

News & views

Evolution

Why humans reciprocate but animals usually do not

Sarah Mathew

Reciprocal cooperation can be advantageous, but why it is more common in humans than in other social animals is a puzzle. A modelling and experimental study pinpoints the conditions needed for reciprocity to evolve.

Reciprocity is so intuitive to humans that its evolutionary logic can seem self-evident. If there is a high chance that individuals will interact again, it pays to be nice to those who might return the favour. A rich body of theoretical work has confirmed this idea, showing that — as long as there is a high probability of interacting with the same person again, and individuals preferentially help those who have previously helped them — reciprocal cooperation is advantageous despite its short-term cost. However, writing in *Nature*, Efferson *et al.* report evidence suggesting that the evolutionary path to reciprocity is treacherous at best, and impossible at worst — unless natural selection favours not only individuals, but also groups, that cooperate more.

As counterintuitive as the finding might be, it could clarify a key paradox about reciprocity theory. Despite the long-term gains that reciprocal cooperation offers, most animals do not cooperate with individuals that are not related to them, even when they have many opportunities for future interactions¹. By contrast, humans exchange a wide variety of goods and services with unrelated individuals during daily life (Fig. 1) in a manner that is consistent with reciprocity theory². A satisfactory theory should explain not just why humans cooperate, but also why other animals do not when the conditions for cooperation to evolve seem to be met.

Despite theoretical shortcomings in explaining why most animals do not behave reciprocally, researchers continue to ascribe cooperation in repeated interactions to reciprocity, and have turned their gaze to a more unusual phenomenon — cooperation in one-off interactions. In a conspicuous deviation

If the recipient cannot return the favour later, then how does the helper recoup the cost of helping? Some think that cooperation in such one-off interactions is a 'mismatch' in modern settings, resulting from a reciprocity-driven psychology that evolved when humans lived in smaller groups in which interactions between individuals were almost always repeated³. Others think that such cooperation arises through group selection, in which competition between groups of people with different cooperative behaviours and norms favours those with high levels of in-group cooperation, including in one-off interactions⁴. Testing apart which of these explanations is correct is difficult.

fueling a debate over the roots of our altruistic disposition⁵.

To try to settle this argument, Efferson *et al.* developed a model that simulates which cooperation strategies evolve in populations over time when interactions are repeated and when group selection occurs, to derive precise predictions of the scenarios that give rise to one-off cooperation. Contrary to both sides of the debate, neither repeated interactions nor group selection consistently produced one-off cooperation. More surprisingly, repeated interactions did not yield the most obvious outcome, reciprocal cooperation. These results emerged because the model was constructed in a way that did not make standard simplifying assumptions, thus ensuring that it did not sidestep certain realities of the natural world that have long eluded effects.

First, rather than having the model consider cooperation and non-cooperation as two discrete options, individuals could cooperate to any extent along a continuous scale. Second, any conceivable cooperation strategy could arise through chance and compete with existing strategies in the population. In standard models, the strategies that can arise are predetermined to make the model more straightforward, so existing strategies in the population are artificially protected from their full range of competing strategies. These two decisions exposed a fundamental weakness of repeated interactions as a mechanism by which cooperation can evolve — when



Sarah Mathew (2024). [Why humans reciprocate but animals usually do not](#). *Nature*, 626 (8001), 955-956.

Reciprocity is so intuitive to humans that its evolutionary logic can seem **self-evident**. If there is a high chance that individuals will interact again, it pays to be nice to those who might return the favour. **A rich body of theoretical work has confirmed this idea**, showing that — as long as there is a high probability of interacting with the same person again, and individuals preferentially help those who have previously helped them — reciprocal cooperation is advantageous despite its short-term cost. However, writing in *Nature*, Efferson *et al.* report evidence suggesting that **the evolutionary path to reciprocity is treacherous at best, and impossible at worst** — unless natural selection **favours** not only individuals, but also **groups**, that cooperate more.

Altruism



- Helping
- Human societies
- Communication
- Collective efficiency
- Moral
- Norms
- Sacrifice
- ...

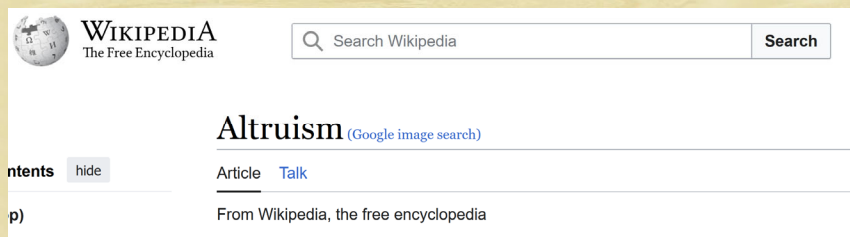
Altruism



"This is not only an attack against WCK, this is an attack on humanitarian organizations showing up in the most dire of situations where food is being used as a weapon of war. This is unforgivable," said World Central Kitchen CEO Erin Gore.
The seven killed are from Australia, Poland, United Kingdom, a dual citizen of the U.S. and Canada, and Palestine.

- ☀ Helping
- ☀ Human societies
- ☀ Communication
- ☀ Collective efficiency
- ☀ Moral
- ☀ Norms
- ☀ Sacrifice
- ☀ ...

