

Appendix from L. Lehmann et al., “Strong Reciprocity or Strong Ferocity? A Population Genetic View of the Evolution of Altruistic Punishment”

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Strong Reciprocity or Strong Ferocity

Associations

In order to evaluate explicitly the change in frequency of the helping and punishment alleles (eqq. [9], [10]), we first express all the gene frequencies appearing in the fecundities (f_{ij} , f_i , and f) in terms of the centered variables

$$\zeta_{A(ij)} = p_{A(ij)} - p_A, \quad (\text{A1})$$

and then we follow the same developments as presented in Roze and Rousset (2005). Products of ζ variables are noted $\zeta_{U(ij)} = \prod_{A \in U} \zeta_{A(ij)}$, where U is the set of loci within an individual. These variables can be averaged over single and pairs of individuals within demes according to

$$\zeta_{U(i)} = \frac{1}{N} \sum_{j=1}^N \zeta_{U(ij)} \quad (\text{A2})$$

and

$$\zeta_{U/V(i)} = \frac{1}{N(N-1)} \sum_j^N \sum_{k=1, k \neq j}^N \zeta_{U(ij)} \zeta_{V(ik)}, \quad (\text{A3})$$

where the “/” symbol separates sets of genes sampled from different individuals in the same deme. When centered variables involve repeated indices, as will occur below, they can be simplified by using the relation $\zeta_{AA/V(i)} = p_A(1 - p_A)\zeta_{V(i)} + (1 - 2p_A)\zeta_{A/V(i)}$ (Kirkpatrick et al. 2002).

Genetic associations are then obtained as averages of $\zeta_{S(i)}$ variables over all demes

$$D_S = E[\zeta_{S(i)}], \quad (\text{A4})$$

where the set S can contain one or several loci in the same or in different individuals. For instance, $D_{HH} = E[\zeta_{H(ij)}^2]$ is the genetic variance at the helping loci, $D_{PH} = E[\zeta_{H(ij)}\zeta_{P(ij)}]$ measures the covariance of both the helping and punishment alleles within the same individual (i.e., linkage disequilibrium) and $D_{H/H} = E[\zeta_{H(ij)}\zeta_{H(ik)}]$ is the covariance of two helping alleles in two individuals.

Fecundity Functions in Terms of Centered Variables

In terms of centered variables, the fecundity of individual j in deme i is given by

$$\begin{aligned} f_{ij} = & (B - C)p_H - (C_P + D)(1 - p_H)p_P + \frac{1}{N-1} \sum_{k=1, k \neq j}^N \{-C_H\zeta_{H(ij)} + B\zeta_{H(ik)} - C_P[(1 - p_H)\zeta_{P(ij)} \\ & - p_P\zeta_{H(ik)} - \zeta_{P(ij)}\zeta_{H(ik)}] + D[p_P\zeta_{H(ij)} - (1 - p_H)\zeta_{P(ik)} + \zeta_{H(ij)}\zeta_{P(ik)}]\}. \end{aligned} \quad (\text{A5})$$

When selection is evaluated on the helping allele, the first term appearing in equation (9), averaged over all individuals in deme i , then becomes

$$\begin{aligned} \frac{1}{N} \sum_{j=1}^N f_{ij} \zeta_{H(ij)} &= [(B - C)p_H - (C_P + D)(1 - p_H)p_P] \zeta_{H(i)} - C_H \zeta_{HH(i)} + B \zeta_{H/H(i)} \\ &- C_P [(1 - p_H) \zeta_{HP(i)} - p_P \zeta_{H/H(i)} - \zeta_{HP/H(i)}] + D [p_P \zeta_{HP} - (1 - p_H) \zeta_{H/P(i)} + \zeta_{HH/P(i)}]. \end{aligned} \quad (\text{A6})$$

