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Harsh childhood environmental characteristics predict exploitation and retaliation in humans

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Across and within societies, people vary in their propensities towards exploitive and retaliatory defection in potentially cooperative interaction. We hypothesized that this variation reflects adaptive responses to variation in cues during childhood that life will be harsh, unstable and short—cues that probabilistically indicate that it is in one's fitness interests to exploit co-operators and to retaliate quickly against defectors. Here, we show that childhood exposure to family neglect, conflict and violence, and to neighbourhood crime, were positively associated for men (but not women) with exploitation of an interaction partner and retaliatory defection after that partner began to defect. The associations between childhood environment and both forms of defection for men appeared to be mediated by participants' endorsement of a 'code of honour'. These results suggest that individual differences in mutual benefit cooperation are not merely due to genetic noise, random developmental variation or the operation of domain-general cultural learning mechanisms, but rather, might reflect the adaptive calibration of social strategies to local social–ecological conditions.

1. Introduction

Cooperation has played unique roles in hominid reproduction, survival and parental care for several million years [1]; so the psychological mechanisms that regulate distinctly human forms of cooperation have plausibly been subject to natural selection [1,2]. For ancestral humans, everyday social relations were characterized by repeated cooperative interactions over long time horizons, which created selection pressure for reciprocity—that is, for cooperating with co-operators and punishing (or terminating interactions with) individuals who seek to exploit co-operators [2–4].

However, humans vary in their tendencies to cooperate and in their readiness to withdraw from cooperation with (or to punish) defectors [5,6]. Recent attempts to explain such individual differences based on cultural group selection have relied on the premise that people acquire norms through cultural learning, and that internalization of these norms leads to within-culture commonalities and between-culture differences. Norms for cooperating, and for punishing defectors, it is argued, proliferate because they suit people for life in large societies in which social and economic life increasingly incorporates non-kin and interactions that cannot be stabilized through direct reciprocity [7]. The sufficiency of this theoretical approach, however, is called into question by recent evidence that the variation among populations within a single culture [8], and even neighbourhoods within the same city [9], is as substantial as is the variance between cultures—not to mention the substantial individual differences among individuals from the same subject pools [10]. Thus, other theories for these individual differences merit consideration.

(a) Adaptationism, life history and childhood social ecology

An adaptationist approach to these individual differences arises from the premise that natural selection produces organisms whose behaviours are not necessarily constrained to single, inflexible strategies: instead, organisms (including humans)

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subject (P1)

	C	D
C	P1 : 2 P2 : 2	P1 : 3 P2 : 0
D	P1 : 0 P2 : 3	P1 : 1 P2 : 1

partner (P2)

Figure 1. The iterated Prisoner's Dilemma. Two players are paired and complete multiple rounds of play, making decisions independently and anonymously. Participants receive points (later converted to real money) depending on their joint outcomes in each round. Players have two possible choices—cooperate (C) or defect (D)—yielding four potential outcomes per round: Both players cooperate (CC), one cooperates and the other defects (CD and DC) or both defect (DD). Each joint outcome corresponds to different payoffs for the players: CC yields moderate and equal payoffs for both players (2,2), CD and DC yield zero for the co-operator and the maximum payoff for the defector (0,3), and DD yields small, equal payoffs for both players (1,1). With this payoff matrix, the decision that maximizes one's income on any single round is to defect (because it produces better payoffs than cooperating irrespective of one's partner's choices), but if repeated rounds are expected, mutual cooperation will maximize income if one can assume that one is playing against another actor who wishes to do likewise.

can often choose (not necessarily consciously) from a suite of strategies in response to environmental cues that contain information about which strategies will fit best with local conditions, based on ancestral correlations between those cues and the behaviours that raised fitness when those behaviours were enacted in response to those cues [9,11]. To wit, girls with stressful family relationships reach reproductive maturity faster than those with more positive family relationships [12], age at first conception is lower and rates of violence are higher in neighbourhoods with low life expectancies [13], and people from homes in which nurturance, discipline and parental care were inconsistent, or from neighbourhoods in which violence and economic disadvantage were high, engage in more impulsive and risky behaviour as young adults [14,15]. More generally, harsh, violent conditions are valid cues (not necessarily processed consciously) that it is in one's reproductive interests to allocate energetic and somatic resources to reproductive maturity and mating effort in the short-term, rather than to investments that will redound to fitness only over a longer time horizon [16]. Here, we explored whether this 'live fast, die young' principle [17] explains individual differences in cooperation with a highly cooperative partner and retaliatory defection in an Iterated Prisoner's Dilemma (IPD; figure 1).

