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The Co-Evolution of Love and Hate

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Abstract

Experimental and other evidence demonstrates that many individuals willingly give to strangers, reward good deeds and punish violations of norms by others even at a significant cost to oneself, and favor fellow group members over others. These behaviors exhibit aspects of both *altruism* – benefitting other group members at a cost to oneself– and *parochialism*, conditioning one's behavior towards others on the degree of similarity in ascriptive characteristics.

Both altruism and parochialism are puzzling from an evolutionary perspective as both would appear to reduce individual payoffs (whether fitness or material well-being) by comparison to other members of one's group who eschewed these behaviors. Lower payoffs, in turn, are expected to result in the elimination of these behaviors in a population governed by any dynamic in which lower relative payoffs result in a declining frequency of the behavior. The view advanced here is that altruism and parochialism co-evolved, each providing an environment favoring the evolutionary success of the other, and neither being singly capable of proliferation in human populations under conditions approximating those experienced by our Late Pleistocene ancestors.

The plausibility of this view is suggested by extensive simulations with an agent-based model of individual-level and group-level selection representing the long term evolution of human behaviors. Altruistic behaviors are modeled at both the individual and group level (groups practice varying degrees of resource sharing), while parochialism is captured by small group size, within- group social segmentation, group boundary maintenance resulting in limited inter-group migration, and hostility towards out group members.

JEL Codes: C73, B52, D74, O30, P14.

Keywords: agent based model, evolutionary game theory, property rights, altruism, social preferences, war, hunter gatherer societies. .

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...Selfish and contentious people will not cohere, and without coherence, nothing can be effected. A tribe possessing ... a greater number of courageous, sympathetic and faithful members, who were always ready to warn each other of danger, to aid and defend each other... would spread and be victorious over other tribes...Thus the social and moral qualities would tend slowly to advance and be diffused throughout the world.

Charles Darwin (1873), *The Descent of Man*, p. 134

Whether .. the extra-group struggle .. takes the form of actual warfare or of still keener competition for trade and food supply, that group in which unchecked internal competition has produced a vast proletariat with ... no 'stake in the state' will be the first to collapse.

Karl Pearson (1894), *Socialism and Natural Selection*, p. 17

1. Introduction

Far from being uniquely modern, the welfare state is just the most spectacular example of a virtually ubiquitous aspect of society over the entire life course of anatomically modern humans, namely, the sharing of food, information, and other valued resources among genetically unrelated members of a group. The frequent electoral endorsement of this process of sharing suggests that the altruistic predisposition to help those in need and to contribute to the pursuit of common goals is quite widespread.[1] Equally ubiquitous, both in modern society and over the millennia, is a predisposition to favor one's own kind in friendships, economic activities, mating, and coalitions, and to hold an unfavorable evaluation of "outsiders" and even a willingness to inflict severe harm on them.[2] These parochial predispositions are often manifested in and heightened by institutions governing residential patterns, access to resources, sexual reproduction, and inter-group warfare.

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[1] See Fong (2001) and the literature surveyed in Fong, Bowles, and Gintis (2003)

[2] See Lazarsfeld and Merton (1954), Thibaut and Kelly (1959), Homans (1961), Tajfel, Billig, Bundy, and Flament (1971) and the literature summarized in Bowles and Gintis (2000). Yamagishi (2002), however, shows that negative evaluations of outsiders need not motivate experimental subjects to treat outsiders in disadvantageous ways.

Both altruism and parochialism are puzzling from an evolutionary perspective, as both would appear to reduce individual payoffs (fitness or material well-being) by comparison to other members of one's group eschewing these behaviors. Lower payoffs, in turn, are expected to result in the elimination of these behaviors in any population governed by any dynamic in which lower relative payoffs result in a declining frequency of the behavior. The view advanced here is that altruism and parochialism co-evolved, each providing an environment favoring the evolutionary success of the other, and neither being singly capable of proliferation in human populations under conditions approximating those experienced by our Late Pleistocene ancestors.

The plausibility of this view is suggested by extensive simulations with an agent-based model of individual-level and group-level selection representing the long term evolution of human behaviors. Altruistic behaviors are modeled at both the individual and group level (groups practice varying degrees of resource sharing), while parochialism is captured by small group size, within-group social segmentation, group boundary maintenance resulting in limited inter-group migration, and hostility towards out group members.

The evolutionary mechanisms involved in this account are multi-level selection processes with the novel features (adapted from Bowles (2001)) that both genetically transmitted influences on individual behaviors as well as culturally transmitted group-level institutional characteristics are subject to selection, with intergroup conflicts playing a decisive role in group-level selection. The model is thus an example of a gene-culture evolutionary process (Cavalli-Sforza and Feldman (1981), Boyd and Richerson (1985) and Durham (1991)).

It has been long recognized that in populations composed of groups characterized by a markedly higher level of interaction among members than with outsiders, evolutionary processes may be decomposed into between-group and within-group selection effects (Lewontin (1965), (Price (1972), Crow and Kimura (1970), Uyenoyama and Feldman (1980)). Where the rate of replication of a trait depends on the frequency of the trait in the group and where group differences in trait frequencies are substantial and persistent, group selection contributes to the pace and direction of evolutionary change. But most who have modeled evolutionary processes under the joint influence of group and individual selection have concluded that the group selection pressures cannot override individual-level selection except where special circumstances (e.g. small group size, limited migration) heighten and sustain differences between groups relative to within-group differences (Eshel (1972), Boorman and Levitt (1973), Maynard Smith (1976)).