The product of the centered variable $\zeta_{H(ij)}$ and the effect of actors on average deme fecundity f_i averaged over all individuals within deme i (second term in eq. [9]) is given by

$$\begin{aligned} \frac{1}{N} \sum_{j=1}^N f_i \zeta_{H(ij)} &= [(B - C)p_H - (C_P + D)(1 - p_H)p_P] \zeta_{H(i)} + [(B - C_H) + p_P(D + C_P)] \zeta_{H^R/H(i)} \\ &- (1 - p_H)(D + C_P) \zeta_{H^R/P(i)} + (D + C_P) \zeta_{P^R/(P/H)(i)}, \end{aligned} \quad (\text{A7})$$

where

$$\zeta_{U^R/V(i)} = \frac{1}{N} \zeta_{UV(i)} + \left(\frac{N-1}{N} \right) \zeta_{U/V(i)} \quad (\text{A8})$$

and

$$\zeta_{U^R/(V/X)(i)} = \frac{2}{N} \left(\frac{1}{2} \zeta_{UVX(i)} + \frac{1}{2} \zeta_{UX/V(i)} \right) + \left(\frac{N-2}{N} \right) \zeta_{U/VX(i)} \quad (\text{A9})$$

are associations where individuals can be sampled with replacement, and $\zeta_{U/VX(i)}$ is the association between the genes sampled in three different individuals in deme i .

Weak Selection (First-Order Effects)

Helping

Substituting equations (A5) and (A7) into equation (9) and taking the expectation over all demes and noting that $E[\zeta_{H(i)}] = 0$, we find that the change in frequency of the helping allele H is given to the first order in phenotypic effects by

$$\begin{aligned} \Delta p_H &= -C_H D_{HH} + B D_{H/H} - C_P [(1 - p_H) D_{PH} - (p_P D_{H/H} + D_{PH/H})] \\ &+ D [p_P D_{HH} - p_H D_{P/H}] - (1 - m)^2 \{ [(B - C_H) + p_P(D + C_P)] D_{H^R/H} \\ &- (1 - p_H)(D + C_P) D_{H^R/P} + (D + C_P) D_{P^R/(P/H)} \} + O(\delta^2). \end{aligned} \quad (\text{A10})$$

Notice that in this equation and in subsequent ones, the phenotypic effect on fitness D should not be confused with the indexed $D_{X/Y}$ for the associations. The change in frequency of the helping allele is made of five components. First, we have the direct cost of helping, which is weighted by the genetic variance D_{HH} in the population. Second, we have the benefit stemming from the partners of the focal individual expressing helping, which depends on the association $D_{H/H}$ of allele H in a focal individual and another individual randomly sampled from its deme. Third, we have the cost of punishment, which is expressed conditionally on the partners not bearing allele H when the focal individual bears allele P . This cost thus varies directly with the association D_{PH} of allele H and P within an individual. But the cost of punishment also varies indirectly with the association $(p_P D_{H/H} + D_{PH/H})$ of alleles H and P in the same individual and a second allele H in another individual. This last term represents the reduction in punishment cost expressed by the focal individual because its neighbors bear allele H in higher frequency than an individual sampled at random from the population. Fourth, we have the benefit of not being damaged, which varies directly with the frequency of punishers in the focal deme and indirectly with the association of allele H and P in different individuals. This last term represents the decrease in the relative advantage of a focal helper also bearing the punishment allele (and thus not being punished) because

its neighbors, which are relatives, are also more likely to bear the punishment allele. Fifth, we have the change in competition in the focal deme resulting from the expression of helping in that deme.

In the neutral model, the association of pairs or triplets of genes sampled from the same or from different individuals at different loci are null (see the appendix in Roze and Rousset 2005); hence, $D_{PH} = D_{P/H} = D_{PH/H} = D_{P/P/H} = 0$. By contrast, associations between pairs of homologous genes remain positive, and we have $D_{HH} = p_H(1 - p_H)$ and $D_{H/H} = p_H(1 - p_H)R$, where

$$R = \frac{D_{H/H}}{D_{HH}} \quad (\text{A11})$$

is the coefficient of relatedness between two different individuals sampled from the same patch in the absence of selection (i.e., neutral model). Inserting these values into equation (A10) produces equation (16) of the main text.

