Five rules for the evolution of cooperation

Martin Nowak, Harvard University
What is cooperation?

Donor pays a cost, $c$

Recipient gets a benefit, $b$

Cost and benefit are measured in terms of fitness. Reproduction can be genetic or cultural.
The Prisoner’s Dilemma payoff matrix

<table>
<thead>
<tr>
<th></th>
<th>I cooperate</th>
<th>I defect</th>
</tr>
</thead>
<tbody>
<tr>
<td>you cooperate</td>
<td>$b - c$</td>
<td>$-c$</td>
</tr>
<tr>
<td>you defect</td>
<td>$b$</td>
<td>$0$</td>
</tr>
</tbody>
</table>

you get

$b > c$
What is the dilemma?

Two *rational* players defect and end up with a low payoff, 0.

Two *irrational* players might cooperate and receive a higher payoff, $b - c$. 
Natural selection chooses defection

In any mixed population, defectors have a higher payoff than cooperators.

Here natural selection reduces the average fitness of the population.
Natural selection needs help to favor cooperators over defectors.

Why do we care?
Evolution needs cooperation to construct new levels of organization:

nucleic acids - proteins

cells

cells with organelles

multi-cellular organisms

animal societies

humans

Cooperation is needed for ‘evolvability’ on a large scale.
Five mechanisms for the evolution of cooperation:

Kin selection
Direct reciprocity
Indirect reciprocity
Graph selection
Group selection
Kin selection

The interaction occurs between genetic relatives.

‘I will jump into the river to save 2 brothers or 8 cousins’

J.B.S Haldane
Kin selection

Hamilton’s rule

\[ r > \frac{c}{b} \]

- \( r \) … coefficient of relatedness
- \( c \) … cost of cooperation
- \( b \) … benefit of cooperation
Direct reciprocity

‘I help you, you help me.’

Robert Trivers, 1971
Repeated Prisoner’s Dilemma

Player 1 : C D C D C C C C ....
Player 2 : D C D D C C C C ....

What is a good strategy for playing this game?

Robert Axelrod
Tit-for-tat

- I start with cooperation.
- If you cooperate, then I will cooperate.
- If you defect, then I will defect.

Anatol Rapaport

Axelrod & Hamilton, Science, 1981
Tit-for-tat is unforgiving

Errors destroy cooperation

Tit-for-tat : CCCCCDCDCDCDDDDDDDDDDDDDD....
Tit-for-tat : CCCCCCDCDCDCDDDDDDDDDDDDDD....
Let natural selection design a strategy
Let natural selection design a strategy

Always defect

Random
Let natural selection design a strategy

- Tit-for-tat
- Always defect
- Random
Let natural selection design a strategy

- Tit-for-tat
- Generous Tit-for-tat
- Always defect
- Random
Generous Tit-for-tat

- If you cooperate, then I will cooperate.
- If you defect, then I will cooperate with probability $1 - \frac{c}{b}$.

Evolution of forgiveness: in a world of errors it is important to forgive

Nowak & Sigmund, *Nature*, 1992
Let natural selection design a strategy

- Tit-for-tat
- Generous Tit-for-tat
- Always defect
- Random
Let natural selection design a strategy

- Tit-for-tat
- Always defect
- Random

- Generous Tit-for-tat
- Always cooperate
Let natural selection design a strategy

Tit-for-tat \rightarrow Generous Tit-for-tat

\uparrow

Always defect \rightarrow Always cooperate

War and peace
Let natural selection design a strategy

- Tit-for-tat
- Generous Tit-for-tat
- Always defect
- Always cooperate
- Win-stay, lose-shift
Win-stay, lose-shift

- If I am doing well (payoff $b$ or $b-c$) then I will repeat my move.
- If I am doing badly (payoff 0 or $-c$) then I will change my move.

Nowak & Sigmund, *Nature*, 1993
Win-stay, lose-shift

- **WSLS**: CCCCCD*DCCCC..... corrects errors
- **WSLS**: CCCCCCDDCCCCC..... dominates ALLC
- **WSLS**: CCCCCD**DDDDDDDD....** is stable against invasion by ALLD if \( b / c > 2 \)
- **ALLC**: CCCCCCCCCCCCCC.....
- **WSLS**: CDCDCDCDCDCDCD.....
- **ALLD**: DDDDDDDDDDDDDDD.....

For \( b / c < 2 \) a stochastic variant of WSLS is stable against ALLD.
Direct reciprocity

... allows the evolution of cooperation if

\[ w > \frac{c}{b} \]

\( b \) ... benefit
\( c \) ... cost
\( w \) ... probability of another round
Indirect reciprocity

‘I help you.
Somebody will help me.’
Direct reciprocity: repeated encounters between the same two individuals. My strategy depends on what you have done to me.

