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Spontaneous similarity discrimination in the evolution of cooperation

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ABSTRACT

The similarity discrimination effect occurs when a single gene or gene cluster causes its carriers to display both a variable phenotypic trait and a behavioural predisposition to cooperate preferentially with recognisably similar carriers. We distinguish this from the greenbeard effect, in which cooperation evolves through fixed phenotypic tags and genetically linked cooperative behaviour with others displaying the same tag. Our agent-based simulations show that the evolution of cooperation through similarity discrimination, in contrast to the greenbeard effect, does not depend on population viscosity or other restrictive conditions. Similarity discrimination evolves spontaneously in well mixed populations, not only in the Prisoner's Dilemma game but also across a range of different binary-choice strategic interactions, provided that agents can distinguish reliably between similar and dissimilar co-players.

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1. Introduction

Darwin's theory of evolution rests on a competitive process of natural selection in which only the fittest individuals survive. But cooperation abounds in nature, despite its costliness in individual fitness, and Darwin (1859) knew that this posed the most serious problem for his theory. The existence of highly cooperative and altruistic sterile workers in colonies of ants presented a problem that seemed to him, at first, "insuperable, and actually fatal to my whole theory" (p. 236). The solution that he suggested tentatively was that natural selection can occur between families as well as between individuals. More than a century later, Hamilton (1964) developed this inchoate idea into a rigorous theory according to which natural selection operates through *inclusive fitness*, a gene being favoured not merely if it increases the fitness of its carrier, but more generally if it increases the fitness of all of its carriers.

According to Hamilton's (1964, 1970) rule, the relative frequency within a population of a gene encoding cooperative or altruistic behaviour will increase if $rb > c$, where r is the coefficient of genetic relatedness between the cooperator and the recipient, or more specifically a statistical measure of their genetic similarity relative to the average similarity of all population members; b is the fitness benefit to the recipient of the behaviour; and c is the fitness cost to the cooperator. Fitness benefits and costs are defined as increases or decreases in expected lifetime reproductive success. Thus, according to Hamilton's rule, a gene for cooperative or altruistic behaviour will

spread if the benefit to the recipient, discounted by the coefficient of genetic relatedness, exceeds the cost to the cooperator. The rule encapsulates the current interpretation of natural selection in its most general form (Grafen, 2009; West and Gardner, 2010). It formalizes a logical implication of natural selection arising from the fact that individuals can pass on genes to later generations not only via their own immediate offspring (direct fitness) but also via the offspring of genetically related individuals carrying copies of the same genes (indirect fitness).

The most familiar form of inclusive fitness is *kin selection* (Maynard Smith, 1964), whereby a gene increases the fitness of its carriers' close relatives, but there are other mechanisms through which inclusive fitness can operate, without kin selection. The research reported in this article focuses on what we call the *similarity discrimination effect*, whereby a gene, or a tight cluster of genes, is favoured by natural selection if it produces a phenotypic trait that exhibits variability within the population and simultaneously causes its carriers to cooperate selectively with recognisably similar carriers, even if they are not close relatives by descent and are genetically related only at the locus or loci encoding for the variable phenotypic trait and the behavioural similarity discrimination. In this case, the coefficient of genetic relatedness r applies only to the relevant genes and not to the entire genome (Hamilton, 1964, 1970).

The similarity discrimination effect is related to, but subtly distinct from the mechanism whereby a gene, or a cluster of genes, is favoured by natural selection if it produces a recognisable phenotype or tag and simultaneously causes its carriers to cooperate selectively with other carriers displaying the same tag. Ever since Dawkins (1976) suggested a green beard as a vivid though intentionally fanciful example of a suitable phenotypic tag, this form of

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inclusive fitness has been called the *greenbeard* effect.¹ A variant form – the so-called *spiteful greenbeard* effect – occurs when the behavioural discrimination takes the form of costly behaviour selectively harming carriers that do not display the tag, rather than cooperating with those that do (Grafen, 1985; Hamilton, 1970). In contradistinction to the greenbeard effect, the similarity discrimination effect does not involve an individual conditioning its behaviour on any specific phenotypic tag displayed by another individual, but rather on whether or not the other individual's phenotype, *whatever it is*, is similar to its own.

Researchers were initially sceptical about the greenbeard effect (Dawkins, 1976; Hamilton, 1964; Maynard Smith, 1976), largely because, on the one hand, it seemed improbable that a single gene could carry the pleiotropic burden of encoding both a recognisable phenotypic tag and the necessary similarity-discriminative cooperative (or spiteful) behaviour. If, on the other hand, the tag and the behaviour were assumed to be encoded at separate loci, then the greenbeard strategy would be evolutionarily unstable, because cheating *falsebeards*, displaying the tag but not the cooperative behaviour, could emerge through recombination and mutation and displace the greenbeards. Nevertheless, a clear instance of a spiteful greenbeard effect was discovered in the red fire ant *Solenopsis invicta*, when it was shown that *Bb* heterozygote workers, at the locus *GP-9*, distinguish *Bb* from homozygote *BB* queens on the basis of a recognisable odour and kill the *BB* queens (Keller and Ross, 1998; Ross and Keller, 2002), the allele *b* being prevented from fixing by the fact that the *bb* genotype is lethal in adults. Several instances of cooperative greenbeard effects were subsequently discovered, including most strikingly cell adhesion in the social slime mould *Dictyostelium discoideum*, in which only carriers of the *csA* gene adhere to one another and form cooperative fruiting bodies (Queller et al., 2003). Close or complete linkage between tag and behaviour are assumed to exist in these cases – in fact, the effect in the slime mould *D. discoideum* appears to be a single-gene effect – and it is therefore reasonable to assume that similar linkage between genes encoding variable phenotypic traits and similarity-discriminative behaviour may at least be possible.

Greenbeard effects may be far more common in nature than is generally recognised, because it is difficult or impossible to observe the effect after selection has driven it to fixation. In such cases, individuals lacking the tag and the associated behaviour will no longer be present in the population, and the behavioural discrimination will therefore not be apparent, although it will still be exhibited and will still have beneficial fitness consequences (Gardner and West, 2010; Haig, 1996). For the same reason, similarity discrimination may also be partly hidden in natural populations and difficult to uncover. It must be acknowledged that there is likely to be strong evolutionary pressure to weaken the link between the variable phenotypic trait and behaviour involved in the similarity discrimination effect, unless the two are completely linked, because recombinants will be at a selective advantage if they can exploit those that retain the link. However, provided that complete or at least very strong linkage can be maintained, as appears possible with the greenbeard effect, the research described below suggests that similarity discrimination may evolve relatively easily and robustly across a wide range of strategic interactions.