Punishment

Following a similar procedure as for the helping allele, we find that the change in frequency of the punishment allele is obtained to the first order in phenotypic effects by

$$\begin{aligned} \Delta p_P = & -C_H D_{PH} + B D_{P/H} - C_P [(1 - p_H) D_{PP} - (1 - p_P) D_{P/H}] - D [(1 - p_H) D_{P/P} - (p_P D_{PH} + D_{HP/P})] \\ & - (1 - m)^2 \{ [(B - C_H) + p_P (D + C_P)] D_{P^R/H} - (1 - p_H) (D + C_P) D_{P^R/P} + (D + C_P) D_{H^R/(P/H)} \} + O(\delta^2). \end{aligned} \quad (\text{A12})$$

The change in frequency of the punishment allele is also made of five components. First, we have the direct cost of helping, which depends on the association D_{PH} between allele P and H in the same individual. Second, we have the benefit stemming from the neighbors of the focal individual expressing helping, which depends on the association $D_{P/H}$ between allele P in the focal individual and allele H in one of its neighbors. Third, we have the direct cost of punishment, which depends on the genetic variance D_{PP} in the population and on frequency of individuals not bearing the helping allele. The net cost of punishing decreases with the covariance $D_{P/H}$ between the punishment and helping alleles in two different individuals, which measures the extent to which the focal individual does not express punishment because its neighbors are bearing the helping allele. Fourth, we have the damage of being punished, which depends on the probability that a focal punisher does not bear the helping allele and on the extent to which he is then punished by its neighbors. Fifth, we have the change in competition in the focal deme resulting from the expression of punishment in that deme.

As was the case for the previous model, the associations of pairs or triplets of genes sampled from the same or from different individuals at different loci are null at steady state, while the associations between homologous genes remain positive in that case. Thereby, $D_{PH} = D_{P/H} = D_{HP/P} = D_{H/P/H} = 0$, $D_{PP} = p_P(1 - p_P)$, and $D_{P/P} = p_P(1 - p_P)R$, which, once substituted into equation (A12) produces equation (19) of the main text.

Strong Reciprocity without Recombination

The change in the frequency of strong reciprocators can be obtained either from equation (A10) (by substituting all subscripts H with P) or from equation (A12) (by substituting all subscripts P with H). Since both equations are equivalent in this case, we use the subscript A , and the resulting change in frequency of strong reciprocators is given after simplification by

$$\begin{aligned} \Delta p_A = & [-C_H - (1 - p_A)C_P + p_A D] D_{AA} + [B + (1 - p_A)C_P - p_A D] D_{A/A} \\ & - (1 - m)^2 \{ [B - C_H - (1 - 2p_A)(C_P + D)] D_{A^R/A} + (C_P + D) D_{A^R/(A/A)} \} + O(\delta^2). \end{aligned} \quad (\text{A13})$$

The associations appearing in this model are given by $D_{AA} = p_A(1 - p_A)$, $D_{A/A} = p_A(1 - p_A)R$,

$$D_{A^R/A} = \frac{1}{N} D_{AA} + \left(\frac{N-1}{N} \right) D_{A/A}, \quad (\text{A14})$$

and

$$D_{A^R/(A/A)} = \frac{2}{N}D_{AA/A} + \left(\frac{N-2}{N}\right)D_{A/A/A}. \quad (\text{A15})$$

In the last equation, $D_{AA/A} = (1 - 2p_A)D_{A/A}$ and $D_{A/A/A}$ is the association between allele A sampled in three different individuals, which satisfies the recursion

$$D_{A/A/A} = (1 - m)^3 \left[\frac{1}{N^2}D_{AAA} + \frac{3(N-1)}{N^2}D_{AA/A} + \frac{(N-1)(N-2)}{N^2}D_{A/A/A} \right], \quad (\text{A16})$$

where $D_{AAA} = (1 - 2p_A)p_A(1 - p_A)$.

When the number of demes is large, we have, to the first order in $1/N$, $D_{A/A/A} = O(1/N^2)$, with the result that equation (A14) can be written as

$$\begin{aligned} \Delta p_A = p_A(1 - p_A) \{ & -C_H - (1 - p_A)C_P + p_A D + [B + (1 - p_A)C_P - p_A D]R \\ & - (1 - m)^2 [B - C_H - (1 - 2p_A)(C_P + D)]R^R \} + O(\delta^2) + O\left(\frac{1}{N^2}\right), \end{aligned} \quad (\text{A17})$$

which is equation (11) of the main text.

