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1 Genetic differentiation and the evolution of cooperation in chimpanzees and humans

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18 SUMMARY

19 It has been proposed that human cooperation is unique among animals for its scale and
20 complexity, its altruistic nature, and its occurrence among large groups of individuals that
21 are not closely related or are even strangers. One potential solution to this puzzle is that the
22 unique aspects of human cooperation evolved as a result of high levels of lethal competition
23 (i.e., warfare) between genetically differentiated groups. Although between-group migration
24 would seem to make this scenario unlikely, the plausibility of the between-group competition
25 model has recently been supported by analyses using estimates of genetic differentiation
26 derived from contemporary human groups hypothesized to be representative of those that
27 existed during the time period when human cooperation evolved. Here we examine levels of
28 between-group genetic differentiation in a large sample of contemporary human groups
29 selected to overcome some of the problems with earlier estimates, and compare them with
30 those of chimpanzees. We find that our estimates of between-group genetic differentiation in
31 contemporary humans are lower than those used in previous tests, and not higher than those
32 of chimpanzees. Because levels of between-group competition in contemporary humans and
33 chimpanzees are also similar, these findings suggest that the identification of other factors
34 which differ between chimpanzees and humans may be needed to provide a compelling
35 explanation of why humans, but not chimpanzees, display the unique features of human
36 cooperation.

37 1. INTRODUCTION

38 Human cooperation is apparently unique among vertebrates in its combination of three
39 features: the large number of individuals that can cooperate together, the high frequency
40 of cooperation that involves individuals incurring a cost to their personal reproduction
41 (i.e., ‘altruistic’ cooperation), and its occurrence within such large groups that
42 cooperators are not closely related or are even strangers [1-4]. Thus, the long-term social
43 relationships based on kin selection and reciprocity that underlie cooperation in many
44 other animals, particularly other primates, appear to be insufficient to account for the
45 evolution of cooperation in humans [1-4].

46 One potential solution to this puzzle is that high levels of lethal competition between
47 groups (i.e., warfare) may have played a key role in the evolution of the unique facets of
48 human cooperation [5-8]. A large body of empirical research suggests that humans pay
49 special attention to in-group membership when cooperating [9-11], while theory suggests
50 that altruistic cooperation can evolve via between-group competition provided that groups
51 containing a higher proportion of altruists out-reproduce groups with fewer altruists more
52 quickly than non-altruists out-reproduce altruists within groups [12]. For this process to
53 occur, there should be sufficiently high levels of genetic differentiation between groups so
54 that there are large differences among groups in the fraction of altruists that they contain.
55 While the homogenizing effects of between-group migration would appear to make this
56 scenario unlikely [13,14], it is only recently that attempts have been made to assess the role
57 of between-group competition in the evolution of human cooperation using empirical data.
58 Bowles [15,16] estimated levels of mortality due to between-group competition as well as
59 levels of between-group genetic differentiation in contemporary and recently living hunter-

60 gatherers, and concluded that altruistic cooperation could evolve in humans if similar
61 conditions applied during the period when this behaviour evolved (presumably the Late
62 Pleistocene).

63 However, there are several limitations to our understanding of between-group
64 genetic differentiation in humans that limit our ability to evaluate the role of between-
65 group competition in the evolution of human cooperation. First, as his benchmark value
66 of between-group genetic differentiation, Bowles [15] used the median F_{ST} values from a
67 number of studies that assayed genetic variation using a variety of different marker
68 systems, including Y-chromosome and mitochondrial DNA. In contrast to biparentally-
69 inherited autosomal markers, such uniparentally-inherited markers can be very poor
70 indicators of patterns of genome-wide genetic differentiation, and thus of the assortment
71 of altruistic alleles within and between groups, if between-group migration is female- or
72 male-biased, respectively, as typically occurs in human societies [17,18]. Second, most
73 groups in these studies were separated by such large distances that they were very
74 unlikely to have interacted. However, groups tend to be further away from one another
75 and exchange fewer migrants the longer the time since they split from a common
76 ancestral population, and so the amount of between group genetic differentiation usually
77 increases with geographical distance [19-21]. Thus, it is currently unknown if levels of
78 between-group genetic differentiation measured at the more local scale at which most
79 between-group competition occurs are sufficiently high for the evolution of altruistic
80 cooperation in humans. Third, we have very little understanding of how levels of genetic
81 differentiation between local competing human groups compare to those of other group-
82 living animals. This comparison is important because any compelling explanation of the

83 evolution of human cooperation must also explain why other animals do not display the
84 unique features of human cooperation.

