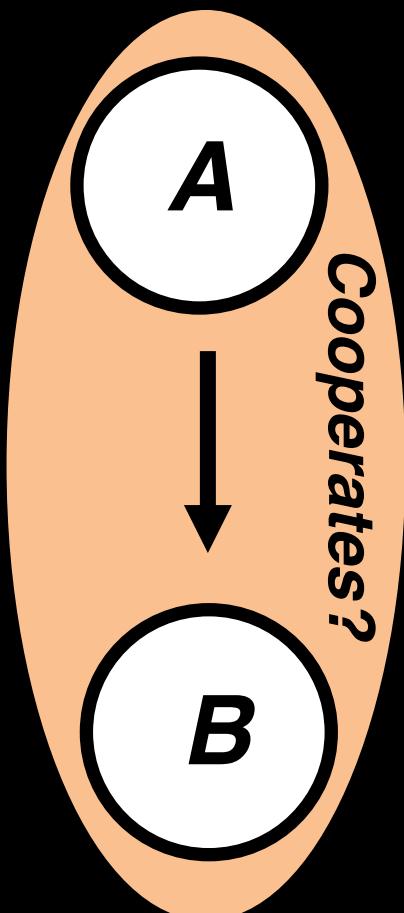
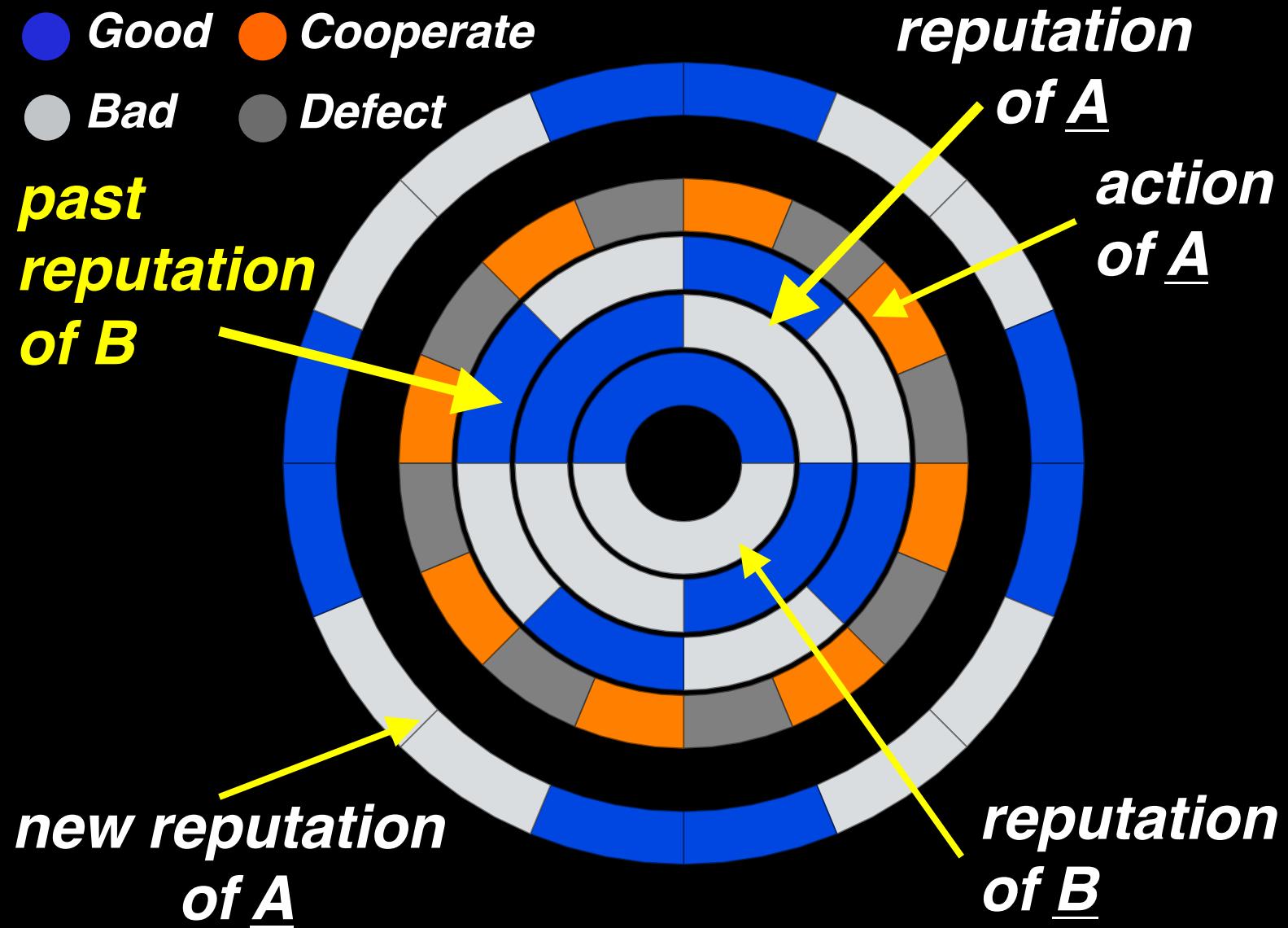


## 4<sup>th</sup> order norms (16 bits): adding the previous reputation of the receiver

$2^{16}$  norms

- Good
- Bad
- Cooperate
- Defect

*past  
reputation  
of B*



Who should be considered good for cooperation to thrive?

What's the most “efficient” social norm?