Explanations of altruism

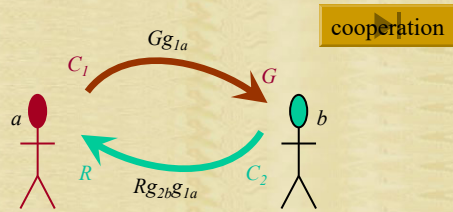


- ☀ Evolutionary explanations of altruism
 - ◉ (Vested interest)
 - ◉ Kin selection
 - ◉ ~~Reciprocal altruism~~
 - ◉ Costly signaling ←
 - ◉ ~~Group selection~~

Reciprocation vs. social signaling

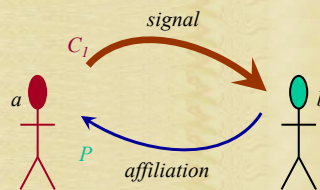
Reciprocal cooperation

- $\text{€} \leftrightarrow \text{€}$
- wealth creation
- cheating
- unstable



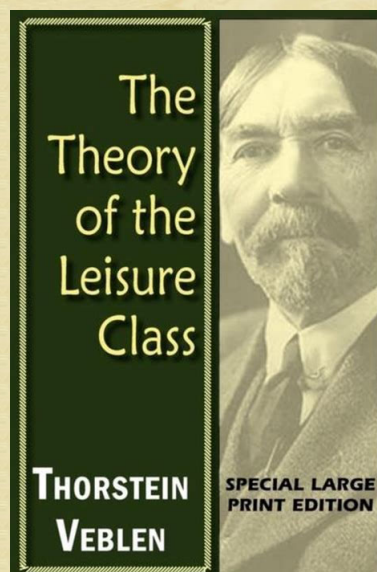
Social signaling

- Social bond $\leftrightarrow$ display
- no cheating
- Stable / robust



- Veblen, T. (1899).
The theory of the leisure class.
Macmillan.

However widely, or equally, or "fairly", it may be distributed, no general increase of the community's wealth can make any approach to satiating this need, the ground of which is the desire of every one to excel every one else in the accumulation of goods.
(Veblen 1899:23)



Conspicuous consumption

☀ Explain why people may

- ◉ spend much time
- ◉ spend money, resources
- ◉ take risks

with no obvious material return.

**People are real funny.
They spend money that they
don't have to buy things that
they don't need in order
to impress people they
don't like.**

☀ Examples:

- ◉ first Iphone
- ◉ cars
- ◉ clothing
- ◉ tourism
- ◉ ...

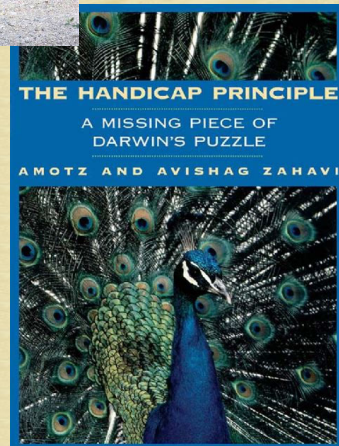


Costly signalling



- Zahavi, A. & Zahavi, A. (1997).
The handicap principle.
New York: Oxford University Press.

If guarding were based on reciprocity, there would be no point in striving to do more guard duty than others. Even if one asserts that such competition is necessary to ensure that the group is never without a sentinel, one would still have to explain why each bird interrupts the watch of the one nearest to it in rank, rather than attempting to replace younger, more inexperienced babblers.
(Zahavi & Zahavi 1997:135)



Bénabou, R. & Tirole, J. (2006).
[Incentives and prosocial behavior](#).
American Economic Review, 96 (5), 1652-1678.



Bénabou, R. & Tirole, J. (2006).
Incentives and prosocial behavior.
American Economic Review, 96 (5), 1652-1678.

$$R(a, y) = \alpha [(\gamma_a E(v_a|a, y) - \gamma_y E(v_y|a, y))]$$

$$\max_a [(v_a + v_y y) a - C(a) + R(a, y)]$$

Bénabou, R. & Tirole, J. (2006).
Incentives and prosocial behavior.
American Economic Review, 96 (5), 1652-1678.

The model postulate an exogenous social reward for being able to produce the positional signal.

$$R(a, y) = \alpha [(\gamma_a E(v_a|a, y) - \gamma_y E(v_y|a, y))]$$

• Where does social utility come from?

Reputation models

☀ Where does social utility come from?

- ◉ ~~Future cooperation?~~
- ◉ Social signaling



Social signaling

☀ Individuals benefit from making friends

- ◉ sharing time together
 - security
 - solidarity
- ◉ "good" friends
 - competent
 - reliable



Signaling (altruism included)

Model 0: asymmetrical bonds

→ stardom

+ Model 1: time sharing

→ friendship

Model 2: praise

→ heroes

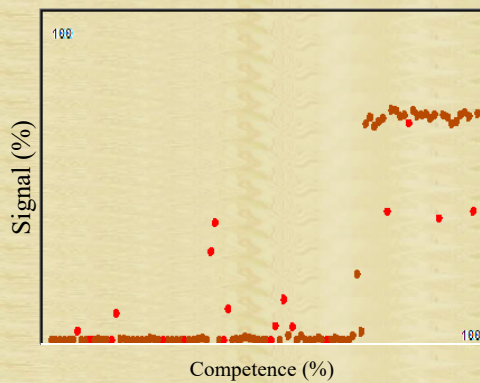
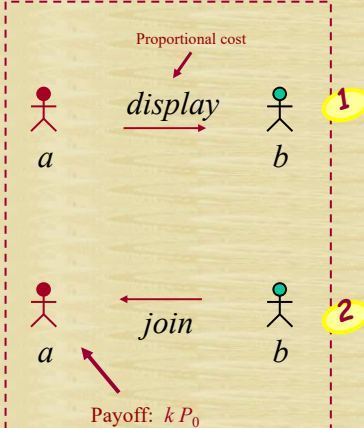
Model 3: outrage

→ norms

Asymmetrical bonds (Twitter-like network, one quality)

Sabine Hossenfelder

Social signals



See also:
Gintis, H., Smith, E. A. & Bowles, S. (2001).
[Costly signaling and cooperation](#)
Journal of Theoretical Biology, 213, 103-119.

