

## The evolution of fairness: explaining variation in bargaining behaviour

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# The evolution of fairness: explaining variation in bargaining behaviour

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Conceptions of fairness vary across the world. Identifying the drivers of this variation is key to understanding the selection pressures and mechanisms that lead to the evolution of fairness in humans. Individuals' varying fairness preferences are widely assumed to represent cultural norms. However, this assumption has not previously been tested. Fairness norms are defined as culturally transmitted equilibria at which bargainers have coordinated expectations from each other. Hence, if fairness norms exist at the level of the ethno-linguistic group, we should observe two patterns. First, cultural conformism should maintain behavioural homogeneity within an ethno-linguistic group. Second, bargainers' expectations should be coordinated such that proposals and responses to proposals should covary. Here we show that neither of these patterns is observed across 21 populations of the same ethno-linguistic group, the Pahari Korwa of central India. Our findings suggest that what constitutes a fair division of resources can vary on smaller scales than that of the ethno-linguistic group. Individuals' local environments may play a central role in determining conceptions of fairness.

## 1. Introduction

Variation in cooperative and bargaining behaviour across human populations [1–7] is assumed to reflect culturally transmitted fairness norms. This untested assumption has been widely used to interpret results from empirical studies of bargaining behaviour across disciplines [1–3,5–9]. There are at least two ways of defining fairness in the context of a bargaining situation. The first is an absolute definition whereby a fair outcome is one where a pie is always divided equally between bargainers. The second is a relativist definition whereby a fair outcome is any division of a pie that is mutually agreed upon by bargainers, irrespective of whether the shares are equal or not. An absolute fairness norm cannot account for the variation in bargaining behaviour observed across human populations. Thus, here we consider whether relativist fairness norms operating at the level of the ethno-linguistic group drive bargainers behaviour.

Relativist fairness norms are defined as culturally transmitted equilibria at which bargainers have coordinated expectations from each other [10,11]. Hence, if fairness norms at the level of the ethno-linguistic group drive behaviour in a bargaining situation, then we should observe two patterns. First, cultural conformity should maintain behavioural homogeneity within the ethno-linguistic collective despite variation in the characteristics of individuals and their local environments. Second, proposals and responses to proposals should be coordinated in the sense that first-movers should only make high offers because second-movers would reject low offers. We show that neither of these patterns is observed empirically in a set of real-world populations. Thus, we find no evidence for the operation of a fairness norm at the level of the ethno-linguistic collective. Our findings suggest that environmental factors may be more important determinants of fairness in humans than cultural norms.

We implemented one-shot, anonymous ultimatum games (UGs) in 21 discrete populations of the *same* ethno-linguistic group, a forager-horticulturist society called the Pahari Korwa of central India (details are provided in the electronic

supplementary material). The UG is a two-player bargaining experiment that has been extensively used as a behavioural measure of fairness across disciplines [e.g. 3,5–7,12–14]. One of a pair of individuals, the ‘proposer’, must divide a sum of money (the stake,  $S$ ) between herself and an unknown ‘responder’. If the responder accepts the proposer’s offer ( $x$ ), the responder earns  $x$ , and the proposer earns  $S - x$ . If the responder rejects the offer, neither player earns anything. In this game, the income-maximizing strategy entails that a responder accepts any offer made by the proposer. Assuming that the responder will play the income-maximizing strategy, the income-maximizing strategy for a proposer is to make the smallest possible offer.

We find significant variation in proposers’ offers across these populations. By contrast, responders rarely rejected any offers and their behaviour varies little across the same 21 populations. Thus, proposer behaviour does not covary with responder behaviour. Our finding that proposer behaviour varies significantly across populations of the same ethno-linguistic group demonstrates an absence of cultural conformity within the ethno-linguistic group as a collective. Moreover, proposer behaviour does not covary with responder behaviour, which demonstrates that bargainers do not have coordinated expectations. Hence, we do not find any evidence for the operation of a fairness norm at the level of the ethno-linguistic group in these populations.

