Focus on the success of others leads to selfish behavior

Pieter van den Berg^{a,1}, Lucas Molleman^{a,b,1}, and Franz J. Weissing^{a,2}

^aTheoretical Biology Group, University of Groningen, 9747 AG Groningen, The Netherlands; and ^bThe Centre for Decision Research and Experimental Economics, University of Nottingham, Nottingham NG7 2RD, United Kingdom

Edited by Marcus W. Feldman, Stanford University, Stanford, CA, and approved January 21, 2015 (received for review September 8, 2014)

It has often been argued that the spectacular cognitive capacities of humans are the result of selection for the ability to gather, process, and use information about other people. Recent studies show that humans strongly and consistently differ in what type of social information they are interested in. Although some individuals mainly attend to what the majority is doing (frequency-based learning), others focus on the success that their peers achieve with their behavior (success-based learning). Here, we show that such differences in social learning have important consequences for the outcome of social interactions. We report on a decision-making experiment in which individuals were first classified as frequency- and success-based learners and subsequently grouped according to their learning strategy. When confronted with a social dilemma situation, groups of frequency-based learners cooperated considerably more than groups of success-based learners. A detailed analysis of the decision-making process reveals that these differences in cooperation are a direct result of the differences in information use. Our results show that individual differences in social learning strategies are crucial for understanding social behavior.

social learning | cooperation | individual differences | cultural evolution | personality

Acquiring information about others is a prominent feature of the human behavioral repertoire (1–3). Observing the behavior of others can allow individuals to improve their own knowledge and skills, but it can also be instrumental in anticipating how others will behave in future social interactions. Clues that help to predict how others will behave can allow for better coordination, or for being able to outsmart others for personal gain (4, 5). Indeed, the ability to keep a mental tab about the past actions of others has been put forward as one of the main mechanisms that allowed for the evolution of cooperation in humans (6, 7).

This focus on social information comes with a spectacular capacity to imitate. Imitation and other forms of social learning govern the spread of information between individuals and are therefore at the basis of cultural change. Indeed, it has been argued that these mechanisms of transmission underlie a process of cultural evolution, which is in many ways analogous to genetic evolution (8–10). Social learning has allowed humans to rapidly adapt to all kinds of environmental circumstances and is ultimately responsible for the wide variety of languages, habits, forms of organization, and social norms that are found across cultures (11–14). Because of this, social learning and its group-level consequences have been the object of considerable scientific scrutiny. Laboratory studies and theoretical models have gone hand-in-hand in respectively identifying the social learning strategies that people use (15–18) and determining how these different strategies are shaped by selection (19–21) and affect the outcome of cultural evolution (22–26). The framework of cultural evolution has been successfully applied for a range of purposes, such as understanding the spread and the loss of technologies in human societies (27, 28) and inferring the ancestry of cultural traits such as language and political organization (29–31).

Although there has been extensive focus on identifying the rules that humans use to learn from each other, the possibility that people may differ in the way they learn from others has long been ignored. Only recently, several studies (32–36) have

suggested that there is substantial individual variation in how much social information people use, and in the type of information they are interested in. Some focus on information about the success of others (paying attention to both their decisions and the associated payoffs), whereas others are only interested in the frequencies with which behaviors occur in their social group (disregarding information about the payoffs others obtained). Moreover, individuals tend to use the same social learning strategy across different (social and nonsocial) contexts (35). However, it is unclear how the focus on different types of social information might affect the outcome of social interactions.

In this study, we examine the consequences of individual variation in human social learning strategies on the outcome of cooperative interactions. For this, we conducted a decision-making experiment that consisted of two parts that took place 1 month apart. In part 1, subjects were divided in groups and confronted with a number of different interaction settings. In each interaction round, they were allowed to view a limited amount of information about their peers' previous behavior and earnings. In part 2, we assorted the same subjects in groups based on the social learning strategies they had used in part 1, creating groups of success-based learners and frequency-based learners. These groups were confronted with a cooperation setting, in which each subject had to decide between a selfish option and an option that benefitted the group. We analyze the outcome of the interactions in these groups and investigate whether, and to what extent, differences in cooperation can be traced back to differences in social learning style.

