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Birth order affects behaviour in the investment game: firstborns are less trustful and reciprocate less

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Explaining the behavioural variations observed between individuals is an important step for understanding the evolution of human cooperation and personality traits. Birth order is a potentially important variable that implies physical and cognitive differences between siblings and differential access to parental resources during childhood. These differences have been shown to influence several personality characteristics in adulthood. We tested the hypothesis that birth order can shape adult cooperative behaviours towards nonkin. An anonymous investment game was played by 510 unrelated students. The results of the game show that firstborns were less trustful and reciprocated less than others. No significant differences in trust or reciprocity were found among laterborn and only children based on birth order. Firstborn status was a better predictor of cooperativeness than age, sex, income or religion. These results constitute some of the first experimental evidence that birth order differences established within the family can persist in adult behaviour among nonkin. We discuss the implications of this finding for the evolution of human cooperation.

Understanding the evolution of human cooperation remains a challenging problem for economists (Fehr & Fischbacher 2003) and evolutionary biologists (Boyd 2006). Cooperative behaviours provide a benefit to the recipient and can only be selected for if they also provide benefits to the same actor that accepted the costs of the cooperative action (Clutton-Brock 2002; Fehr & Fischbacher 2003; Lehmann & Keller 2006; Nowak 2006; Lehmann et al. 2007; West et al. 2007). Therefore, cooperation can evolve and spread in populations provided that it entails either direct benefits to the actors or indirect benefits (through an increase in inclusive fitness, i.e. benefits to the actors' kin). In animals, cooperative behaviours are almost exclusively restricted to kin groups, apart from rare and specific cases of repeated encounters between pairs of individuals (Dugatkin 1997; Fehr & Fischbacher 2003). In humans, individuals cooperate in large groups involving nonrelatives, in situations where no direct reciprocity is possible (Nowak & Sigmund 1998; Fehr & Gachter 2002; Fehr & Fischbacher 2003; Fehr 2004; Boyd 2006). Examples include blood donation and charity, but also everyday food sharing in traditional populations and rubbish sorting in industrial societies. Despite active research in this area, we only have a partial understanding of human characteristics that promote specific conditions in which cooperation could evolve and be maintained.

Most studies on cooperative behaviours report important interindividual variation within populations. Empirical studies of this variation are essential to understand the evolution of human cooperation (Zahavi 1995; Lotem et al. 1999; McNamara et al. 2004). Nevertheless, studies of this nature are still scarce (Scheres & Sanfey 2006). A few studies have related interindividual variability to sex and age (e.g. Murnighan & Saxon 1998; Andreoni & Vesterlund 2001; Solnick 2001), but results are often inconsistent, and a large part of the variability remains unexplained.

In humans, as in other species with altricial young, parental investment (Trivers 1974) has profound effects on offspring survival (Hill & Hurtado 1996; Pavard et al. 2005) and reproductive success (Lindström 1999; Lummaa 2003). However, parental investment is not unlimited (Stearns 1992; Kaplan 1996). The potential fitness benefits of investment in different offspring are seldom equal, potentially leading to selection pressures on parents to invest differentially in their offspring (Biermann & Robertson 1983; Slagsvold 1997; Jeon 2008). In humans, parents need to divide their limited resources between several simultaneously dependent

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offspring of different ages and developmental stages (Keister 2003; Gurven & Walker 2006), which exacerbates sibling competition (Mock & Parker 1997).

Sulloway (1996) argued that many psychological differences between siblings result from different adaptive strategies based on differential access to parental investment and, more specifically, on the microenvironment defined by birth order. Firstborn, middleborn or lastborn status affects the relative competitive ability of each child (Sulloway 1996). During childhood, a firstborn has an advantage merely because he/she is older, and thus physically stronger and cognitively more advanced than laterborn children. In addition, at a given time, the potential fitness gain that parents can obtain from firstborns is higher, because: (1) they are more likely to survive to adulthood, as they have already survived the first years of life when mortality is highest; and (2) they are likely to start reproducing earlier, thereby shortening the generation time (Trivers 1974; Voland 1998; Draper & Hames 2000). If parents are going to invest differentially in offspring, they should thus increase investment in firstborns from which fitness benefits are likely to be greatest (Jeon 2008). The widespread primogeniture system (inheritance by the eldest son of a large share or the entirety of a parent's wealth) exemplifies biased investment dependent on birth order (Hrdy & Judge 1993). Therefore, birth order influences (1) the differential ability of children to compete for this investment, and (2) differential allocation of care from the parents. Both have consequences for personality traits measured in adults (Sulloway 1996). In this study we tested the hypothesis that birth order can shape adult cooperative behaviours in a similar way.

