

rspb.royalsocietypublishing.org

Research



Cite this article: Molleman L, van den Broek E, Egas M. 2013 Personal experience and reputation interact in human decisions to help reciprocally. Proc R Soc B 280: 20123044. http://dx.doi.org/10.1098/rspb.2012.3044

Received: 20 December 2012 Accepted: 31 January 2013

Subject Areas:

behaviour, ecology

Keywords:

reciprocal altruism, cooperation, direct reciprocity, indirect reciprocity, repeated games, experimental economics

Author for correspondence:

Lucas Molleman e-mail: l.s.molleman@rug.nl

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2012.3044 or via http://rspb.royalsocietypublishing.org.



Personal experience and reputation interact in human decisions to help reciprocally

Lucas Molleman¹, Eva van den Broek^{2,3} and Martijn Egas⁴

There is ample evidence that human cooperative behaviour towards other individuals is often conditioned on information about previous interactions. This information derives both from personal experience (direct reciprocity) and from experience of others (i.e. reputation; indirect reciprocity). Direct and indirect reciprocity have been studied separately, but humans often have access to both types of information. Here, we experimentally investigate information use in a repeated helping game. When acting as donor, subjects can condition their decisions to help recipients with both types of information at a small cost to access such information. We find that information from direct interactions weighs more heavily in decisions to help, and participants tend to react less forgivingly to negative personal experience than to negative reputation. Moreover, effects of personal experience and reputation interact in decisions to help. If a recipient's reputation is positive, the personal experience of the donor has a weak effect on the decision to help, and vice versa. Yet if the two types of information indicate conflicting signatures of helpfulness, most decisions to help follow personal experience. To understand the roles of direct and indirect reciprocity in human cooperation, they should be studied in concert, not in isolation.

1. Introduction

A key mechanism proposed to explain the evolution of cooperation is reciprocity [1,2]. When individuals interact repeatedly with the same partner, reciprocal donation can lead to mutual cooperation if the probability of future interaction is large enough (direct reciprocity) [3,4]. This mechanism becomes less relevant as group size increases, and thus the probability of two members meeting again decreases. In such situations, indirect reciprocity can favour cooperation if individuals can base the decision to help others on reputation (i.e. information about helping behaviour of individuals in previous interactions with others) [5].

In humans, experimental work on helping behaviour confirms that both direct and indirect reciprocity can promote cooperation [6–8]. Such controlled experiments have focused on one of the two mechanisms in isolation, using designs that ensure the participant's information is either based on earlier interactions with the same individual (personal experience) or based on interactions of the recipient with other individuals (reputation). Other studies have compared effects of each of the two mechanisms, but in separate treatments. Some find higher helping rates towards recipients when information is available from personal experience rather than by reputation [9]. Others report the reverse [10]. Simulations suggest that helping strategies based on reputation can survive in a population with other strategies based on personal experience [11]. However, to the best of our knowledge, strategies based on both types of information were not yet taken into account. When making real-life decisions,

¹Theoretical Biology, University of Groningen, Nijenborgh 7, Groningen 9747 AG, The Netherlands ²Center for Research in Experimental Economics and Political Decision Making, University of Amsterdam, Roetersstraat 11, Amsterdam 1018 WB, The Netherlands

³Department of Economics, University of Munich, Geschwister-Scholl-Platz 1, Munich 80539, Germany ⁴Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, PO Box 94240, Amsterdam 1090 GE, The Netherlands

humans typically use their own experience with another person and the experiences of others with this person. This raises the question how both types of information affect each other in the decision to help.

Here, we report on an experiment in which subjects are allowed to condition helping behaviour on both personal experience and reputation. In a repeated helping game [7,8,12,13], participants are randomly paired, and within pairs one participant is randomly assigned the role of donor and the other the role of recipient. In each game, the donor must decide to (i) give a benefit to the recipient at a cost to himself or (ii) to pass, resulting in no change in payoff for either of them. This helping game is iterated at least 100 times in groups of 12 subjects. To investigate the effects of personal experience and reputation, the game itself is preceded by an information stage in which donors can request costly information about their partner's past behaviour towards the donor (when roles were reversed) and/or towards others. Below, we refer to past behaviour towards the donor or others as 'direct' and 'indirect information', respectively. Donors choose to request either direct and/or indirect information at the same time, but may also decide not to request any information. A request for direct information provides the donor with the recipient's most recent decisions towards the donor, but not the order of decisions. For our baseline experiment, we impose six as a maximum to the number of decisions so that behaviour in the more distant past is ignored [7] (see §2). Donors have no other way to retrieve this information, because subjects cannot be identified. A request for indirect information gives donors insight in the recipient's interaction history by presenting up to the last six decisions of this recipient when paired as a donor with other participants. Hence, indirect information excludes previous direct interactions with the donor. Additionally, we test for two factors that may affect the role of information in our baseline experiment. First, in reality, information on interaction histories with third parties is likely to be noisy owing to mistakes in information transfer (e.g. in gossip). To mimic this, we superimpose noise to the indirect information ('noise' treatment). Second, under random matching, indirect interactions are more frequent than direct interactions. To mimic this, we changed the available information on a recipient's history from six each to two direct decisions and twenty indirect decisions ('asymmetric' treatment).