85 Chimpanzees represent a particularly relevant test for the human between-group
86 competition model, as they are one of humanity's two closest living relatives and
87 represent the base-level of relatively simple, reciprocity- and kinship-based cooperation
88 from which human cooperation evolved [22,23]. Like humans, chimpanzees are one of
89 the few species in which members of one group make lethal coalitionary attacks against
90 members of other groups, a behaviour that has long drawn attention for its similarity to
91 warfare or raiding in traditional human societies [24,25]. Although direct comparisons are
92 difficult, the available evidence suggests that the fitness consequences of between-group
93 competition are as high in chimpanzees as they are in humans; for example, the fraction
94 of adult mortality due to between-group violence in chimpanzees may match [26] or even
95 exceed [27] that of humans living in traditional societies. However, whether levels of
96 genetic differentiation between competing groups are higher in humans than chimpanzees
97 is unknown, as almost all studies on genetic differentiation in chimpanzees have been
98 conducted at broad geographical scales [28,29] or have used uniparentally inherited
99 markers [30,31], and thus suffer from the same limitations as the data used in Bowles'
100 [15,16] models.

101 There are several reasons to suspect that levels of genetic differentiation between
102 competing groups may be higher in humans than in other primates. The first stems from
103 the fact that in contrast to most non-human primates, humans have a hierarchical social
104 structure, where multiple local groups are subsumed within a larger ethnolinguistic group
105 that shares a common language, culture, and ethnic identity [32]. Ethnographic evidence

106 suggests that most people marry within their ethnolinguistic group [33], and genetic
107 evidence indicates that ethnolinguistic identity predicts genetic differentiation between
108 groups independently of the effects of geographical distance and barriers [19-21]. The
109 second is that while dispersal in non-human primates usually involves a single individual
110 or small number of individuals dispersing from their natal group to join a nearby,
111 established group [34], in humans whole groups can engage in long-distance migrations
112 to settle new lands. This process can lead to competition between neighboring groups
113 whose genetic differentiation is elevated due to the previous long-distance geographical
114 separation between them. While a similar phenomenon occurs in chimpanzees when the
115 extinction of geographically intermediate groups brings previously separated groups into
116 competition [35,36], its frequency and scale throughout evolutionary history is likely
117 lower than in humans.

118 Here we determine whether levels of autosomal genetic differentiation between
119 local human groups reach the levels previously suggested [15,16] as sufficient to allow
120 the evolution of unique facets of human cooperation via group competition, and further
121 examine whether values in humans exceed those in chimpanzees. In an attempt to
122 compensate for the necessity of using samples of contemporary humans to infer levels of
123 between-group genetic differentiation that existed during the time period when human
124 cooperation evolved, we examined between-group genetic differentiation in a large
125 sample of many different types of human societies across the world. While previous
126 studies [15,16] only considered hunter-gatherers, it has been argued that recent hunter-
127 gatherers live in more marginal habitats than those of Pleistocene hunter-gatherers, whose
128 resource-rich habitats (e.g., oceanic coasts) may have resulted in higher levels of

129 sedentism, population density, polygyny, and endogamy that are more similar to those of
130 contemporary food-producing societies [37,38]. Thus, rather than limiting our
131 comparisons to hunter-gatherers, we also examined levels of between-group genetic
132 differentiation in traditional (i.e., non-industrialized) food-producing human societies. As
133 a further step towards ensuring that our sample of contemporary human groups was
134 representative of the full range of between-group genetic differentiation values possibly
135 characteristic of Pleistocene hunter-gatherers, we also performed additional tests where
136 we limited comparisons to pairs of human groups that belonged to different
137 ethnolinguistic groups and spoke languages belonging to different language families.

138

139 2. MATERIALS AND METHODS

140 We used autosomal microsatellite genotypes to estimate levels of genetic differentiation
141 between potentially competing groups of chimpanzees and humans. Using DNA
142 extracted from feces [39], we genotyped 19 autosomal loci in 486 individuals from 18
143 chimpanzee groups from 3 locations (Figure 1). Genotypes from five chimpanzee groups
144 were previously published [22,40-42], while genotypes for 13 groups were newly
145 generated for this study. We used a two-step amplification method, where all 19 loci
146 were combined with template DNA in an initial multiplex PCR reaction, with dilutions of
147 the resultant PCR products subsequently amplified in singleplex PCR reactions using
148 fluorescently labeled forward primers and unlabelled nested reverse primers [43]. We
149 performed the necessary number of PCR replications to produce error rates of < 1%, as
150 established in previous work [43]. Eleven of the chimpanzee groups were habituated or
151 semi-habituated to human observation, facilitating the collection of fecal samples from

152 identified adult individuals. In the remaining seven unhabituated chimpanzee groups,
153 genotypes were assigned to individuals and individuals assigned to groups following
154 procedures described in [42]. We classified as potentially competing 25 pairs of
155 chimpanzee groups that were separated from one another by ≤ 20 km, as determined by
156 the centre of their sampling locations (unhabituated groups) or the centre of their territory
157 (habituated groups).