Stronger Selection (Second-Order Effects)

The calculation of the various associations appearing in equation 10 when selection is evaluated to the second order have been carried out with the automated recursions developed by F. Rousset and D. Roze (unpublished manuscript). The resulting full selective pressures on the helping and punishment allele are very complicated functions and are presented in the Mathematica notebook “Strong reciprocity.” We give here only the expressions of the associations involved in equation (10) and that are evaluated to the first order in phenotypic effects on fitness because they allow us to gain some insight on the selective pressure. We also report the effects of the traits on the fitness of a single actor. All the equations presented below are evaluated to the first order in $1/N$ (large N), and we drop all the residues of order $1/N^2$.

Kinship Associations and Linkage Disequilibrium

The association between one allele H and one allele P sampled from the same individual (linkage disequilibrium) is given by

$$D_{PH} = \frac{(C_P + D)(1 - m)^2 [(2 - m)m(1 - r) + r] p_H(1 - p_H)p_P(1 - p_P)}{r(2 - m)^2 m^2 N}, \quad (\text{A18})$$

which shows that selection generates, through the harming of nonhelpers, a positive association between alleles H and P within individuals whenever $C_P + D > 0$. This linkage disequilibrium is generated by an interaction of selection and identity by descent. The correlations between alleles brought by identity by descent depends on the probability $(1 - m)^2/N$ that two gametes sampled in a deme originate from the same individual. The linkage disequilibrium tends toward 0 when dispersal is complete ($m \rightarrow 1$) or when patch size becomes very large ($N \rightarrow \infty$).

The association between one allele H and one allele P sampled from two different individuals reads

$$D_{P/H} = \frac{(C_P + D)(1 - m)^2 p_H(1 - p_H)p_P(1 - p_P)}{(2 - m)^2 m^2 N}, \quad (\text{A19})$$

which is again positive if $C_P + D > 0$.

The association between two alleles H sampled from two different individuals is given by

$$D_{H/H} = \frac{(1-m)^2[(2-m)m - (1-2p_H)(C_H - p_P D)]p_H(1-p_H)}{(2-m)^2 m^2 N}. \quad (\text{A20})$$

When the frequency of allele H is below one half ($p_H < 1/2$), this association is lower than expected under the action of drift alone (obtained by setting $C_H = 0$ and $D = 0$) provided that $C_H > p_P D$, whereas when $p_P > 1/2$, the association is increased relative to the neutral expectation. The association between two P alleles sampled from two individuals is given by

$$D_{P/P} = \frac{(1-m)^2[(2-m)m - (1-p_H)(1-2p_P)C_P]p_P(1-p_P)}{(2-m)^2 m^2 N}. \quad (\text{A21})$$

When the frequency of allele P is below one half ($p_P < 1/2$), this association is again lower than expected under the action of drift alone (obtained by setting $C_P = 0$), whereas when $p_P > 1/2$, the association is increased relative to the neutral expectation.

The association between alleles H and P sampled from the same individual and another allele H sampled from a second individual is given by

$$D_{HP/H} = -\frac{C_P(1-r)(1-m)^2 p_H(1-p_H)^2 p_P(1-p_P)}{[m(1-r) + r][2 - m(1-r) - r][(2-m)m(1-r) + r]N}, \quad (\text{A22})$$

while the association between alleles H and P sampled from the same individual and another allele P sampled from a second individual is given by

$$D_{HP/P} = \frac{(-C_H + Dp_P)(1-r)(1-m)^2 p_H(1-p_H)p_P(1-p_P)}{[m(1-r) + r][2 - m(1-r) - r][(2-m)m(1-r) + r]N}. \quad (\text{A23})$$

Finally, the associations $D_{P/P/H}$ and $D_{P/H/H}$ tend to 0 under large deme size.