Results

In part 1 of the experiment, 200 subjects were divided in groups of 5 and confronted with four different interaction contexts in

Significance

We report on a two-step decision-making experiment. The first part shows that humans differ consistently in the way they learn from others. Some individuals are success-based learners, who try to identify successful peers and mimic their behavior. Others are frequency-based learners, who tend to adopt the most frequent behavior in their group. The second part reveals that these differences in social learning have important consequences for the outcome of social interactions. In situations where participants had to choose between a selfish option and an option benefitting their group, groups of frequency-based learners achieved considerably higher levels of cooperation than groups of success-based learners. This is the first clear experimental evidence that learning strategies are an important determinant of social behavior.

Author contributions: P.v.d.B., L.M., and F.J.W. designed research; P.v.d.B. and L.M. performed research; P.v.d.B. and L.M. analyzed data; and P.v.d.B., L.M., and F.J.W. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹P.v.d.B. and L.M. contributed equally to this work.

²To whom correspondence should be addressed. Email: F.J.Weissing@rug.nl.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1417203112/-DCSupplemental.

randomized order (nonsocial, cooperation, coordination, and evasion). In each context, they made decisions between two options for 20 consecutive interaction rounds. Each decision resulted in a payoff that depended on the interaction type, the decisions of fellow group members, and also included an element of random noise. Before making a decision, subjects were given the opportunity to view up to four “pieces of information” about their fellow group members at a small cost, where one piece of information consisted of either a previous payoff or a previous decision of a fellow group member. The four interaction contexts we offered are consistent with those considered in our earlier study (35), but here we focus on the three social contexts.

The results of part 1 fully confirm the earlier observation that there are marked individual differences in both the amount of

social information that individuals request, and the type of information they are interested in (35). A large majority of information requests (86.7%) were of two types: individuals either requested the decisions of the four fellow group members in the previous round (henceforth referred to as frequency-information), or they requested both the decision and the payoff of two fellow group members (success-information). Fig. 1*A* classifies all individuals with respect to what type of information they requested in each social context. In all contexts, we find U-shaped distributions, indicating that most subjects consistently focused on either frequency-information or success-information. Fig. 1*B* demonstrates that most subjects were also consistent across the different contexts; almost two-thirds of individuals

Fig. 1. Consistent individual differences in social learning strategies. In part 1 of the experiment, 86.7% of all information requests fell into two categories: subjects either asked for frequency-information (i.e., the decisions of all four group members in the previous round) or they asked for success-information (i.e., the combination of decision and corresponding payoff for two group members in the previous round). (A) Classification of individuals with respect to the fraction of requests an individual targeted at success-information in part 1 of the experiment. In each social context, the histogram reveals a U-shaped distribution: most individuals had extreme social learning strategies, either requesting mainly success-information or requesting mainly frequency-information. (B) Consistency of social learning strategies across the three social contexts in part 1 of the experiment. For each context, individuals were classified as either focused on frequency (more than 50% of their requests used for frequency-information) or focused on success (more than 50% used for success-information). The graph depicts the eight possible combinations of frequency- and success-focus across the three social contexts; the size of the circles indicates the number of individuals falling in each category. The individuals that were consistent over all social contexts are highlighted; consistent frequency-based learners (69) in orange and consistent success-based learners (23) in purple. Ninety-two of the 145 subjects (63.4%) who requested information in at least one round of each social context were consistent across all three contexts. (C) Consistency in the number of information requests over time (between part 1 and part 2 of the experiment, summed over all social contexts) and (D) consistency in type of information requested between part 1 and part 2 (the fraction of information pieces requested that were used for success-information, over all social contexts). In both C and D, the size of the dots indicates number of individuals (the smallest dots representing single individuals), and the red lines represent linear regressions (in both cases, $R^2 = 0.454$, $P < 0.001$).

always focused on the same type of information in all three social contexts.

In part 2, 160 of the subjects that had participated in part 1 were assorted in groups of 5 based on their social learning strategies, resulting in 16 groups of frequency-based learners, 8 groups of success-based learners, and 8 mixed groups (consisting of individuals with varying social learning strategies) as a control. These groups were confronted with the same interaction settings as in part 1, again for 20 consecutive rounds, but the settings were presented in a different way (see *Materials and Methods* for details). Fig. 1 *C* and *D* shows that individual information use was strongly correlated between part 1 and part 2. Subjects were consistent in both the extent to which they requested social information (Fig. 1*C*) and the type of information that they focused on (Fig. 1*D*). Apparently, subjects stuck to their social learning strategy for the 1-month period separating parts 1 and 2. In conclusion, the experiment provides independent confirmation for individual variation in social learning strategies and their consistency across different contexts, and it suggests that these differences are stable over longer time periods.