158 We used published autosomal microsatellite genotypes to measure levels of
159 genetic differentiation between potentially competing human groups (Africans [44,45],
160 Aboriginal Australians [46], Pacific islanders [47], and Native Americans [48]). Details
161 of the laboratory procedures followed to produce autosomal genotypes are provided in
162 the individual publications. Because the seafaring technology that would have allowed
163 frequent competition between groups separated by oceans likely did not evolve until late
164 in the Holocene, we only considered human groups that occupied the same land mass.
165 Distances between human groups were determined by their sampling location, or if
166 unavailable, the centre of their traditional territory. As the geographical scale at which
167 most between-group competition occurred during the period when human altruism
168 evolved is unknown, we examined several different cut-off points for potentially
169 competing human groups: those separated by ≤ 100 km, ≤ 200 km, ≤ 300 km, ≤ 400 km,
170 and ≤ 500 km. As expected, we found the highest levels of between-group genetic
171 differentiation among potentially competing groups when we included pairs separated by
172 up to 500 km. As we found that between-group genetic differentiation was not higher in
173 humans than chimpanzees even when including human groups separated by up to 500 km
174 (see results section below), we do not present the results for the more geographically

175 restrictive classifications of potentially competing human groups, even if it is more likely
176 that most competition occurs at these more local scales, particularly among direct
177 neighbors.

178 Genetic differentiation between groups was calculated using D [49] and F_{ST} [50].

179 D measures the actual relative degree of differentiation of allele frequencies among the
180 groups of a population. F_{ST} , in contrast, was designed to estimate one of the causes of
181 differences in allele frequencies between groups, the amount of migration (other factors
182 include mutation rate, bottlenecks, founder effects, etc.). Unlike F_{ST} , which is
183 mathematically bound by the amount of within-population diversity, D increases
184 monotonically with increasing levels of allelic differentiation. Thus, D is a more
185 appropriate measure to approximate the assortment of altruistic alleles within- and
186 between-groups, and we used D values for statistical comparisons of levels of between-
187 group genetic differentiation in chimpanzees versus humans.

188 We used a bootstrapping procedure to assess the statistical significance of
189 differences in the mean of pairwise between-group D values of chimpanzees and humans.
190 Here we generated 95% confidence intervals (C.I.s) by calculating means based on
191 10,000 resamples (with replacement) of the pairwise D values, and determined the
192 statistical significance of differences by examination of the overlap of the 95% C.I.s. We
193 also repeated all of our analyses with F_{ST} , but as they did not qualitatively change any of
194 our conclusions concerning average levels of between-group genetic differentiation in
195 chimpanzees versus humans, we only report F_{ST} when making comparisons with the F_{ST}
196 values used by Bowles in his earlier work on this topic. In addition to comparing average
197 pairwise F_{ST} , we also examine the percentage of pairwise F_{ST} values in chimpanzees and

198 our newly assembled human data sets that are as large or larger than the benchmark
199 value Bowles used in his original work on this topic (0.076, [15]), as well as the
200 minimum value he considered in subsequent work (0.022, [16]). We make these
201 comparisons because it is possible that although chimpanzees and humans do not differ in
202 average pairwise genetic differentiation, values that are sufficiently high for the evolution
203 of altruism may occur more frequently in humans than in chimpanzees.

204 We compare levels of between-group genetic differentiation in chimpanzees with
205 three sets of human groups: (1) both groups in a dyadic comparison are hunter-gatherers
206 (HG-HG comparisons), (2) both groups are food-producers (FP-FP), and (3) one group is
207 a hunter-gatherer and the other group is a food-producer (HG-FP). We repeated each of
208 these comparisons with restricted human data sets that only included pairs of groups that
209 belonged to different ethnolinguistic groups and spoke languages belonging to different
210 language families.