Asymmetrical bonds (Twitter-like network, one quality)



turdoides squamiceps

Signal $s(q) = g(q) q$

Cost: $Cg(q)$

Profit: $k P_0$

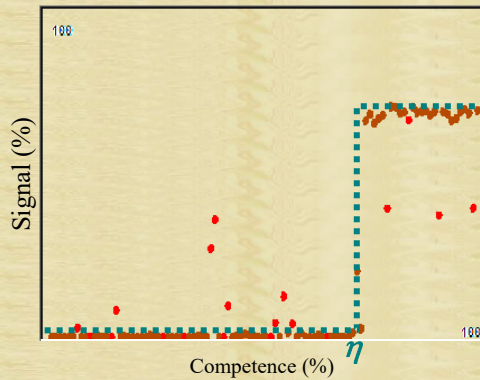
$s(q) = 0$ for $q < \eta$

For $q > \eta$:

Benefit: $B(q) = kP_0 - Cs_0/q$

$$s_0 = \eta = 1 - 1/k$$

$$\rightarrow 1 - 2/k \leq s_0 \leq 1 - 1/k$$



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Dessalles (2014). Optimal investment in social signals. *Evolution*, 68 (6), 1640-1650.

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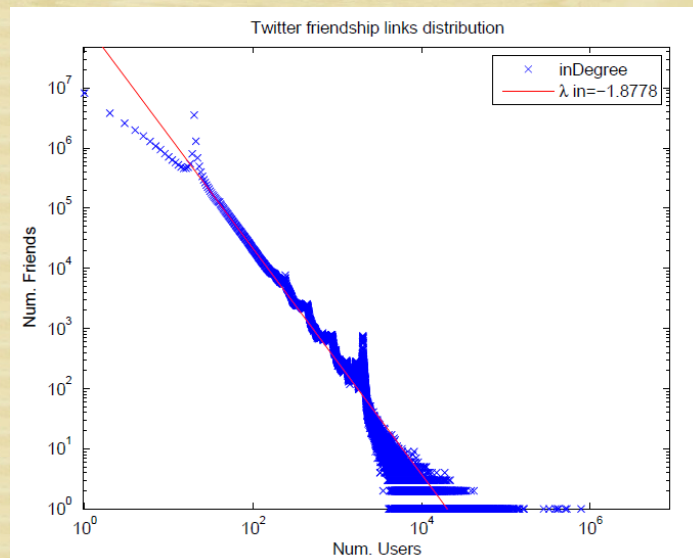
https://friendorfollow.com/twitter/most-followers/ | twitter most follow |

Plans & Pricing | FAQ | Sign In

ND of LOW | Most Followe | 11:14 | 181

The top 100 people and brands with the most Twitter followers.

	followers	following	tv
1. KATY PERRY @katyperry Bio: Love. Light.	107,312,083	216	9
2. Justin Bieber @justinbieber Bio: Let's make the world better. Join me on @bkstg at 'justinbieber'. PURPOSE OUT NOW	104,769,005	304,358	3
3. Barack Obama @BarackObama Bio: Dad, husband, President, citizen. Location: Washington, DC	102,770,287	618,710	1
4. Rihanna @rihanna Bio: New @fentybeauty #STUNNA shades out now!	88,083,690	1,102	1

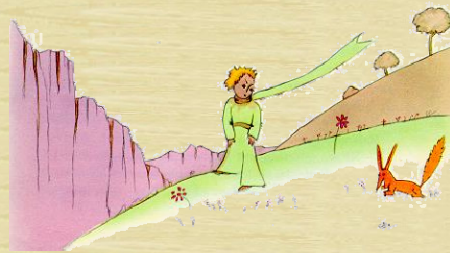


Aparicio, S., Villazón-Terrazas, J. & Álvarez, G. (2015). [A model for scale-free networks: application to twitter](#). *Entropy*, 17 (8), 5848-5867.

Signaling (altruism included)

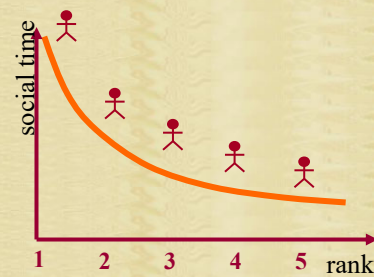
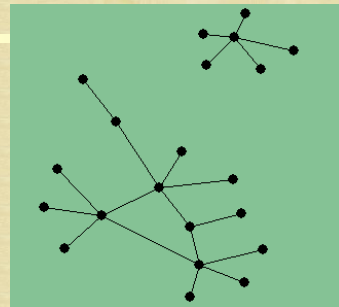
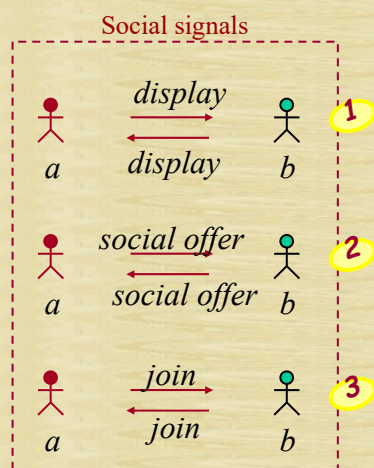
- ✶ Model 0: asymmetrical bonds → stardom
- + Model 1: time sharing → friendship
- ✶ Model 2: praise → heroes
- ✶ Model 3: outrage → norms

C'est le temps que tu as perdu pour ta rose
qui fait ta rose si importante.