Beginning with Darwin, a number of evolutionary theorists have suggested that human evolution might provide an exception to this negative assessment of the force of multi-level selection. Among the distinctive human characteristics which may enhance group selection

effects on genetic variation is our capacity for the suppression of within-group phenotypic differences in reproductive or material success, our patterns of social differentiation supporting positive assortation (non-random pairing), and the frequency of intergroup conflict. Thus, the two key features of our model will be intergroup conflicts and culturally transmitted group differences in institutional structure. We stress intergroup conflicts for empirical reasons: the central role of war and the extinction or reduced fitness of loser populations in the spread of behavioral traits. The institutions we model are the commonly observed human practices of resource sharing among group members including non-kin and patterns of residence and social differentiation that result in a greater likelihood of like types interacting (positive assortation). Our model could easily be extended to study other group level institutions that, like resource sharing, reduce the within group variance of material and hence reproductive success. Included are information sharing, consensus decision making, and monogamy.

Group differences in institutional structure persist over long periods of time due to the nature of institutions as conventions. A convention is a common practice that is adhered to by virtually all group members because the relevant behaviors – for example sharing meat, or not engaging in extra-pair copulations – are mutual best responses conditional on the expectation of similar behaviors by most others (Young (1995)). We do not here model the reasons why the behavior prescribed by the institution is a mutual best response, but plausible accounts are not difficult to provide. Those violating sharing norms may bear fitness costs of ostracism, for example (Boehm (1993)). The conventional nature of institutions accounts for their long term persistence and also their occasional rapid demise under the influence of shocks. We study institutional evolution in ways analogous to the evolution of individual traits. Just as the individuals in our model are the bearers of genes, groups are the bearers of institutions, and a successful institution produces many replicas, while unsuccessful ones are eliminated. The inheritance of group-level institutions results from a cultural transmission process based on learned behaviors: as new members of the population mature or immigrate, they adhere to the existing institutions, not due to any conformist predisposition, but because this is a best response as long as most others do the same. The resulting behavioral uniformity in adherence to a group's institutions permits us to treat the institution as a group-level characteristic.

By contrast, the group beneficial individual traits in our model are replicated by a standard fitness-based mechanism in which the above pressures for uniformity are absent. We consider a single individually costly but group-beneficial trait relevant to dyadic interactions among group members. Those behaving in this way are termed altruists or A's. Other formally altruistic traits could be modeled in a similar manner. Included are individual contributions in an n-person public good interaction (common defense, insurance, or the punishment of those who fail to contribute in such situations, and other ways that cheating is sanctioned (e.g. Clutton-Brock and Parker (1995), Boyd, Gintis, Bowles, and Richerson (2003) and Bowles and Gintis (2003).

Our simulations explore the causal relationships among the individual and group-level measures of altruism and parochialism mentioned above. Our findings for a parameter set approximating Late Pleistocene human environments may be summarized. First, the evolutionary success of a genetically transmitted predisposition to contribute to the wellbeing of others at a cost to oneself is favored by small group size, within-group segmentation, limited between group migration, extensive within group redistribution of resources and frequent between-group hostilities. Second the conditions that foster the proliferation of altruism also favor the evolution of group level institutions implementing significant levels of egalitarian redistribution and social segmentation within groups. Specifically over the empirically relevant range, increases in the frequency of between group conflicts fosters higher levels of within group redistribution. Third, when the group level institutions – segmentation and resource sharing – and the individual trait – altruism – are all endogenous, they co-evolve: each influencing the movement of the other. This co-evolutionary dynamic is sufficiently strong that under empirically plausible parameter values, the evolution of altruism does not occur if social segmentation and egalitarian redistribution are precluded; and correspondingly the evolution of segmentation and resource sharing does not occur if altruism is precluded.

The fundamental causal processes at work in these results are the following. Group level selection favors the A trait because groups with a higher faction of altruists win wars. But within group selection always works against the A's, so the multi level selection dynamic is a race between the two levels of selection: only if the group level predominates can the A's proliferate. This is more likely to occur when between-group conflicts are more frequent. The within-group institutions – segmentation and resource sharing – effectively slow the pace of within-group selection against the A's, for two reasons. First, in a more segmented society the A's are less likely to encounter the non-A's (called N's). The second reason is that egalitarian resource sharing reduces the A's relative payoff disadvantage when they do encounter N's. Finally, the strength of group selection pressures depends on the between group variance in the frequency of A's relative to the average within group variance in this frequency, and small group size and low between group migration rates tend to elevate the between group variances.[3]

2. Variance Reduction, Segmentation, and Conflict

The idea that the suppression of within-group competition may be a strong influence on evolutionary dynamics has been widely recognized in eusocial insects and other species

[3] Random migration among groups is a form of population mixing that will reduce differences between groups. Small size contributes to between group variance because when successful groups fission and successor groups are created by a random draw, the expected absolute value of the difference in the means of the successor groups is greater for smaller groups.