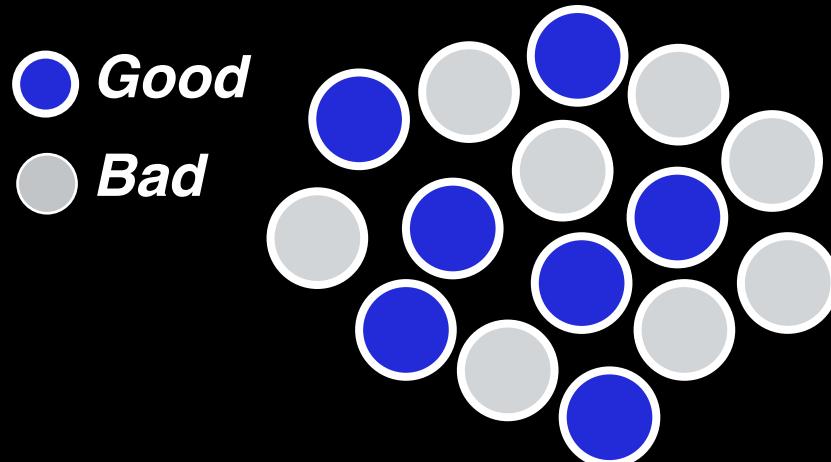
Let evolution decide!

Ohtsuki, H., & Iwasa, Y.,  
J Theor. Biol. (2004, 2006 & 2007)

FP Santos, FC Santos, JM Pacheco,  
Nature 2018, Plos Comput. Biol. 2016, 2007, etc.

Each individual has a reputation...

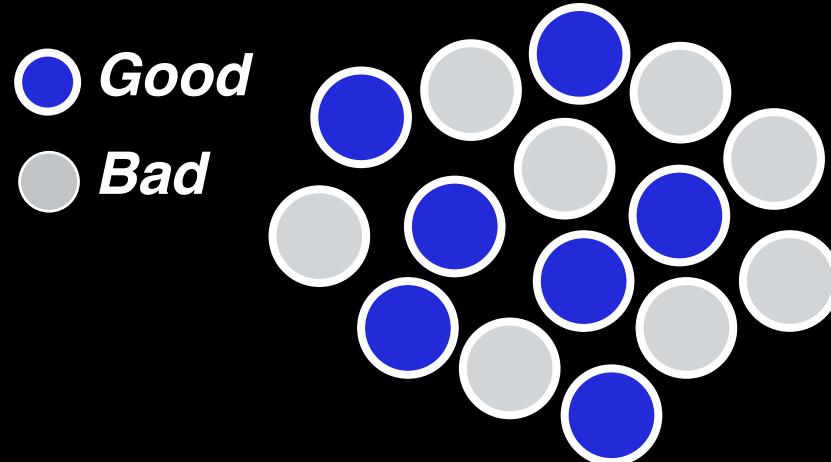
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Each individual has a reputation...  
and a strategy (or action rule)