Effects of Actors on Their Fitness

The effect of an individual bearing the helping allele on its fitness when the initial frequency of helpers in the population is rare ($p_H \rightarrow 0$) is given by

$$\begin{aligned} -c_H = & -(C_H - p_P D)[1 + p_P(D + C_P)] - \beta_{PH \cdot H} \left[C_P - \frac{(1-m)^2(D + C_P)}{N} \right] \\ & - \frac{(1-m)^2}{N} \{ (B - C_H)(1 - C_H + p_P D) + p_P \{ (D + C_P)[1 + B - 2C_H - D + p_P(C_P + 3D)] \} \}, \end{aligned} \quad (\text{A24})$$

where $\beta_{PH \cdot H} = D_{PH}/D_{HH}$ is the regression of the punishment allele in an individual on the helping allele in that individual and D_{PH} is given by equation (A18). The effect of a focal individual bearing the punishment allele on its fitness when the initial frequency of punishers in the population tends to 0 ($p_P \rightarrow 0$) reads

$$\begin{aligned} -c_P = & -C_P(1-p_H)[1 - p_H(B - C_H)] - \beta_{PH \cdot P} \left[C_H + \frac{(1-m)^2(B - C_H)}{N} \right] \\ & + \frac{(1-p_H)(1-m)^2}{N} \{ (C_P + D)[1 - (1-p_H)C_P] - p_H(B - C)(D + 2C_P) \}, \end{aligned} \quad (\text{A25})$$

where $\beta_{PH \cdot P} = D_{PH}/D_{PP}$ is the regression of the helping allele in an individual on the punishment allele in that individual. When the frequency of the helping allele is rare in the population ($p_H \rightarrow 0$), the linkage disequilibrium D_{PH} is equal to 0, and this last equation reduces to equation (22) of the main text.

Cultural Transmission of Strong Reciprocity

In this section, we assume that helping and punishment are coded by a single cultural variant (a meme) following vertical and/or oblique transmission. The life cycle is assumed to be similar to the one described in the main text with the only difference being that between the reproduction and the dispersal stage, cultural variants are transmitted from the parental to the offspring generation. Hence, the behavior of individuals is culturally determined, but it affects their Darwinian fitness (e.g., Cavalli-Sforza and Feldman 1981; Feldman et al. 1985). With these assumptions, the dynamics of strong reciprocity are given by equation (11), and in order to obtain the explicit expression of this equation, it remains to evaluate the probability R that two adults in a deme bear the same cultural variant (i.e., cultural kinship). We will consider here two different transmission schemes: transmission primarily by parents and transmission primarily by teachers (e.g., Cavalli-Sforza and Feldman, 1981, chap. 3.11).

Transmission Primarily by Parents

For transmission primarily by parents, we assume that each offspring adopts the cultural variant from its parent with probability τ and, with complementary probability $1 - \tau$, adopts the cultural variant of one of the $N - 1$ other individuals of the parental generation (e.g., Cavalli-Sforza and Feldman 1981, chap. 3.11). In order to evaluate the coefficient of cultural kinship, we define

$$\alpha_s \equiv \tau^2 + \frac{(1 - \tau)^2}{N - 1}, \quad (\text{A26})$$

which is the probability that two juveniles descending from the same parent have adopted a meme from the same cultural ancestor. We also define

$$\alpha_d \equiv \frac{2(1 - \tau)\tau}{N - 1} + \frac{(1 - \tau)^2(N - 2)}{(N - 1)^2} = \frac{1 - \alpha_s}{N - 1}, \quad (\text{A27})$$

which is the probability that two individuals descending from two different parents have adopted a meme from the same cultural ancestor. With these variables, the coefficient of kinship satisfies at equilibrium the recursion

$$R = (1 - m)^2 \left\{ \frac{1}{N} [\alpha_s + (1 - \alpha_s)R] + \left(\frac{N - 1}{N} \right) [\alpha_d + (1 - \alpha_d)R] \right\}. \quad (\text{A28})$$