The 'tit-for-tat' strategy for the IPD—which involves cooperating initially, always reciprocating cooperation, always retaliating against defection and immediately resuming cooperation when a defector has done likewise [18]—is a venerated model for effective self-interested social cooperation in repeat interactions. Applying a tit-for-tat strategy, however, requires overcoming an impulsive temptation to defect because defection yields the largest short-term outcomes in the IPD [19]. Consequently, temporal discount rates (i.e. rates at which people downgrade the subjective value of future rewards as a function of the time until their receipt) are negatively associated with cooperation during the IPD and similar social dilemmas [20]. Given the effects

of childhood exposures to harsh conditions on impulsive choice generally [15], we hypothesized that childhood exposures to conflict, neglect and violence in the family and neighbourhood—the same exposure variables that appear to accelerate female sexual maturation, and increase impulsivity, risk-taking and violence—also are associated with higher rates of unprovoked defection in the IPD. Similarly, quick retaliatory defection reduces one's exposure to future exploitation—if that defection is a reliable cue to one's partner's future moves—but too-hasty retaliation can damage potentially beneficial long-term social relationships (particularly when co-operators might inadvertently defect because of error [18,21]). Like unprovoked defection, retaliation for unfairness in other economics games appears to have a basis in impulsive choice [22]; so we predicted that childhood exposure to harsh social conditions—which generally shift organisms towards a preference for actions that yield immediate benefits (or deter immediate harms)—would also be associated with higher levels of retaliatory defection.

Social scientists have noted that harsh environmental conditions, combined with weak policing or other institutional controls, create a behavioural syndrome that encompasses social distrust, a preoccupation with reputation and honour, and the approval of retaliation for its direct and indirect deterrence benefits [23,24]. Here, we hypothesized that endorsement of this so-called *code of honour*—which has been shown previously to predict individual differences in violence [25]—would appear to mediate the associations of exposure to harsh social conditions with unprovoked and retaliatory defection in the IPD.

(b) Anticipated sex differences

Finally, adaptationist thinking about individual differences in human cooperation also leads to a hypothesis about sex differences in the associations we posited earlier. In species in which females provide more parental care than males, individual differences in male reproductive fitness are more dependent than are women's on differential success at resource acquisition and retention that can be converted into mating effort—that is, attracting and retaining mates [16]. This male-specific reproductive constraint has led some theorists to posit for humans a so-called *young male syndrome*, whereby men whose early environments are rich in cues that ancestrally were predictive of reproductive failure (i.e. Hobbesian cues that life will be solitary, poor, nasty, brutish and short) are expected to adopt a risky style of social decision-making in the service of improving their reproductive prospects. More germane to our goals here, young males are hypothesized to respond to ancestrally valid cues of reproductive failure by adopting an impulsive style of decision-making, a taste for risk, and a readiness to retaliate against cost impositions and affronts to their social status [26].

Extant evidence indicates that young males experience and witness more violence [27] than do women. In addition, they more frequently perpetrate lethal retaliatory violence [28] and engage in non-lethal retaliatory aggression in the laboratory [29] than do women. Here, in keeping with Daly & Wilson's [26] theorizing, we tested the hypothesis that the associations of harsh childhood conditions (e.g. low socioeconomic status (SES), weak police presence, violence, conflict and neglect within the family, exposure to neighbourhood crime) with exploitation and retaliation in the iterated PDG apply to men to a greater extent than to women.

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2. Methods

(a) Participants

Participants were 244 (131 female; M age = 19.35, s.d. = 2.69, range = 17–53) undergraduate psychology students at the University of Miami, whom we ran in groups of six to 24 individuals. Participants received partial course credit and $7–10, depending on their outcome in the IPD. Data from seven participants (2.8% of total) were excluded from all analyses because they expressed scepticism during debriefing that they had been interacting with other people.