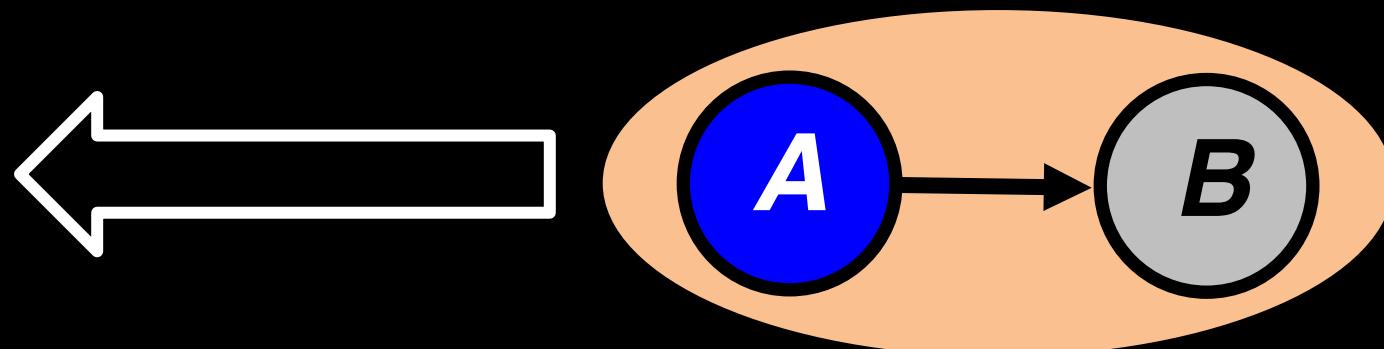
2<sup>nd</sup> order

Rep.	AllC	AllD	Disc	pDisc
G	C	D	C	D
B	C	D	D	C



*Action rules that do well spread in the population*

New reputation  
based on the  
social norm

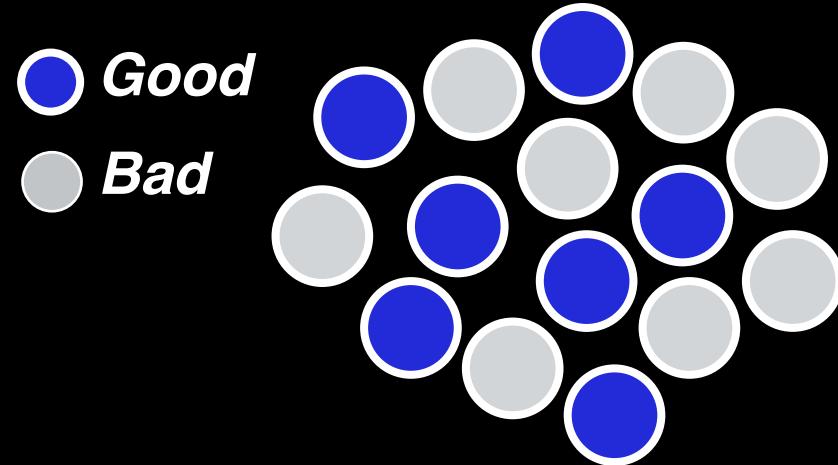


Choose C/D based on the  
adopted action rule

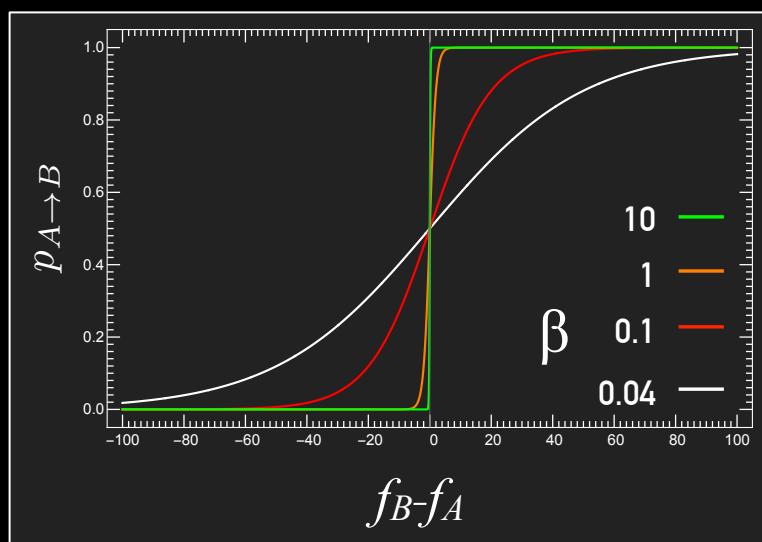
Each individual has a reputation...  
and a strategy (or action rule)

*2<sup>nd</sup> order*

Rep.	AllC	AllD	Disc	<i>p</i> Disc
G	C	D	C	D
B	C	D	D	C



*Action rules that do well spread in the population*



*A imitates a random individual B with a probability that increases with the fitness difference.*

$$p = [1 + e^{-\beta(f_B - f_A)}]^{-1}$$

## The model

---

social norms  
are fixed in the  
population



different norms lead to  
different reputations

different levels of  
cooperation



Reputations influence  
the success and  
frequency of strategies

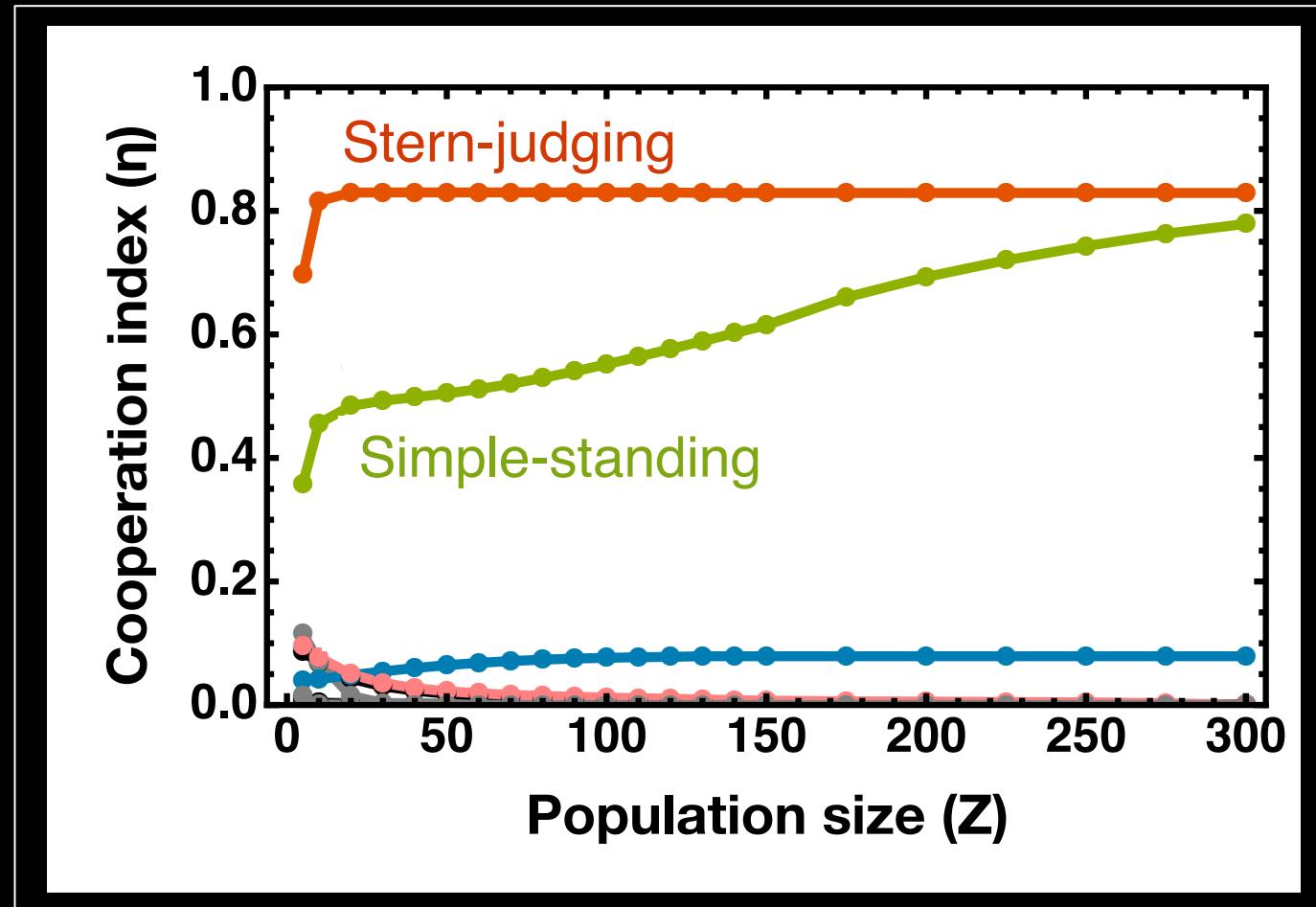
Who should be considered good for cooperation to  
thrive?