Here, we provide a detailed analysis of the effect of group assortment with respect to social learning on the subjects' behavior in the cooperation setting (see *SI Appendix*, Fig. S1, for the two other types of social interaction). The cooperation setting was a social dilemma; a situation in which individuals have to choose between their own interest (defection) and the interest of the group they are in (cooperation). In our experiment, cooperation raised the payoffs of all fellow group members but came at a cost to the cooperating individual. Accordingly, it is advantageous to be in a group of cooperators, but defection is associated with an individually higher payoff irrespective of the behavior of the others. Also in this part, there was some random noise added to each payoff, so that it could occur that cooperation paid off better than defection (see *Materials and Methods* for details).

As shown in Fig. 2, the group composition with regard to learning strategy had a systematic and significant effect on the

Fig. 2. Groups of frequency-based learners achieved higher levels of cooperation than groups of success-based learners. Bars show average cooperation rates (± 1 SEM) over all rounds of the social dilemma context in part 2. Data are based on 16 groups of frequency-based learners, 8 mixed groups, and 8 groups of success-based learners. The *P* value shown in the graph refers to a Tukey–Kramer test.

level of cooperation achieved in the group (one-way ANOVA, $F = 4.772$, $P = 0.016$). Particularly, cooperation levels were significantly higher in groups of frequency-based learners than in groups of success-based learners (Tukey–Kramer test, $P = 0.013$), whereas cooperation levels in mixed groups (mostly composed of individuals with inconsistent learning strategies) were intermediate. Due to the higher cooperation levels, average payoffs were significantly higher in groups of frequency-based learners than in groups of success-based learners (one-way ANOVA, $F = 5.083$, $P = 0.013$; Tukey–Kramer test, $P = 0.014$). These results strongly suggest that differences in social learning strategies affect the outcome of social interactions.

How do the observed differences in cooperation level arise? One possibility is that frequency-based learners simply have a stronger tendency to cooperate. Our data do not support this: in the first round of the interaction, when decisions were not yet influenced by social information, cooperation levels did not differ between frequency-based learners and success-based learners (0.362 ± 0.054 and 0.350 ± 0.076 , respectively; Fisher's exact test, $P = 0.839$). Another possibility is that the different cooperation levels are the direct result of the different social learning strategies. To investigate this in more detail, we zoom in on how different types of social information affect subsequent behavior.

Fig. 3*A* shows how subjects behaved after viewing success-information (both the decisions and the payoffs of two fellow group members in the previous round). Subjects were most likely to switch behavior (from cooperation to defection or vice versa) if they observed that others achieved substantially higher payoffs with the opposite behavior. Interestingly, this effect was equally strong for subjects that defected in the previous round and subjects that cooperated. In addition, subjects were generally conservative; if the observed payoff difference in favor of the other behavior was small, they tended not to change their behavior. Apart from this tendency to conservatism, the observed patterns are consistent with success-based learning as it is often implemented in models of cultural evolution (22, 26).

Fig. 3*B* illustrates how subjects behaved after viewing frequency-information (the decisions of their four fellow group members in the previous round). In this case, the response to information was strongly affected by an individual's own previous behavior. After having defected in the previous round, subjects were relatively likely to switch to cooperation (35% of the cases). Interestingly, this switching rate did not depend on the social information they just viewed; it was the same irrespective of the number of fellow group members that cooperated in the previous round. In contrast, subjects who had cooperated in the previous round were responsive to the information they received. The more cooperators they observed among their fellow group members, the more likely they were to continue cooperating themselves. Although this latter pattern has an element of conformism, frequency-based learning as observed in our experiment is quite distinct from conformism as it is generally represented in models of cultural evolution (10, 25, 26). In such models, conformism is typically modeled by a symmetric S-shaped function, indicating that copying a behavior becomes disproportionately more likely the more common the behavior is in the population, causing the common behavior to become even more common over time.