(Smith and Szathmary (1995), Frank (1995), Michod (1996), Buss (1987), Ratnieks (1988)) and Frank (2003). Christopher Boehm (1982) and Irenaus Eibl-Eibesfeldt (1982) first applied this reasoning to human evolution, exploring the role of culturally transmitted practices which reduce phenotypic variation within groups.[4] Examples of such variance-reducing practices are leveling institutions, such as monogamy and food sharing among non-kin, namely those which reduce within-group differences in reproductive fitness or material well-being. Monogamous or polygamous mating systems, distinct systems of resource sharing, and the like may be termed institutions, by which we mean a uniformity in the structure of human interactions, that is characteristic of a group but may differ among groups. Such structures may have attenuated within-group selection operating against individually-costly but group-beneficial practices, resulting in higher group average fitness or material success. If so, groups adopting these variance-reducing institutions would have had advantages in coping with climatic adversity, intergroup conflicts and other threats. A group's institutions thus constitute a niche, that is, a modified environment capable of imparting distinctive direction and pace of evolutionary change (Laland, Odling-Smee, and Feldman (2000), Bowles (2000)). According to this view, the evolutionary success of variance-reducing social institutions may be explained by the fact that they retard selection pressures working against in-group-beneficial individual traits coupled with the fact that high frequencies of bearers of these traits reduces the likelihood of group extinctions (or increases the likelihood of a group's expanding and propagating new groups).

A common form of variance reduction, widely practice among mobile foraging bands, is within-group sharing of meat, honey, and other large-package forms of nutrition. To be concrete, suppose, some fraction of the resources an individual acquires -- perhaps specific kinds of food as among the Ache (Kaplan and Hill (1985)) -- is deposited in a common pot to be shared equally among all group members.This sharing institution may be modeled as a linear tax, $t \in [0,1)$, collected from the members payoffs with the proceeds distributed equally to all members of the population.

In addition to resource sharing, most groups are characterized by what may be termed assortative meeting. so that in the pairing process *within* groups that determines who interacts with whom at what frequency, one's likely partners are conditional on ones own type. Thus if there are two types, tin the population -- Altruists (As) and Non-altruists (Ns) -- A's are more likely to interact with A's and N's with N's than would occur by random matching. Suppose that the probability that an A-member of group j is matched with an A is not p_j, the fraction of group j who are As, but $s_j + (1- s_j)p_j > p_j$ and the probability that a N-member of group j is matched with an A is $(1- s_j)p_j < p_j$. Then we define $s_j \geq 0$ as the degree of segmentation in group j, or the difference in the conditional probability of an A meeting an A and an N meting an A in the within-group pairing. A transparent interpretation of s_j is that it represents

[4] Boehm (2002) surveys the recent literature.

the fraction of interactions that take place with one's own type for reasons such as common residence and the like, the remaining $(1-s_j)$ pairings being random. But it could arise for other reasons, deliberate but imperfect attempts by the A's to avoid interactions with the N's, for example, or a preference to interact with people with ones own ethnic markers, coupled with a difference across ethnic groups in the distribution of traits.

Segmentation by type favors the evolution of the A-trait, because As confer benefits on those with whom they interact, and by enhancing an A's likelihood of interacting with a fellow A segmentation thus increases the expected payoffs of the As. For analogous reasons the expected payoffs of the N's are reduced. For sufficiently high levels of s, the expected payoffs to the As will exceed the payoffs to the N's. In this case the within group selection process will favor the As. We restrict the possible values of s to those for which this is not the case.

The model shows how group level institutions may retard individual level selection and thus facilitate the proliferation of an otherwise unviable trait by means of group selection. But the analysis is incomplete. The Price equation gives the stationarity condition for p, but it does not account for the movement of the variances upon which the movement in p is based. For most species, the between-group variance-enhancing mechanisms (mutation, genetic drift) are weak and tend to be swamped by the homogenizing effects of selection itself, along with migration among groups. This is the reason why group-selection pressures among non-human animals are thought to be weak. However, among humans, where effective group size is small (e.g. the members of a foraging band) and where groups frequently divide either in response to increased size or to interpersonal tensions within the group, a process of even random (rather than associative) division will increase between-group variance.

Thus small group size and frequent group division coupled with social institutions that attenuate the within-group selection against the A-trait constitute an environment favorable for multi-level selection pressures to support the evolution of the A-trait. For any model even minimally faithful to the empirical circumstances of human evolution, the only practical way to determine if these between group variance-enhancing effects and withing group attenuation of individual level selection are strong enough to make group selection an important influence on evolution is to simulate a group-structured population under reasonable parameter values.

3.*Simulating the Co-evolution of Love and Hate*

We simulated an artificial population living in 20 groups. For each simulation, total population size is given and group size is approximately constant, modified only by random migration among groups and by the outcomes of group conflict, as explained below. In the model above, groups with a high frequency of A's produce more offspring and thus grow in size. In the simulations to follow, a group's size is restricted by its site, and a high frequency

of A's contributes to the group's success in intergroup conflicts, allowing it to occupy a new site and thus to increase in size.

Reflecting the effect of payoffs on fitness, an individual's expected share of the group's next generation's offspring is equal to the individual's share of the group's total payoffs.We assume that each individual has access to material resources from sources other than the interaction we are modeling and set these "baseline payoffs" at 10 units. Because offspring are produced in proportion to the individual's share of the group's total material payoffs and the expected difference in payoffs is c = 1 (in the absence of segmentation and resource sharing), the N's produce ten percent more offspring than the A's. Individual replication is subject to mutations, such that with a small probability, *e*, the offspring of an A will be an N or an A with equal probability and conversely.