# A special norm: Stern-judging (in small-scale societies)

**Help the good and refuse help to the bad ; otherwise you will become *bad*.**



Fernando P. Santos  
Amsterdam & Princeton  
Recruiting PhD students:  
<https://fp-santos.github.io/>



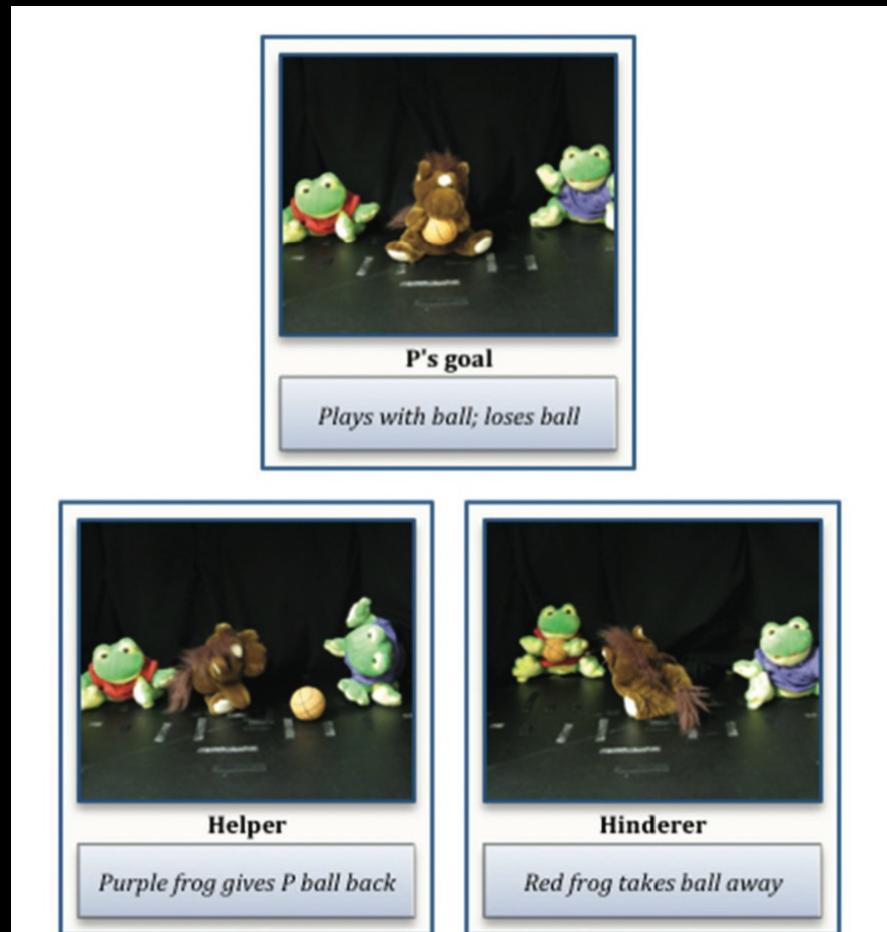
## A special norm: Stern-judging

---

**Help the good and refuse help to the bad ; otherwise you will become bad.**

# ***Experiments:*** infants prefer puppets that help others and puppets that defect against hinderers

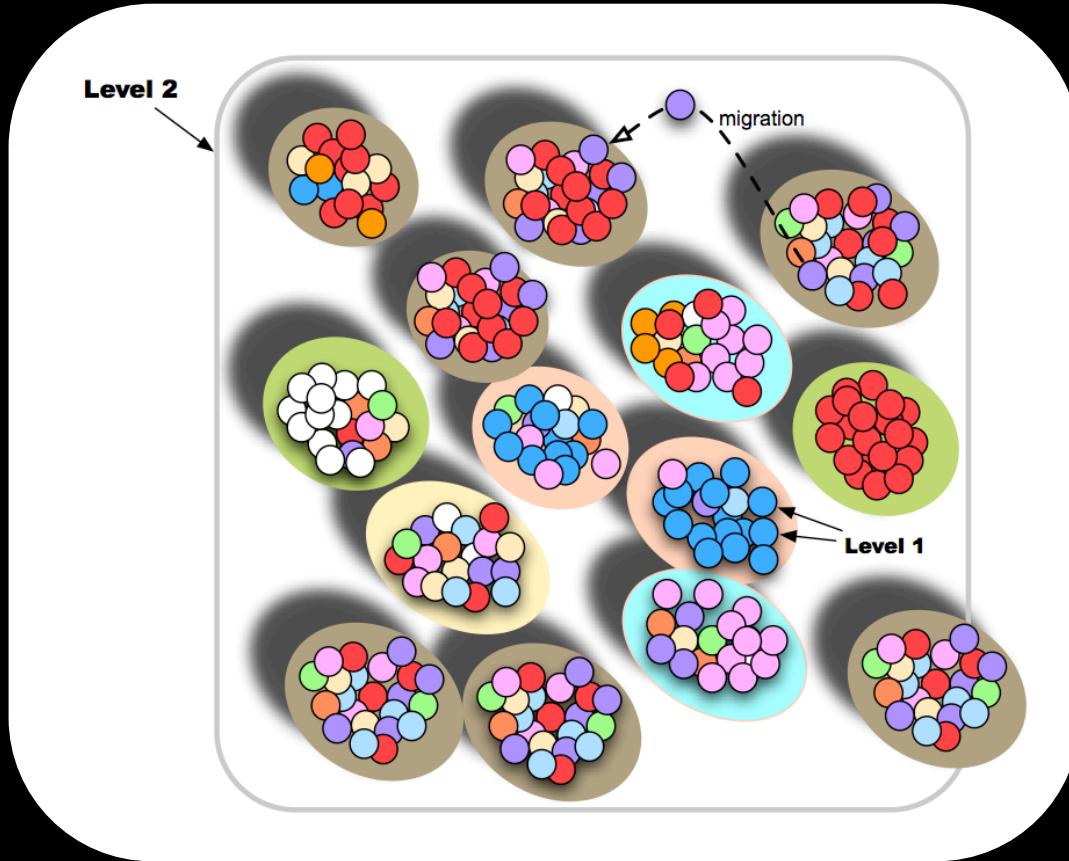
**Help the good and refuse help to the bad**



*Hamlin, J. K. (2013). Moral Judgment and Action in Preverbal Infants and Toddlers Evidence for an Innate Moral Core. Current Directions in Psychological Science*

*Hamlin, J. K. (2011) How infants and toddlers react to antisocial others. PNAS*

# Other types of models



- **strategies evolve in a tribe under a single norm**
- **individual fitness is the payoff of a cooperation game in each tribe;**
- **tribes compete with each other;**
- **the loosing tribe changes towards the norm of the winning tribe;**

# Conclusion: bits of good and evil!

---

- A single norm maximizes cooperation, while minimizing its cognitive complexity & order (particularly, in small societies).
- Cooperate with good and defect against bad; all else is *bad*... Even toddlers know it! ☺
- Cooperative societies can be sustained by very simple moral judgments that neglect past reputations.