Many studies have examined the relationship between birth order and personality traits (Sulloway 1995). They can sometimes provide more or less direct information on cooperativeness because several personality traits are associated with it (see Jefferson et al. 1998 and references therein; Paulhus et al. 1999; Sulloway 2001 and references therein). Overall, results reported in these studies appear relatively inconsistent. Moreover, these studies used subjective measures of cooperation (peer- or self-reported) rather than measurement of actual cooperative behaviours. In contrast, the development of economic games opens the possibility of objectively measuring cooperation. We used the investment game, a tool to study trust (or risk taking) and positive reciprocity in social interactions (Berg et al. 1995). We investigated whether and how behaviour in an investment game played with nonrelated adults is affected by birth order.

METHODS

The Investment Game

We used an investment game based on the protocol introduced by Berg et al. (1995). Two players (A and B) are each given 30 monetary units (MU). Player A has to decide how much, if any, of this 30 MU he/she wants to send to player B. This amount x is then tripled by the experimenter before being delivered to player B. Hence, at this stage A has $30 - x$ and B has $30 + 3x$. Player B then has to decide how much, if any, of his/her total amount he/she wants to send back to player A, called amount y. Here, y can take any value in $[0, 30 + 3x]$, in contrast to the original game of Berg et al. (1995), where y was bounded within $[0, 3x]$. Finally, A gets $30 - x + y$ and B gets $30 + 3x - y$. The game sequence was not repeated.

The game theory prediction based on the assumptions of narrow self-regarding preferences and common knowledge of these rational preferences is that player B will send back nothing, inducing player A to send no money in the first place. Economic experiments have shown, however, that these predictions fail, at least in one-shot encounters (Berg et al. 1995). Departures from rational choices (if x or y differs from zero) constitute departures from selfishness, and thus reveal trends towards cooperation with unrelated individuals. As a consequence, this experiment provides measures of two important aspects of cooperative behaviour: trust and reciprocity. As player A is not sure that B will reciprocate and send back an amount equal to or greater than x, sending money to player B is interpreted as a risky behaviour. Consequently, x is seen as a quantitative measure of trust. In the same way, y allows us to quantify reciprocation behaviour.

Experimental Design

Volunteer subjects were enrolled during March and April 2005 on the campus of the University of Montpellier 2, France. Each subject was randomly assigned the role of the A or B player. The subjects were given written instructions and had to write down on a form the amount x (for A players) or the amount y (for B players) that they wanted to send to the other player. To study the interindividual variation in reciprocity independently of the interindividual variability in trust, we used an experimental design focused on B players' responses to a fixed amount received from A players. As this amount could potentially influence B players' behaviours during the experiment, we chose two different values: each B player was randomly assigned a fictional A player who sent either 10 MU or 30 MU. Below, x refers to the amount sent by A players, whereas x_F refers to the amount that B players received from fictional A players.

Both players were informed of the whole sequence before starting, and they were also aware that their final financial gain would be converted into real money with 10 MU = 1 €. For B players, the compensation was indeed directly obtained by their payoff, that is $(30 + 3x_F - y)/10$ €. However, because no real B players played with A players, the compensation of a focal A player was calculated by randomly drawing an amount y^* from the responses of B players who received 30 MU. The compensation paid to the focal A player was $(30 - x + y^*)/10$ €, except when y^* was higher than $30 + 3x$ (the maximum amount that could have been played by a B player responding to this focal A player); in this latter case, the compensation paid to A was $(60+2x)/10$ €.

The participants in each game session all played at the same time and had no opportunity to communicate with each other. In a single game session, all players were assigned to the same type of player (A or B). All players subsequently filled in questionnaires concerning personal and familial characteristics such as age, sex, nationality, religious belief, number and ages of siblings, parental ages at birth, personal income and parental income.

Ethical Note

Anonymity and confidentiality of subjects were guaranteed. The experimental protocol was approved by the scientific committee of 'ANR', the national research funding agency.