*It is the time you have wasted for your rose
that makes your rose so important.*

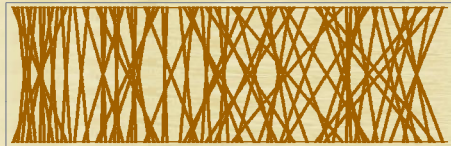
The time sharing (TS) model



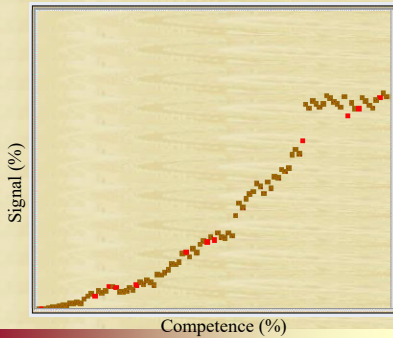
The time sharing (TS) model

profit

$$P(q) = 1 - \prod_i (1 - K r^i q)$$



assortativeness



Competence (%)

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Homophily in Twitter

Homophily in networks

Homophily in humans

Social offer :

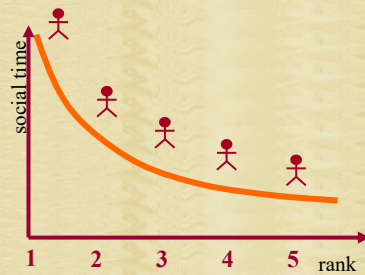
Competence $\times$ Time

$$s(q) \quad r^i$$



i : B's potential rank in A's contact list

r^i : amount of time offered by A to B ($0 \leq r \leq 1$).



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Competitive signaling

profit

$$P(q) = 1 - \prod_i (1 - K r^i q)$$

Signal $s(q) = g(q) q$

Cost: $Cg(q)$

assortativeness

Benefit: $B_c(q) = P(q) - C s(q)/q$

Suppose a mutant with competence q sends the signal normally sent with competence $q+dq$.

The recruitment of a better partner provides

$P(q+dq)$

by dint of an augmented cost $C s(q+dq)/q$.

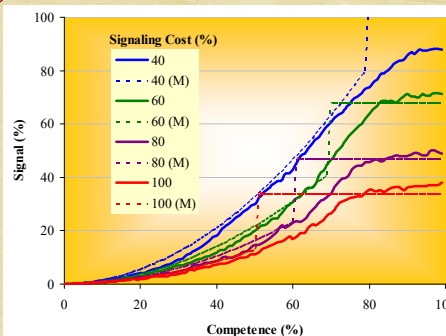
Benefit variation

$$dB_c = P'(q) dq - C s'(q) dq / q$$

must be zero for the equilibrium to be stable:

$$s'(q) = q P'(q) / C$$

$$s(q) = [q P(q) - \int P(q) dq] / C$$



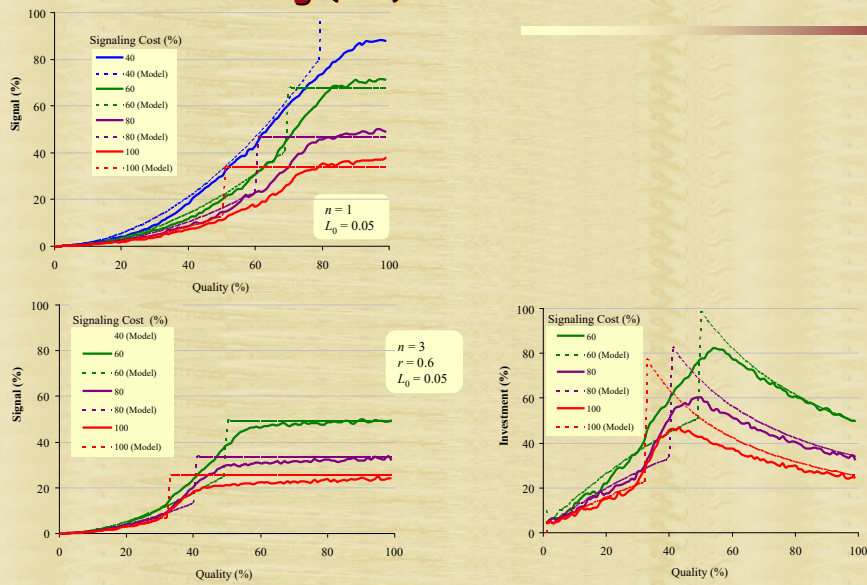
$n = 1, K = 1, L_0 = 0.05$

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Dessalles, J.-L. (2014).
Optimal Investment in Social Signals.
Evolution, 68 (6), 1640-1650.