Could the differences in cooperation level between groups of frequency-based learners and groups of success-based learners (as shown in Fig. 2) be fully explained by the response patterns to both types of information (Fig. 3)? To investigate this, we implemented simplified cartoon versions of the observed learning strategies in a simulation model. In the simulations, we used the same payoff functions (and payoff noise level) as in the experiment and assumed that individuals are equally likely to request information as observed in the experiment. The probability of cooperating after not requesting information was also parameterized from our experimental observations. As illustrated

Fig. 3. Cooperation rates after viewing frequency-information and success-information. (A) Probability of cooperation after viewing success-information about two fellow group members, as a function of the difference between the own previous payoff and the observed previous payoffs of others (only instances where the opposite behavior was observed are included). Both after cooperation (blue circles and lines) and after defection (red circles and lines), individuals were more likely to switch their behavior if they observed that the opposite behavior had yielded a higher payoff (logistic regressions, $df = 282$, $P < 0.001$; $df = 268$, $P < 0.001$, respectively). (B) Probability of cooperation after viewing frequency-information about all four fellow group members, as a function of the number of fellow group members that cooperated in the previous round. Individuals that cooperated in the previous round (blue circles) were more likely to cooperate again if they observed that more fellow group members cooperated (blue line: logistic regression, $df = 703$, $P < 0.001$). The number of observed cooperators did not have an effect on cooperation rates when individuals defected in the previous round (red circles; red line: logistic regression, $df = 763$, $P = 0.937$). In both A and B, the size of the circles (as well as the numbers inside them) represent the number of observations. Data are based on pooled results from part 1 and part 2 of the experiment (the patterns are similar for both parts separately; see [SI Appendix, Fig. S2](#)).

in Fig. 4, the differences in social learning rules can indeed account for the observed differences in cooperation.

Discussion

The results of our study can be summarized in three main points. First, our study confirms with an independent experiment that individuals differ systematically and consistently in their social learning strategies. Second, we show for the first time (to our knowledge) that the differences in learning strategies are stable over a longer time period, much like aspects of personality. Third, we demonstrate that individual differences in social learning strategies can strongly affect the outcome of social interactions. In particular, groups of success-based learners reach lower levels of cooperation than groups of frequency-based learners.

Our experiment was designed to investigate the effect of social learning strategies on the outcome of social interactions. Accordingly, we consider the finding that the cooperation level achieved in groups of success-based learners is considerably lower than cooperation in frequency-based learners the main result of this study. There were no differences in cooperation levels between frequency-based learners and success-based learners in the first interaction round. This suggests that the diverging cooperation levels do not result from differences in general cooperation tendencies but are a direct result of how the learning strategies affect behavior. This is also supported by our simulation model. Intuitively, the effect of an individual's social learning strategy on their cooperative behavior can be understood as follows. In a social dilemma, defection yields individually higher payoffs than cooperation, so success-based learning is likely to lead to low levels of cooperation. Frequency-based learners are not as focused on information about payoffs and are therefore less inclined to adopt the individually better-paying option (in this case, defection). Additionally, high levels of cooperation can be sustained by a positive feedback in groups of frequency-based learners: the more fellow group members are observed to cooperate, the higher the inclination of individuals to continue cooperation themselves.

Although this was not the main focus of our study, we provide strong support for our earlier finding (35) that humans differ consistently in their social learning strategies. On purpose, we modified the setup of our experiment in several ways from that of our earlier study: groups were smaller, payoffs and information

cost were different, the degree of random noise on payoffs was higher, and subjects were allowed to request fewer pieces of information. Despite these differences, the vast majority of subjects in both studies consistently used one of two social learning strategies, irrespective of the social context. This strongly suggests that individual differences in social learning strategies are a robust phenomenon. This conclusion is further strengthened by the finding that the subjects of the present study tended to use the same learning strategy in part 2 of the experiment as in part 1. In other words, differences in social learning strategy seem to be stable over time, at least over a period of 1 month. Model studies suggest that such time stability can have important

Fig. 4. Simulation of the effect of social learning strategy on cooperation in a social dilemma. Change in cooperation rates over time for groups of five, containing only frequency-based learners (orange lines) or only success-based learners (purple lines). Lines represent averages over 100,000 replicate simulations. For both scenarios, all possible starting conditions with regard to the initial number of cooperators are shown. The social learning strategies used in the simulations are simplified cartoon versions of the learning rules observed in the experiment (as shown in Fig. 3).

implications, e.g., for signaling intentions and for coordinating behavior within groups (32, 37–39). However, such time stability is rarely investigated in experimental studies. Our study is a first step, but experiments spanning a longer time period and specifically designed to study time stability are required to really judge the stability of differences in social learning strategies.