## 2. Material and methods

### (a) Study populations

Pahari Korwa populations present an excellent model system for this study: a set of real-world, uni-ethnic meta-populations of the same endogamous ethno-linguistic group with distinct population boundaries. Pahari Korwas are heavily reliant on gathered forest products, which are a primary source of food and income, but they also practice agriculture on small tracts of land [15]. These economic resources are supplemented by opportunistic hunting, fishing and wage labour. They live in mostly uni-ethnic villages that have well-defined boundaries; tracts of forest and hills separate neighbouring villages. In this endogamous society, exogamous marriages usually incur severe penalties, entailing ostracism and expulsion from the tribe and village. Table 1 presents summary statistics for our study populations (see the electronic supplementary material for further details).

### (b) Experimental set-up

The size of the stake ( $S$ ) for each game was 100 Indian rupees (henceforth rupees), equivalent to a little over 2 days’ wages in the region. Offer values were restricted to multiples of five. Each individual played the game once and in one role, as a proposer or a responder, under anonymous conditions. Pairs of players were constituted by randomly matching token numbers. In 16 of the 21 populations where the UG was played, once a responder had made her decision regarding whether she wished to accept or reject the offered amount, we additionally asked her what minimum offer from a proposer she was willing to accept; this was recorded as the minimum acceptable offer (MAO) for that individual. The game outcome and payoffs were determined on the basis of the accept/reject response and players were fully aware of this. Hence, the MAO is a self-reported figure and players knew that its value did not affect their actual payoffs in the game. We use MAO values to examine

whether players’ self-reported behavioural strategies agree with their game behaviour.

To summarize the key features of our standardized protocol. (i) Instructions were delivered from standardized scripts and real money was used to demonstrate game rules and examples. Only individuals who correctly answered a set of questions played the game; the questions were designed to assess their understanding of the game and experimental set-up. (ii) Decisions were made individually at a private location and no names were recorded; a player’s only identification was a numbered token. (iii) Those who had played the games were prevented from interacting with those who had not yet played. (iv) All games in all villages were administered by S.L. usually on the second and third day after arrival in the village and usually completed in 2 days; prior to this study, S.L. had no contact with any individual from any of the 21 villages included in this study.

Our study design excludes the following confounding causes of variation across populations (see the electronic supplementary material for details): (i) context and framing effects, (ii) experimenter variation, (iii) experimenter familiarity, (iv) differences in recruitment methods and time periods over which games were conducted in different populations, and (v) differences in protocols. Previous cross-cultural studies [5–7,16], mostly administered by multiple researchers, did not exclude and could not test for these confounding causes of variation between their study populations.

### (c) Demographic and individual data

Demographic and other data on individuals were collected via a standardized questionnaire administered by a research assistant. Descriptions of the village and individual descriptors are in the electronic supplementary material. Once all games in a village had been completed, a population census was conducted and the geographical coordinates for every house in the village were recorded using a global positioning system (Garmin GPS 12XL). Geographical information systems (GIS) data were processed and analysed in ARCGIS (v. 9.2; Environmental Systems Research Institute).

### (d) Analyses

We employ multilevel normal linear models [17] to explicitly analyse variation in UG behaviour at the village and individual levels in our data (structured as individuals within villages). We mainly use an information-theoretic model-fitting approach [18] to analyse data and interpret results. The Deviance Information Criterion (DIC) was used to compare models [19]. The DIC is a Bayesian measure of model fit and complexity; it accounts for the change in degrees of freedom between nested models. Models with a lower DIC value provide a better fit to the data and, as a rule of thumb, a difference in DIC values of 5–10 units or more is considered substantial [18,19]. Details of the analyses are in the electronic supplementary material.