To address the question of how personal experience and reputation affect helping behaviour, we focus on the following three issues. Do humans base their decisions to help on personal experience as well as on reputations? How do personal experience and reputation affect helping behaviour? Are the effects of personal experience and reputation on decisions to help independent?

2. Material and methods

We conducted a computerized experiment (programmed in z-Tree [14]) in laboratories at the CREED laboratory of the University of Amsterdam and the sociology laboratory of the University of Groningen, the Netherlands. A total of 180 students were recruited to take part in 15 independent sessions (five sessions per treatment) with 12 participants each. In each session, subjects were randomly assigned to cubicles. No communication was allowed. Written instructions for the experiment (in Dutch; see the electronic supplementary material for an English translation) were provided

and a quiz was used to ensure the subjects understood the instructions. Subjects knew that after 100 periods, a next period started with a probability of 0.9 (this was done to minimize end game effects). Each session lasted for approximately 90 min. In addition to a show-up fee of €7, subjects received an initial endowment of 3000 points (300 points = €1). Parameters were chosen such that requesting any type of information had a cost of five points, whereas helping had a cost of 150 to the donor, and a benefit of 250 to the recipient. To avoid income effects as much as possible, no information was given about the subjects' current earnings during the experiment. In principle, however, subjects could calculate their own earnings with pen and paper.

Whenever a participant was assigned the role of donor, two information request boxes were displayed. Choices to help or pass were shown as yellow and blue choices, respectively. When a donor requested information on previous decisions of the recipient, only the *number* of blue and yellow choices in the most recent decisions was given, not the order. In the baseline and the noise treatment, both direct and indirect information was limited to the six most recent decisions, giving subjects an opportunity to 'clean their record' [7]. In our treatments, we use random matching, which implies for the baseline and the noise treatment that direct information is on average less recent than indirect information. Also, for direct information it would take a larger number of periods for an individual to clean its record compared with indirect information. The asymmetric treatment takes into account these arguments by limiting direct information to two decisions, and indirect information to 20 decisions, making both kinds of information equally recent.

We impose a cost of five points for each information request, to ensure that subjects deliberately click on the information they are interested in. In the early phase of the experiment, the total number of decisions presented to the donor may be smaller than the maximum (6 and 6 in the baseline and noise treatment; or 2 and 20 in the asymmetric treatment), or even zero. After decisions have been made, the donors and recipients are informed about their earnings in that period. At the end of the experiment, subjects completed a short questionnaire with topics such as age, gender and educational background. On average subjects earned €36.75 (≈

Requested information of direct interactions was fully accurate. We added some noise to the indirect information in the five sessions of the noise treatment to mimic distorting effects of gossip. One out of six pieces of information was randomly chosen and its content was flipped (i.e. from yellow to blue or vice versa). This implementation is slightly biased against extreme scores, because a 5:1 score is more likely to stem from 6:0 than from 4:2.

Statistical analyses were conducted in R [15]. We used a mixedeffects logit regression model to analyse how decisions to help or requests for direct and/or indirect information depended on various factors. We analysed these generalized linear mixed models (GLMM) using the R package 'lme4' [16]. All GLMM analyses included controls for period/100, and period²/100², correcting the model for temporal patterns in the experiment (e.g. decreasing helping rates in the ending phase of the experiment). Unless stated otherwise, subject was included as random factor, nested in session replicate. As a check of the robustness of the effects obtained, we fitted another mixed-effects logit model to all data, including those decisions preceded by no information. In order to test for the robustness of the statistical findings, we verified that found effects are insensitive to the assumed cumulative probability distributions to help (i.e. probit versus logit).