This equation can be understood as follows. Two adults sampled in a deme originate from the same deme with probability $(1 - m)^2$, in which case they either descend from the same parent (with probability $1/N$) or from two different parents (with probability $1 - 1/N$). Whether the two individuals descend from the same or from two different parents from the same deme, the probability that they bear the same meme depends on two different events. Either the two individuals have adopted an identical meme from the same common cultural ancestor or they have each adopted a meme from a different individual, in which case they bear an identical meme with probability R . Independently of the value of τ , the recursion for cultural kinship simplifies to

$$R = (1 - m)^2 \left[\frac{1}{N} + \left(\frac{N - 1}{N} \right) R \right], \quad (\text{A29})$$

which is equivalent to equation (13) of the main text. Therefore, under cultural transmission primarily by parents, the dynamics of strong reciprocity is the same as under genetic transmission.

Transmission Primarily by Teachers

For transmission primarily by teachers, we assume that each offspring inherits the cultural variant from the same teacher with probability τ and, with complementary probability $1 - \tau$, adopts the cultural variant of one of the $N - 1$ other individuals of the parental generation in their deme (e.g., Cavalli-Sforza and Feldman 1981, chap.

3.11). In each generation, the teacher is chosen at random among the N individuals of the parental generation. In this model, the probability that two juveniles sampled at random after reproduction and before dispersal have adopted their cultural variant from the same individual of the parental generation is given by

$$\alpha \equiv \tau^2 + \frac{(1 - \tau)^2}{N - 1}. \quad (\text{A30})$$

With this variable, the coefficient of cultural kinship satisfies at equilibrium the recursion

$$R = (1 - m)^2[\alpha + (1 - \alpha)R], \quad (\text{A31})$$

which yields

$$R = \frac{(1 - m)^2 \alpha}{(2 - m)m(1 - \alpha) + \alpha}. \quad (\text{A32})$$

When the value of τ is high (i.e., transmission primarily by teachers), this coefficient of kinship exceeds the value obtained under genetic transmission or transmission primarily by parents (compare with eq. [13] or eq. [A32]). Hence, under cultural transmission primarily by teachers (i.e., “one to many transmission”), the selective pressure on strong reciprocity can be higher than under genetic transmission of the trait. Finally, to complete the model and have all the associations involved in equation (A13), we need to evaluate the association $D_{A/A/A}$ between three cultural strong-reciprocity variants sampled in three different individuals. Following along equation (A16), we have

$$D_{A/A/A} = (1 - m)^3(\alpha_1 D_{AAA} + \alpha_2 D_{AA/A} + \alpha_3 D_{A/A/A}), \quad (\text{A33})$$

where

$$\alpha_1 = \tau^3 + \frac{(1 - \tau)^3}{(N - 1)^2}, \quad (\text{A34})$$

$$\alpha_2 = 3 \left[\tau^2(1 - \tau) + \frac{\tau(1 - \tau)^2}{N - 1} + \frac{(1 - \tau)^3(N - 2)}{(N - 1)^2} \right], \quad (\text{A35})$$

and $\alpha_3 = 1 - \alpha_1 - \alpha_2$ are the probabilities that three juveniles sampled after reproduction and before dispersal have adopted their cultural variants from, respectively, the same individual, two distinct individuals, and three distinct individuals of the parental generation. Note that neither equation (A32) nor the solution to equation (A33) vanishes under large deme size.

Cultural Transmission by Imitation of Strong Reciprocity

In this section, we assume again that helping and punishment are coded by a single cultural variant but which now follows cultural transmission through imitation. The stage of social interactions is assumed to be the same as the one described in the life-cycle section of the main text. After the stage of social interactions, individuals imitate the strategies of other individuals. We will consider two different imitation schemes: one where individuals compare their payoff with the average payoff of demes, and the other where individuals compare their payoff with the payoff of individuals during pairwise interactions.