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The time sharing (TS) model

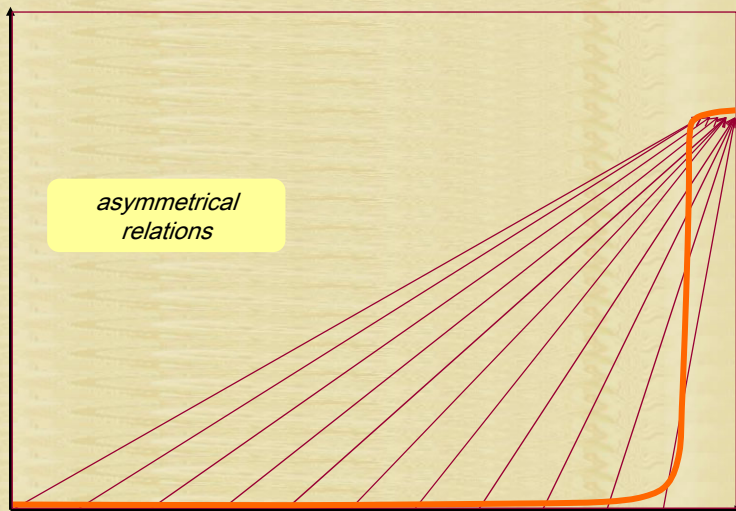


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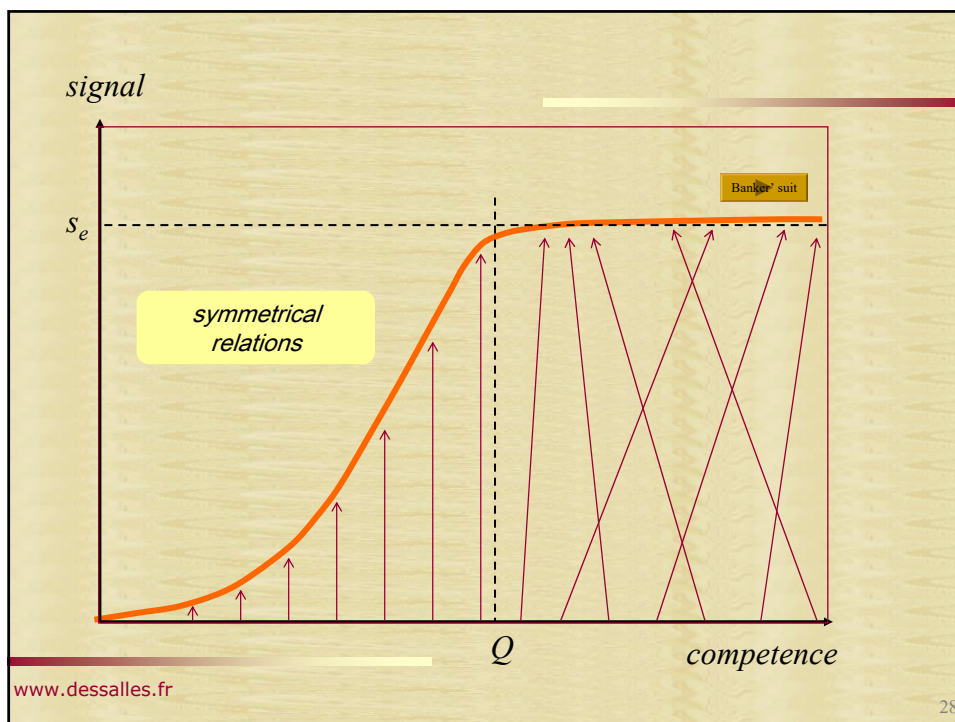
signal



competence

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Last updated: January 25, 2013 6:34 pm

‘Strong’ repayment of ECB cheap funding

By FT Reporters

Banks across Europe pledged to repay more than a quarter of the first tranche of cheap funding they took from the European Central Bank at the height of the debt crisis, the central bank said on Friday, in a further sign of a gradual improvement in the eurozone’s financial system.

Some analysts noted that some banks in southern Europe could be tempted to pay back symbolic amounts of the LTRO money so as to avoid appearing weak in comparison to their rivals.

“Maybe there will be banks that **will try to look better** by paying back **at least a small part** of the money early, and also to reflect their improved liquidity position in comparison to last year,” said Daragh Quinn, a Spanish banking analyst at Nomura.

BBC NEWS BUSINESS

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25 January 2013 Last updated at 13:59 GMT

ECB loans: European banks to repay early

Some of the banks in Europe that received billions in cheap loans to keep them afloat during the eurozone debt crisis are to repay them early.

The European Central Bank (ECB) said that 278 eurozone banks will repay 137.16bn euros (\$185bn, £117bn) of three-year loans they borrowed.

The money, lent in December 2011 and February 2012, will be paid on 30 January, it says.

The loans were made when fear that the euro would collapse was at its peak a year ago

In Spain, [BBVA](#) and [Banco Popular](#), [Banco Sabadell](#) and [Bankinter](#) plan to pay back some LTRO money. Senior bankers have noted that the opportunity to repay early risks **stigmatising banks who do not do so**, heaping pressure on those lenders who still need the cheap funding to at least start their repayments.

Signaling (altruism included)

- Model 0: asymmetrical bonds → stardom
- + Model 1: time sharing → friendship
- Model 2: praise → heroes
- Model 3: outrage → norms

Emergence of acclaimed heroes

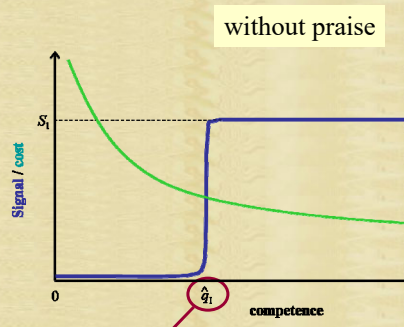
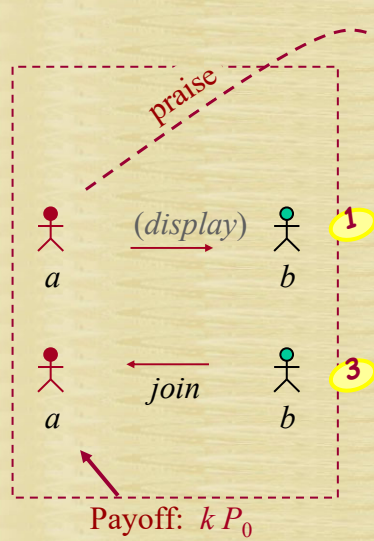
- Some rare people achieve costly feats
... that are often totally altruistic
 - Why?
- Why is there a cheering audience?
- Why not let others cheer?