3. Results

Subjects displayed a high degree of helpful behaviour in all treatments of our experiments (figure 1). Helping rates did

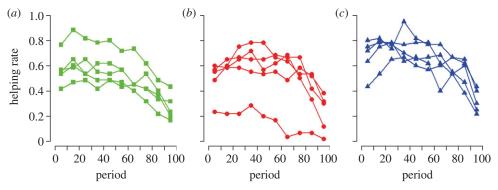


Figure 1. Direct and indirect reciprocity combined lead to high levels of cooperation. Panels show helping rates in the (a) absence and (b) presence of noise in indirect information, and (c) when indirect information was 10 times as abundant as direct information. Symbols represent 10-period averages of helping rates throughout the experimental sessions. Each line represents one replicate session; n = 60 per data point (10 periods \times 6 decisions per period).

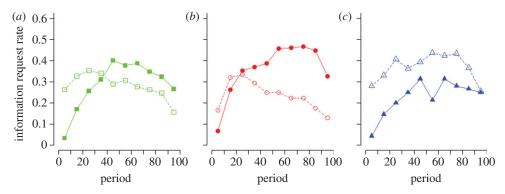


Figure 2. People condition their decision to help on both direct and indirect information. Panels show aggregate rates of information requests in the (a) absence and (b) presence of noise in indirect information, and (c) when indirect information was more abundant than direct information (ratio 20:2). Solid lines and symbols reflect requests for direct information, dashed lines and open symbols reflect requests for indirect information. Symbols represent 10-period averages of the frequency of information requests; n = 300 per data point (5 sessions \times 10 periods \times 6 decisions per period).

not differ between treatments (see the electronic supplementary material, table S1a; Tukey contrasts for treatment effects in GLMM: p > 0.115 for each pair of treatments), and in all replicate sessions of the three treatments helping rates declined towards the end of the experiment (see the electronic supplementary material, table S1a; p < 0.001).

(a) Subjects use information on both direct and indirect interactions

Averaged over all sessions, donors based 49.3 per cent of their decisions on past decisions of the recipient. In an early phase, information on interaction histories is likely to be scarce and is therefore less frequently requested (figure 2; electronic supplementary material, table S1b; p < 0.001). This is particularly true for direct information. Initially, under random matching, subjects are unlikely to have interacted with each other before; as the session progresses, direct information becomes relatively more useful and is therefore requested more often (see the electronic supplementary material, table S1b; p < 0.001). The overall proportion of requests for indirect information tends to decrease over time (see the electronic supplementary material, table S1d; p < 0.001). Overall, adding noise to indirect information decreases its relative proportion of requests compared with direct information (figure 2b; electronic supplementary material, table S1d; p < 0.001). When indirect information is available in higher amounts, it is requested relatively more often (figure 2c; electronic supplementary material, table S1d; p < 0.001). When we control for variation at the individual level, treatments do not significantly differ in request rates for direct information (see the electronic supplementary material, table S1*b*; p = 0.280 and p = 0.460 for the noise and the asymmetric treatment, respectively). However, subjects do tend to increase requests for indirect information in the asymmetric treatment (figure 2c; electronic supplementary material, table S1c; p = 0.043). In §S2 of the electronic supplementary material, we describe patterns of variation at the individual level in the use of information, helping rates and performance in the experiment. Individual rates of requests for direct and indirect information suggest that many individuals are biased towards either direct or indirect information (see the electronic supplementary material, figure S2).

(b) Direct and indirect information affect helping differently

For both direct and indirect information, we find a strong positive correlation between the recipient's helping rate and the rate of being helped (figure 3; electronic supplementary material, table S2; p < 0.001). The two types of information differ, however, in their effect on helping behaviour. We illustrate this with an analysis that contrasts the decisions preceded by requests for direct information only with the

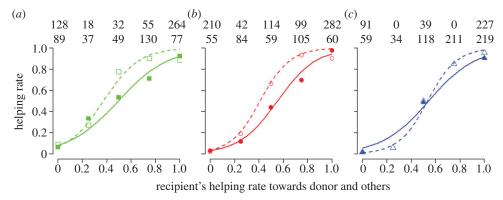


Figure 3. Reciprocal motives prevail in decisions to help. Panels show helping rates preceded by requests for either direct (solid symbols) or indirect (open symbols) information in the (a) absence and (b) presence of noise in indirect information, and (c) when indirect information was more abundant than direct information (ratio 20:2). For each data point, the number of observations is shown above (top row, direct information; bottom row, indirect information). Lines represent logistic regressions fitted to decision data when only direct information was requested (solid lines) or only indirect information was requested (dashed lines).