1.1. Simulation and modelling

Agent-based computational simulation and mathematical modelling have confirmed that cooperation can evolve if agents

¹ Researchers refer jocularly to the study of greenbeard effects as *chloropogonology*, from Greek *chloros* pale green + *pogon* a beard + *logos* word, discourse, or reason.

are assigned uniform arbitrary tags and are programmed to cooperate with individuals carrying the same tags (Riolo et al., 2001), but only if cooperation is mandatory with recipients displaying the tag, thus arbitrarily and unrealistically excluding the possibility of unconditionally competitive or selfish agents who do not cooperate even with similarly tagged recipients (Roberts and Sherratt, 2002; Tanimoto, 2007), or if the mutation rate is high for the tag and low for the behaviour (Antal et al., 2009). If cooperation with recipients displaying the tag is not pre-programmed but is allowed to evolve naturally, without close linkage between tags and behaviour, then cheating tends to erode the tag variability on which the mechanism depends (Gardner and West, 2010). This can be overcome by an oscillating process of *beard chromodynamics* in which continual mutation causes old tags to be replaced by new ones (Jansen and van Baalen, 2006; Van Baalen and Jansen, 2003), but research findings suggest that this works only in viscous populations with limited dispersal, in which all interactions tend to be with close relatives.

Spontaneous evolution of stable cooperation has been reported in a few studies, but once again only in very viscous populations (Axelrod et al., 2004; Hammond and Axelrod, 2006), in set structured populations with payoff parameters assuming certain restrictive values (Tarnita et al., 2009), or under conditions of incomplete information, when individual thresholds for cooperation with others are sometimes, but not always, known to the other population members (Masuda and Ohtsuki, 2007). Taken together, these findings appear to suggest that cooperation with other individuals displaying an identical fixed tag can evolve spontaneously, but only with difficulty and under restrictive conditions.

For the similarity discrimination effect, in contrast, our findings suggest that such restrictive conditions may be unnecessary. By avoiding the problems associated with independently inherited fixed tags and behaviour (Fehr and Fischbacher, 2005; Pepper and Smuts, 2002; West and Gardner, 2010), we show that mandatory cooperation, population viscosity or structure, beard chromodynamics, incomplete information, and other special conditions and mechanisms are unnecessary, and that mutual cooperation evolves spontaneously and easily through similarity discrimination across a remarkably wide range of strategic structures. Using much simpler models than those used to study the greenbeard effect, we allow similar individuals to recognise one another by direct comparison of their genomes. From an evolutionary point of view, this is equivalent to the process that occurs if a recognisable and variable phenotypic trait is encoded by the same gene as the associated behaviour or, what amounts to the same thing, if the genes encoding the variable phenotypic trait and the behaviour are completely linked, ensuring that similarity can be recognised reliably. Our results show that, in these circumstances, stable mutual cooperation evolves through the spontaneous emergence of similarity discrimination, even in well mixed populations, provided that the evolving propensity to cooperate with similar individuals varies continuously and sufficient variability is preserved across generations to provide a purchase for similarity discrimination. If these conditions are satisfied, then similarity discrimination evolves not only in the Prisoner's Dilemma game, but also across a range of other strategic structures.

2. Prisoner's dilemma and other strategic structures

In the Prisoner's Dilemma game, and some other strategic structures, cooperation and altruism are inextricably linked. Consider any strategic interaction in which two players each have a choice between one action (altruism) that involves paying a cost c to provide a benefit b to the recipient and is thus altruistic by definition, and an alternative action (defection) that entails no cost or benefit to either player. Provided that $c < b$, mutual altruism

results in a payoff of $b - c$ to each player, which is clearly preferable to the zero payoff for mutual defection; but a unilateral defector receives the benefit b without any cost (the best of all possible payoffs), while a unilateral altruist pays the cost c without any benefit (the worst of all payoffs). This payoff structure is a simple (decomposable) Prisoner's Dilemma game, in which it is easy to see that mutual cooperation corresponds precisely to mutual altruism. Properly understood, mutual cooperation is reciprocated beneficial behaviour between two or more individuals—it is an irreducibly interactive phenomenon that cannot be understood or even adequately defined at the individual level.

If players recognise each other as *identical* to themselves, then cooperation is the optimal strategy, even in one-shot, unrepeated Prisoner's Dilemma interactions between strangers. Howard (1988) and Danielson (1992) independently proved that rational decision makers have a reason to cooperate if they recognise their co-players to be identical to themselves. Both researchers formalized the problem in terms of game-playing automata that can compare their programs and identify co-players identical to themselves when they meet them. The gist of the argument is that each player, knowing that the co-player is identical, can reason validly that any strategy choice is bound to be mirrored by the co-player's choice, because an identical co-player must make the same choice in the same situation; therefore, because mutual cooperation pays better than mutual defection, it is rational for a self-interested agent to cooperate. Furthermore, a population of identical cooperators must be evolutionarily stable against invasion by mutants or migrants who invariably defect. Both Howard and Danielson implemented this argument computationally, showing that if all players use the self-recognition programme and cooperate only against identical co-players, then every game will be played cooperatively. The relevance of this argument to cooperation in nature is limited by the requirement that the cooperating players must be literally identical, but we have easily proved that if players are similar but not identical, and if the probability that both will choose the same strategy is π , then the fitness payoff from cooperation exceeds that from defection whenever $\pi > (b+c)/2b$ (see Appendix A). This suggests that similarity, even when it is incomplete or partial, may play a part in the evolution of cooperation.

There are other strategic structures apart from the Prisoner's Dilemma game that afford opportunities for cooperation, although they have not received as much attention from researchers as they merit, considering that there is no obvious reason to suppose that they occur any less frequently in natural strategic interactions. We studied six symmetric 2×2 games (Fig. 1) in which mutual cooperation pays better than mutual defection but players nevertheless have reasons to defect. Players are tempted to defect by the possibility of the best payoff in Games 1a and 1f, and to avoid the worst payoff in Games 1b, 1c, and 1d. Game 1a is the Prisoner's Dilemma game in which, in addition, the defecting D strategy is dominant, in the sense that it yield a better payoff than the cooperative C strategy against both counterstrategies of the co-player. In Game 1e, a strategy choice has no effect on the payoff of the player who chooses it, each player's payoff depending exclusively on the co-player's choice, but the only way to obtain a higher payoff than the co-player is by defecting, and this reason for defecting exists also in all of the other games.

