Genetic differentiation and the evolution of cooperation in chimpanzees and humans

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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-gather/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-gather 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

316   5. ACKNOWLEDGEMENTS

327

328   6. REFERENCES

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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

N

N2 (8)

N3 (3)

N1 (4)

North (22)

GTZ (11)

Meteo (17)

East (18)

Middle (11)

South (57)

**Budongo
Forest Reserve**

Sonso (29)

Busingiro (41)

Kasokwa (6)

Kanyawara (40)

Ngogo (119)

Kanyantale (49)

**Kibale
National Park**

G2 (17)

G4 (7)

**Taï
National Park**

0   10   20   Kilometers