decisions preceded by requests for indirect information only. A GLMM fit to data detects a significant interaction effect between the observed helping rate of the recipient and the type of requested information (direct or indirect), indicating that direct and indirect information affect decisions to help differently (see the electronic supplementary material, table S2a; p = 0.030). This is in line with the finding that helping rates tend to be higher when donors observed indirect information as opposed to direct information, both in absence and presence of noise (figure $3a_b$). When we consider the difference between the number of helping and passing decisions instead of helping rates, we find the same effects (see the electronic supplementary material, table S2b). On the same range of 'image scores', direct information has a steeper slope in all treatments (see the electronic supplementary material, figure S6 and table S4), suggesting that subjects react to direct information in a more extreme way. No relationship was found between individuals' reliance on reputation and overall helping rate (see the electronic supplementary material, figure S4).

(c) Direct and indirect information are not independent

When we consider decisions preceded by requests for both direct and indirect information, we find that reciprocity effects are significant: positive information (helping the donor in the past, helping others in the past) has positive effects on helping rates (table 1; p < 0.001). The estimated effect of direct information ('help donor') is marginally larger than the estimated effect of indirect information ('help others'), confirming the findings in §3b (effect sizes $(\pm s.e.)$ are 4.620 (0.432) and 3.838 (0.542) for 'help donor' and 'help others', respectively). Also, whenever a recipient's helping rates from direct and indirect information show values on opposing extremes, subjects follow direct information more often; number of helping versus passing decisions equals 41:18 when direct information is positive (greater than 0.5) and indirect information is negative (less than 0.5). In the reverse case, helping versus passing equals 24:29 (Fisher exact test: p = 0.013).

The statistical model shows a significant interaction effect between direct and indirect information. The estimate of the interaction effect is negative (i.e. higher observed helping rates in either type of information are associated with a lower impact of the other type on helping behaviour). The

Table 1. Direct and indirect information are not independent. Values represent regression model estimates of factors affecting decisions to help. The analysis only considers decisions preceded by requests for both direct and indirect information. Significant effects include the recipients' fraction of helpful decisions towards the donor and others, as well as their interaction. Treatments do not affect helping rates significantly. Subject nested in session was included as random effect. Helping rates are centred before entering analysis. Period (squared) was included to control for the decreasing trend in helping rates over time.

	estimate	p
intercept	1.130	0.266
period	3.842	0.223
period ²	- 5.561	0.033
help donor	4.620	< 0.001
help others	3.838	< 0.001
help donor $ imes$ help others	- 3.883	0.006
noise in indirect information	— 0.193	0.793
asymmetric information	- 0.605	0.401

effect of indirect information becomes weaker as direct information is more positive (and vice versa; table 1). When direct information about the recipient indicates this subject often helped the donor, indirect information has a smaller effect on the decision of the donor to help than when the recipient hardly helped the donor. Similarly, when indirect information reveals the recipient often helped others, the effect of direct information is mitigated (figure 4; electronic supplementary material, figure S7 and table S5).

4. Discussion

Our results show how people integrate direct and indirect information about past social interactions (figure 2), confirming the commonly held belief that people use both personal experience and reputations to decide whether or not to help others. Even though information is costly, subjects often condition their decisions about whether to help a recipient on the decisions that this person made previously. Cooperation levels are far above zero in all sessions (figure 1), which is

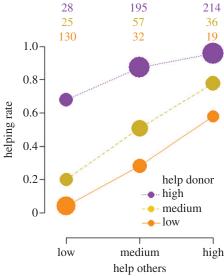


Figure 4. Personal experience and reputations interact in decisions to help. Data points correspond to rates of receiving help when both direct and indirect information were requested, for various categories of recipients' helping rate. The recipients' helping rate towards the donor (help donor) and towards third parties (help others) are both categorized as 'low' (less than or equal to 0.3), 'medium' (0.3-0.7) or 'high' (greater than or equal to 0.7). The sizes of the plotted dots indicate the natural log of the number of constituent data points. These numbers are also given above the graph. Receiving rates are plotted as a function of helping rates towards others, for the three categories of help donor. Effects of indirect information are largest for low values of help donor (solid line). When direct information provides a high signature of helpfulness (dotted line), indirect information has weaker effects (compare the slopes of dotted and solid lines). Thus, the effect or reputation is weak when personal experience is good. A similar pattern emerges in the reverse case: when helping rates towards others are low, the effect of direct information is stronger (data points on the left-hand side, where 'help others' is low, are farther apart than the data points on the right-hand side, where 'help others' is high).