The institutions represented by *s* and *t* differ among groups, and they also evolve. When conflict occurs between groups, the group with the higher total payoff wins. The losing group's members die and the winning group populates the site occupied by the losers with replicas of themselves.[5] The new inhabitants of the site adopt the institutions of the group from which they descended. Institutions are also subject to stochastic variation, increasing or lowering *t* and *s* by chance each period. Both segmentation and resource sharing impose costs on the groups adopting them. More segmented groups may fail to capture the benefits of diversity or of economies of scale, and resource sharing may reduce incentives to acquire the resources to be shared. Neither of these costs are modeled formally, but to capture their impact, group average benefits are reduced by an amount that is rising and convex in both *s* and *t*. Unlike many institutions, both *s* and *t* may be introduced at low levels, so the initial emergence of resource sharing and segmentation could readily take place through the extension to an initially small number of unrelated individuals of the practice of within-family resource sharing or a preference for interaction with individuals sharing common traits, proximity, or other similarities.

The benchmark values of the parameters in the simulations, and the range of alternative values that we explored appear in Table 1. The structure of our simulation is described in Figure 1 and its notes. (Additional details are available at http:\www.santafe.edu). The key parameters concern the rate of (random) migration among groups, group size, and the probability in any period that a group will engage in a between-group conflict.

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[5] An alternative formulation would have the losing group survive as a subject people with less access to resources and hence reduced fitness. We have modeled group conflict in this way elsewhere but will not pursue it here.

	Benchmark Values	Range explored
Mean group Size (n/g)	20	7 to 47
Migration Rate (m)	0.2	0.1 to 0.3
Probability of conflict (k)	0.25	0.18 to 0.4
Mutation rate (e)	0.001	0.01 to 0.000001

Note: Total population size is n, and there are g groups; m, k and e are per generation. Other Parameters: Benefit (b): 2; Cost (c): 1; Baseline payoffs: 10. We varied group size by varying n. For reasons explained in the text, we restricted s to not exceed ½ while $t \in [0,1]$ The costs imposed on the group by these institutions are $\frac{1}{2}(s^2 + t^2)$.

Table 1 Key Parameters for the Simulations

Because our group conflicts are lethal for the losers, we have chosen a benchmark probability of conflict giving an expected frequency of a single war every four generations. Of course group conflicts more commonly result in fitness differentials between winners and losers without group extinctions. Our benchmark likelihood of an extinction is chosen to reflect the long term consequences of plausible values of differential reproductive success between adjacent stronger and weaker groups engaged in on going conflict. The other benchmark values were also chosen on grounds of empirical plausibility, the evidence for which we review in the penultimate section.

Notes to Figure 1. We assign n individuals to g groups. At t=0 all are N. 1. *Pairing*. In each period, each member of a group is randomly paired to play the PD game once, with another member with payoffs given in the text (in some runs modified by the resource-sharing rule). With segmentation, the member interacts with a similar type with probability s and is paired randomly with probability 1- s. 2. *Reproduction*. Replicas of the current generation constitute the next generation. They are produced by drawing (with replacement) from the current group membership with the probability that any member will be drawn equal to that member's share of the total payoffs of the group. 3. *Mutation.* With probability e a member of the next generation is not a replica of its parent, but is A or N. with equal probability. 4. *Migration.* With probability m each member of the new generation relocates to a group randomly selected from the other groups. 5. *Group competition.* With probability k each group is selected and among those selected competition takes place between randomly paired groups. The winning group is that with the highest total payoff (net of the costs of sharing and segmentation, if any). 6. *Repopulation and fission.* The members of the losing group are replaced by replicas of the members of the winning group, and the resulting (temporarily enlarged) winning group splits with members assigned randomly to two new groups. (In simulations with resource sharing or segmentation, the two new groups adopt the institutions of the winning group.)