Emergence of acclaimed heroes

Partially visible signals

- Punctual
- Few witnesses



$$1 - m / (p_1 N)$$

p_1 : default visibility of signals

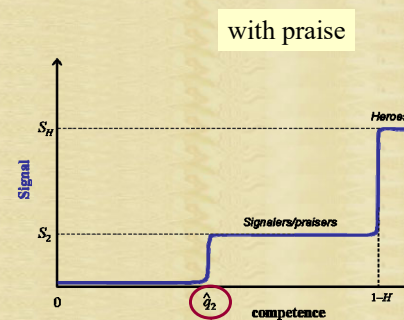
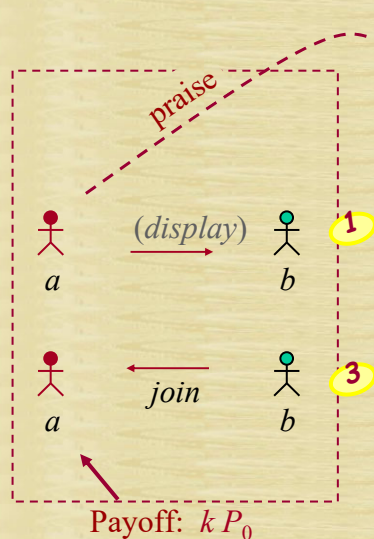
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Emergence of acclaimed heroes

Partially visible signals

- Punctual
- Few witnesses



$$1 - m / (p_2 N)$$

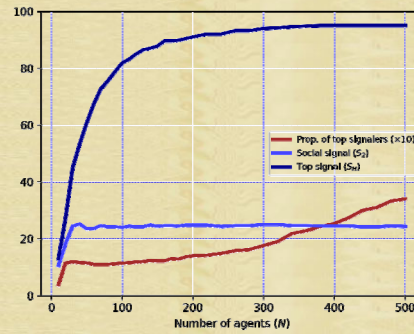
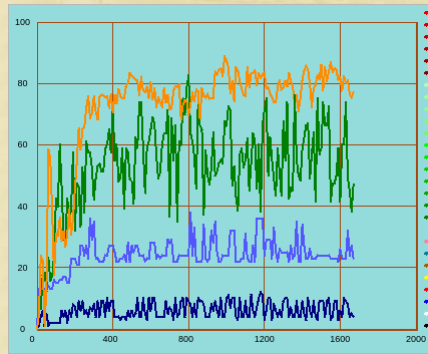
p_2 : visibility of gossipers' signals

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Heroes

Emergence of a few disproportionate signals

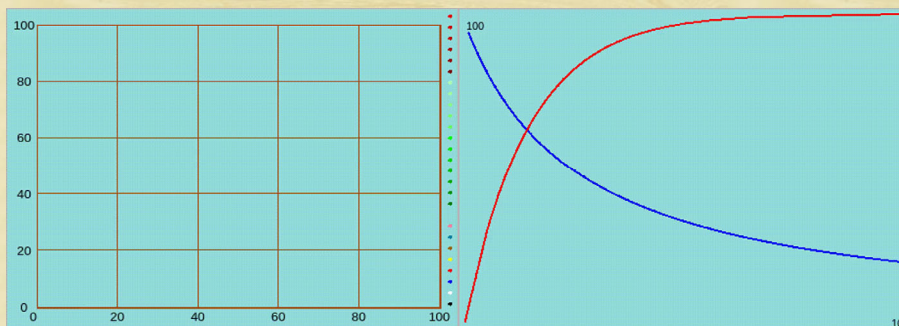


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Dessalles, J.-L. (2025). [Why honor heroes?](#)
The emergence of extreme altruistic behavior
as a by-product of praisers' self-promotion.
Evolution and human behavior, 46 (1), 106656.

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Emergence of acclaimed heroes

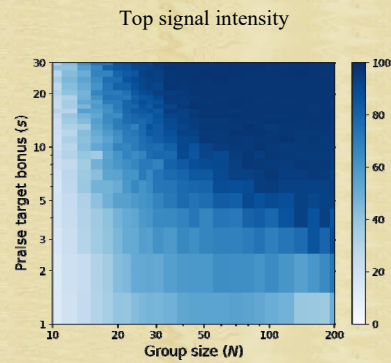
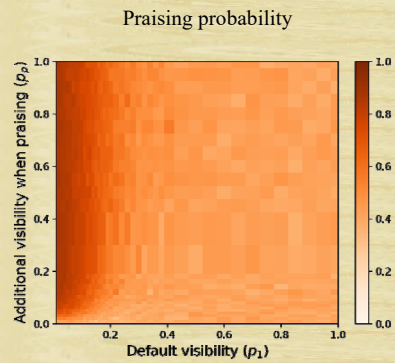


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Emergence of acclaimed heroes

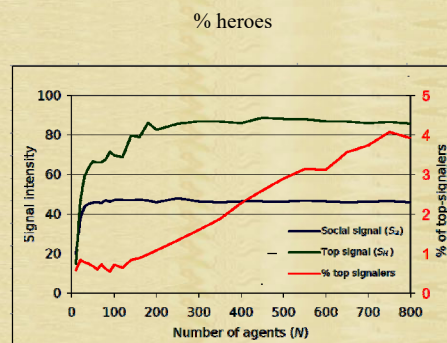
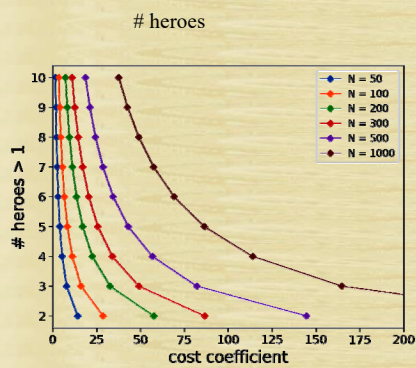