in agreement with a comparable experiment in which subjects always received information but could not distinguish direct from indirect information [7]. The past behaviour of recipients, reflected in direct and indirect information, has strong effects on decisions of donors to help (figure 3, table 1; electronic supplementary material, figure S6, tables S1a, and S2), marking direct and indirect reciprocal motives. It has been argued that indirect reciprocity is likely to wane in large groups because of the noisy nature of information (e.g. owing to gossip [12]; but see [17,18]). In contrast, we find that people show sensitivity to noise not by a lower propensity to help but, at the aggregate level, people react to noise by higher proportions of requests for direct information (figure 2; electronic supplementary material, table S1d). In the asymmetric treatment subjects rely more on indirect information (see the electronic supplementary material, table S1d). Despite the fact that under these conditions direct information was less information-rich (ratio 2:20) but equally costly, subjects frequently rely on direct information in making their decisions to help. This suggests that people have a preference to rely on personal experience, even when it gives a limited picture of a recipient's helpfulness.

Subjects react more strongly to information from personal experience than to reputational information (figure 3a,b, table 1; electronic supplementary material, figure S6, tables S2 and S4). This effect does not appear to be due to differences in individual strategies; individuals relying to different degrees on direct and/or indirect information did not show differences in helping rates (see the electronic supplementary material, figure S4). The inherent contrast between the direct and concrete effects of first-person experience and the indirect and abstract notion of reputation, however, may partly explain the observed pattern. Refusing to help may infuriate a direct partner, whereas the same thing happening to others does little more than eliciting empathy. Alternatively, the relative impact of direct and indirect information could depend on the type of interactions that subjects encounter in their everyday life. For example, public information may guide behaviour of individuals from a small village. In a large city, however, interaction partners are mostly reputation-free strangers to each other. Hence, our results may be influenced by the fact that most participants were students from large cities.

Our results show that reputation has the potential to substantially increase helping rates when personal experience is negative (figure 4). Conversely, however, when personal experience is positive, a bad reputation does not lead to severe decreases in helping. These results are robust to changes in assumptions on the evaluation of (in)direct information in the regression models (see electronic supplementary material, figure S7, table S5). When personal experience is positive, helping rates are generally high, and a good reputation has little scope to increase helping rates even more. Such 'ceiling effects' may partly explain the detected interaction between personal experience and reputations. We believe that these effects are not particular to our experiment. In real life, personal experience and reputations may compensate for each other: people might help others with a bad reputation if personal experience is good. Conversely, people may be more helpful to others after a bad personal experience, if these others have a good reputation (figure 4).

In our experiment, as in previous experiments on reciprocity [6,7,8], the aim is to measure effects of first-order information. Hence, subjects do not know whether previous decisions of their interaction partners are based on any information, and it is impossible to examine if a donor reciprocated the earlier decisions of the recipient. In our experiment it was thereby impossible to use (theoretically superior) strategies that make use of second-order information, such as the reputations of subjects that were refused help by a recipient (e.g. the 'standing' strategy [19-21]). It seems plausible that insight in secondorder information will influence helping behaviour: subjects might forgive a refusal to help more easily when they themselves refused help to a recipient before (but see [22]). In addition, second-order information is likely to affect the frequency and distribution of information requests, as well as the payoffs of reciprocal strategies. Our experimental design can be readily extended to address such scenarios.

Previous theoretical and experimental work on mechanisms driving human cooperative behaviour has focused on direct and indirect reciprocity in isolation. Building theory on the basis of these two mechanisms would require assumptions on how the two types of information—direct experience and reputation—are integrated in social decision making. However, how humans integrate these pieces of information is unknown, as yet. Our experiment shows that the effects of information on personal experience and reputations are interdependent in determining whether to help others: cooperation prevails when either personal experience or reputation is positive. This suggests that a higher level of cooperation can be attained, relative to a situation where only one of the two types of information is available. To understand the roles of direct and indirect reciprocity in human cooperation, these mechanisms should be studied in concert, not in isolation.

We thank Arthur Schram, Martin Kocher, Franjo Weissing, Maurice Sabelis, Dirk Engelmann and two anonymous reviewers for helpful comments and suggestions. The manuscript benefitted from comments by members of the ESA 2007 in Pasadena and the seminar audience at the University of Munich. This paper is part of the research project 'Simultaneous evolution of social norms and social behaviour: a combined theoretical and experimental approach' funded by The Netherlands Organization for Scientific Research (NWO).