The income-maximizing offer (IMO) was calculated as follows [20]. A binary logistic regression was run with responder response (accept/reject) as the dependent variable and proposer offer as the only explanatory variable. This regression estimates the relationship between the probability of acceptance and proposer offer, from the distribution of offers accepted and rejected. The parameter values derived from the regression equation ( $\beta$  and  $c$ ) were used to estimate the probability of acceptance ( $p_i$ ) for each offer value ( $i$ ) from 0 to 100 ( $p_i = \exp(\beta_i + c) / \{1 + \exp(\beta_i + c)\}$ ), with  $i$  increasing in increments of five. The estimated probability of acceptance ( $p_i$ ) for each offer value ( $i$ ) was multiplied with the payoff received by a proposer if that offer value was accepted; this is the expected payoff (payoff <sub>$i$</sub> ) from an offer (payoff <sub>$i$</sub>  =  $p_i(S - i) = p_i(100 - i)$ )

**Table 1.** Summary statistics of demographic variables and sample sizes for the study populations. Three hundred and forty-four individuals participated as proposers and 340 as responders in UGs played across 21 villages. The total number of proposers differs from the total number of responders since in eight villages an odd number of individuals participated in the games. In these villages, one individual was paired randomly with two other players from the village in order to determine the payoff to all participating players. The mean age  $\pm$  s.d. of participants was  $35.57 \pm 12.49$  years and 44% were female.

village number	village name	population size <sup>a</sup>	percentage of migrants in sample <sup>b</sup>	percentage of non-Korwas <sup>c</sup>	distance from the major town (km) <sup>d</sup>	proposers (n)	responders (n)
1	Chipni Paani	27	92 (12)	0	24	6	6
2	Mahua Bathaan	61	32 (22)	16	44	11	11
3	Jog Paani	64	53 (19)	25	47	10	9
4	Semar Kona	64	29 (17)	17	24	9	8
5	Bihidaand	73	48 (21)	21	33	11	10
6	Khunta Paani	97	52 (31)	27	36	16	15
7	Kaua Daahi	102	41 (32)	0	46	16	16
8	Pareva Aara	111	44 (36)	14	42	18	18
9	Musakhhol	117	37 (30)	26	35	15	15
10	Kharranagar	125	42 (38)	0	50	19	19
11	Tedha Semar	141	40 (30)	3	45	15	15
12	Jamjhor	144	37 (30)	44	25	15	15
13	Vesra Paani	157	25 (44)	25	27	22	22
14	Mirgadaand	163	56 (32)	35	5	16	16
15	Barghaat	194	31 (42)	10	41	21	21
16	Gotidoomar	195	36 (50)	0	31	25	25
17	Chaur Paani	197	40 (30)	1	33	15	15
18	Aama Naara	207	33 (43)	6	69	21	22
19	Bakrataal	254	54 (39)	7	26	19	18
20	Kheera Aama	290	29 (42)	18	31	20	21
21	Ghatgaon	957	15 (47)	5	13	24	23

<sup>a</sup>Includes all adults and children residing in the focal village.

<sup>b</sup>Numbers in parentheses indicate size of sample used to estimate the proportion of migrants. Migrants are individuals (Pahari Korwas) currently residing in the focal village but born in another village. Migration often follows marriage, particularly for females.

<sup>c</sup>Percentage of the focal village population who were not Pahari Korwas.

<sup>d</sup>Distance from Ambikapur, the largest town in the study region.

given its probability of acceptance. The IMO is then the offer value with the highest expected payoff.