The finding that individuals differ systematically and consistently in their learning strategies has important implications for the design and interpretation of empirical studies, irrespective of whether they are conducted in the laboratory or the field. For example, an interesting recent study on social learning strategies in a social dilemma in 14 Indian villages found support neither for conformism nor for success-based learning (40). This conclusion is based on statistical analyses (one to test for the use of conformist learning, and one to test for the use of success-based learning) that implicitly assume that the population is homogeneous with regard to social learning strategies. However, even if neither conformism nor success-based learning can be detected at the aggregate level, it is well possible that the population is heterogeneous, harboring significant variation in social learning strategies.

The idea that humans differ fundamentally in the way they gather information was already suggested by Jung (41) but has received relatively little attention in modern systems of personality categorization such as the five-factor model (42, 43). This may be an important shortcoming; if individuals differ systematically in the way they collect, interpret, and respond to information, they will also differ systematically in their behavior. This insight can have important implications for the interpretation of individual differences. Observed behavioral variation need not reflect differences in mental, physiological, or motivational states, but may instead result from differences in social learning strategies. Experimental studies designed to distinguish between these potential causes can help provide proximate explanations of how consistent individual differences in behavior come about.

From where do individual differences in social learning strategies originate? Recent evidence suggests that social learning strategies are at least partially culturally determined (44), but this does not explain the variation in social learning strategies found in the culturally homogeneous sample in this study. Are these differences perhaps “adaptive”; have they been shaped by evolution? Such questions currently play a central role in animal behavior studies (37, 45), where consistent individual differences have been described in hundreds of species across the entire animal kingdom (46, 47). Theoretical studies show that individual differences in social responsiveness (or “social sensitivity”) can arise through frequency-dependent selection, leading to the stable coexistence of responsive types (that condition their behavior on social information) and unresponsive types (that do not use social information) (48). Differences in social learning strategies may also be the result of evolution; modeling studies could elucidate whether and how evolution could lead to this outcome.

In the cooperation setting investigated in our study, groups of frequency-based learners achieved higher payoffs than groups of success-based learners. If frequency-based learning generally leads to superior payoffs, how can we explain that success-based learning still occurs in a social dilemma? This may be an ill-posed question. The fact that individuals consistently use the same social learning strategy in different social contexts suggests that learning rules have not been tailored to perform optimally in every single context. This is in line with the view that evolution does not produce perfect behavior for every circumstance, but rather leads to the emergence of general-purpose strategies, or heuristics, that perform relatively well across the whole range of circumstances that an organism may face (49, 50). It is conceivable that frequency-based learning is superior under some circumstances, whereas success-based learning is superior under other circumstances. Moreover, learning strategies might complement each

other, leading to a faster spread of insights and technologies in groups harboring different learning strategies (35).

The link between frequency-based learning and cooperation has received quite some attention in the literature around the topic of “cultural group selection.” This literature discusses the spread of cooperation through competition between groups, when individuals use conformist learning: the disproportional tendency to copy the majority behavior. Because this type of frequency-based learning reduces variation within groups relative to variation between groups, it makes selection between groups more effective. Some argue that this increases the scope for the cultural evolution of group-beneficial traits (10, 51–55). However, conformism is neutral with regard to behavioral content—it makes it very difficult for any behavior, including cooperation, to spread when initially rare (25, 56). Our experiment does not consider competition between groups but measures the consequences of different learning strategies for the spread of cooperation within groups. Although many of our subjects used frequency-based learning, it was quite distinct from conformism as it is often modeled. In fact, the frequency-based learning we observed did not reduce variation within groups; it led to intermediate levels of cooperation. Also, our results suggest that frequency-based learning in a social dilemma is not neutral with respect to behavior; subjects that defected in the previous round responded to information differently from those who cooperated. It would be interesting to develop models of cultural group selection including individual differences in social learning strategies and more refined versions of frequency-based learning (as observed in our experiment). Such models may help explain both the evolutionary stability of cooperation due to cultural group selection, and the spread of cooperation when initially rare.