(b) Procedure

Participants were seated in individual, private cubicles. After providing consent, participants were told they would be anonymously paired (via the computer network) with another person in the room to play between 20 and 40 rounds of a decision-making game. In reality, this 'partner' was a pre-programmed computer script; without deception, this research would have been impossible (see the electronic supplementary material, section S1.3). Here, we focus only on the first 19 rounds of the game, which occurred before an experimental manipulation [30]. Participants were told they would play the game for points and would be paid 10 per cent of their total points in dollars after the game ended. Participants followed along while the experimenter read aloud a 10-min tutorial about how to play the IPD [31], which included a 2×2 payoff matrix depicting participants' and their partners' possible earnings from a single round of play as a function of whether they, and their partners, 'cooperated' or 'defected'. The tutorial did not note the strategic complexities of iterated play or refer to notions such as 'exploitation', 'retaliation' or 'forgiveness' that arise during iterated games. The experiment began after all participants confirmed that they understood how to play.

In Rounds 1–12, the computer played a generous tit-for-tat (GTFT) [21] strategy (also known as 'tit for two tats' [18]). It cooperated in round 1 and in every successive round, unless the participant defected; if so, the computer responded with a retaliatory defection with a 50 per cent probability (GTFT elicits high levels of cooperation, which is why we used it here. Indeed, 85% of participants' choices were cooperative during this regime). In rounds 13–19, the computer defected unconditionally; so participants' defections (64% of their choices) in rounds 14–19 can be considered retaliatory.

(c) Measures

(i) Exposure to family neglect, conflict and violence

We measured participants' perceptions of the extent to which they were exposed to neglect, conflict and violence in their childhood families with the mean of five items ($\alpha = 0.80$). The items (e.g. 'When I was growing up, someone in my house was always yelling at someone else', 'Some of the punishments I received when I was a child now seem too harsh to me', 'I guess you could say that I wasn't treated as well as I should have been at home') were rated on a seven-point Likert-type scale (1 = strongly disagree and 7 = strongly agree).

(ii) Exposure to neighbourhood crime and violence

We measured participants' perceptions of violence and crime in their childhood neighbourhoods with a factor score based on a seven-item scale ($\alpha = 0.89$). The items (e.g. 'Someone being mugged or robbed on the streets', 'Someone being injured during a fight so badly that he/she had to go to the hospital', 'Someone's home being burglarized') were rated on a five-point Likert-type scale (1 = never and 5 = more than 10 times) in response to the question, 'How many times do you remember witnessing or hearing about the following events in your neighbourhood when you were growing up'.

(iii) Perceived efficacy of neighbourhood policing

We measured participants' perceptions of the efficacy of the police in the neighbourhoods in which they grew up with the mean of four items ($\alpha = 0.82$) based on items from Tyler [32]. The items (e.g. 'How effective are the police in your neighbourhood in fighting crime?') were rated on five-point Likert-type scales (e.g. 1 = totally ineffective and 5 = extremely effective).

(iv) Socioeconomic status

We measured participants' SES with a modified version of Hollingshead's [33] social status index, the Barratt simplified measure of social status (BSMSS) [34], which involves calculations based on participants' (and their parents') degree of educational attainment and occupational status. We were interested in participants' SES during childhood; so we incorporated only their parents' information here. The BSMSS assesses education level from *less than seventh grade* to *Graduate degree* and occupational status in nine categories ranging in prestige from, for example, *day labourer* or *janitor* to *physician* or *attorney*. Each education level and occupation status are assigned a weighted number of points for each parent, and parents' scores are averaged together (in the case of single-parent homes, the single parent's score was used by itself) to form a measure of SES.

(v) Code of honour endorsement

We measured endorsement of the 'code of honour' with a factor score based on participants' scores on three separate multi-item scales. The first scale was an 'attitude towards revenge' scale (seven items; $\alpha = 0.86$) comprising items from several previously published scales [25,35,36] such as 'If someone treats me badly, I feel I should treat them even worse'. The second scale measured endorsement of 'street code' beliefs (10 items; $\alpha = 0.81$), with items from elsewhere [25,35,36] such as 'Sometimes, you have to fight to uphold your honour or put someone in his or her place'. The third scale, which measured attitudes towards forgiveness, included seven items (reverse coded; $\alpha = 0.76$) from Berry *et al.* [37] such as 'I try to forgive others even when they don't feel guilty for what they did'. The three scales, which we derived using factor-analytic methods, were then themselves factored, yielding one factor that accounted for 67 per cent of the standardized variances of the three scales.