# Conclusion: bits of good and evil!

---



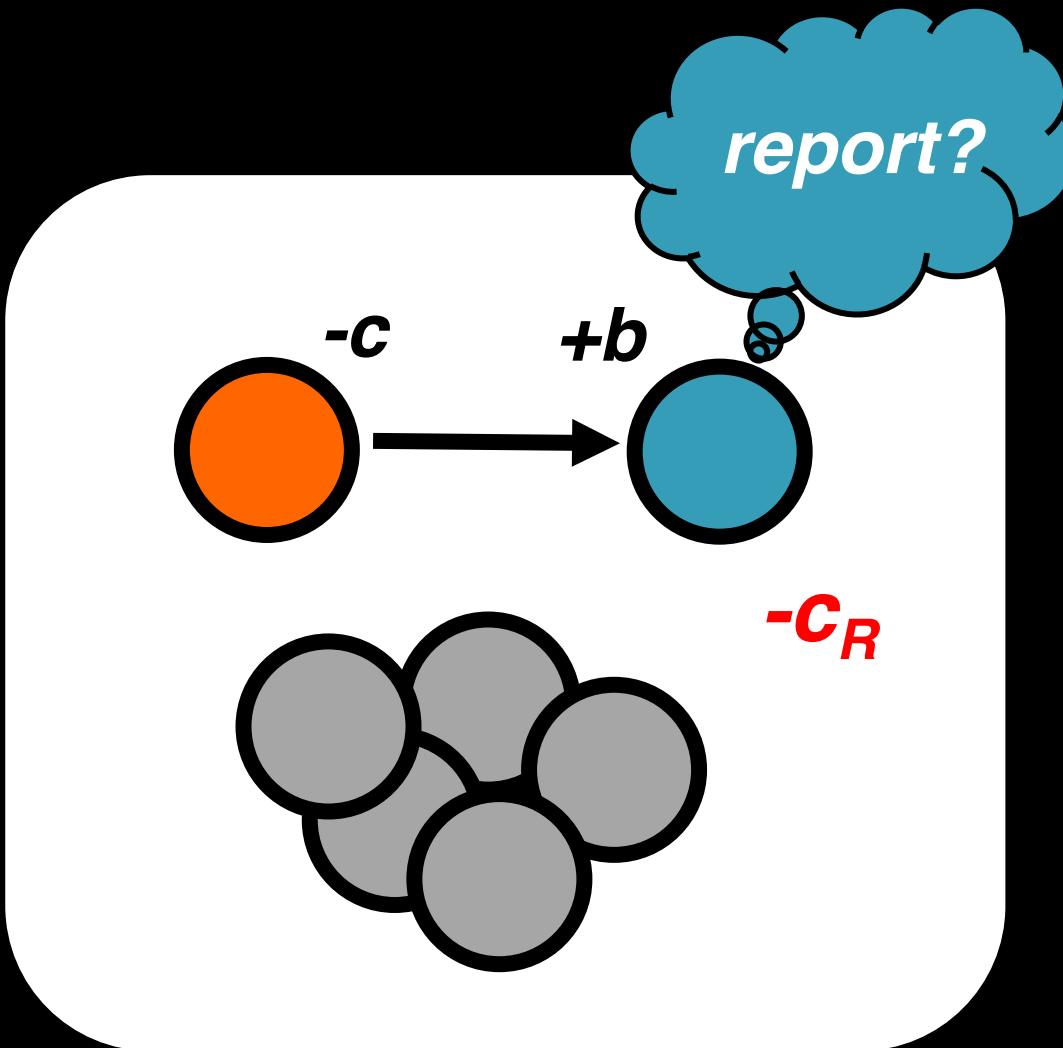
*Indirect reciprocity allows the characterization of the evolution of complex cultural concepts, such as:*

- **Punishment**
- **Forgiveness**
- **Evolution of laws and moral systems**
- **Appealing definitions of GOOD and EVIL.**