Materials and Methods

A total of 200 subjects (mostly students; mean age, 22.9; 68.5% female) participated in the study in a laboratory at the University of Groningen. Participation was by informed consent, and the experimental setup was approved by the Sociological Laboratory of the University of Groningen. Part 1 and part 2 consisted of 10 and 8 sessions of 20 subjects each, respectively. In both parts, subjects were confronted with four interaction contexts (in random order) of 20 rounds each, in groups of five. At the start of each session, subjects received written general instructions that were also read aloud by the experimenters. Before each interaction context, groups were reshuffled randomly, and subjects received specific instructions on their computer screens (see *SI Appendix* for screen shots and the general instructions of both parts). After this, subjects completed a short questionnaire to ensure they had understood the payoff structure of the following context. In part 1, decision making was framed in a context of a choice between planting different crops on a farm. In part 2, the context of decision making was framed as investment choices in a stock market. The basic payoff structures of the contexts were the same between both parts, but the payoffs, noise on payoffs, and information cost in part 2 were scaled with a factor 1.5 compared with part 1 (here, values for part 1 are given). Subjects were not aware of the identity of their group members and were unable to see the computer screens of other participants. The experiment was run with the experimental software z-Tree (57) (code available upon request).

In each context, subjects decided between two options that remained the same in all rounds of that context [we used actual crop names (part 1) and fictitious company names (part 2), but here we will refer to the options as A and B]. All subjects made their choice simultaneously and were then shown the resulting payoff. Before each decision, subjects could choose to collect information about the members of their group, at a cost of 2 points. At the end of part 2, subjects were paid in private proportional to the payoffs they had accumulated over both parts (100 points = 1 euro; mean earnings of subjects that participated in both parts, € 69.93; max earnings, € 94.30; min earnings, € 50.40). We ensured that participants could not end with a negative point total, by giving them a large enough endowment at the start of the experiment. Sessions lasted for ~90 min.

In the social dilemma (see *SI Appendix* for other contexts), payoffs of choosing respectively A and B in part 1 were given by $\pi_A = 40p - 20(1-p) + \varepsilon$ and $\pi_B = 60p + \varepsilon$, where p denotes the fraction of subjects in the group that chose option A, and ε is a stochastic component, drawn from a normal

distribution with mean 0 and SD σ ($\sigma = 20$). The one-shot version of this game has a single Nash equilibrium at $p^* = 0$, even though all subjects obtain a higher payoff at $p = 1$. This shows that collective interests and individual interests are opposed to each other in this context.

Simulations were programmed in C++ (code available upon request). We tracked the cultural evolution of cooperation through 20 rounds for groups consisting either of only frequency-based learners or only payoff-based learners. In each round, individuals received payoffs for cooperation and defection as in the experiment (including noise on payoffs). Individuals used social information with a 36% probability (as in the experiment). If they did not request information, they had a 63% or 16% probability to cooperate, depending on whether they cooperated or defected in the previous round (as in the experiment). If they did request information, the probability of

cooperation was determined by the logistic regressions shown in Fig. 3. Success-based learners viewed two randomly chosen peers—if both these individuals had the same behavior as the focal individual in the previous round, the focal individual was assumed to stay with their previous behavior (with a probability of 1% to switch).

ACKNOWLEDGMENTS. We thank the Department of Sociology at the University of Groningen for access to its recruitment system and laboratory facilities. P.v.d.B. was supported by Grant NWO 022.033.49 of the Graduate Programme of The Netherlands Organisation for Scientific Research. L.M. was supported by an Ubbo Emmius scholarship of the University of Groningen and European Research Council Grant Project COOPERATION (ERC-AdG 295707). The experiments were subsidized by the Dr. J. L. Dobberke Foundation.