(vi) Unprovoked and retaliatory defection

We measured unprovoked defection as the number of rounds participants defected during rounds 1–12. Scores for this variable were zero-inflated and over-dispersed ($M = 1.81$, s.d. = 2.39), as is common with count variables; so we used zero-inflated negative binomial regression for this variable [38] (see the electronic supplementary material, section S1.2). We measured retaliatory defection with its complement—a count of the number of rounds participants cooperated during the seven-round defection regime by the computer (because decisions were made simultaneously, participants could not possibly respond to the defection in round 13 until round 14; so this variable comprises participants' choices during the six rounds following the computer's initial defection in round 13). Thus, this variable measures how much participants retaliated to repeated defection: lower values imply more retaliation; higher values indicate more tolerance of defection. To account for the fact that cooperation after defection was a count variable with a non-normal distribution ($M = 2.16$, s.d. = 1.51), we used Poisson regression for this variable [38].

190 After the 19 rounds of iterated PDG play and other pro-
191 cedures that are not relevant to the present study, participants
192 completed questionnaires that included (i) a block of self-report
193 items for measuring honour code endorsement and family
194 environment amidst other items for measuring trust and grati-
195 tude; (ii) a block of items including the police efficacy items;
196 (iii) a block of items including the perceived neighbourhood
197 crime items; and (iv) the items for measuring SES.

3. Results

201 Table 1 includes descriptive statistics for major study variables
202 for men and women separately. Men and women's means
203 and variances for major study variables were generally
204 comparable, although men reported having witnessed or
205 heard about more crime in their childhood neighbourhoods
206 ($p < 0.05$, effect size $d = 0.268$). Men also had slightly fewer
207 unprovoked defections during the first 12 rounds of the IPD
208 ($p < 0.05$, effect size $d = 0.255$), which is consistent with
209 meta-analytic results regarding sex differences in cooperation
210 in iterated games [39].

211 In addition, Levene's test indicated that men's numbers of
212 retaliatory defections were 26 per cent more variable than were
213 women's ($F = 10.68$, $p < 0.01$), but their coefficient of variation
214 was only trivially larger (i.e. 0.70 and 0.67 for men and women,
215 respectively). Thus, although this difference in men's and
216 women's variances was unlikely to attenuate associations due
217 to range restriction (given the comparable coefficients of vari-
218 ation), it does suggest that men are slightly more variable in
219 their proneness to retaliatory defection than are women. Table 1
220 also shows that men's (but not women's) rates of unprovoked
221 defection were significantly associated at the zero-order level
222 with family neglect, conflict and violence, and that men's
223 (but not women's) rates of provoked defection were signifi-
224 cantly associated at the zero-order level with exposure to
225 neighbourhood violence and endorsement of the code of honour.

226 To test our hypotheses (i.e. that the four childhood
227 variables are associated with unprovoked and provoked defec-
228 tion, and that these associations obtain in part via the
229 intermediate associations of the four childhood with endorse-
230 ment of the code of honour), we conducted path models in
231 MPLUS v. 6 [39] using maximum-likelihood estimation with
232 robust standard errors. Given the relatively small size of the
233 sample ($n = 244$), only manifest variables were used.
234 Maximum-likelihood estimation with robust standard errors
235 does not produce a measure of overall model fit. Additionally,
236 MPLUS cannot calculate indirect effects for count outcomes; so
237 indirect effects were hand-calculated using the delta method
238 to adjust the s.e. [40] (see the electronic supplementary
239 material, section S1.2) in R (v. 2.12.1) with package 'msm'
240 (v. 0.7.4). We ran the model in figure 2 separately for men
241 and women, and the acceptabilities of the various models
242 were compared using the Bayesian Information Criterion
243 (BIC) [41].