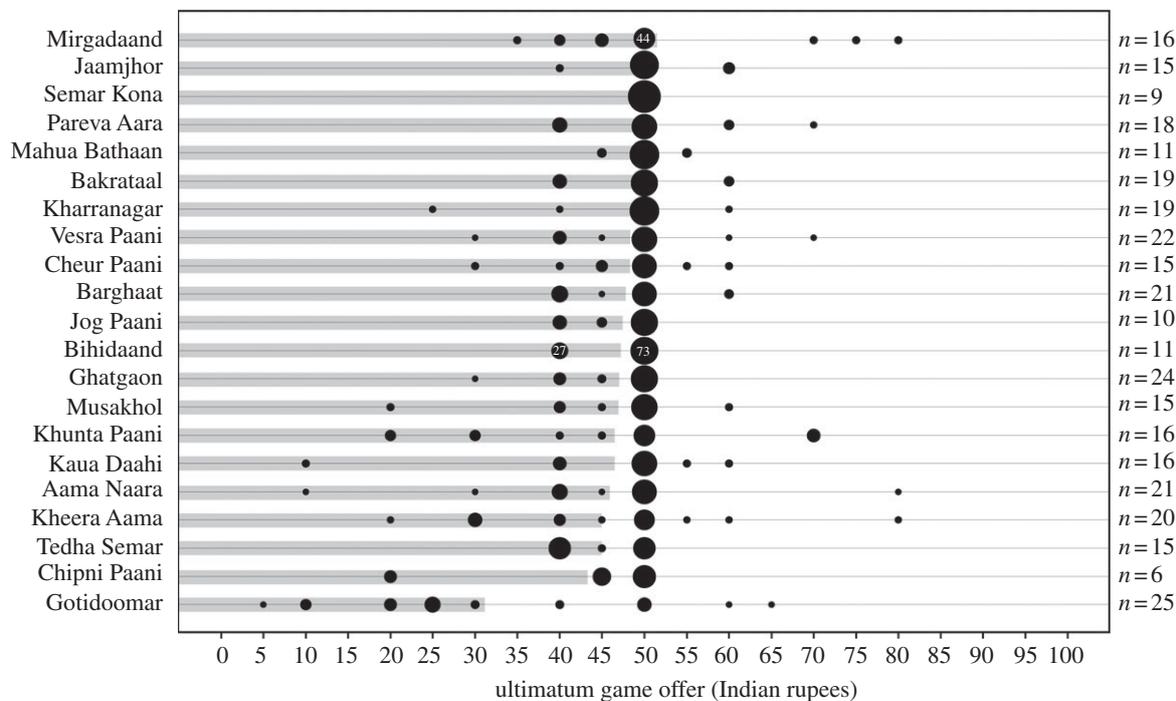
### 3. Results

#### (a) Proposer behaviour varies across populations of the same ethno-linguistic group

Distributions of proposer offers (figure 1) vary significantly across villages. Offers vary from 5 to 80 per cent of the stake across villages. The modal offer across all villages is 50 rupees (50% of the stake). While the primary mode (the most frequently made offer) varies little across villages, the secondary mode (the second most frequently made offer) varies between 30 and 70 rupees across villages. Mean offers vary between about 31 and 52 rupees. 14.4 per cent (95% Bayesian confidence interval (BCI) = 6.3, 27.3) of the variance in offers occurs between villages (table 2b; null model (multilevel)). The DIC value for the null model with village-level intercepts (multilevel) is about 44 units lower

than for the null model without village-level intercepts (single level), indicating that the multilevel model accounting for village effects provides a significantly better fit to the data (table 2a; null models). Once village and individual descriptors are included in the model, the unexplained between-village variance reduces to 11.2 per cent (95% BCI = 4, 22.8) (table 2b; full model (multilevel)).

We tested whether properties of populations and individuals are associated with proposer offers (details are presented in table 2a, and a discussion of these results is provided in the electronic supplementary material). One population descriptor and two individual descriptors are associated with proposer offers. The proportion of non-Korwas (village residents who are not Pahari Korwas) has a substantial positive effect on proposer offers. Each additional non-Korwa living in the village is associated with offer values that are about 14 rupees (14% of the stake) higher on average. Note that non-Korwas did not participate in the games in any village. A player's household size has a small negative effect on her offer. Each additional person in the household reduces offers by about half a rupee on average. Finally, people



**Figure 1.** Distributions of UG proposer offers across 21 villages. For each village on the y-axis, the areas of the black bubbles represent the proportion of individuals from the village who made an offer of the value on the x-axis. To indicate scale, the numbers in some bubbles are the percentage proportions represented by those bubbles. Grey horizontal bars indicate the mean offers for villages. Villages are ordered by their mean offers; the bottom village (Gotidoomar) has the lowest mean. Counts on the right ( $n$ ) represent the number of proposers from each village (total  $n = 344$ ). The overall mode across villages is 50 rupees (mean  $\pm$  s.d. = 46.61  $\pm$  10.40).