- Dunbar RIM (1998) The social brain hypothesis. *Curr Anthropol* 6(5):178–190.
- Dunbar RIM, Shultz S (2007) Evolution in the social brain. *Science* 317(5843):1344–1347.
- Mesoudi A, Whiten A, Dunbar R (2006) A bias for social information in human cultural transmission. *Br J Psychol* 97(Pt 3):405–423.
- Byrne RW, Whiten A, eds (1988) *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans* (Clarendon, Oxford).
- Whiten A, Byrne RW, eds (1997) *Machiavellian Intelligence II: Extensions and Evaluations* (Cambridge Univ Press, Cambridge, UK).
- Nowak MA, Sigmund K (1998) Evolution of indirect reciprocity by image scoring. *Nature* 393(6685):573–577.
- Wedekind C, Milinski M (2000) Cooperation through image scoring in humans. *Science* 288(5467):850–852.
- Dawkins R (1976) *The Selfish Gene* (Oxford Univ Press, Oxford).
- Cavalli-Sforza LL, Feldman M (1981) *Cultural Transmission and Evolution* (Princeton Univ Press, Princeton).
- Boyd R, Richerson PJ (1985) *Culture and the Evolutionary Process* (Univ of Chicago Press, Chicago).
- Gintis H (2000) *Game Theory Evolving: A Problem-Centered Introduction to Evolutionary Game Theory* (Princeton Univ Press, Princeton).
- Boyd R, Richerson PJ, Henrich J (2011) The cultural niche: Why social learning is essential for human adaptation. *Proc Natl Acad Sci USA* 108(Suppl 2):10918–10925.
- Mesoudi A (2011) *Cultural Evolution: How Darwinian Theory Can Explain Human Culture and Synthesize the Social Sciences* (Univ of Chicago Press, Chicago).
- Whiten A, Erdal D (2012) The human socio-cognitive niche and its evolutionary origins. *Philos Trans R Soc Lond B Biol Sci* 367(1599):2119–2129.
- Traulsen A, Semmann D, Sommerfeld RD, Krambeck HJ, Milinski M (2010) Human strategy updating in evolutionary games. *Proc Natl Acad Sci USA* 107(7):2962–2966.
- Morgan TJH, Rendell LE, Ehn M, Hoppitt WJE, Laland KN (2011) The evolutionary basis of human social learning. *Proc R Soc B Biol Sci* 279(1729):653–662.
- Atkisson C, O'Brien MJ, Mesoudi A (2012) Adult learners in a novel environment use prestige-biased social learning. *Evol Psychol* 10(3):519–537.
- Hoppitt WJE, Laland KN (2013) *Social Learning: An Introduction to Mechanisms, Methods and Models* (Princeton Univ Press, Princeton).
- Laland KN (2004) Social learning strategies. *Learn Behav* 32(1):4–14.
- Kendal J, Giraldeau LA, Laland K (2009) The evolution of social learning rules: Payoff-biased and frequency-dependent biased transmission. *J Theor Biol* 260(2):210–219.
- Nakahashi W, Wakano JY, Henrich J (2012) Adaptive social learning strategies in temporally and spatially varying environments: How temporal vs. spatial variation, number of cultural traits, and costs of learning influence the evolution of conformist-biased transmission, payoff-biased transmission, and individual learning. *Hum Nat* 23(4):386–418.
- Henrich J (2001) Cultural transmission and the diffusion of innovations: Adoption dynamics indicate that biased cultural transmission is the predominate force in behavioral change. *Am Anthr* 103(4):992–1013.
- Sigmund K, De Silva H, Traulsen A, Hauert C (2010) Social learning promotes institutions for governing the commons. *Nature* 466(7308):861–863.
- Rendell L, et al. (2011) Cognitive culture: Theoretical and empirical insights into social learning strategies. *Trends Cogn Sci* 15(2):68–76.
- Molleman L, Pen I, Weissing FJ (2013) Effects of conformism on the cultural evolution of social behaviour. *PLoS One* 8(7):e68153.
- Molleman L, Quiñones AE, Weissing FJ (2013) Cultural evolution of cooperation: The interplay between forms of social learning and group selection. *Evol Hum Behav* 34(5):342–349.
- Henrich J (2004) How adaptive cultural processes can produce maladaptive losses: The Tasmanian case. *Am Antiq* 69(2):197–214.
- Henrich J, Henrich N (2010) The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. *Proc R Soc B Biol Sci* 277(1701):3715–3724.
- Gray RD, Drummond AJ, Greenhill SJ (2009) Language phylogenies reveal expansion pulses and pauses in Pacific settlement. *Science* 323(5913):479–483.