Statistical Analysis

The data obtained for x and y have two peculiar characteristics that interfere with classical statistical analysis. First, multimodal distributions of raw data (Fig. 1) and residuals prevent the use of generalized linear models. Second, the large number of ties in the data (same values are repeated several times) leads to an incorrect estimate of the critical values from tables used in nonparametric tests. Consequently, as suggested by Manly (2007), two statistical analyses were performed based on randomization tests: test 3 (Manly 1995) and test DO (Manly & Francis 1999). These two tests allow one to test differences between means of several samples in the situation where the samples may be drawn from distributions

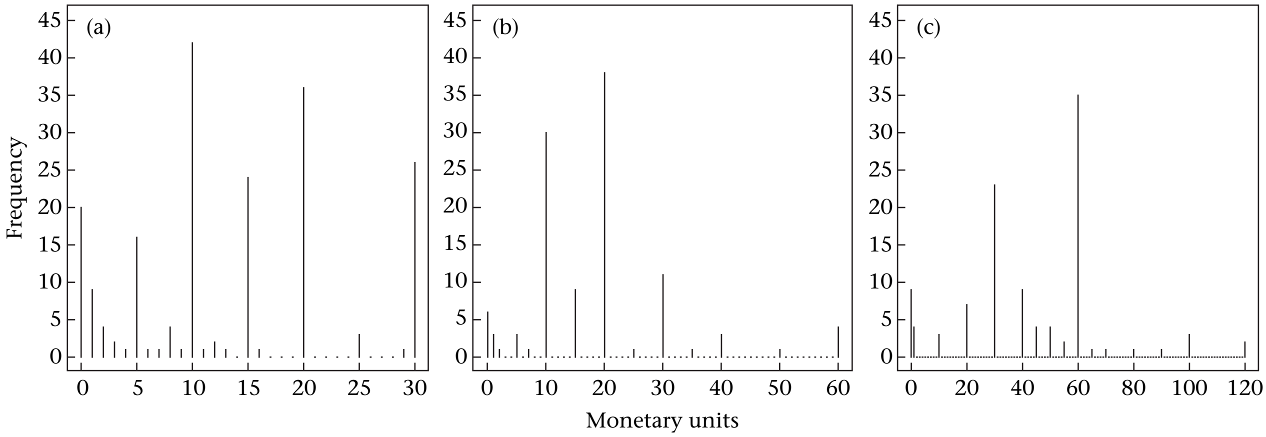

Figure 1. Frequency distributions of the amounts sent in the investment game. (a) Distribution of amounts (monetary units) sent by A players. (b) Distribution of amounts sent back by B players when they received 10 monetary units or (c) 30 monetary units.

with different variances. Both tests rely on the classical *F* statistic used in AN(C)OVA, and therefore can be interpreted straightforwardly as in their original context (see Appendix for details).

Birth order was taken into account as a factorial variable with four categories: firstborn, middleborn, lastborn and only child. All middleborn children were pooled together because families of more than three children were rare in the sample. For A players, the effect of birth order category on x was investigated. For B players, the effect of birth order category on y was investigated, while controlling for x_F and its interaction with birth order category. The variable x_F is factorial, with two categories: 10 and 30 MU.

In such an analysis, putative confounding effects may remain undetected. This possibility was evaluated by investigating the association between x (or y) and the variables that could potentially create an artefactual birth order effect (because they are associated with birth order): parents' age at birth and number of siblings (see Appendix for details).

To assess the relevance of birth order effects on trust and reciprocity, we compared them with the effects of several other covariates characterizing the subjects: sex, age, number of siblings, personal income, parental income, parents' age at birth and whether the subject believed in a god or not. Randomization procedures (test 3 and test DO) used to analyse birth order effects do not allow simultaneous consideration of more than two covariates. Moreover, as previously mentioned, the distributions of amounts sent are such that linear modelling cannot be used. Thus, we considered a binary dummy variable indicating whether or not the subject sent an amount greater than the median of amounts sent by all players of the same category (either A or B players). Although this method implies a loss of information, it allows simultaneous modelling of the influence of all covariates. Two generalized linear models were built: first, a logistic regression model to explain the amount sent by A players, and second, a model to explain the amount sent by B players. For B players, the amount received from A was considered in addition to the other covariates. Once models were fitted, Nagelkerke R^2 values were computed to measure the proportion of deviance explained. Parameter estimates and significance levels obtained for each covariate are indicated in Table 1.