**Table 2.** (a) Associations of each predictor term (fixed effect) with proposer offers in the null (intercept only) and full models. (b) Village- and individual-level variance components for proposer offer in the null and full models.<sup>a</sup> (The variance partition coefficient (VPC = village-level variance/(village-level variance + individual-level variance)) is 0.144  $\pm$  0.054 (95% BCI<sup>b</sup> = 0.063, 0.273) in the null model, and 0.112  $\pm$  0.049 (95% BCI<sup>b</sup> = 0.040, 0.228) in the full model. \*\*\* $p < 0.01$ ; \*\* $p < 0.05$ ; \* $p < 0.10$ .)

(a) fixed effect	proposer offer (Indian rupees)			
	$\beta \pm$ s.e.	95% BCI <sup>b</sup>	DIC <sup>c</sup>	
null models				
intercept (single level)	46.624 $\pm$ 0.562***	45.506, 47.717	2590.199	
intercept (multilevel)	46.928 $\pm$ 1.031***	44.903, 49.037	2546.072	
full model (multilevel)			2528.601	
intercept	45.888 $\pm$ 1.853***	42.304, 49.607		
proportion of non-Korwas	13.821 $\pm$ 7.256*	-1.045, 27.509		
household size (individuals)	-0.400 $\pm$ 0.213*	-0.819, 0.024		
day on which game was played: day 2+ (ref: day 1)	4.940 $\pm$ 1.162***	2.658, 7.189		
(b)				
	village-level	individual-level		
	variance $\pm$ s.e.	95% BCI <sup>b</sup>	variance $\pm$ s.e.	95% BCI <sup>b</sup>
null model (multilevel)	15.720 $\pm$ 7.090	6.314, 33.725	91.781 $\pm$ 7.310	78.660, 107.180
full model (multilevel)	11.234 $\pm$ 5.674	3.705, 25.155	87.018 $\pm$ 6.873	74.694, 101.473

<sup>a</sup>For the two multilevel models (null and full), fixed-effect parameters in each model are specified in table 2a, while table 2b presents the village- and individual-level variances in proposer offers for each model, respectively. For instance, in table 2a, the full model (multilevel) has four fixed effects including the intercept; for each fixed effect (column 1), the associated  $\beta$ -value (column 2) and its 95% BCI<sup>b</sup> (column 3) can be read in the corresponding row. The DIC<sup>c</sup> value for the model is presented in column 4 of table 2a. The variance components for the full model (multilevel) can be read in the last row of table 2b; column 2 represents the village-level variance in proposer offers with its 95% BCI<sup>b</sup> (column 3), and column 4 represents the individual-level variance in proposer offers with its 95% BCI<sup>b</sup> (column 5). The fixed effect parameters for the single-level null model are presented in table 2a; this model does not have variance components.

<sup>b</sup>Bayesian credible interval.

<sup>c</sup>Deviance Information Criterion.

**Table 3.** UG responder responses (total  $n = 340$ ) for each of 21 study villages. (Players' payoffs in the game were determined on the basis of these accept/reject responses and they were fully aware of this.)

village number	village name	responses		
		total ( $n$ )	accept ( $n$ )	reject ( $n$ ) <sup>a</sup>
1	Chipni Paani	6	6	0
2	Mahua Bathaan	11	11	0
3	Jog Paani	9	9	0
4	Semar Kona	8	8	0
5	Bihidaand	10	10	0
6	Khunta Paani	15	15	0
7	Kaua Daahi	16	16	0
8	Pareva Aara	18	18	0
9	Musakhol	15	15	0
10	Kharranagar	19	19	0
11	Tedha Semar	15	15	0
12	Jamjhor	15	15	0
13	Vesra Paani	22	22	0
14	Mirgadaand	16	15	1 : 35
15	Barghaat	21	21	0
16	Gotidoomar	25	23	2 : 25, 50
17	Cheur Paani	15	14	1 : 50
18	Aama Naara	22	22	0
19	Bakrataal	18	18	0
20	Kheera Aama	21	20	1 : 50
21	Ghatgaon	23	23	0

<sup>a</sup>Values listed after the colons are the values of the offers (in rupees) rejected.