References

- 1. Fehr E, Fischbacher U. 2003 The nature of human altruism. Nature 425, 785-791. (doi:10.1038/ nature02043)
- Nowak M. 2006 Five rules for the evolution of cooperation. *Science* **314**, 1560 – 1563. (doi:10. 1126/science.1133755)
- 3. Trivers RL. 1971 The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 35–57. (doi:10.1086/406755)
- 4. Axelrod R, Hamilton W. 1981 The evolution of cooperation. *Science* **211**, 1390 – 1396. (doi:10. 1126/science.7466396)
- Nowak M, Sigmund K. 2005 Evolution of indirect reciprocity. Nature 437, 1291-1298. (doi:10.1038/ nature04131)
- Wedekind C, Milinski M. 1996 Human cooperation in the simultaneous and the alternating Prisoner's Dilemma: Pavlov versus Generous Tit-for-Tat. Proc. Natl. Acad. Sci. USA 93, 2686-2689. (doi:10.1073/ pnas.93.7.2686)
- Seinen I, Schram A. 2006 Social status and group norms: indirect reciprocity in a repeated helping experiment. Eur. Econ. Rev. 50, 581-602. (doi:10. 1016/j.euroecorev.2004.10.005)
- Wedekind C, Milinski M. 2000 Cooperation through image scoring in humans. Science 288, 850-852. (doi:10.1126/science.288.5467.850)

- Bolton GE, Katok E, Ockenfels A. 2005 Cooperation among strangers with limited information about reputation. J. Public Econ. 89, 1457-1468. (doi:10. 1016/j.jpubeco.2004.03.008)
- 10. Dufwenberg M, Gneezy U, Güth W, Van Damme E. 2001 Direct versus indirect reciprocity: an experiment. Homo Oeconom. 18, 19-30.
- 11. Roberts G. 2008 Evolution of direct and indirect reciprocity. *Proc. R. Soc. B* **275**, 173 – 179. (doi:10. 1098/rspb.2007.1134)
- 12. Engelmann D, Fischbacher U. 2009 Indirect reciprocity and strategic reputation building in an experimental helping game. Games Econ. Behav. **67**, 399 – 407. (doi:10.1016/j.qeb.2008.12.006)
- 13. Nowak M, Sigmund K. 1998 Evolution of indirect reciprocity by image scoring. *Nature* **393**, 573 – 577. (doi:10.1038/31225)
- 14. Fischbacher U. 2007 z-Tree: Zurich toolbox for ready-made economic experiments. Exp. Econ. 10, 171 – 178. (doi:10.1007/s10683-006-9159-4)
- 15. R Development Core Team. 2010 R: a language and environment for statistical computing. See http:// www.R-project.org.
- Bates D, Maechler M, Bolker B. 2012 Linear mixedeffects models using S4 classes. See http://lme4.rforge.r-project.org.

- 17. Sommerfeld RD, Krambeck H-J, Semmann D, Milinski M. 2007 Gossip as an alternative for direct observation in games of indirect reciprocity. Proc. Natl Acad. Sci. USA 104, 17 435 – 17 440. (doi:10. 1073/pnas.0704598104)
- 18. Sommerfeld RD, Krambeck H-J, Semmann D, Milinski M. 2008 Multiple gossip statements and their effect on reputation and trustworthiness. *Proc. R. Soc. B* **275**, 2529–2536. (doi:10.1098/rspb.
- 19. Leimar O, Hammerstein P. 2001 Evolution of cooperation through indirect reciprocity. Proc. R. Soc. Lond. B 268, 745-753. (doi:10.1098/rspb.2000.
- 20. Ohtsuki H, Iwasa Y. 2004 How should we define goodness? Reputation dynamics in indirect reciprocity. J. Theor. Biol. 231, 107-120. (doi:10. 1016/j.jtbi.2004.06.005)
- 21. Ule A, Schram A, Riedl A, Cason T. 2009 Indirect punishment and generosity toward strangers. *Science* **326**, 1701 – 1704. (doi:10.1126/science. 1178883)
- 22. Milinski M, Semmann D, Bakker TC, Krambeck HJ. 2001 Cooperation through indirect reciprocity: image scoring or standing strategy? Proc. R. Soc. Lond. B **268**, 2495 – 2501. (doi:10.1098/rspb.2001.1809)