211 The ethnolinguistic identities, language families and subsistence systems of
212 human groups were determined from information reported in the original publications
213 from which we got the genetic data, and along with human and chimpanzee D and F_{ST}
214 values, are reported in the Electronic Supplementary Material. Despite the fact that
215 African Pygmies typically speak languages that combine their native tongues with those
216 of their immediate non-Pygmy neighbours [51], we classified all pairs of African Pygmy
217 groups as having languages of the same language family, and all Pygmy/non-Pygmy pairs
218 as having languages of different language families, as we felt that this classification
219 would more closely reflect the purpose of the language family variable, namely, to assay

220 levels of genetic differentiation between groups where large cultural differences may
221 inhibit between-group migration.

222

223 3. RESULTS

224 Overall, we found that genetic differentiation was the same or greater between pairs of
225 chimpanzee groups than between human groups (Figure 2). Using D, the most appropriate
226 measure of genetic differentiation for assaying the assortment of altruistic alleles within- and
227 between-groups, we found that average genetic differentiation was significantly higher in
228 chimpanzees ($D = 0.076$, 95% C.I. = 0.063 - 0.088, $N = 25$ pairs of groups) than in hunter-
229 gatherers ($D = 0.040$, 95% C.I. = 0.035 - 0.045, $N = 253$). The average D of hunter-gatherers
230 doubled to 0.085 when comparisons were made only between groups with different
231 ethnolinguistic affiliations and speaking languages belonging to different families, but did
232 not significantly differ (95% C.I. = 0.073 - 0.099, $N = 14$) from that of chimpanzees.

233 Similarly, although genetic differentiation was higher in hunter-gatherer/food-producer ($D =$
234 0.068, 95% C.I. = 0.065 - 0.071, $N = 223$) and food-producer/food-producer ($D = 0.075$,
235 95% C.I. = 0.071 - 0.078, $N = 539$) comparisons than in hunter-gatherer/hunter-gatherer
236 comparisons, in neither of these sets of groups were average D values significantly higher
237 than in chimpanzees. Unlike in the hunter-gatherer/hunter-gatherer comparisons, average D
238 values among hunter-gatherer/food-producer ($D = 0.068$, 95% C.I. = 0.065 - 0.071, $N = 178$)
239 and food producer/food-producer ($D = 0.080$, 95% C.I. = 0.076 - 0.085, $N = 254$)
240 comparisons did not substantially increase when restricted to comparisons of groups with
241 different ethnolinguistic affiliations and speaking languages from different families.

242 Very similar results were obtained with the more widely used estimator of genetic
243 differentiation, F_{ST} (Table 1). The average genetic differentiation of hunter-gatherers was
244 once again low, and values for none of the sets of human groups were higher than among
245 chimpanzees. Notably, human pairwise F_{ST} values rarely reached levels used in prior
246 assessment of the models exploring the potential for the evolution of human cooperation via
247 between-group competition [15,16] (Table 1). It was actually more common for
248 chimpanzees to reach the minimum pairwise F_{ST} value (0.022) recently suggested necessary
249 for the evolution of altruism [16] than it was for hunter-gatherer/hunter-gatherer and hunter-
250 gatherer/food-producer pairs. Only in food-producer/food-producer pairs was the percentage
251 of pairwise comparisons that met the minimum value of 0.022 higher than in chimpanzees.

252

253 4. DISCUSSION

254 Using the measure of genetic differentiation (D) most appropriate for interpopulation
255 and interspecies comparisons, we showed that average levels of small-scale genetic
256 differentiation between human groups, even when limited to groups exhibiting marked
257 cultural differences, are not higher than levels observed in chimpanzees. In addition, while
258 individual pairwise estimates of Fst infrequently reached threshold levels deemed sufficient
259 for the evolution of cooperation via group competition [15,16], this occurred in both humans
260 and chimpanzees with no consistent difference between the two species. The apparent lack of
261 higher local genetic differentiation in humans relative to chimpanzees is surprising given our
262 expectations based on how cultural barriers to between-group migration could lead to higher
263 levels of genetic differentiation between local competing groups of humans than
264 chimpanzees. However, it is also important to consider how other differences between the

265 species could produce the opposite effect. Of particular relevance in this regard is the lower
266 level of autosomal genetic variation in humans than chimpanzees, likely due to a bottleneck
267 at the recent origin of *Homo sapiens* some 200 kya, which may limit the extent of
268 differentiation in allele frequencies between groups that have all recently diverged from the
269 same source population [29].