We included the Leader game (1f) mainly for comparison and did not expect it to support the evolution of cooperation or similarity discrimination. It is the only one of our games with no symmetric pure-strategy *Nash equilibrium*. In a Nash equilibrium, each player's strategy is a *best reply* to the co-player's, in the sense that it yields a higher payoff than the alternative strategy, given the strategy that the co-player has chosen. Mutual defection is a Nash equilibrium in the Prisoner's Dilemma game, and mutual cooperation is a Nash equilibrium in all of the other

a		II		b		II	
		C	D			C	D
I	C	3, 3	0, 5	I	C	9, 9	0, 8
	D	5, 0	1, 1		D	8, 0	7, 7
c		II		d		II	
		C	D			C	D
I	C	3, 3	0, 2	I	C	3, 3	0, 1
	D	2, 0	1, 1		D	1, 0	2, 2
e		II		f		II	
		C	D			C	D
I	C	1, 1	0, 1	I	C	1, 1	3, 4
	D	1, 0	0, 0		D	4, 3	0, 0

Fig. 1. Games used in agent-based simulations. (a) Prisoner's Dilemma game, (b) Aumann's Stag Hunt game, (c) Lewis's Stag Hunt game, (d) Assurance game, (e) Mutual Fate Control game, and (f) Leader game. In each game, Player I chooses row C or D, Player II independently chooses column C or D, the payoffs in each cell are the payoffs to Players I and II, respectively, for that outcome, and mutual cooperation is better for both players than mutual defection. The payoffs represent Darwinian fitness: they determine changes in expected lifetime reproductive success.

games apart from Leader (in Mutual Fate Control, all four outcomes are weak Nash equilibria). Leader has two pure-strategy Nash equilibria located asymmetrically at (C, D) and (D, C) . Previous research has shown that a form of cooperative turn-taking can evolve in games of this type, but only if they are repeated many times (Browning and Colman, 2004; Colman and Browning, 2009). There is no scope for turn-taking in the unrepeated, one-shot Leader game that we studied. Nonetheless, the small-world microanalysis reported in Section 4.2 and the threshold probabilities calculated in Appendix A suggest that, theoretically, cooperation could evolve through the similarity discrimination effect, even in the Leader game.

3. Agent-based simulations

We investigated the evolution of cooperation in agent-based simulations using the games shown in Fig. 1 embedded in a specially designed genetic algorithm. In our simulations, agents played unrepeated, one-shot versions of the games and had no capacity to observe one another's interactions. In each simulation, an evolving population of 20 agents, programmed to generate a unique move (C or D) probabilistically, depending on the co-player's similarity, played one of the test games in pairs. Each agent's genome comprised two haploid genes, specifying the probabilities of cooperating against similar and dissimilar co-players respectively. In each evolutionary generation, each member of the population was paired with every other member for a single round of the game. Pairs were classified as similar if their genomes differed by half a standard deviation or less, so that, in the first generation of each simulation, slightly over 1/7 of interactions occurred between similar pairs (see Appendix B). From members of each generation, 20 offspring were created for the following generation, with an agent's probability of selection for parenthood being proportional to its total payoffs against the 19 co-players in the population. This process was repeated over 10,000 generations in each simulation. We repeated each simulation 20 times.

3.1. Genetic algorithm

We designed our genetic algorithm along the lines of earlier published algorithms (Browning and Colman, 2004; Colman and Browning, 2009; Holland, 1975). Our algorithm incorporates noise at

various levels, because this is known to be important in evolutionary processes (Blume, 2003). We implemented the algorithm in the following 14 steps:

1. Assign payoff values according to one of the test games shown in Fig. 1.
2. Set the population size N to 20 automata and the number of evolutionary generations to 10,000.
3. For each automaton in the population, randomly select two real numbers from the uniform distribution on the interval $[0, 1]$. These two numbers function as the two adaptively variable haploid genes, labelled SIM and DIS, in every automaton's genome, the SIM gene determining the automaton's probability of making a C choice against a *similar* co-player, and the DIS gene determining the probability of making a C choice against a *dissimilar* co-player, similarity being defined as in Step 5 below.
4. Calculate the standard deviation of the SIM values and the standard deviation DIS values for the current generation.
5. For every pair of automata, calculate the absolute differences between their SIM values in units of standard deviations, and repeat the calculation for their DIS values. Calculate the mean d of these two standardized differences, and define the pair as *similar* if $d \leq 1/2$ and *different* if $d > 1/2$. Because the variance of a uniform distribution on the interval $[a, b]$ is $\sigma^2 = (b-a)^2/12$, this arbitrary criterion d has the effect of defining slightly over 1/7 of pairs as similar in the random population of the first (randomized) generation (see Appendix B).
6. Pair each automaton with one of the others in the population, determine whether the pair is similar or dissimilar, and introduce *misidentification noise*, at the level of the pair, such that the automata are treated as similar when they should be dissimilar, or vice versa, with probability $\gamma = 0.01$. The similarity or dissimilarity of the pair is misidentified if either member of the pair misidentifies it; hence this amounts to assuming that the probability of individual misidentification is approximately 0.005.
7. Generate results for a single round of the game for the pair of automata. If the pair is similar, then both choose C with probabilities specified by their SIM genes; if they are dissimilar, both choose C with probabilities specified by their DIS genes.
8. Introduce random *misimplementation noise* for every C or D move, independently for each automaton, switching C to D or D to C with probability $\delta = 0.01$.
9. Award payoffs according to the relevant payoff matrix and record a running total for each automaton.
10. Pair each automaton in the population with a different co-player, and repeat Steps 5–9 until every automaton has played a single round with each of the others in the population. Compute each automaton's total payoff over its 19 pairwise interactions and assign a mating probability proportional to this total payoff.
11. Generate a subsequent population of 20 automata by selecting two distinct parents for each offspring randomly, with replacement, from the current population, with the probability of selection for parenthood being proportional to mating probabilities defined in Step 10.
12. Assign genes from parents to offspring by randomly selecting the offspring's SIM gene from either of its parents, with equal probability, then randomly selecting the offspring's DIS gene from either of its parents, again with equal probability. Thus the offspring is equally likely to have its SIM and DIS genes from different parents or from the same parent.