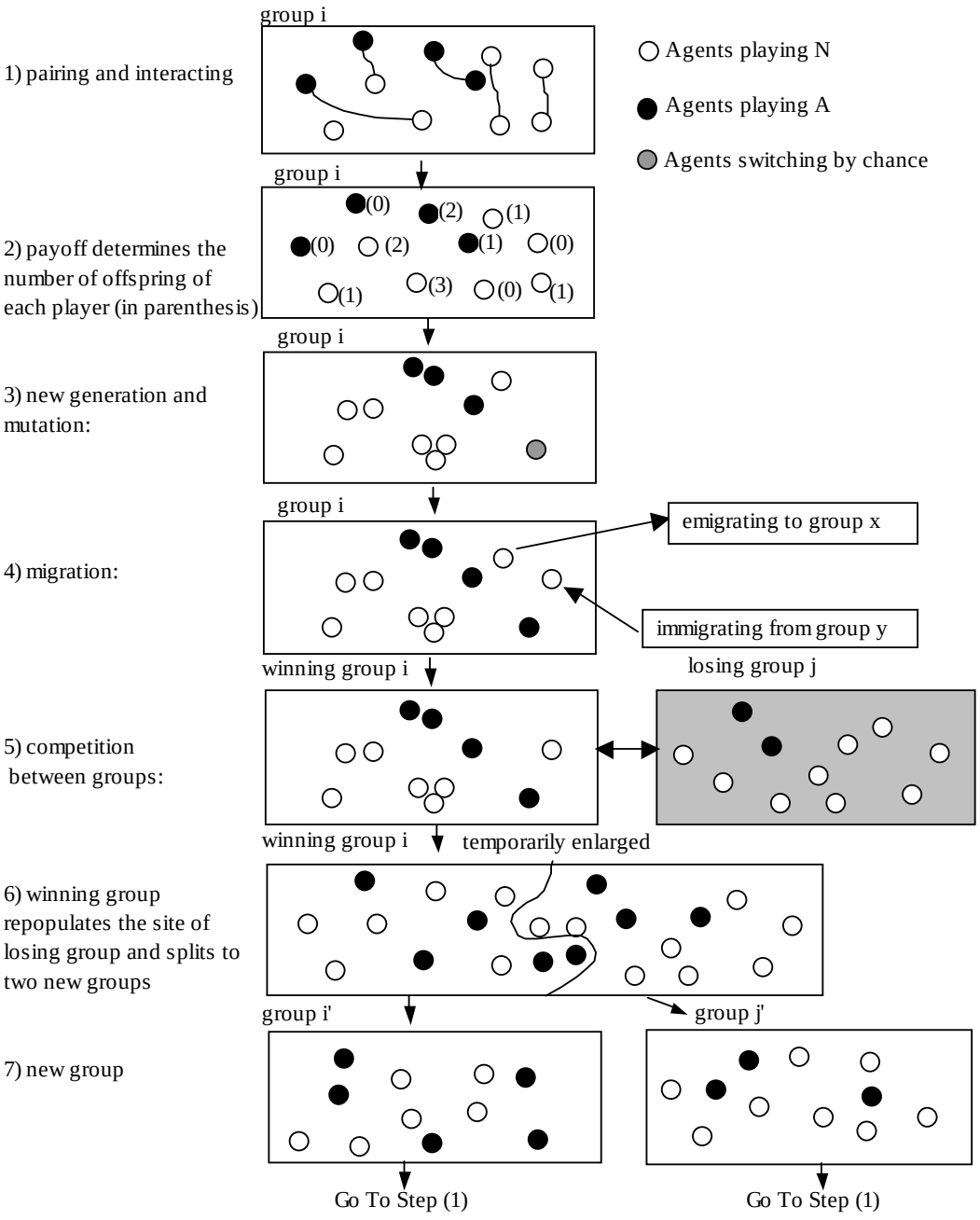


Figure 1 Individual and group-level selection in the simulation (see notes, next page)

We initiated each simulation with altruists and institutions absent at time zero, to see if both the individual A-trait and the group level institutions would proliferate if initially rare (the individual and institutional mutation process will introduce some variability in the population). To explore the effects of varying parameter values, we ran at least ten simulations of at least 10,000 generations for each parameter set investigated, as indicated in the notes to Figure 6.

4. Artificial histories

The early generations of a typical simulation appear in Figure 2.The rise in p is supported by the chance increase in both s and t (between periods 100 and 150). When p reaches high levels (periods 532 to 588, for example) both s and t decline, typically leading to a sharp decline in p. The subsequent rise in s or t occurs by chance. This pattern emerges for the following reason. When the population is evenly divided between A's and N's, many groups are also approximately evenly divided. From equation (6), we know that the beneficial effects of institutions – the retarded within-group selection gained by higher levels of t or s -- are maximized in this region. When p is well above 0.5, the benefits of the protection of A's offered by the institutions is of less value. But the institutions are costly to bear, so when p is high, groups with substantial levels of segmentation or resource sharing are likely to lose conflicts with other groups, and the sites they occupied are then populated by the descendants of winners, who typically bear lower levels of these institutional variables. As a result, both s and t fall.

To explore further the impact of institutions on the within group selection process, we estimated the pace of within group updating while constraining s, t, both, or neither to zero. Recall that the expected effect of both segmentation and resource sharing is to attenuate the within group selection against the As. Using data from four simulations of 10,000 generation each, we found just this. The combined effect of resource sharing and segmentation is to reduce by half the extent of within-group selection against the altruists.[6]

[6] The details of these estimates are given in Bowles, Choi, and Hopfensitz (2003).

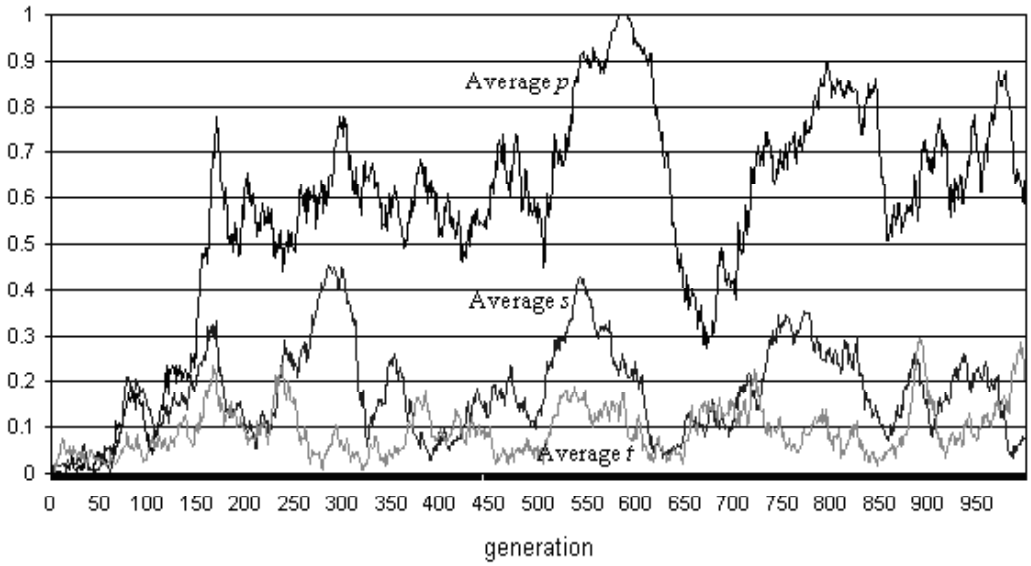


Figure 2.The dynamic interaction between group institutions and individual behaviors. The figure presents a 1000 period history of a run using the benchmark parameters from Table 1. The population average frequency of altruists is *p*, while *t* and *s* give the average across the 20 groups of the level of resource sharing and segmentation. Altruism and both group-level institutions are initially rare. The particular time frame shown in Figure 4 was selected because it clearly reveals this dynamic, which is observed over long periods in many runs.