244 Among men, childhood exposure to family neglect, con-
245 flict and violence ($b = 0.324$, s.e. $= 0.067$, $p < 0.001$) and to
246 neighbourhood violence and crime ($b = 0.179$, s.e. $= 0.088$,
247 $p = 0.041$) significantly predicted endorsement of the code of
248 honour (figure 2). Moreover, endorsement of the code
249 of honour was positively associated with unprovoked defec-
250 tion ($b = 0.271$, s.e. $= 0.129$, $p = 0.036$) and negatively with
251 cooperation during the defection regime ($b = -0.142$,
252 s.e. $= 0.061$, $p = 0.020$)—that is, positively related to retaliatory

Table 1. Descriptive statistics, comparisons of men's and women's means and s.d. and associations among variables. POL, police efficacy; VIO, neighbourhood crime/violence; FAM, family conflict, neglect, violence; CH, code of honour; DEF, unprovoked defection; COOP, cooperation after being exploited.

variable	range	men M	men s.d.	women M	women s.d.	M diff.	F^c	1	2	3	4	5	6	7
1. SES	8.50–66.00	52.03	12.44	51.44	12.25	0.59	0.54	—	0.02	-0.22^a	-0.06	-0.21^a	0	0
2. POL	1.00–4.75	3.64	0.65	3.60	0.75	0.04	2.08	0.13	—	-0.23^a	-0.08	-0.06	0.02	-0.08
3. VIO	-1.58–3.25	0.14	1.05	-0.13	0.95	0.27^a	3.06	-0.04	-0.39^b	—	0.13	0.12	-0	0.04
4. FAM	1.00–7.00	2.19	1.18	2.12	1.09	0.07	0.68	-0.06	-0.15	0.06	—	0.16	-0.07	-0.03
5. CH	-2.34–2.23	0.01	1.02	-0.10	0.98	0.11	0.26	-0.02	-0.17	0.22^a	0.39^b	—	0.11	-0.06
6. DEF^d	0–10.00	1.49	2.28	2.09	2.44	-0.60^a	2.95	-0	0.12	0.13	0.22^a	0.27	—	0.03
7. COOP^d	0–6.00	2.38	1.68	1.97	1.33	0.41	10.68^b	-0	0.11	-0.18^b	-0.03	-0.14^a	-0.01	—

correlations (men below diagonal)

$^a p < 0.05$.
$^b p < 0.01$.
^{c} Levene's test for equality of variances.
^{d} Difference was examined with Mann–Whitney U-test. Correlations cannot be computed for count variables [39], so unstandardized regression coefficients from zero-inflated negative binomial (DEF) and Poisson (COOP) regressions are reported.
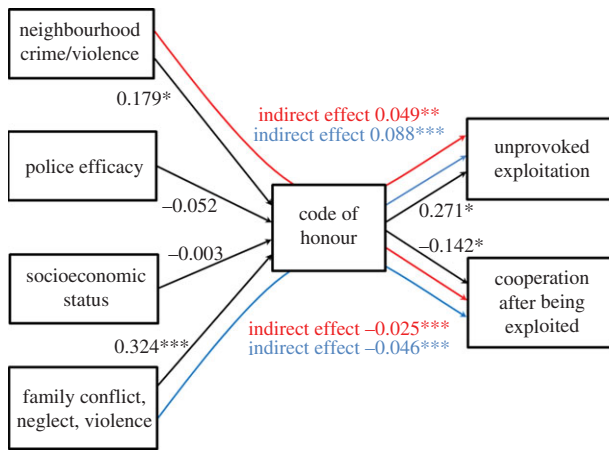
Figure 2. Path model linking characteristics of childhood social environment with unprovoked exploitation and cooperation after being exploited via their intermediate effects on code of honour endorsement. Unstandardized path coefficients for men are in black. Indirect paths and coefficients are colour-coded red (neighbourhood crime and violence) and blue (family conflict, neglect and violence). Predictor variables were allowed to covary freely; notation left out of diagram for clarity (likewise for variances; see the electronic supplementary material, tables for complete results).

defection. The rate ratios that resulted from exponentiating these coefficients (the dependent variables were counts [38]) were 1.311 for the path from code of honour endorsement to unprovoked defection (implying that every one-unit increase in endorsement of the code of honour led to a 31.1% increase in unprovoked defection) and 0.868 for the path from endorsement of the code of honour to cooperation after defection (indicating a $1-0.868 = 0.132$, or 13.2% reduction in cooperation after defection). Childhood exposure to family neglect, conflict and violence had significant indirect associations with both unprovoked defection ($b = 0.088$, s.e. $= 0.014$, $p < 0.001$) and cooperation during defection ($b = -0.046$, s.e. $= 0.003$, $p < 0.001$) via its intermediate associations with endorsement of the code of honour. Rate ratios of 1.092 and 0.955 for these indirect associations imply that, through its intermediate associations with code of honour endorsement, a one-unit change in childhood exposure to family neglect, conflict and violence would be expected to lead to a 9.2 per cent increase in unprovoked defection and a 4.5 per cent reduction in cooperation with a defector, respectively.