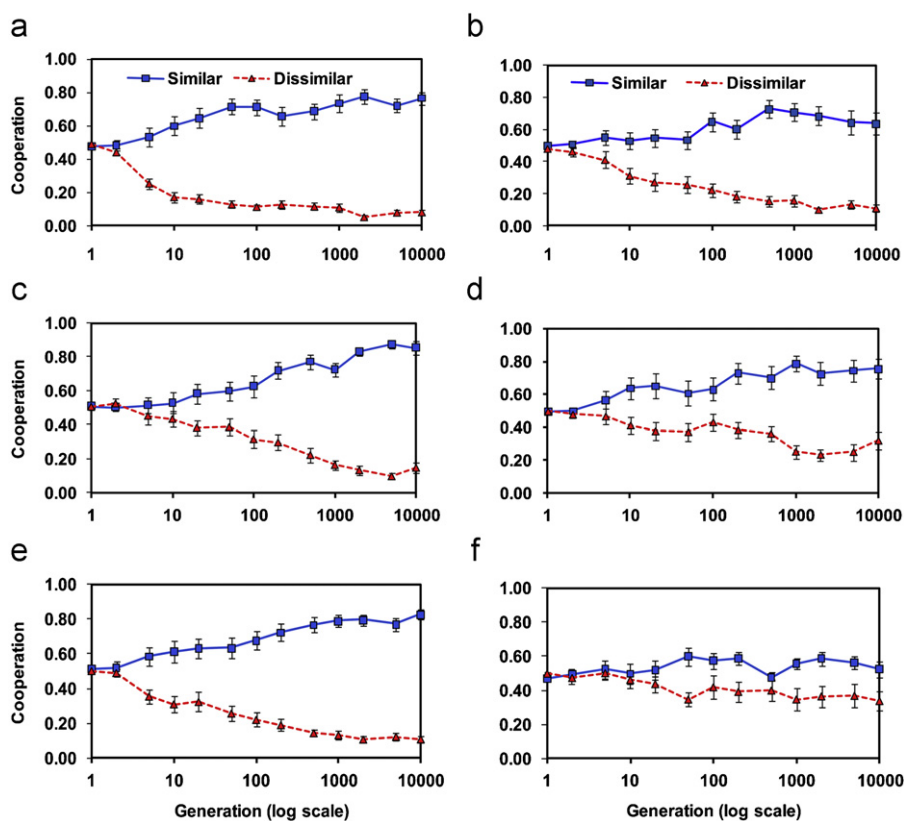


Fig. 2. Relative frequencies of cooperative choices over generations. Mean cooperative choices per generation in one-shot interactions between similar and dissimilar pairs. (a) Prisoner's Dilemma game, (b) Aumann's Stag Hunt game, (c) Lewis's Stag Hunt game, (d) Assurance game, (e) Mutual Fate Control game, and (f) Leader game. For visual clarity, generations are shown on a log scale. Data are averaged over 20 replications, and error bars represent ± 1 standard errors of the means.

13. Simulate genetic mutation by substituting each gene in the offspring's genome with a different gene, with probability of substitution $\varepsilon=0.01$. When mutation occurs, a SIM or DIS gene is replaced by a new real number selected randomly from the uniform distribution on the interval [0, 1].
14. Having replaced 20 parents with 20 offspring to form a new generation, loop back to repeat Steps 4–13 for 10,000 generations, then stop.

A key assumption in this algorithm is that members of the population can judge whether others are similar or different, relative to population variability, before interacting with any of them. We assume that they use variable phenotypic traits that are not explicitly modelled in our simulations but are assumed to be completely linked with behavioural similarity discrimination. The range of applicability of our model to natural populations depends crucially on this assumption, of course.

4. Results

Fig. 2 shows the evolution of different levels of cooperation between similar and dissimilar players, averaged over 20 replications of each simulation. It is obvious from the sharply diverging curves, representing cooperative choices in similar and dissimilar pairs, that similarity discrimination – more frequent cooperation in similar than dissimilar pairs – evolved early in every simulation and increased over subsequent generations. Cooperation in similar pairs evolved strongly in five of the six simulations (Games 2a to 2e) and weakly in the last (Game 2f). Cooperation between dissimilar players declined steadily over generations in all games.

Chi-square contingency tests of cooperation in the final Generation 10,000, in similar and dissimilar pairs, confirmed that, after evolution had run its course, mutual cooperation was significantly more frequent between similar than dissimilar players in all six simulations. Table 1 shows the relative frequencies, including all 20 replications of each simulation, of the outcomes of one-shot interactions in the final generation, in similar and dissimilar pairs, expressed as percentages. Chi-square contingency tests confirm that, in all six simulations, the frequencies after evolution had run its course are significantly different, with much more frequent cooperation between similar than dissimilar players. In every simulation, cooperation and mutual cooperation were more frequent with similar than with dissimilar co-players.²

4.1. Time series analysis

Looking beyond the static results for the final generation, the data generated in each of our simulations are mean relative frequencies of cooperative choices, recorded once for similar pairs and once for dissimilar pairs every 10,000 generations. Such data sequences, representing variables recorded repeatedly over time, are not independent, have dispersions that tend to vary over time, and generally exhibit correlated error terms. For these reasons, they cannot be analysed using conventional statistical procedures that assume independent and identically distributed data. The appropriate techniques for analysis of such data are various

Table 1

Relative frequencies of game outcomes in Generation 10,000 in similar and dissimilar pairs (percentages).

Simulation	(C, C)	(C, D)=(D, C)	(D, D)	$\chi^2(2)$	$p <$
Prisoner's Dilemma					
Similar	62.14	30.55	7.31	1223.01	.001
Dissimilar	2.65	23.82	73.53		
Aumann's Stag Hunt					
Similar	49.94	28.41	21.65	524.99	.001
Dissimilar	4.69	29.10	66.21		
Lewis's Stag Hunt					
Similar	76.28	19.30	4.41	1266.77	.001
Dissimilar	5.32	36.34	58.31		
Assurance					
Similar	66.99	20.91	12.10	882.23	.001
Dissimilar	12.70	29.25	58.05		
Mutual Fate Control					
Similar	69.36	26.16	4.48	1094.78	.001
Dissimilar	2.90	30.43	66.67		
Leader					
Similar	34.09	43.35	23.56	66.91	.001
Dissimilar	19.19	47.34	33.47		

Note: (C, D)=(D, C), because whenever one player chooses C against a co-player who chooses D, the co-player must have chosen D against the first player who chose C.

methods of time series analysis (e.g., Chatfield, 2003; Shumway and Stoffer, 2006; Yanovitzky and VanLear, 2008).

To provide insight into the time course of evolution occurring in each simulation, we performed time series analyses by fitting either an autoregressive integrated moving average (ARIMA) model or a simple exponential smoothing model to the mean values, recorded at each generation, of the SIM and DIS genes that encoded the evolving propensity of players to cooperate with similar and dissimilar co-players respectively. Whenever an ARIMA (p, d, q) model provided the best fit, we estimated the maximum likelihood values of the p and q moving average parameters involved in fitting the model to the SIM or DIS time series, analogous to beta coefficients in multiple regression. In an ARIMA (p, d, q) model, p represents the number of autoregression parameters, d the degree of differencing, indicative of linear or nonlinear trend, and q the number of moving average parameters. When a simple exponential smoothing model provided the best fit, we estimated the maximum likelihood value of the exponential smoothing parameter α , ranging from $\alpha=0$, when previous values are weighted as heavily as recent ones in fitting the model, to $\alpha=1$, when the single most recent value is used exclusively, and generated a value of the t statistic, and the probability level indicating the statistical significance of the parameter α . The results of the time series analyses are summarised in Table 2.