Between-group conflicts play a key role in supporting both group-level institutions and individual-level altruism. In the simulations reported, the expected frequency of conflict was 1/*k*, where *k* is the probability that a group is drawn for a conflict in every generation. It seems likely that over long historical periods, the frequency of conflict varied considerably, perhaps in response to the need to migrate in times of climatic variability. To explore the sensitivity of the simulations to the frequency of conflicts, we varied *k* stochastically using the auto-regressive system described in the notes to Figure 3. During periods in which conflict was frequent (e.g. around the 21000th generation), high levels of altruism were sustained, but periodic outbreaks of relative peace among the groups (around the 25300th, 27000th and 29600th generations) led to sharp reductions in the fraction of A's in the population. The 500-generation period following generation 28500 illustrates the strong path dependency in the model The high level of *p* induced by the sharp rise in the frequency of intergroup conflict around 28500 persists even as the frequency of conflict sharply declines in subsequent generations. But the "lock-in" is not permanent: when *k* remains below 0.2 for a number of periods, *p* crashes.

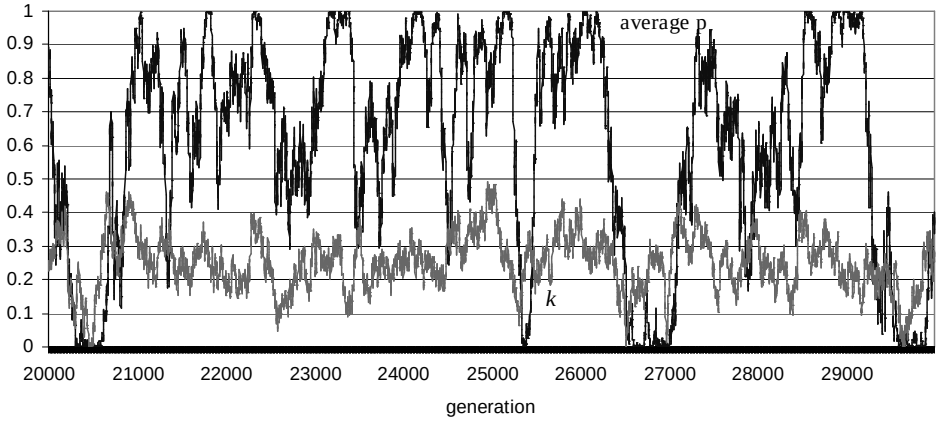


Figure 3. High frequencies of group conflict favor altruism. The figure shows a thousand generation period from a run in which both institutions evolved endogenously, and in which *k*, the frequency of between-group conflict varies over time according to $k_t = k_0 + \rho\, k_{t-1} + \sigma_t$ where $\rho = 0.99$, σ_t is randomly drawn from the uniform distribution [-0.02, 0.02], and k_0 is selected so that the mean of k_t is the same as the baseline k, namely, 0.25.

We sought to answer two other questions as well. Could altruism have evolved had group level institutions not co-evolved with individual level altruism? And how sensitive are our simulations to variations in the key parameters? To answer these two questions, we varied group size from 7 to 47, and for each size ran 10 simulations of 50,000 generations, with the other parameters at their baseline values. We did this with both institutions constrained to not evolve, with each singly constrained to not evolve, and with neither constrained. We performed the same operation for variations in the migration rate from 0.1 to 0.3, and the probability of conflict (*k*) from 0.18 to 0.51. The results appear in Figure 4.[7] The top panel shows that with both institutions constrained not to evolve, a group size of 7 supports high levels of altruism, but group sizes greater than 8 result in a frequency of altruists of less than 0.3. Taking as a benchmark the group size for which $p>0.5$, we see that with no institutions, the critical size is 8, while with both institutions, $p>0.5$ for all group sizes less than 22. The results for the migration rate are similar. Without institutions, sustaining $p>0.5$ requires a (per generation) migration rate of 0.13, but with both institutions free to evolve, the critical migration rate is 0.21.

[7] We also investigated whether the institutions would evolve if *p* is constrained to zero. They do not, because institutions are costly and where there are no altruists in the population they perform no group-beneficial function, thus leading groups that by chance adopt a high level of sharing or segmentation to lose any conflicts in which they are involved.

The bottom panel shows that institutions also allow the evolution of substantial frequencies of altruism with significantly fewer between-group conflicts. A "vertical" reading of the figure is also illuminating: for example, the bottom panel shows that for $k = .3$, p is less than 0.2 without institutions, but is greater than 0.8 with both institutions free to evolve.