Imitation by Comparing Direct Payoff to Group Payoff

Here we assume that individuals imitate another individual from their deme with probability $1 - m$ and imitate an individual from a different deme with probability m . In each case, imitations occur proportional to the average payoff of individuals within demes. With these assumptions, the probability that individual j in deme i is

imitated by any individual in that deme (including himself) is given by $N(1 - m)(1 + f_{ij})/\sum_{k=1}^N (1 + f_{ik})$, where $1 + f_{ik}$ is the payoff of individual k in deme i (i.e., fecundity for fertility models). The probability that individual j in deme i is imitated by an individual from another deme is given by $m(1 + f_{ij})/(1 + f)$. Collecting terms, the direct fitness of individual j in deme i is given by

$$w_{ij} = (1 - m)\left(\frac{1 + f_{ij}}{1 + f_i}\right) + m\left(\frac{1 + f_{ij}}{1 + f}\right), \quad (\text{A36})$$

where the payoffs f_{ij} , f_i , and f are given, respectively, by equations (5), (6), and (7) of the main text. To the first order in phenotypic effects, the fitness function becomes

$$w_{ij} = 1 + f_{ij} - (1 - m)f_i - mf + O(\delta^2). \quad (\text{A37})$$

Substituting this fitness function into the equation for the change in frequency (eq. [4]) allows us to evaluate the change in frequency Δp of strong reciprocators to the first order in phenotypic effects on fitness. This change in frequency is given to the first order in $1/N$ (i.e., neglecting $D_{\Delta/\Delta}$) by

$$\begin{aligned} \Delta p = & p(1 - p)\{-C_H - (1 - p)C_P + pD \\ & + [B + (1 - p)C_P - pD]R - (1 - m)[B - C_H - (1 - 2p)(C_P + D)]R^R\} + O(\delta^2) + O\left(\frac{1}{N^2}\right), \end{aligned} \quad (\text{A38})$$

where R is the probability that two individuals in a deme bear the same cultural variant and $R^R = 1/N + [(N - 1)/N]R$ (eq. [12] of the main text). Under proportional imitation, this kinship coefficient is given by equation (13). Hence, the only difference between this change in frequency and equation (11) is that the intensity of kin competition is greater under cultural than genetic transmission (cf. the second line of eq. [11] with the second line of eq. [A38]). Since $(1 - m)R^R > R$, equation [A38] informs us that the greater the benefit of helping B , the greater selection against strong reciprocity.

Imitation by Pairwise Payoff Comparison

A variant of the imitation scheme presented in the last section is to assume as Boyd et al. (2003) did in their simulations that after the stage of interactions, individuals encounter at random another individual from their own deme with probability $1 - m$ and an individual from another deme with probability m . Individual k from deme l who encounters individual j from deme i then imitates j with probability $(1 + f_{ij})/[(1 + f_{ij}) + (1 + f_{ik})]$ (Boyd et al. 2003, p. 3532). With these assumptions, there are $N - 1$ possible encounters within a deme, each of which may result in a focal individual keeping its cultural variant and the neighbor adopting the variant of the focal individual. Thereby, the fitness function of individual j from deme i is given by

$$w_{ij} = (1 - m)\left[\frac{2}{N - 1} \sum_{k=1, k \neq j}^{N-1} \frac{1 + f_{ij}}{(1 + f_{ij}) + (1 + f_{ik})}\right] + m\left[\frac{2(1 + f_{ij})}{(1 + f_{ij}) + (1 + f)}\right]. \quad (\text{A39})$$

To the first order in phenotypic effects, the fitness function w_{ij} becomes

$$w_{ij} = 1 + \frac{f_{ij}}{2} - (1 - m)\left[\frac{N}{2(N - 1)}f_i + \frac{1}{2(N - 1)}f_{ij}\right] - \frac{mf}{2} + O(\delta^2). \quad (\text{A40})$$

The corresponding change in gene frequency is then given to the first order in $1/N$ by

$$\Delta p = \frac{p(1-p)}{2} \left(\left(1 + \frac{1-m}{N} \right) \{-C_H - (1-p)C_P + pD + [B + (1-p)C_P - pD]R\} \right. \\ \left. - (1-m) \left(1 + \frac{1}{N} \right) [B - C_H - (1-2p)(C_P + D)]R^R \right) + O(\delta^2) + O\left(\frac{1}{N^2}\right). \quad (\text{A41})$$

The dynamics of this equation are slightly different than those given by equation [A38], but again, the greater the benefit of helping B , the greater selection against strong reciprocity.