RESULTS

Sample Characteristics

A total of 510 volunteers were subjected to either the A or the B player version of the investment game and filled in the questionnaire. Foreign students were excluded, because cultural differences in cooperative behaviour have been reported (Henrich 2000). After we excluded incomplete questionnaires, the resulting sample consisted of 417 students (196 A players and 221 B players) aged a mean ± SD of 20.9 ± 2.3 years. Males and females were equally represented (198 and 219, respectively; exact binomial test: $P = 0.33$). The average number of siblings was 1.3 ± 0.9. Average parental income was 2636 ± 1153 € per month, and average personal income was 369 ± 251 € per month. For 89% of the students, their personal income was partially or totally provided by their parents. In this sample, 27% of individuals reported religious beliefs.

Overall, our sample was composed of 178 firstborn, 48 middleborn, 125 lastborn and 66 only children. Firstborns were overrepresented in the sample compared to lastborn children (exact binomial test: $N = 303$, $P = 0.003$), as has been reported in most universities worldwide (Rohde et al. 2003). As expected, maternal, paternal and average parental age at birth differed between birth order categories (Kruskal–Wallis *H* test: $H = 84$, $P < 0.0001$; $H = 81$, $P < 0.0001$; $H = 95$, $P < 0.0001$, respectively; $N = 417$). In addition, birth order and number of siblings were not independent (Fisher's exact test on a 6×4 contingency table: $N = 417$ $P < 0.0001$).

Investment Game Summary Statistics

Among the 417 participants, only 8% (20 A players and 15 B players) played according to the rational prediction (Nash equilibrium). For A players, the average amount sent to B was 13.3 MU (confidence interval, CI: 12.0–14.6). The distribution of the amount sent was multimodal, with an excess of players choosing exactly 0, 10, 20 or 30 MU (Fig. 1a). Among the 112 B players who received 10 MU from fictional A players, the average amount sent back was 18.1 MU (CI: 15.8–20.5; Fig. 1b). Among the 109 B players who received 30 MU from A, the average amount sent back was 42.7 MU (CI: 38–47.6; Fig. 1c). Among all B players, 93% sent back a non-null amount, but 17% sent back less than the amount received ($y < x_F$).

Birth Order Effect on Trust

Randomization tests suggest a slight overall effect of birth order categories on x (test 3: $F = 2.8$, $P = 0.042$; test DO: $F = 2.5$, $P = 0.079$; $N = 196$; see Appendix for details on the methods). Means of x for middleborn, lastborn and only children appeared

Table 1
Results of the logistic regression models explaining the amount sent in the investment game

Subjects	Covariates	Estimates	SE	OR	95% CI for OR	Likelihood ratio	P
A players							
	Birth order (firstborn)	−1.1	0.39	0.34	0.16–0.73	8.1	4.3×10^{-3}
	Sex (male)	−0.34	0.36	0.71	0.35–1.4	0.89	0.34
	Age	7.4×10^{-2}	8.4×10^{-2}	2.1	0.40–11	0.76	0.38
	Number of siblings	0.37	0.21	1.5	0.96–2.2	3.1	7.6×10^{-2}
	Income	-3.8×10^{-4}	7.9×10^{-4}	0.96	0.82–1.1	0.23	0.63
	Parental income	3.8×10^{-4}	1.7×10^{-4}	1.0	1.0–1.1	5.3	2.1×10^{-2}
	Father's age at birth	1.5×10^{-2}	5.0×10^{-2}	1.2	0.44–3.1	9.1×10^{-2}	0.76
	Mother's age at birth	-4.0×10^{-2}	5.1×10^{-2}	0.67	0.24–1.8	0.62	0.43
	Belief in god	0.10	0.40	1.1	0.51–2.4	6.5×10^{-2}	0.80
B players							
	Amount received from A	1.4×10^{-1}	1.9×10^{-2}	16	7.4–34	64	$<10^{-4}$
	Birth order (firstborn)	−1.2	4.6×10^{-1}	0.31	0.13–0.77	6.7	9.5×10^{-3}
	Sex (male)	1.1×10^{-1}	3.8×10^{-1}	1.1	0.52–2.4	7.9×10^{-2}	0.78
	Age	3.4×10^{-2}	1.1×10^{-1}	1.4	0.16–12.2	9.6×10^{-2}	0.76
	Number of siblings	1.1×10^{-1}	2.4×10^{-1}	1.1	0.70–1.8	0.20	0.65
	Income	3.4×10^{-5}	8.9×10^{-4}	1.0	0.84–1.2	1.4×10^{-3}	0.97
	Parental income	4.6×10^{-5}	1.7×10^{-4}	1.0	0.97–1.0	7.2×10^{-2}	0.79
	Father's age at birth	2.1×10^{-2}	4.9×10^{-2}	1.2	0.47–3.2	0.18	0.67
	Mother's age at birth	3.4×10^{-3}	5.6×10^{-2}	1.0	0.34–3.1	3.6×10^{-3}	0.95
	Belief in god	-3.6×10^{-1}	4.5×10^{-1}	0.70	0.29–1.7	0.62	0.43