...but also has several limitations

# The Achilles heel of indirect reciprocity:

*Inaccurate information about reputations*

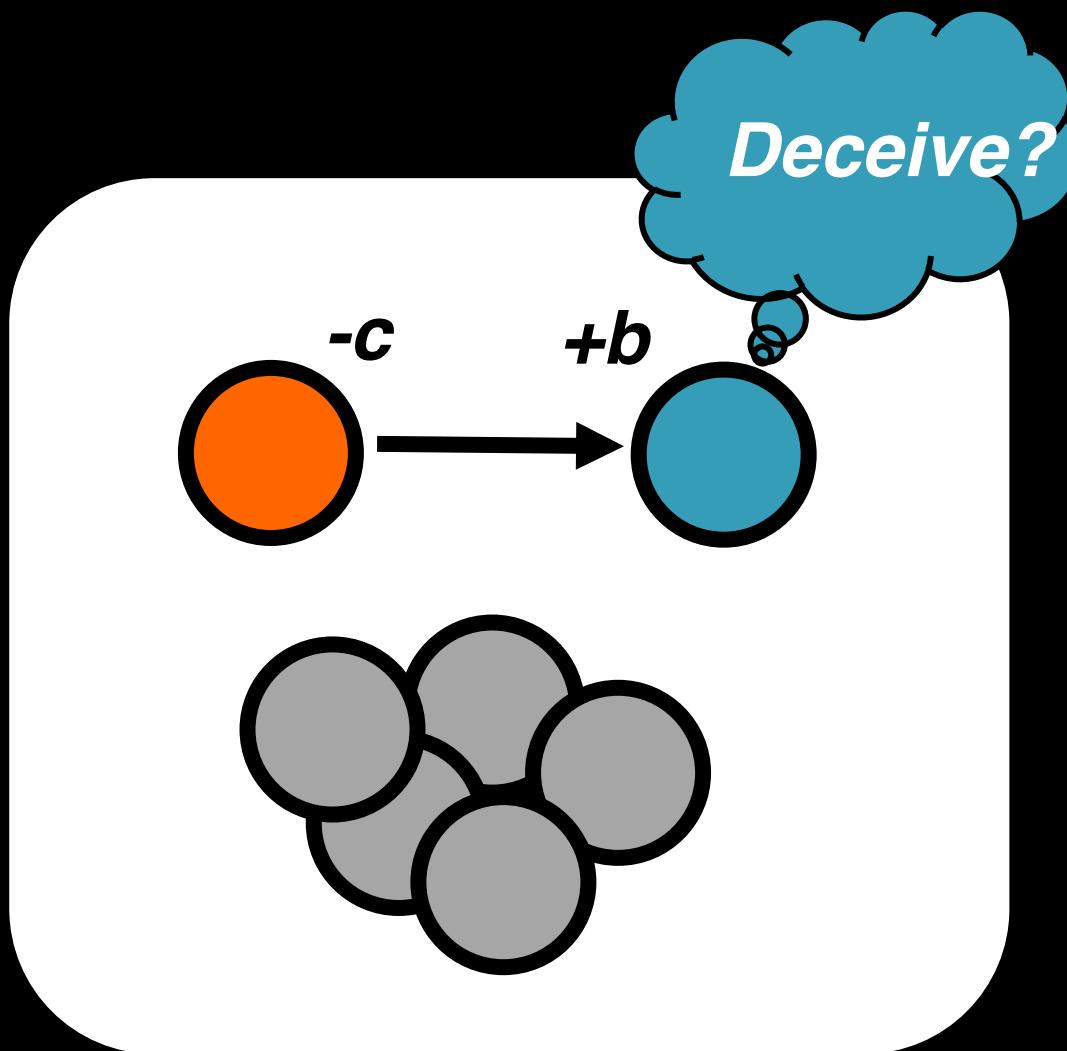


Fernando P. Santos  
Amsterdam & Princeton

*Santos, F. P., Pacheco, J. M. & Santos, F. C. (2018).  
Social Norms of Cooperation with Costly Reputation  
Building. AAAI'2018*

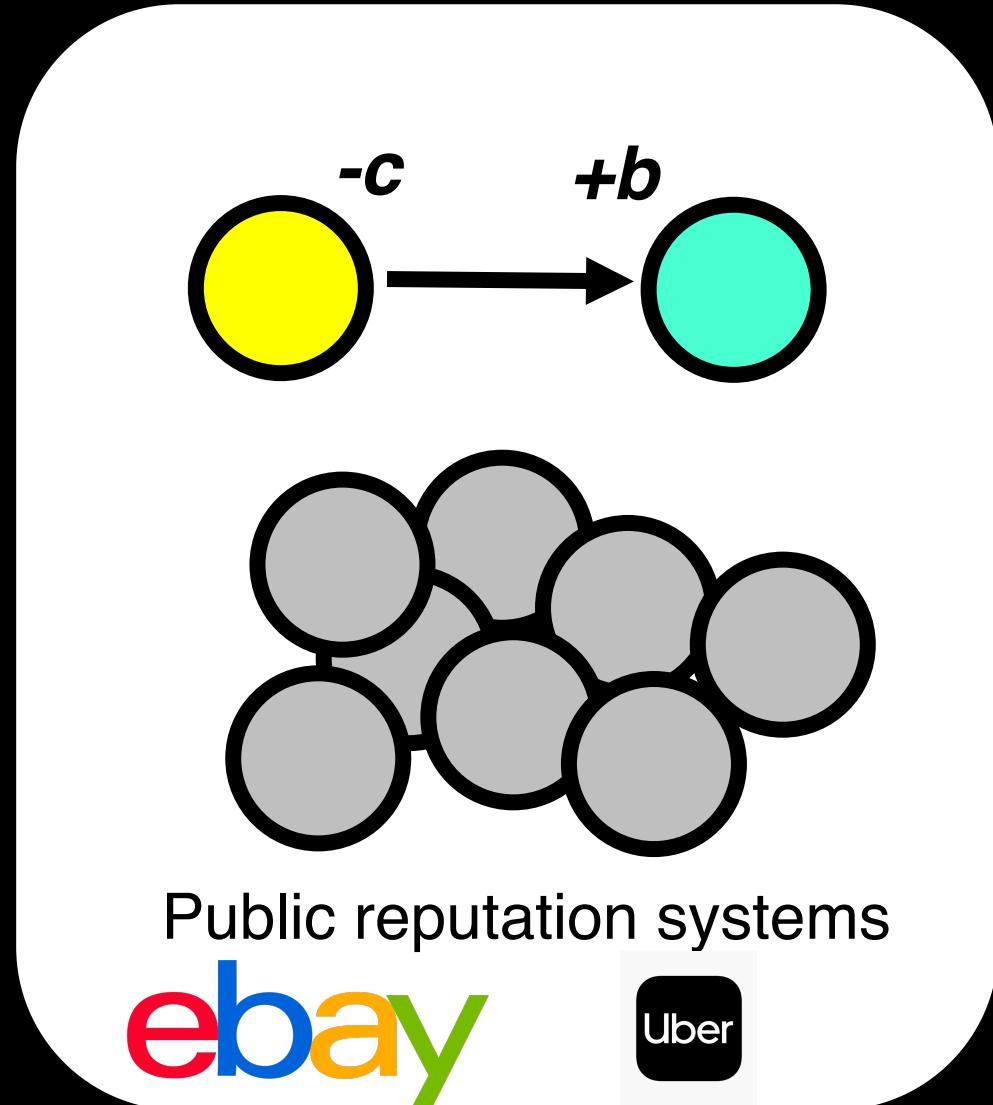
# The Achilles heel of indirect reciprocity:

*Inaccurate information about reputations*



Számadó et al. Deception undermines the stability of cooperation in games of indirect reciprocity PloS one (2016)

# *From public to private information systems*



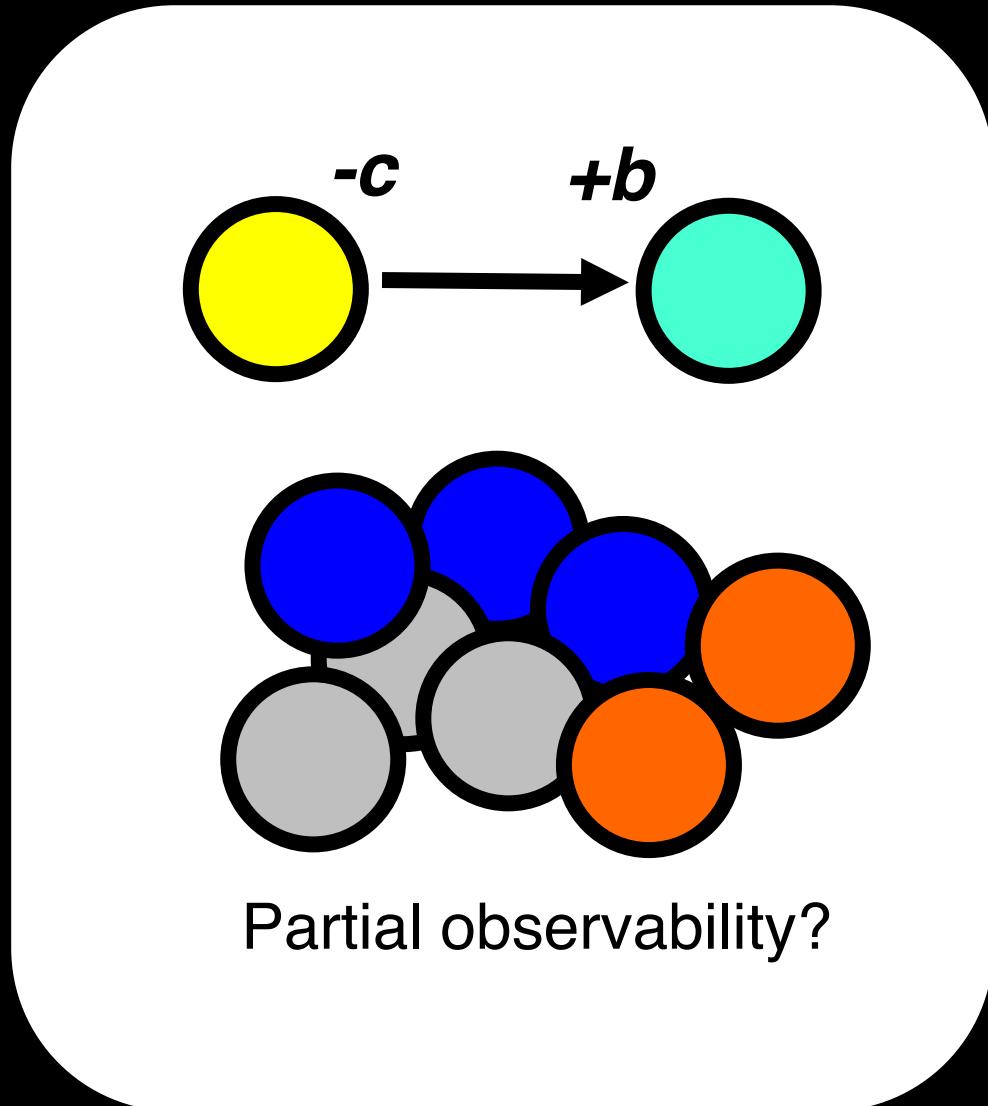
*Binary reputations*



# *From public to private information systems*



H. Fonseca, et al. 2020



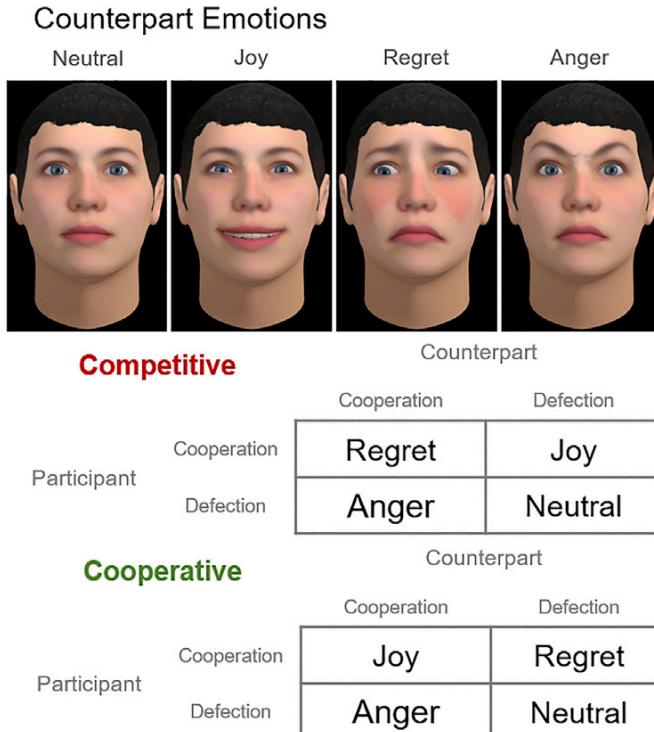
*Ternary reputations*



# Emotion expressions & indirect reciprocity

## Emotion-based reputations and social norms (3x2x3 experiments, n=711)

Emotions are used to forgive those that defect but also to punish those that cooperate.