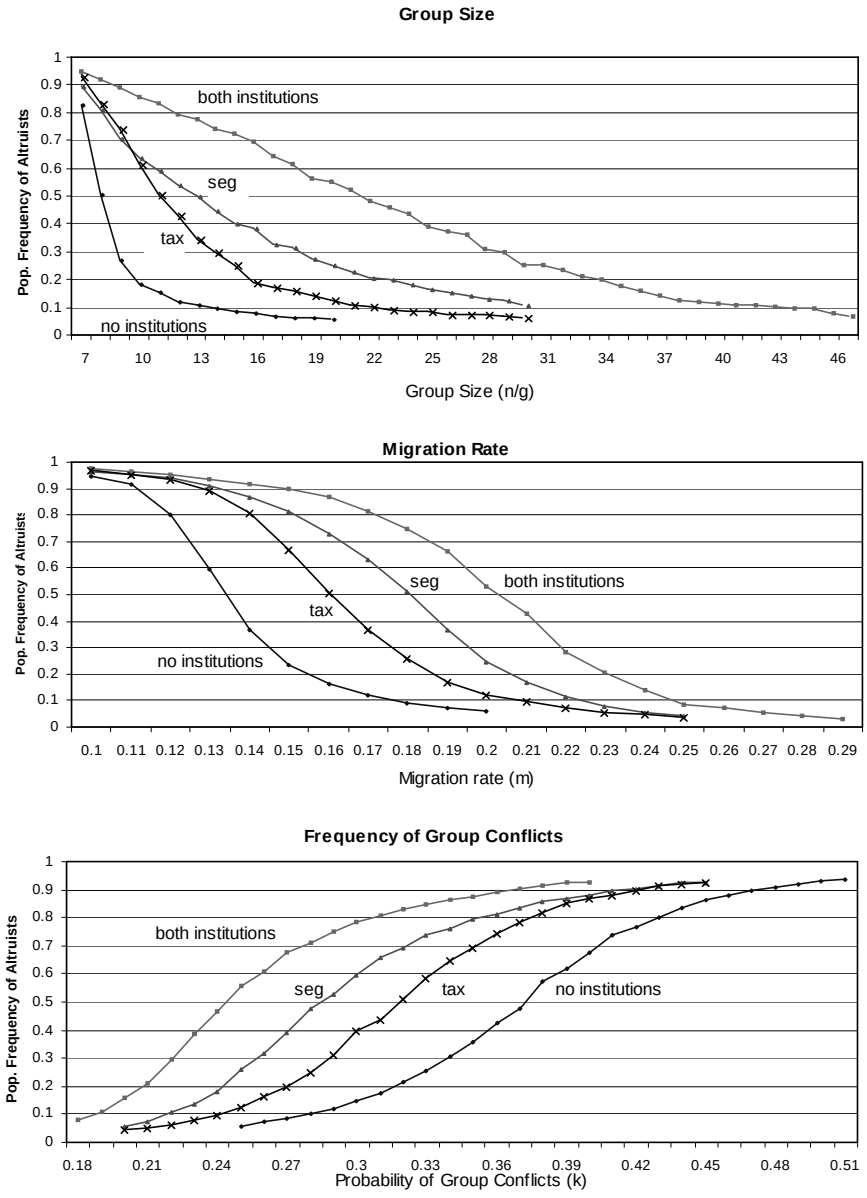


Figure 4. Group-level institutions increase the size of the parameter space for which altruistic behaviors are common. (See notes, next page.)

Notes to Figure 4 (previous page)**.** Each data point is the average frequency of altruists in the entire population over 10 runs of 50,000 periods each for the parameter value indicated on the horizontal axis. In each panel the other parameters are the benchmark values shown in table 1. Each run began with *p*, *t*, and *s* set equal to zero. The curve labeled "none" gives the results for runs in which *t* and *s* were constrained to zero; the other curves indicate runs in which one or both of the institutions were free to evolve. ("Tax" refers to resource sharing.) The horizontal distance between the curves indicates the enlargement of the parameter space made possible by group level institutions. The vertical distance between the curves shows the impact of institutions on average p.

Further study of our simulations reveal another relationship: as we suspected, war and within-group redistribution are institutional complements, at least over a substantial parameter range. We have just seen that when we increase the frequency of wars, *k*, the long term fraction of the population that are A's rises. Figure 5 shows that the extent of within-group redistribution (as measured by the average tax rate, *t*, among groups) also rises with the frequency of intergroup conflicts, at least up to values of *k* around 0.25. For higher levels of *k*, the fraction of A's in the population is high enough that the group benefits of redistribution (retarding the selection against A's) is more than offset by the cost of this institution. As a result, the average level of redistribution falls at higher levels of *k.* Notice, also, that segmentation and redistribution are also complements: when segmentation as well as redistribution is permitted to evolve ("both institutons"), the level of taxation is higher than in the absence of segmentation, at least for levels of $k < 0.32$.

Thus far we have varied the frequency of war exogenously or purely stochastically. A more plausible approach would take account of the fact that the group-oriented behaviors that facilitate cooperation for mutual benefit also make large-scale lethal warfare possible. If this is the case, war, altruism, and redistribution may all co-evolve. In this case, two long term steady states of the model are likely: a highly altruistic population with frequent wars, or a non-altruistic population with infrequent wars. To explore this possibility we let the frequency of intergroup conflicts vary with the fraction of A's in the population. Figure 6 shows that our dismal expectations were confirmed.