An ARIMA (p, d, q) model provided the best fit to the evolving SIM genes in every simulation. For SIM values, all models include one degree of differencing, indicating upward linear trend over generations in the probability of cooperation with similar co-players, plus several moving average parameters indicating persistent effects of random shocks or deviations from trend in earlier generations – presumably arising from mutations, misidentification noise, and misimplementation noise – and in two cases also a single order of autoregression, indicating the influence on SIM values in one generation of SIM values in the previous generation. For DIS values, the best fit is a simple exponential smoothing model in three simulations (Prisoner's Dilemma, Lewis's Stag Hunt, and Mutual Fate Control) and, in the other three, ARIMA models incorporating one degree of differencing, indicating downward linear trend, plus several orders of

² In response to a suggestion of an anonymous reviewer, we ran all six simulations again using the standard deviations of the previous (rather than the current) generation to assign similar and dissimilar pairs, except in Generation 1, where we used the standard deviations from the current generation. Because the standard deviations change very slowly from one generation to the next over the 10,000 generations, this made very little difference to the results. In Appendix C, we compare results from the original and the modified simulations, using previous generation standard deviations.

moving average, reflecting persistent effects of random shocks in earlier generations. In the Leader simulation, the trend of the SIM curve for cooperation with similar co-players is hard to discern with the naked eye, but the ARIMA model confirms a significant upward trend.

We tested differences between the distributions of SIM and DIS values in each simulation for significance. Because the time series are autocorrelated, standard significance tests would underestimate error variance (Yanovitzky and VanLear, 2008). We therefore adopted an alternative *effective degrees of freedom* approach (Dawdy and Matalas, 1964; Meko and Woodhouse, 2005), substituting conservative estimates for the numbers of scores in the data sets. We used the Kolmogorov–Smirnov two-sample test, which is sensitive to any differences between sample distributions, to compare SIM and DIS values in each simulation, but we defined the effective degrees of freedom (the numbers of

observations in each group) as $N_{\text{eff}}=N(1-\rho)/(1+\rho)$, where ρ was the largest autoregressive, moving average, or exponential smoothing parameter in the corresponding ARIMA or exponential smoothing model. This formula reduces the value of N radically when the parameter is large and results in very conservative estimates of error variance; for example, for $\rho=0.50$, N_{eff} is one-third as large as N , and probable errors are therefore increased by a factor of $\sqrt{3}$. For our data, the formula reduced the effective sample sizes by varying amounts, from 10,000 down to 7699 for the Prisoner's Dilemma; 5736 for Aumann's Stag Hunt; 852 for Lewis's Stag Hunt; 8674 for the Assurance game; 828 for Mutual Fate Control; and 752 for Leader. With these N_{eff} values, two-tailed Kolmogorov–Smirnov test results confirm that the differences between the SIM and DIS distributions are significant beyond $p < 0.001$ in all six simulations, corroborating the graphical evidence of cooperative choices in Fig. 2.

Table 2
Time-series analysis of mean SIM and DIS values over 10,000 generations: model type, R^2 , α (simple exponential models only), t , and significance level.

Model type		R^2	Smoothing α	t	$p <$
Prisoner's Dilemma					
SIM	ARIMA (0, 1, 14)	0.99		All > 2.84	0.005
DIS	Simple	0.89	0.47	55.25	0.001
Aumann's Stag Hunt					
SIM	ARIMA (0, 1, 7)	0.98		All > 2.77	0.006
DIS	ARIMA (0, 1, 8)	0.96		All > 3.21	0.001
Lewis's Stag Hunt					
SIM	ARIMA (1, 1, 3)	0.96		All > 2.26	0.024
DIS	Simple	0.99	0.83	83.77	0.001
Assurance					
SIM	ARIMA (0, 1, 4)	0.98		All > 3.07	0.002
DIS	ARIMA (0, 1, 4)	0.99		All > 2.67	0.008
Mutual Fate Control					
SIM	ARIMA (1, 1, 3)	0.77		All > 3.23	0.001
DIS	Simple	0.93	0.62	67.17	0.001
Leader					
SIM	ARIMA (0, 1, 17)	0.97		All > 2.06	0.040
DIS	ARIMA (0, 1, 8)	0.96		All > 2.63	0.009

Note: For the ARIMA models, only the smallest t and largest p values are shown.

4.2. Robustness under parameter variations

To provide an indication of the robustness of the similarity discrimination effect under variations of the model parameters, we ran several variations of the Prisoner's Dilemma simulation with modified parameter values. We examined the effect under both a smaller population size ($N=10$) and a larger population size ($N=30$) than the standard $N=20$ used in the main simulations, under a lower mutation rate of $\varepsilon=0.005$, rather than the $\varepsilon=0.01$ used in the main simulations, and under a more lenient similarity threshold of 1 standard deviation, compared to the threshold of 1/2 standard deviation used in the main simulations, in each case retaining the original values for the remaining parameters. The results of these supplementary simulations, each averaged over five replications, are shown in Fig. 3.

It is clear from Fig. 3 that the similarity discrimination effect is not restricted to the parameter values chosen for the main simulations. The effect emerged, more or less the same, with substantially modified parameter values. The curves are not as smooth as those obtained from in the main simulations, largely because they are averaged over far fewer replications, especially in Fig. 3a where a smaller population size was used, but cooperation through similarity discrimination evolved quickly