Childhood exposure to neighbourhood violence and crime also had significant indirect associations with both unprovoked defection ($b = 0.049$, s.e. $= 0.019$, $p = 0.009$) and retaliatory defection ($b = -0.025$, s.e. $= 0.004$, $p < 0.001$). Rate ratios of 1.050 and 0.975 for these indirect associations imply that through its intermediate associations with code of honour endorsement, a one-unit change in childhood exposure to neighbourhood crime and violence would be expected to lead to a 5.0 per cent increase in unprovoked defection and a 2.5 per cent reduction in cooperation with a defector, respectively. Neither perceived police efficacy nor SES predicted endorsement of the code of honour ($ps > 0.11$), unprovoked defection or retaliatory defection.

As hypothesized, this pattern of results did not hold for women; indeed, the only significant path in the model for women was the association of SES with endorsement of the code of honour ($b = -0.015$, s.e. $= 0.008$, $p = 0.049$; table 2). However, only the path from childhood exposure to family neglect, conflict and violence to endorsement of the

code of honour, and the path from endorsement of the code of honour to unprovoked defection were significantly stronger for men than for women. The other coefficients did not differ significantly between sexes. We also ran the model in figure 2 with data from both sexes. The overall pattern of results was identical to the results for men by themselves, though the associations were unsurprisingly weaker in magnitude for the overall sample (see the electronic supplementary material, table S1).

We tested alternative structural equation models by adding direct paths, one at a time, from each life-history predictor to the PDG variables in the model depicted in figure 2. None of the eight added paths reduced the BIC for either the men's or the women's models. To test the statistical importance of the mediational role we have ascribed to the code of honour, we used two approaches (see the electronic supplementary material, section S1.2). For the first approach, we replaced the indirect paths from the two significant childhood predictors (neighbourhood crime and violence; family neglect, conflict and violence) to the two PDG outcomes through their intermediate associations with the code of honour variable with direct paths to the respective PDG outcomes. These path substitutions resulted in eight alternative models (four for each sex). Of these eight alternative models, only one had a smaller BIC than did the model in figure 2: for men, a model with a direct effect (rather than an indirect effect) from neighbourhood crime and violence to retaliatory defection had a smaller BIC than did the figure 2 model. The difference in BIC was 3.19, which is considered 'positive' evidence that the alternative model is better, but with less confidence than one would ascribe to a p-value equal to 0.05 in a frequentist hypothesis-testing framework—a BIC difference of at least 6 is needed to reach the analogous 0.05 level of confidence [41]. In addition, the conclusion that a model with a direct effect (but no indirect effect) between neighbourhood violence/crime and retaliatory defection is superior to the results in figure 2 at odds with the statistical evidence that the indirect effect from neighbourhood violence and crime to retaliatory defection via endorsement of the culture of honour was statistically significant. The rest of the BIC differences ranged from 0.10 to 21.05, all in favour of our model.

For the second approach, we ran the model with the code of honour excluded entirely—that is, with direct paths from all four predictors to both outcomes—which resulted in BIC increases of 43.77 for men and 24.37 in women (BIC differences greater than 10 are considered 'very strong' evidence in favour of the model with the smaller BIC; [41]), in favour of our model.

4. Discussion

In recent years, research on individual variability in human cooperation has focused conspicuously on ideas from cultural group selection theory [5–7], which draws attention to between-culture differences that are presumed to spread locally via cultural learning mechanisms and to spread geographically through cultural group selection. However, the fact that people from Accra have different mean levels of cooperation (or punishment) than do people from Aberdeen or Atlanta does not imply that all of the meaningful between-persons variation is attributable to broad cultural differences: indeed, people from different neighbourhoods

6

Table 2. Unstandardized path analysis parameter estimates, s.e. and their significance. POL, police efficacy; VIOL, neighbourhood crime/violence; FAM, family conflict, neglect, violence; CH, code of honour; DEF, unprovoked defection; COOP, cooperation after being exploited.