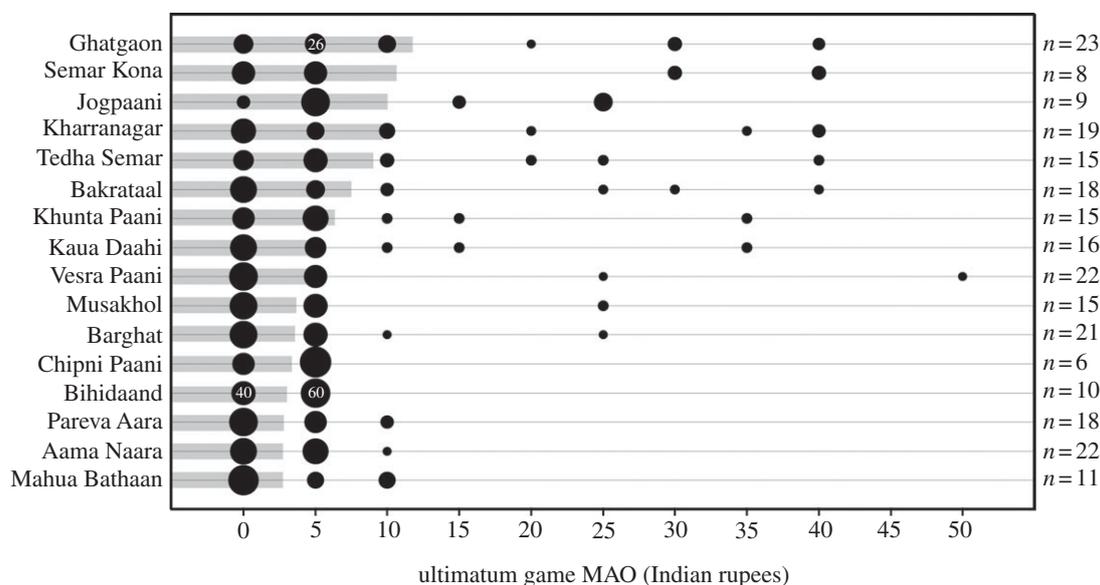
who played on the second or third day of the games in any village made offers that were about five rupees higher on average. Pseudo- $r^2$  values indicate that about 22 per cent of variance between populations and 9 per cent of variance within populations are explained by these three descriptor variables. Players' migration histories, frequency of market contact and multiple measures of wealth have little effect on their offers. The size of a player's social network and the number of kin that she has living, living in the same village, or living elsewhere, are also not associated with her offers.

### (b) Responder behaviour does not vary across populations of the same ethno-linguistic group

In contrast to proposer offers, we find almost no variation in response distributions across villages. Of the 340 offers that responders were presented with across 21 villages, only five offers of any value were rejected (table 3); three of these five rejected offers had a value of 50 rupees (50% of the stake) and the remaining two rejected offers had values of 25 and 35 rupees, respectively. Individuals virtually never reject offers in these populations, despite the fact that offers vary from 5 to 80 per cent of the stake. Only 1.5 per cent of responders across 21 Pahari Korwa villages rejected offers of any value. Thus, there is no variation in responder behaviour across villages. Hence, responders across this ethno-linguistic

group appear to follow the same income-maximizing strategy. Given the small number of rejections, no further analyses were conducted on responders' game responses.

Responders' self-reported strategies confirm this pattern. The modal self-reported MAO across all villages is zero (figure 2). Eighty per cent of responders reported that they were willing to accept either nothing or the smallest possible division of the stake, i.e. five rupees. In fact, the modal MAO in all villages is either zero or five rupees and very few individuals stated MAOs greater than 10. 4.9 per cent of the variance in MAOs occurs between villages (table S3B; null model (multilevel)). The DIC value for the null model with village-level intercepts (multilevel) is about 3.5 units lower than for the null model without village-level intercepts (single level), indicating that the multilevel model accounting for village effects provides only a slightly better fit to the data (see the electronic supplementary material, table S3A; null models). Once individual descriptors are included in the full model, the unexplained between-village variance reduces to 2.7 per cent (see the electronic supplementary material, table S3B; full model (multilevel)). Considering the low rate of actual rejections in these populations (even of small offers), these results suggest that the Pahari Korwa do as they say. If responders were simply justifying their accept/reject decisions, then we should expect a closer resemblance between the distributions of proposer offers and responder MAOs; we find no relationship between the two.