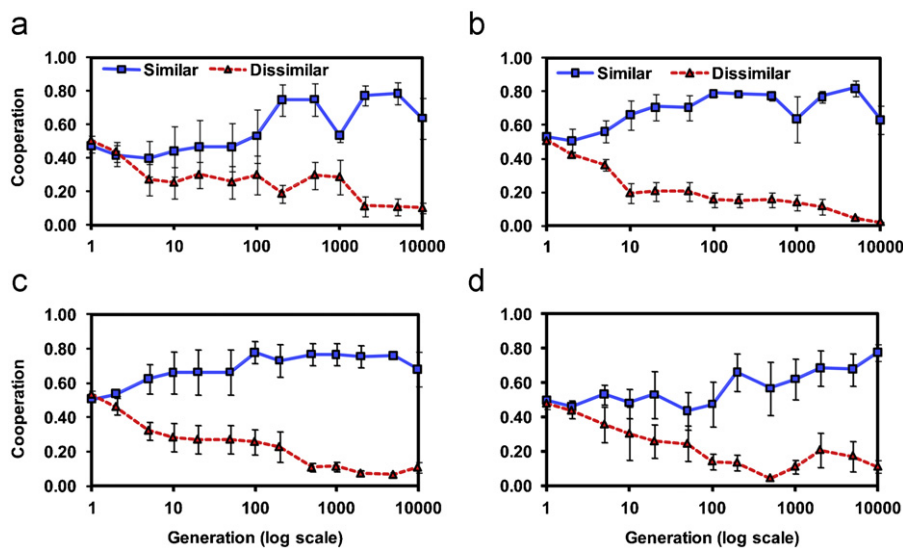


Fig. 3. Prisoner's Dilemma simulations with different parameter values from those used in the main simulations. (a) Smaller population size ($N=10$), (b) larger population size ($N=30$), (c) lower mutation rate ($\varepsilon=0.005$), (d) More lenient similarity threshold ($d \leq 1$ SD). Generations are shown on a log scale, data are averaged over five replications, and error bars represent ± 1 standard errors of the means.

and strongly in every case. Chi-square tests of cooperation in the final Generation 10,000, in similar and dissimilar pairs, confirmed that mutual cooperation was significantly more frequent between similar than dissimilar individuals in all four simulations. The chi-square values are as follows: for the smaller population size, (Fig. 3a), $\chi^2(1)=19.70$, $p < 0.001$; for the larger population size, (Fig. 3b), $\chi^2(1)=83.38$, $p < 0.001$; for the lower mutation rate, (Fig. 3c), $\chi^2(1)=19.60$, $p < 0.001$; and for the more lenient similarity threshold, (Fig. 3d), $\chi^2(1)=24.20$, $p < 0.001$. The effect is highly significant in all cases.

4.3. Small-world microanalysis

In any natural population of organisms, some pairs of individuals are bound to be genetically more similar than others. In the first generation of our artificial populations, even though genes were assigned randomly, between one-sixth and one-seventh of pairs satisfied our criterion of similarity. These similar pairs were favoured by natural selection, producing more copies of themselves than dissimilar pairs. The following microanalysis, based on hypothetical small-world populations, throws light on the mechanism through which cooperation evolves through similarity discrimination in the Prisoner's Dilemma game and a wide range of other strategic structures.

Consider a population consisting of just four individuals, W, X, Y, and Z, with the same properties as the automata that we investigated in our simulations. Suppose that W and X have similar genes encoding for similarity discrimination (SIM=3/4, DIS=1/4), indicating that W and X cooperate with probability 3/4 against similar co-players and with probability 1/4 against dissimilar co-players; that Y cooperates and defects with equal probability against with both similar and dissimilar co-players (SIM=DIS=1/2); and that Z is highly cooperative against both similar and dissimilar co-players (SIM=DIS=3/4). The population standard deviation for the four SIM values is 0.125, and for the four DIS values it is approximately 0.239. The procedure in Step 5 of the genetic algorithm confirms that members of the pair (W, X) differ by less than half a standard deviation ($d < 1/2$) and are therefore similar according to the formal criterion of our algorithm, whereas all other pairs (W, Y), (W, Z), (X, Y), (X, Z), and (Y, Z) have $d > 1/2$ and are dissimilar.

Suppose that these four individuals play a one-shot Prisoner's Dilemma game (Fig. 1a) against each of the others. The probability that W and X cooperate is the joint probability of their SIM values $3/4 \times 3/4$, because they are similar; the probability that W cooperates and X defects is $3/4 \times 1/4$, the probability that W defects and X cooperates is $1/4 \times 3/4$, and the probability of joint defection is $1/4 \times 1/4$. Taking into account the payoffs associated with these mutually exclusive outcomes, the expected payoff to W in the one-shot encounter with X is therefore $(3/4 \times 3/4 \times 3) + (3/4 \times 1/4 \times 0) + (1/4 \times 3/4 \times 5) + (1/4 \times 1/4 \times 1) = 2.69$. Applying the same procedure, we find that W's expected payoff against Y is 2.62, and against Z is 3.94, and W's aggregate expected payoff after playing all three other members of the population is therefore $2.69 + 2.62 + 3.94 = 9.25$. The aggregate expected payoff of X is also 9.25, because X is identical to W. In contrast, Y's aggregate expected payoff is 6.14, and Z's is 7.50, both of these aggregates lagging some way behind those of W and X. If mating probability is proportional to aggregate payoff, as it was in our simulations, then W and X are likely to produce more offspring for the following generation than Y and Z, and this effect will be amplified in subsequent generations. As a consequence, the relative frequencies within the population of the two parameters of player choice, SIM and DIS, evolve in opposite directions, and mutual cooperation between similar individuals increases from generation to generation. This shows how similarity discrimination, arising initially from random mutations, spreads

through a population and drives the evolution of cooperation. The process is illustrated in Fig. 4.

The phenomenon is not peculiar to the particular SIM and DIS values used in the example above. Consider, for example, the following small-world population in which W and X cooperate selectively with similar others, Y shows no behavioural bias, and Z cooperates selectively with dissimilar others: W (SIM=3/4, DIS=1/4), X (SIM=3/4, DIS=1/4), Y (SIM=1/2, DIS=1/2), and Z (SIM=1/4, DIS=3/4). The population standard deviations of the SIM and DIS values are both approximately 0.21. Members of the pair (W, X) differ by less than half a standard deviation, hence $d < 1/2$, and the pair is therefore similar, all other pairs being dissimilar, with $d > 1/2$. In this population, aggregate expected payoffs after one-shot interactions in the Prisoner Dilemma Game are W: 8.87, X: 8.87, Y: 5.88, Z: 4.00. Once again, the similar and similarity-discriminative individuals W and X produce more offspring than the others. The same phenomenon occurs in the other strategic structures that we investigated. In Aumann's Stag Hunt game (Fig. 1b), the aggregate expected payoffs are W: 21.25, X: 21.25, Y: 16.75, Z: 12.25. In Lewis's Stag Hunt game (Fig. 1c), W: 5.50, X: 5.50, Y: 4.00, Z: 3.26. In the Assurance game (Fig. 1d), W: 5.00, X: 5.00, Y: 4.25, Z: 3.50. In the Mutual Fate Control game (Fig. 1e), W: 2.00, X: 2.00, Y: 1.25, Z: 1.00. Even in the Leader game (Fig. 1f), W: 6.50, X: 6.50, Y: 5.75, Z: 6.24. In this last case the aggregate expected payoffs to W and X are only slightly higher than to Y and especially Z, providing some insight into why cooperation through similarity discrimination evolved only