parameter	men				women			
	value	s.e.	t	p	value	s.e.	t	p
SES → CH	−0.003	0.007	−0.412	0.680	−0.015	0.008	−1.967	0.049
POL → CH	−0.052	0.139	−0.375	0.707	−0.038	0.117	−0.323	0.746
VIO → CH	0.179	0.088	2.045	0.041	0.058	0.082	0.706	0.480
FAM → CH	0.324	0.067	4.874	0.000	0.122	0.076	1.603	0.109
CH → DEF	0.271	0.129	2.100	0.036	0.111	0.078	1.435	0.151
CH → COOP	−0.142	0.061	−2.331	0.020	−0.064	0.058	−1.099	0.272
epsilon → CH	0.824	0.103	7.972	0.000	0.896	0.106	8.474	0.000
Cov$_{SES,POL}$	1.019	0.810	1.259	0.208	0.097	0.789	0.123	0.902
Cov$_{SES,VIO}$	−0.442	1.286	−0.343	0.731	−2.562	1.086	−2.359	0.018
Cov$_{SES,FAM}$	0.889	1.247	0.713	0.476	−0.805	1.283	−0.628	0.530
Cov$_{POL,VIO}$	−0.259	0.063	−4.092	0.000	−0.162	0.073	−2.223	0.026
Cov$_{POL,FAM}$	−0.113	0.091	−1.244	0.214	−0.059	0.081	−0.721	0.471
Cov$_{VIO,FAM}$	0.071	0.110	0.648	0.517	0.137	0.089	1.535	0.125

within the same city cooperate [9] and retaliate [42] at different rates; the same is true for people from different villages within the same broad cultural group [8]. These within-population individual differences are, in principle, amenable to individual-level explanations, as the architects of the cultural group selection approaches to cooperation readily concede [5,43].

Consistent with Daly & Wilson's [26] characterization of the *young male syndrome*, the associations that emerged here suggest (though, owing to the correlational nature of the data, do not demonstrate definitively) that men's (but not women's) childhood experiences with crime, violence, neglect and conflict—both within the family and the neighbourhood—predispose them towards stronger propensities for impulsive defection against cooperatively disposed players, as well as to greater retaliation when their interaction partners suddenly become uncooperative. Contradicting previous claims [42,44], the perceived efficacy of local police and SES played no unique predictive role. Moreover, we found that for men (but not women), these associations appear to arise from the intermediate association of childhood ecological characteristics with endorsement of the code of honour, which is a social strategy encompassing low trust, a preoccupation with reputation, and readiness to defend one's reputation with violence. Previous work has documented that young men are more touched by violence in their daily lives [27] and more prone to retaliatory aggression in the laboratory [29] and on the streets [28], but our results are the first of which we are aware to suggest that young men's tendencies towards unprovoked and provoked defection are more sensitive to cues of reproductive failure than are women's. We hasten to note that the sex differences we discovered here are not inconsistent with recent meta-analytic results indicating that men in general tend to be more cooperative than women in iterated cooperation games such as the PD [39]: it is possible for men to be more cooperative on average in the iterated PDG than are women (as we found during the first 12 rounds here) and also for men to calibrate their

levels of exploitation and retaliatory defection on the basis of childhood cues to reproductive failure to a greater extent than women do. In addition, it is worthwhile to note that women are sensitive to these early developmental factors in sex-specific ways (e.g. childhood exposures to family stress accelerate puberty for women but not for men; [45]) just as men appeared to be in this study.

Our results, when combined with ethnographic observations from many different parts of the world [23,42], lead us to propose that impulsive exploitation and retaliation against defectors—at least for males—might be caused in part by evolved cognitive adaptations that process cues about local social conditions to estimate whether it is in one's reproductive interests to allocate energetic and somatic resources to reproductive maturity and mating effort in the short-term, rather than to investments that will redound to fitness only over a longer time horizon [26]. However, the data we analysed here were non-experimental and cross-sectional in nature, which limits confident causal inference. In the light of this caveat, future work with more diverse samples of participants, longitudinal or experimental designs that can more rigorously test cause-and-effect relations—and perhaps even genetically informative designs that can partition purely environmental effects from genetic effects that could be mediated by parents' selection of children's rearing environments [46]—might yield more rigorous tests of the hypotheses evaluated here. We also encourage researchers who are interested in evolutionary approaches to human cooperation to go beyond simply demonstrating the plausibility of group-selectionist or individual-level adaptationist models, and instead, to design studies that can simultaneously put predictions from both types of models in jeopardy of falsification.

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