Indirect reciprocity: repeated encounters in a population of individuals. My strategy also depends on what you have done to others.
Indirect reciprocity works via reputation

A helps B

- The reputation of A increases.

A does not help B

- The reputation of A decreases.

<table>
<thead>
<tr>
<th></th>
<th>donor</th>
<th>recipient</th>
<th>donor’s reputation</th>
</tr>
</thead>
<tbody>
<tr>
<td>cooperate</td>
<td>-c</td>
<td>+b</td>
<td>+1</td>
</tr>
<tr>
<td>defect</td>
<td>0</td>
<td>0</td>
<td>-1</td>
</tr>
</tbody>
</table>

Experimental confirmation:

People help those who have helped others.

People refuse to help those who have refused to help others.

Helpful people have a higher payoff in the end.

‘give and you shall receive’

Wedekind & Milinski, Science, 2000
Gossip spreads reputation

Observers

Rest of the population

either A helps B

or A does not help B

Reputation of A is updated.

gossip

A

B
David Haig:
“For direct reciprocity you need a face.
For indirect reciprocity you need a name.”
Indirect reciprocity leads to social intelligence and human language

Games of indirect reciprocity are cognitively demanding; individuals need to monitor the social network of a group.

=> evolution of social intelligence

Individuals must be able to talk to each other about others.

=> evolution of human language
A rule for indirect reciprocity

$q > \frac{c}{b}$

$q \ldots$ probability to know someone’s reputation
$c \ldots$ cost of cooperation
$b \ldots$ benefit of cooperation
The graph describes a spatial structure or a social network.

‘Evolutionary graph theory’ (Lieberman et al, Nature 2005)
Cooperators pay a cost $c$ for each neighbor to receive benefit $b$. 
Spatial games are special cases

Cooperators
Defectors
Spatial games are beautiful …

Simulations by Christoph Hauert
Graph selection favors cooperation if

$$\frac{b}{c} > k$$

$k$... (average) number of neighbors

‘There can be no doubt that a tribe including many members who [...] are always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over other tribes; and this would be natural selection.’

Charles Darwin, The Descent of Man, 1871
Group selection

Play the game with others in your group.

Offspring are added to the group.

Groups divide when reaching a certain size.

Groups die.
Group selection

favors cooperators if

\[ \frac{b}{c} > 1 + \frac{n}{m} \]

\(n\) ... group size
\(m\) ... number of groups (\(m>>2\))

(weak selection, rare group splitting)

Traulsen & Nowak, PNAS, 2006
Five mechanisms for cooperation

Kin selection: cooperate with genetic relatives.

Direct reciprocity: I help you, you help me.

Indirect reciprocity: I help you, somebody helps me.

Graph selection: clusters of cooperators do well.

Group selection: groups of cooperators out-compete other groups.
Five rules for cooperation

Kin selection : \( \frac{b}{c} > \frac{1}{r} \)  
\( r \)…coefficient of relatedness

Direct reciprocity : \( \frac{b}{c} > \frac{1}{w} \)  
\( w \)…probability of another round

Indirect reciprocity : \( \frac{b}{c} > \frac{1}{q} \)  
\( q \)…probability to know reputation

Graph selection : \( \frac{b}{c} > k \)  
\( k \)…number of neighbors

Group selection : \( \frac{b}{c} > 1 + \frac{n}{m} \)  
\( n \)…group size  
\( m \)…number of groups

Nowak, Science, 2006
Punishment is not a mechanism for the evolution of cooperation.

If you punish someone who has defected with you, then you are using direct reciprocity.

If you punish someone who has defected with others, then you are using indirect reciprocity.

(Winners don’t punish)
The five mechanisms fall into two groups:

- **Network reciprocity**
- **Group selection**
- **Kin selection**
- **Direct reciprocity**
  - uses own experience
- **Indirect reciprocity**
  - uses also experience of others

Unconditional cooperation can win.

Conditional cooperation can win.
Direct and indirect reciprocity are the key components for understanding the evolution of any pro-social behavior in humans.

But ‘what made us human’ is indirect reciprocity, because it provided the selective pressure for both social intelligence and human language.
Cooperators:

Tibor Antal (Harvard)
Anna Dreber (Harvard)
Drew Fudenberg (Harvard)
Christoph Hauert (Harvard)
Lorens Imhof (Bonn)
Yoh Iwasa (Kyushu)
Erez Lieberman (Harvard)
Lord May of Oxford
Hisashi Ohtsuki (Harvard)
Jorge Pacheco (Lisbon)
David Rand (Harvard)
Karl Sigmund (Vienna)
Corina Tarnita (Harvard)
Christine Taylor (Harvard)
Arne Traulsen (Ploen)