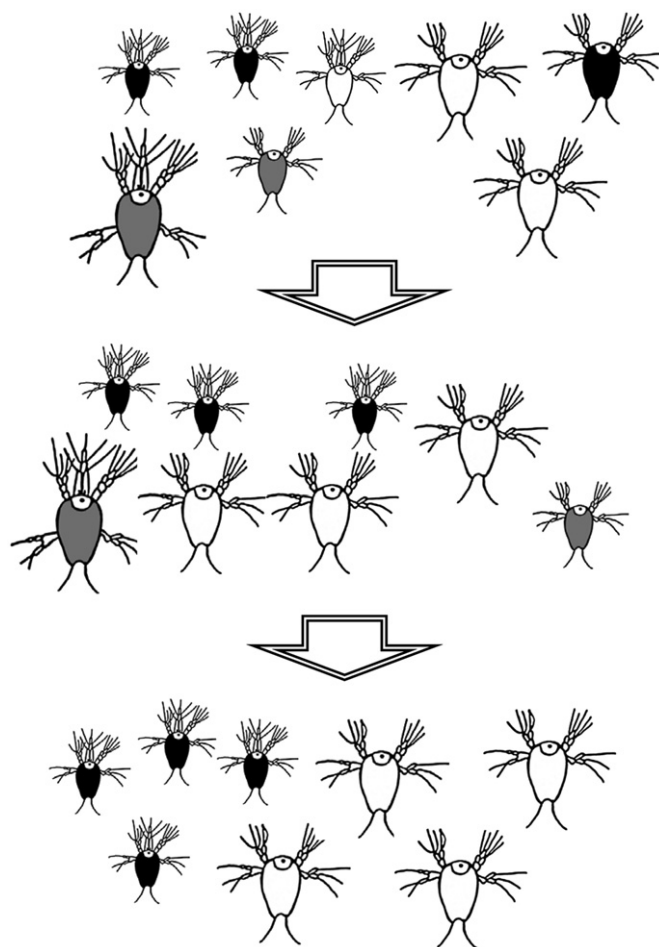


Fig. 4. The similarity discrimination effect in a hypothetical population of microorganisms, starting with a diverse population containing two similar pairs.

weakly in the Leader game simulations. Although this microanalysis is based on arbitrary and artificially contrived mini-populations, it suffices to illustrate the mechanism whereby similarity discrimination can emerge spontaneously and drive the evolution of cooperation.

5. Conclusions

In our simple models, we avoided the problems associated with the fixed tags and linked behaviour that have been used in studies of the greenbeard effect. In contrast to the greenbeard effect, similarity discrimination evolved spontaneously and powerfully, by natural selection alone, without population viscosity or other restrictive conditions, across a wide range of strategic structures. Because each agent played just one round of a game with each of the co-players and had no capacity to observe or respond to the behaviour of other individuals, there was no scope for direct or indirect reciprocity (Masuda and Ohtsuki, 2007; Nowak and Sigmund, 2005; Trivers, 1971). Although our agents had no tags and were genetically heterogeneous, they were capable of distinguishing reliably between co-players genetically similar and dissimilar to themselves, and cheating was therefore impossible.

If we assume that each individual's pair of genes was part of a larger genome, not explicitly included in our model, and that individuals could distinguish reliably, on the basis of variable phenotypic traits also not explicitly modelled, between co-players similar and dissimilar to themselves in these two genes, then in early generations of the simulations, when individuals are not related by descent, the evolutionary process is functionally equivalent to a pure similarity discrimination effect, with complete linkage between variable phenotype and behaviour precluding the possibility of separation through genetic recombination (Rousset and Roze, 2007; West et al., in press). Genes encoding for preferential cooperation with similar individuals (high-value SIM genes coupled with low-value DIS genes) are favoured by natural selection because they increase the fitness of their carriers and of other population members sharing similar genes. In later generations, as individuals manifesting similarity discrimination tend to produce more offspring than others, this form of inclusive fitness begins to blur into kin selection, because similar individuals tend also to be related by descent. Alternatively, if we interpret our model to imply that each individual's pair of genes constitutes its entire genome, rather than being merely a portion of a larger genome, then the similarity discrimination effect is a form of kin selection from the start, individuals cooperating selectively with other population members above a certain threshold of genetic relatedness across the entire genome.

Similarity discrimination evolved less strongly in the Leader game (Game 2f) than in any of the others. Players cooperated significantly more with similar than dissimilar co-players, but cooperation increased only slightly between similar players over 10,000 generations, and declined less steeply between dissimilar players than in the other simulations. We did not expect cooperation to evolve through the similarity discrimination effect in this game, because it has no symmetric pure-strategy Nash equilibrium. The fact that cooperation evolved significantly even in the Leader game shows how powerful the similarity discrimination effect is, compared with the greenbeard effect, at least in theory.

If variable phenotypic traits and similarity-discriminative behaviour are encoded by different, though tightly linked genes, then there will be a tendency for the genes eventually to become unlinked and the similarity discrimination effect to decay, although empirical evidence from research into the greenbeard

effect suggests that tight linkage can be maintained in some circumstances. However, there are reasons to suspect that the similarity discrimination effect may be less likely to evolve in human than in biologically simpler species. The phenotypic traits of the microorganisms and ants in which the greenbeard effect has been observed have been simple and monogenic, but heritable human traits are generally complex and multigenic. If the phenotypic traits and behaviour involved in the similarity discrimination effect are multigenic, then recombinants between linked loci are more likely to arise, and exploitative cheating will tend to evolve (Gardner and West, 2010; Rousset and Roze, 2007; West et al., in press).

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Appendix A. Threshold probabilities for similarity discrimination

Suppose a pair of players in a 2×2 game independently choose between a cooperative and a defecting strategy. The cooperative strategy provides a benefit $b > 0$ to the recipient at a cost $c > 0$ to the cooperator, with $c < b$, and the defecting strategy yields no benefit or cost to either player. Then the payoff to each player if both cooperate is $b - c$, the payoff to each if both defect is 0, the payoff to a cooperator if the co-player defects is $-c$, and the payoff to a defector if the co-player cooperates is b . The payoffs are all assumed to represent Darwinian fitness, that is, changes in expected lifetime reproductive success.

If the players are similar but not identical, let us assume that the probability that they will choose the same strategy is π , with $0 < \pi$. The expected payoff from a cooperative choice is $\pi(b - c) + (1 - \pi)(-c)$, and the expected payoff from a defecting choice is $(1 - \pi)b$. Cooperation yields a higher fitness payoff than defection when

$$\pi(b - c) + (1 - \pi)(-c) > (1 - \pi)b,$$

or when

$$\pi > \frac{b + c}{2b}.$$

More generally, any symmetric 2×2 game can be specified by setting the players' strategy sets to $\{C, D\}$ and representing the payoff functions by the following symbols:

R = payoff to each player if both players choose C .