Initial Reputation	Strategy	Emotion	Final Reputation
Negative	Competitive	Competitive	Negative
		Neutral	Negative
		Cooperative	Negative
	Cooperative	Competitive	Neutral
		Neutral	Neutral
		Cooperative	Positive
Unknown	Competitive	Competitive	Negative
		Neutral	Negative
		Cooperative	Neutral
	Cooperative	Competitive	Positive
		Neutral	Positive
		Cooperative	Positive
Positive	Competitive	Competitive	Negative
		Neutral	Neutral
		Cooperative	Positive
	Cooperative	Competitive	Positive
		Neutral	Positive
		Cooperative	Positive

Emotion expressions shape human social norms and reputations  
C. de Melo, K.Terada, and F.C. Santos  
iScience, 24, 102141, Cell Press, Feb 2021.



Celso de Melo  
U.S. ARL, Los Angeles

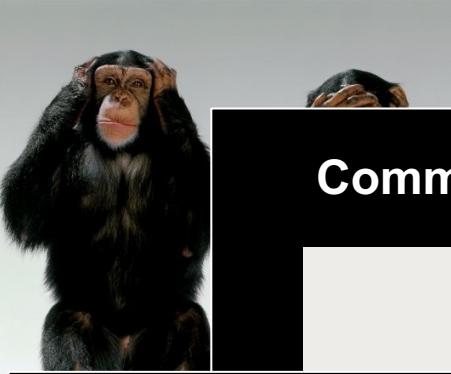
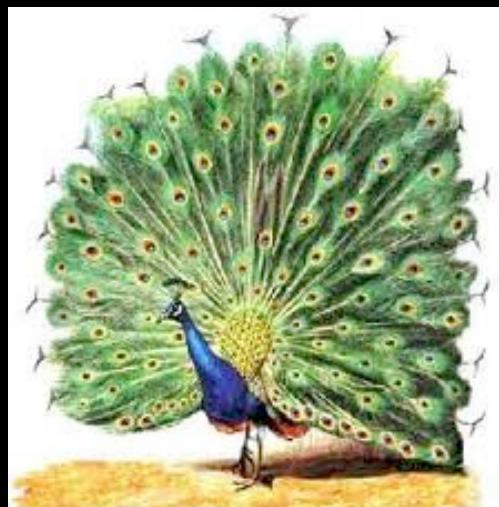


Kazunori Terada  
Gifu Univ., Japan

# Other ways out of the dilemma

Tag-based cooperation

## Signaling for cooperation



Commitments



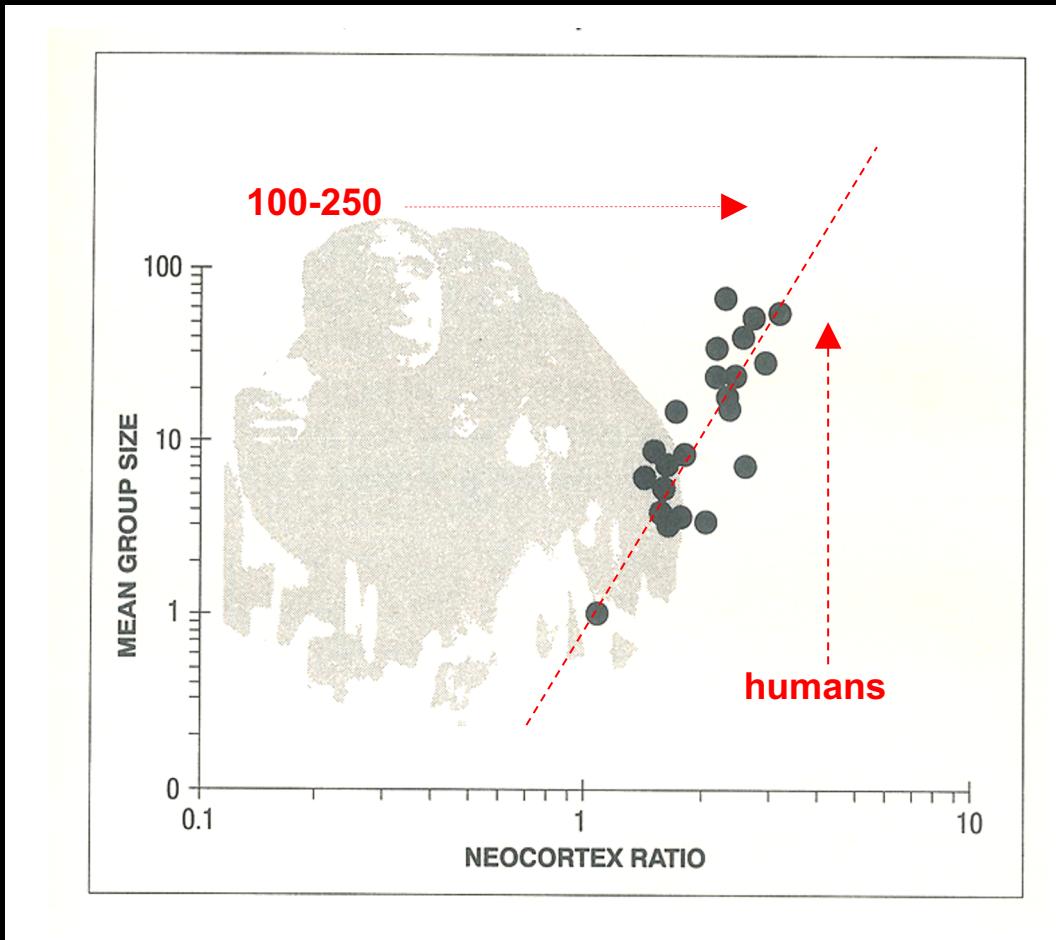
Co-evolution of Cognitive/Social Skills & Cooperation



# Evolution of social-cognition & cooperation

## Co-evolution of different features

- i) Social cognition
- ii) Group size
- iii) Cooperation and social cohesion



# A new evolutionary paradigm

Evolution in networked populations