**Figure 2.** Distributions of UG responder MAOs across 16 villages. The MAO is a self-reported figure and players knew that its value did not affect their actual payoffs in the game. For each village on the *y*-axis, the areas of the black bubbles represent the proportion of individuals from the village who have an MAO of the value on the *x*-axis. To indicate scale, the numbers in some bubbles are the percentage proportions represented by those bubbles. Grey horizontal bars indicate the mean MAO for villages. Villages are ordered by their mean MAOs; the bottom village (Mahua Bathaan) has the lowest mean. Counts on the right (*n*) represent the number of responders from each village (total *n* = 248). The overall mode across villages is 0 rupees (mean  $\pm$  s.d. =  $6.11 \pm 9.67$ ).

### (c) Proposer behaviour is not contingent on responder behaviour

While UG responders in our study populations played the income-maximizing strategy, proposers did not. Proposers often offered substantial proportions of the stake, even though responders rarely rejected offers and appeared willing to accept any offer. Responder behaviour did not vary across the 21 populations even though proposer offers vary significantly across the same populations. The IMO, the offer that provides the highest expected payoff to a proposer given the distribution of rejections across offer values, is zero rupees as estimated from the distribution of rejections pooled across all 21 villages. Hence, the mean proposer offer for every village (figure 1) was much higher than the IMO; this confirms that proposers were not maximizing their income by making such high offers and their offers were not coordinated with responders' responses. In fact, all 344 offers made across 21 villages were higher than the IMO. We estimated the village-specific IMO for the four villages where at least one offer was rejected (see the electronic supplementary material, table S4). The mean proposer offer was much greater than the IMO for all four villages. Moreover, the modal self-reported MAO across populations (zero rupees) is equal to the IMO. Thus, proposer and responder behaviour in the UG is not coordinated across these populations.

## 4. Discussion

### (a) Behavioural variation across populations

We find significant variation in UG proposer behaviour across 21 populations of the same ethno-linguistic group. This result is consistent with our previous findings [21] that contributions to public goods games and decisions regarding the distribution of salt, a locally valued resource, vary significantly and to a similar extent across 16 of the same villages.

Thus, congruent results from three measures of behaviour administered in up to 21 populations provide evidence that levels of cooperation and bargaining behaviour vary substantially across populations of the same ethno-linguistic group.

The low frequency of rejections in UGs observed in Pahari Korwa populations is comparable to that found in several other populations, including populations of the Ache (0%), Tsimane (0%), Kazakh (0%), Quichua (0%), Isanga (3%), Orma (3.5%), Sanquianga (4%), Machiguenga (4.7%), Sangu herders (5%) and Samburu (5%) [7,22]. In about half of the 15 populations sampled in a cross-cultural study [7], responder behaviour was comparable to that observed in our study populations. A meta-analysis of 75 UG studies [3] conducted across 26 countries, largely sampling university students, reveals that the average rejection rate across studies is 16 per cent. However, rejection rates vary significantly by region (group of neighbouring countries). The meta-analysis also demonstrates that, across studies, rejection rates are far more sensitive to changes in the relative proportion of the stake offered than the absolute value of the offered share.

Thus, while responders in some parts of the world are willing to accept any offer made to them and follow the income-maximizing strategy, those in other places care about relative payoffs. What appear to be culturally transmitted fairness norms may be inequity-averse behavioural strategies that are individually adaptive in certain, but not all, environments. The finding that variation in inequality aversion explains some part of the variation in UG behaviour across 15 small-scale societies [22] is consistent with this hypothesis.