P = payoff to each player if both players choose D .

T = payoff to a player who chooses D while the co-player chooses C .

S = payoff to a player who chooses C while the co-player chooses D .

If the probability is π that both players will make the same strategy choice, then a C choice yields a higher fitness payoff than a D choice whenever $\pi R + (1 - \pi)S > (1 - \pi)T + \pi P$, that is, when

$$\pi > \frac{T - S}{R - S + T - P},$$

provided that $R + T > S + P$. For the six test games used in the simulations, the threshold values of π above which C -choosing is

favoured by natural selection are as follows (see Fig. 1): (a) Prisoner's Dilemma, 5/7; (b) Aumann's Stag Hunt, 4/5; (c) Lewis's Stag Hunt, 1/2; (d) Assurance game, 1/2; (e) Mutual Fate Control game, 1/2; (f) Leader game, 1/2.

Appendix B. Probabilities in a uniform distribution

In each generation of our simulations, pairs of individuals were classified as similar if their genes differed by half a standard deviation or less. Because genes were uniformly distributed on the real interval $[0, 1]$ in the first-generation, approximately 1/7 of interactions occurred between pairs that were designated as similar.

The proof is straightforward. First, by definition, the mean value of the uniform distribution in the range $a \leq x \leq b$ is

$$E(X) = \int_a^b \frac{x}{b-a} dx = \frac{1}{b-a} \int_a^b x dx = \frac{b^2 - a^2}{2(b-a)} = \frac{(b-a)(b+a)}{2(b-a)} = \frac{b+a}{2},$$

and the second moment about the origin is

$$E(X^2) = \int_a^b \frac{x^2}{b-a} dx = \frac{1}{b-a} \int_a^b x^2 dx = \frac{b^3 - a^3}{3(b-a)} \\ = \frac{(b-a)(b^2 + ab + a^2)}{3(b-a)} = \frac{b^2 + ab + a^2}{3}.$$

It follows that the variance is:

$$\sigma^2 = E(X^2) - [E(X)]^2 = \frac{b^2 + ab + a^2}{3} - \left(\frac{b+a}{2}\right)^2 \\ = \frac{4b^2 + 4b + 4a^2 - 3b^2 - 6ab - 3a^2}{12} = \frac{(b-a)^2}{12},$$

and the standard deviation is $\sigma = (b-a)/\sqrt{12}$. On the interval $[0, 1]$, value of the standard deviation is therefore $1/\sqrt{12}$, and because the distribution is uniform, the proportion of the area under half a standard deviation is $1/2/\sqrt{12} \approx 0.144$ or slightly over 1/7 of the total area under the curve.

In all of our simulations, the initial proportion of interactions between similar individuals was approximately 0.14 in the first generation, but over successive generations, as the population distributions became non-uniform, the proportions rose to between 0.81 and 0.94, most of the increase usually occurring within the first 50 generations. From Generation 1 to Generation 10,000, the proportions of interactions between similar individuals increased from 0.14 to 0.91 in the Prisoner's Dilemma; from 0.13 to 0.86 in Aumann's Stag Hunt; from 0.13 to 0.91 in Lewis's Stag Hunt; from 0.14 to 0.82 in the Assurance game; from 0.14 to 0.94 in Mutual Fate Control; and from 0.14 to 0.81 in the Leader simulations. Thus, the proportion of dissimilar individuals was never less than 6% of the population and was usually substantially more.

Appendix C. Simulations based on previous generation standard deviations

Reported in this appendix are comparisons of the original simulation results with those of modified simulations using population standard deviations of Generation $g-1$ for assigning similar and dissimilar pairs in Generation g , except in Generation 1, where standard deviations from the current generation were used. We compare the mean relative frequencies of cooperative choices from original and modified simulations at selected generations, each modified simulation having been repeated 10 times.

In the modified simulations, the similarity discrimination effect – increasing cooperation between similar pairs and decreasing cooperation between dissimilar pairs – was clearly evident in all six strategic structures, as in the original simulations. For the Prisoner's

Dilemma (Fig. 2a), the mean relative frequencies of cooperative choices at Generations 1, 2, 5, 10, 20, 50, 100, 200, 500, 1000, 2000, 5000, and 10000 were as follows—original data first, and modified data using $g-1$ standard deviations in parentheses. *Similar pairs*: 0.48 (0.50), 0.48 (0.52), 0.53 (0.53), 0.60 (0.58), 0.65 (0.62), 0.71 (0.69), 0.71 (0.63), 0.66 (0.67), 0.69 (0.70), 0.73 (0.71), 0.78 (0.72), 0.72 (0.74), 0.76 (0.77). The product-moment correlation between the original and modified values is $r=0.949$, $p < 0.001$ (two-tailed significance levels are used here and throughout this appendix). *Dissimilar pairs*: 0.49 (0.50), 0.44 (0.40), 0.25 (0.33), 0.17 (0.26), 0.16 (0.27), 0.13 (0.20), 0.11 (0.15), 0.12 (0.14), 0.11 (0.12), 0.11 (0.08), 0.05 (0.08), 0.08 (0.10), 0.08 (0.08), product-moment correlation between original values and modified values $r=0.946$, $p < 0.001$. It is clear that the modified simulations using $g-1$ standard deviations generated very similar results to the original simulations, which used current generation standard deviations.

The correlations between original and $g-1$ modified values were very high and significant in most of the other simulations. In Lewis's Stag Hunt (Fig. 2c), for similar pairs, $r=0.905$, $p < 0.001$, and for dissimilar pairs, $r=0.963$, $p < 0.001$. In the Assurance game (Fig. 2d), for similar pairs, $r=0.860$, $p < 0.001$, and for dissimilar pairs, $r=0.912$, $p < 0.001$. In the Mutual Fate Control game, (Fig. 2e), for similar pairs, $r=0.968$, $p < 0.001$, and for dissimilar pairs, $r=0.985$, $p < 0.001$. The correlation was slightly lower in Aumann's Stag Hunt game (Fig. 2b) for similar pairs only: $r=0.421$, $p=0.152$, because there was relatively little variance and less increase in cooperation over generations in original and modified data than in most other simulations, but the correlation for dissimilar pairs was very high: $r=0.940$, $p < 0.001$, and similarity discrimination emerged strongly in the modified simulation. In the Leader game, (Fig. 2f), for similar pairs, $r=0.656$, $p=0.015$, and for dissimilar pairs, $r=0.579$, $p=0.038$, both relatively low correlations being explained by the much weaker similarity discrimination in these Leader game simulations than in the others.

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