270 Our results, while suggesting that between-group genetic differentiation in
271 contemporary humans is not greater than in chimpanzees, do not necessarily disprove the
272 hypothesis that high levels of competition between genetically differentiated groups led
273 to the evolution of the unique aspects of human cooperation. Although we found that the
274 frequency of pairwise genetic differentiation values thought to be sufficient for the
275 evolution of altruistic cooperation was not markedly higher in contemporary humans than
276 in chimpanzees, even when comparisons were limited to the most genetically
277 differentiated types of human groups, we cannot definitively rule out the possibility that
278 altruistic cooperation in humans might have evolved due to the existence of occasional or
279 even single instances of high genetic differentiation of an isolated population. In addition,
280 although we have attempted to infer levels of between-group genetic differentiation
281 present at the critical time of the evolution of human cooperation in the Late Pleistocene
282 by examining genetic differentiation in a large and diverse sample of contemporary
283 human groups, there is as currently no way of knowing how successful we have been in
284 this regard. This situation may change in the future as improvements in the ability to
285 extract reliable DNA sequence information from ancient remains [52] may eventually
286 permit the analysis of sufficient samples to describe the population structure of the
287 observed diversity.

288 We suggest that while the direct and indirect fitness benefits that humans derive
289 from between-group competition have likely been important in the evolution of human
290 cooperation, our results imply that additional factors should be considered to explain why
291 cooperation is so different in humans than in other animals, like chimpanzees, who also
292 gain fitness benefits from between-group competition. In his original work on this topic,
293 Bowles [15] argued that unlike non-human primates, where reproduction is skewed
294 towards dominant individuals, humans possess distinctive practices which limit the
295 ability of selfish individuals to outcompete altruists within groups, including culturally-
296 mandated resource and information sharing, consensus decision making, collective
297 restraints on potential aggrandizers, and monogamy. However, as some critics have noted
298 [53,54], these ‘reproductive leveling’ mechanisms may rest on exactly the same altruistic
299 behavior that the model purports to explain, and Bowles’ [16] subsequent model did not
300 include a reproductive leveling term. While it is possible that variance in lifetime
301 reproductive success is lower in humans than in chimpanzees for reasons that do not
302 themselves rely on altruism (i.e, ecological constraints that limit the ability of particular
303 individuals to monopolize fitness-limiting resources), the extremely slow life-history of
304 chimpanzees means that the data necessary to make the necessary comparisons are
305 currently unavailable.

306 Contemporary humans and chimpanzees differ in their cognitive abilities and
307 capacity for language, and such factors may also have played a role in facilitating the
308 evolution of altruistic cooperation in humans. Humans are noteworthy in the extent to
309 which socially learned, culturally transmitted information leads to between-group
310 variation in adaptive behavior. A number of factors, including the tendency of emigrants

311 to adopt the cultural traits of their new group, can lead to more cultural than genetic
312 differentiation between human groups [54,55]. In this regard, our results leave open the
313 possibility that both genetic and cultural differentiation between groups played a role in
314 the evolution of altruistic cooperation [1-3,54,55].

315

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327

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477

478 TABLE AND FIGURE CAPTIONS

479

480 Figure 1. Locations of chimpanzee groups. Number of individuals genotyped per group are
481 shown in brackets.

482

483 Figure 2. Average pairwise D values (and 95% C.I.s) of chimpanzee (empty bars) and
484 human groups (grey bars) with different combinations of subsistence systems. Sample
485 sizes (number of pairs of groups) are shown in brackets. For humans, light grey bars
486 represent values for all pairs of groups, and dark grey bars represent values for the
487 restricted sample consisting only of pairs of groups belonging to different ethnolinguistic
488 groups and speaking languages belonging to different language families. HG: hunter-
489 gatherer, FP: food-producer.

490

491 Table 1. F_{ST} values in chimpanzee and human groups practicing different forms of
492 subsistence. Shown are the sample sizes (number of pairs of groups) and averages of the
493 pairwise F_{ST} values, along with the percentage of pairwise F_{ST} values that reach those
494 used in Bowles' models. For humans, values are shown for all pairs of groups and for the
495 restricted sample consisting only of pairs of groups belonging to different ethnolinguistic
496 groups and speaking languages belonging to different language families. HG: hunter-
497 gatherer, FP: food-producer.

Table 1.

	N	Mean F_{ST}	% $F_{ST} \geq 0.022$	% $F_{ST} \geq 0.076$
Chimpanzees	25	0.014	8.0	0.0
All HG/HG	253	0.005	1.2	0.4
Restricted HG/HG	14	0.013	0.0	0.0
All HG/FP	223	0.011	0.9	0.9
Restricted HG/FP	178	0.010	0.0	0.0
All FP/FP	539	0.015	23.6	0.2
Restricted FP/FP	254	0.015	23.2	0.0