### (b) Absence of coordination between bargainers' behaviour

Proposer and responder behaviour in the UG are not coordinated across our study populations. Our findings agree with those of previous studies demonstrating that mean offers in most populations of small-scale societies are much higher

than IMOs [7] and mean MAOs [5,6]. In populations of large-scale societies, there is much greater variation in rejection rates than in offers [3]; we find the reverse pattern in our study populations. The absence of coordination between bargainers' behaviour observed in previous studies [3,5–7] and this study, contradicts economic models that assume that proposer behaviour is a best response to responder behaviour in a bargaining situation [23,24]. Proposer and responder strategies in a bargaining situation may not simply reflect dyadic relations but may be affected by different factors, especially if they are not wholly regulated by fairness norms. For instance, a recent study demonstrates that while proposers in the UG respond to reputation concerns by increasing their offers in a public context, responders do not do so [25].

### (c) Fairness norms

A fairness norm is a culturally transmitted equilibrium at which bargainers have coordinated expectations from each other [10,11]. We do not find evidence of cultural conformism within the ethno-linguistic group as a collective, nor do we find that proposals and responses covary across this collective. Our findings make clear that current empirical data do not support the hypothesis that fairness norms at the level of the ethno-linguistic group account for the behavioural variation observed across human populations or the homogeneity observed within them.

It is possible that culturally transmitted behavioural norms exist at the level of the village rather than at the level of the ethno-linguistic group. Our finding that responder behaviour is uniform across the ethno-linguistic collective may suggest that responder behaviour is regulated by a norm. However, we find that the behaviour of proposers and responders in the UG did not covary even within our study villages. Thus, since we find that bargainers do not have coordinated expectations even at the level of the village, our findings suggest either that fairness norms do not regulate the behaviour of bargainers, or that behaviour observed in the experimental UG does not reflect the fairness norms that regulate individuals' behaviour in everyday life. It is therefore premature to conclude [1–3,5–9] that behaviour in a bargaining situation is regulated by fairness norms, based on evidence from the experimental UG.

As we have argued before [21], cross-cultural studies that have sampled from one or a few populations per culture confound cultural and environmental (demographic and ecological) differences between populations. Thus, the variation in cooperative and bargaining behaviour across human populations that is currently ascribed to culturally transmitted fairness norms may, in fact, be driven by individuals' sensitivity to local environmental conditions. This process presents a competing hypothesis as an explanation for patterns of behavioural variation that have previously been attributed to conformity to cultural norms.

Many characteristics of individuals are associated with cooperative behaviour, such as age [26], wealth [27] and sex (reviewed in [28]). Substantial empirical evidence demonstrates that individuals share socio-economic traits with their neighbours, a phenomenon termed homophily (reviewed in [29]). If individuals choose their place of residence based on their similarity to others in a neighbourhood, and if such residential homophily is based on individual characteristics that also correlate with cooperative behaviour, this process will give rise to geographically structured (e.g. neighbourhoods, populations) patterns of cooperation. For instance, if individuals buy houses based on where they can best afford to live and an individual's wealth is correlated with how likely they are to cooperate, then we should expect to observe neighbourhoods that are both uniform in their levels of wealth and levels of cooperation; several studies have noted an association between measures of neighbourhood wealth and levels of cooperation [30–32]. Thus, observed within-population similarity and between-population variation in cooperation does not necessarily arise from the cultural transmission of cooperative norms, or even direct assortment on how cooperative an individual's neighbours are, but rather may arise indirectly owing to homophilic residence on individual characteristics that correlate with cooperative behaviour.

Our findings caution against assuming that the modal behaviour in a human population reflects the operation of a cultural norm without explicitly testing this hypothesis. The independent, evolutionarily adaptive responses of individuals to shared local environments or homophilic residence patterns may produce behavioural homogeneity within populations and variation across them even if individuals do not share a cultural norm. Moreover, our findings suggest that what constitutes a fair division of resources can vary on smaller scales than that of the ethno-linguistic group. Individuals' local environments may play a central role in determining what constitutes fair behaviour and explaining the varying conceptions of fairness across the world.

This study has full approval from the Research Ethics Committee at University College London, and informed consent was obtained from all participants.

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