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Emergence of acclaimed heroes



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Signaling (altruism included)

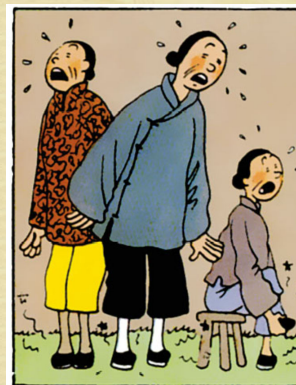
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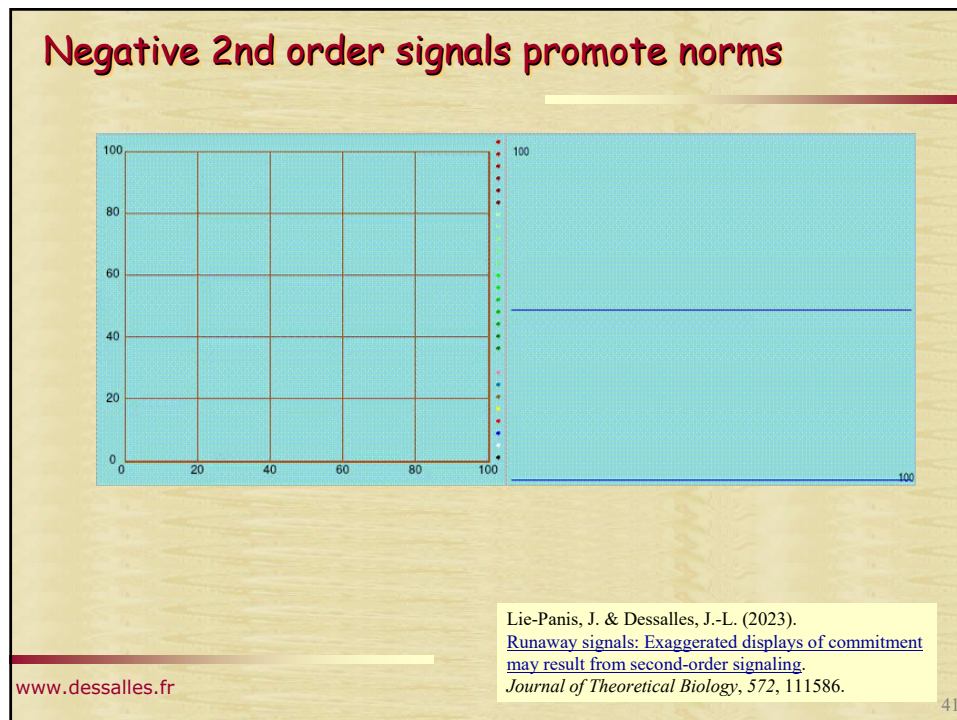
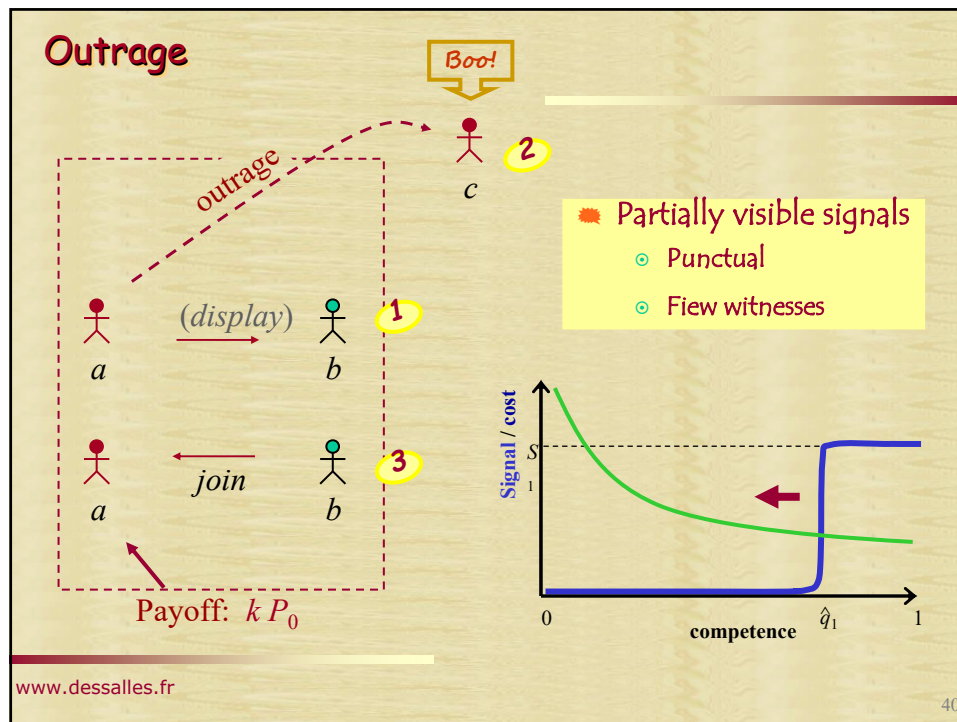
Costly norms