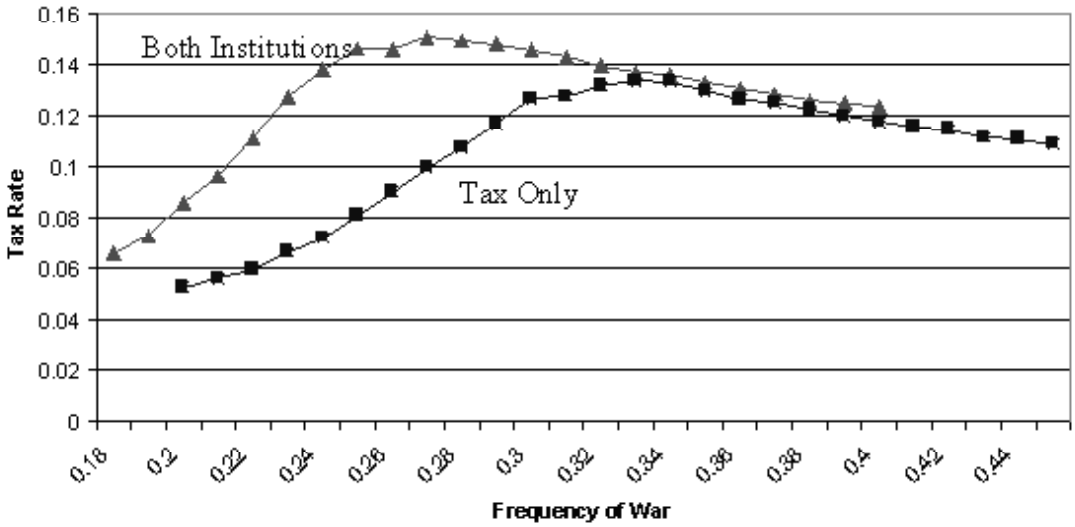


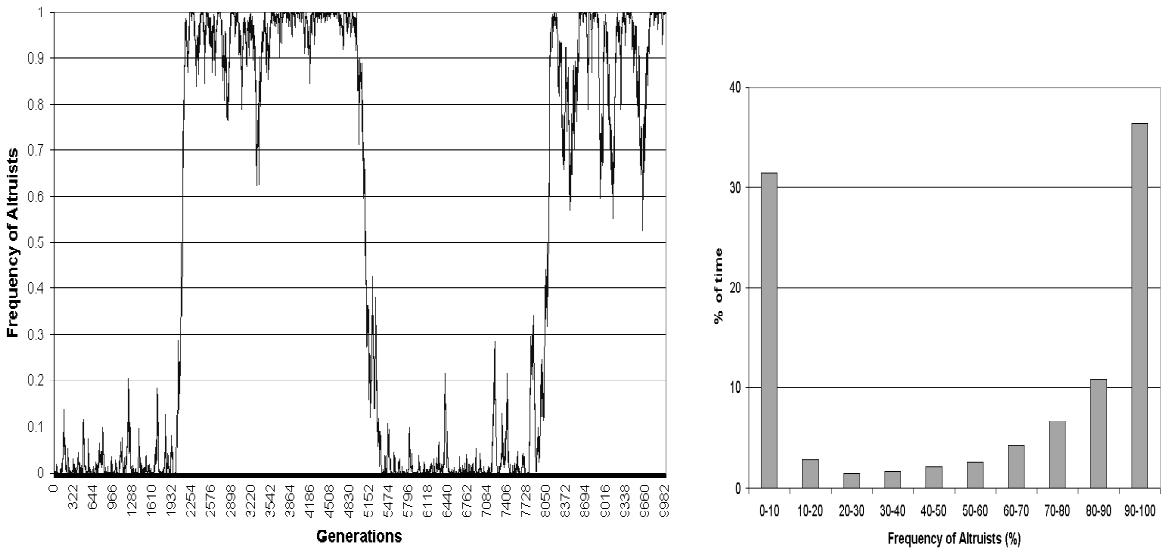
Figure 5. Warfare, redistribution and segmentation are complements. Each data point is the average tax rate over 10 runs of 50,000 periods each for the frequency of war on the horizontal axis. In this figure the other parameters are the benchmark values shown in table 1. Each run began with *p*, *t*, and *s* set equal to zero. The curve labeled tax only gives the results for runs in which *s* were constrained to zero; the other curve indicates runs in which both of the institutions were free to evolve.

5. Conclusion

We have explored the complex evolutionary relationships among a nexus of individual and group characteristics: altruism, segregation, egalitarian redistribution, group size, warfare, and group openness to migrants. We think that a strong case can be made that all of these aspects of human social structure and behavior co-evolved, each contributing to the evolutionary success of the others. Some studies of the modern the welfare state in the English speaking nations (e.g. Semmel (1960) Skocpol (1992), and Luttmer (1998)) provide further evidence for an intimate association of altruism and parochialism. While not surprising, there is something disturbing about the possibility that some of the most admirable aspects of human behavior could have evolved in a symbiotic relationship with some of the most despicable.

The joint provenance of these traits, however, does not mean that they are inextricably linked today. Nor does a comparative study of modern welfare states suggest that they are so linked empirically. The most generous welfare states, for example, are found in nations that contribute comparatively high fractions of their income to foreign aid (Fong (2003) and Fong

and Weibull (2003)). Generosity towards one's fellow citizens does not appear to be linked to indifference toward "outsiders."



(a) (b)

Figure 6. The co-evolution of altruism and war. In this simulation *k* was endogenized by $k(t)=0.1+0.36\,p(t-1)$. Panel (a) shows the average *p* of each generation during the first 10,000 generations. Panel (b) shows the fraction of the time for which p was range of values indicated on the horizontal axis.. The average value of *p* over 50,000 generation was 0.58.

The contemporary project of building societies that are at once solidaristic economically and diverse culturally is proceeding in settings vastly different from the late Pleistocene environments we have modeled. Nor would the project embraced by this workshop– and exemplified by the work of Philippe van Parijs, who we honor today -- be doomed if it were to be the case that human predispositions for both altruism and parochialism had a genetic basis. The project may be more effectively advanced, however, if one recognizes that in the absence of a culture actively promoting the values of economic solidarity and cultural tolerance, loving one's neighbor may seem vastly different from loving a stranger.

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