- Currie TE, Greenhill SJ, Gray RD, Hasegawa T, Mace R (2010) Rise and fall of political complexity in island South-East Asia and the Pacific. *Nature* 467(7317):801–804.
- Dunn M, Greenhill SJ, Levinson SC, Gray RD (2011) Evolved structure of language shows lineage-specific trends in word-order universals. *Nature* 473(7345):79–82.
- Wolf M, Weissing FJ (2012) Animal personalities: Consequences for ecology and evolution. *Trends Ecol Evol* 27(8):452–461.
- Efferson C, Lalive R, Richerson PJ, McElreath R, Lubell M (2008) Conformists and mavericks: The empirics of frequency-dependent cultural transmission. *Evol Hum Behav* 29(1):56–64.
- Mesoudi A (2011) An experimental comparison of human social learning strategies: Payoff-biased social learning is adaptive but underused. *Evol Hum Behav* 32(5):334–342.
- Molleman L, van den Berg P, Weissing FJ (2014) Consistent individual differences in human social learning strategies. *Nat Commun* 5:3570.
- Toelch U, Bruce MJ, Newson L, Richerson PJ, Reader SM (2014) Individual consistency and flexibility in human social information use. *Proc Biol Sci* 281(1776):20132864.
- Wolf M, Weissing FJ (2010) An explanatory framework for adaptive personality differences. *Philos Trans R Soc Lond B Biol Sci* 365(1560):3959–3968.
- McNamara JM, Leimar O (2010) Variation and the response to variation as a basis for successful cooperation. *Philos Trans R Soc Lond B Biol Sci* 365(1553):2627–2633.
- Wolf M, Van Doorn GS, Weissing FJ (2011) On the coevolution of social responsiveness and behavioural consistency. *Proc Biol Sci* 278(1704):440–448.
- Lamba S (2014) Social learning in cooperative dilemmas. *Proc Biol Sci* 281(1787):20140417.
- Jung CG (1971) *Psychological Types*. Collected Works (Princeton Univ Press, Princeton), Vol 6.
- Digman JM (1990) Personality structure: Emergence of the five-factor model. *Annu Rev Psychol* 41:417–440.
- McCrae RR, John OP (1992) An introduction to the five-factor model and its applications. *J Pers* 60(2):175–215.
- Mesoudi A, Chang L, Murray K, Lu HJ (2015) Higher frequency of social learning in China than in the West shows cultural variation in the dynamics of cultural evolution. *Proc Biol Sci* 282(1798):20142209.
- Wolf M, van Doorn GS, Leimar O, Weissing FJ (2007) Life-history trade-offs favour the evolution of animal personalities. *Nature* 447(7144):581–584.
- Gosling SD (2001) From mice to men: What can we learn about personality from animal research? *Psychol Bull* 127(1):45–86.
- Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: An ecological and evolutionary overview. *Trends Ecol Evol* 19(7):372–378.
- Wolf M, van Doorn GS, Weissing FJ (2008) Evolutionary emergence of responsive and unresponsive personalities. *Proc Natl Acad Sci USA* 105(41):15825–15830.
- Gigerenzer G, Todd PM, ABC Research Group (1999) *Simple Heuristics That Make Us Smart* (Oxford Univ Press, New York).
- Fawcett TW, et al.; Modelling Animal Decisions Group (2014) The evolution of decision rules in complex environments. *Trends Cogn Sci* 18(3):153–161.
- Henrich J, Boyd R (1998) The evolution of conformist transmission and the emergence of between-group differences. *Evol Hum Behav* 19(4):215–241.
- Boyd R, Gintis H, Bowles S, Richerson PJ (2003) The evolution of altruistic punishment. *Proc Natl Acad Sci USA* 100(6):3531–3535.
- Guzmán AR, Rodríguez-Sickert C, Rowthorn R (2007) When in Rome, do as the Romans do: The coevolution of altruistic punishment, conformism, and cooperation. *Evol Hum Behav* 28(2):112–117.
- Scheuring I (2009) Evolution of generous cooperative norms by cultural group selection. *J Theor Biol* 257(3):397–407.
- Boyd R, Richerson PJ, Henrich J (2011) Rapid cultural adaptation can facilitate the evolution of large-scale cooperation. *Behav Ecol Sociobiol* 65(3):431–444.
- Lehmann L, Feldman MW, Foster KR (2008) Cultural transmission can inhibit the evolution of altruistic helping. *Am Nat* 172(1):12–24.
- Fischbacher U (2007) z-Tree: Zurich toolbox for ready-made economic experiments. *Exp Econ* 10(2):171–178.