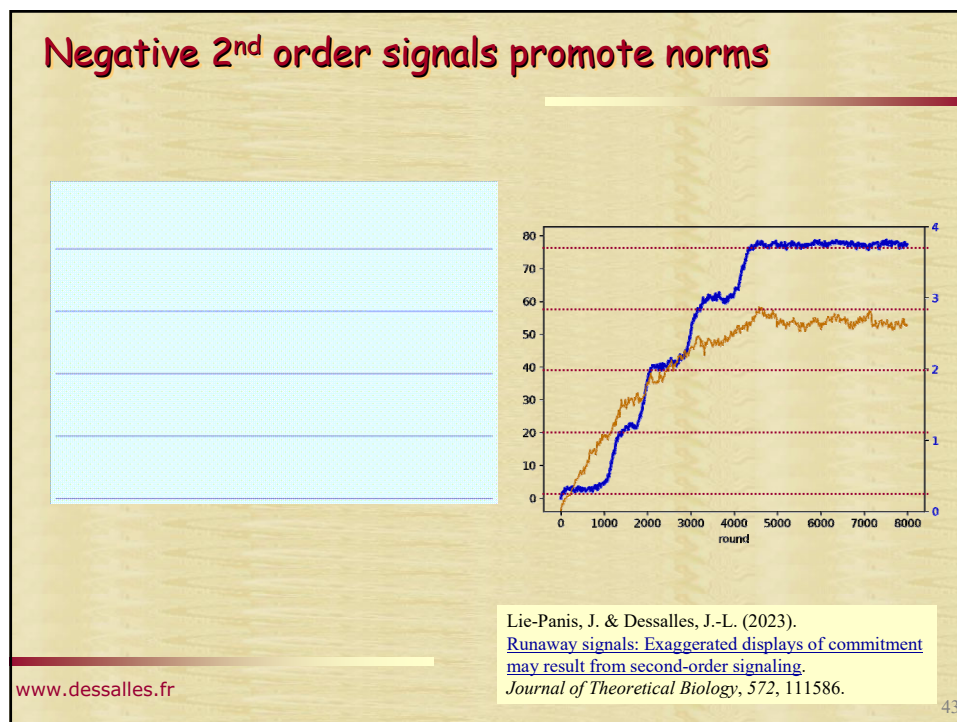
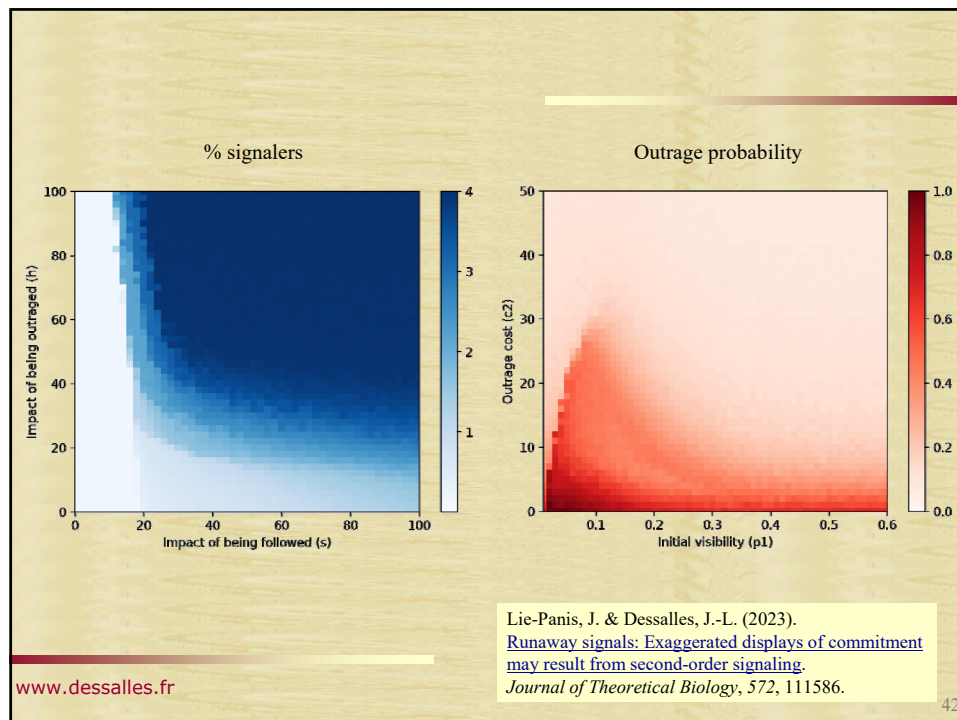
- Costly norms may harm individuals and society as whole

Examples:

- [footbinding](#) lasted for one thousand years in China;
- [infibulation still prevails](#) in some cultures.





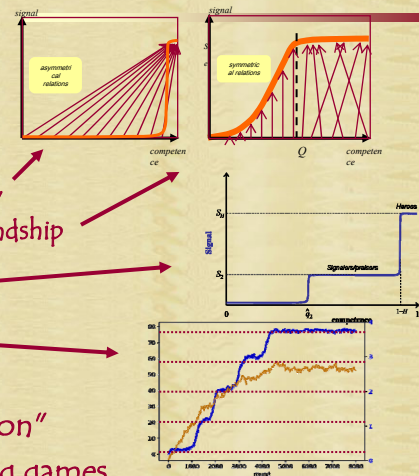


Social signaling

3 social signaling models

- Asymmetrical bonds → stardom,
but symmetrical bonds → friendship
- Praise → heroes
- Outrage → norms

- What authors call "Cooperation"
is embedded in social signaling games



Social signaling

3 social signaling models

- Asymmetrical bonds → stardom,
but symmetrical bonds → friendship
- Praise → heroes
- Outrage → norms



- What authors call "Cooperation"
is embedded in social signaling games

Altruism as a signal