For A players, the dependent variable of the corresponding model is a binary dummy variable indicating whether or not the subject sent an amount greater than the median of amounts sent by all A players (10 monetary units). This model is based on 158 individuals (38 individuals were removed because of missing data). Estimate of the intercept = −2.11; null deviance = 218.4; residual deviance = 201.4; dispersion parameter = 1.36. For B players, the dependent variable of the corresponding model is a binary dummy variable indicating whether or not the subject sent an amount greater than the median of amounts sent by all B players (20 monetary units). This model is based on 191 individuals (30 individuals were removed because of missing data). Estimate of the intercept = −4.77; null deviance = 263.9; residual deviance = 181.3; dispersion parameter = 1.01. For both models, signs of the estimates indicate whether the probability of sending more money than the median increases (if positive) or decreases (if negative) with the corresponding covariate. Odds ratios (OR) and associated confidence intervals are given for both binary and continuous variables. For binary variables, OR indicate the relative odds for the category of reference. For continuous variables, OR are given for increments of 10 years for the three variables referring to ages; for an increment of one sibling for the variable referring to the sibling number; for increments of 100 euros for the two variables referring to income; and for an increment of 20 MU (30 versus 10) for the variable referring to the amount received from A for B players. Significance levels were computed using traditional likelihood ratio tests based on comparing the model with all covariates to the model without the covariate of interest.

much closer to each other than to the mean of x for firstborns (Table 2); these three categories were therefore pooled. On average, firstborns sent 3.7 MU (CI: 1.2–6.2) less than laterborn or only children (Fig. 2a), that is, a 25% lower amount (CI: 8.9–38.4). This difference was significant (test 3: $F = 8.6$, $P = 0.004$; test DO: $F = 7.7$, $P = 0.004$; $N = 196$).

Neither parental age nor sibship size was significantly correlated with x (regression coefficient = 0.13, $N = 189$, $P = 0.40$; regression coefficient = 0.26 $N = 196$, $P = 0.75$, respectively). Consequently, birth order's influence on trust is not likely to result from indirect effects of parents' ages or the number of siblings.

Among all covariates included in the logistic regression model, birth order explained most of the deviance in the probability of sending to B players an amount of money larger than the median of the distribution of x (Table 1). Consistent with randomization tests, firstborn status decreased this probability: the odds that a laterborn or an only child sent an amount larger than the median of x is 2.9 (CI: 1.4–6.3) times higher than the corresponding odds for a firstborn. None of the other covariates was significant except for parental income. Overall, ca. 14% of the total deviance was explained by the model.

Birth Order Effect on Reciprocity

The effects of birth order and x_F (amount received from A) were both significant (test DO: $F = 4.5$, $P = 0.027$ and $F = 74$, $P = 0.0001$, respectively; $N = 221$), but the interaction between these two factors was not (test DO: $F = 1.0$, $N = 221$, $P = 0.41$). Removing the interaction from the model did not influence the F statistics of these two factors. Hence, the interaction was not considered in the following post hoc analysis.

Only children and laterborns were pooled because their average amounts sent (y) were closer to each other than to the average amount sent by firstborns (Table 2). Among B players who received 10 MU, firstborns sent on average 6.1 MU (CI: 1.9–10.7) less than laterborn and only children (Fig. 2b), that is, a 29% lower amount (CI: 10.3–44.0). Among B players who received 30 MU, firstborns sent an average of 10.2 MU (CI: 0.6–19.7) less than laterborn and only children (Fig. 2c), that is, a 22% lower amount (CI: 2.0–38.8). This difference between firstborn and other children was significant (test DO: $F = 9.1$, $N = 221$, $P = 0.002$).

Parental age was not statistically related to y (regression coefficients: for $x_F = 10$: −0.17, $N = 110$, $P = 0.46$; for $x_F = 30$: 0.32,

Table 2
Average amounts sent in the investment game

	Amount sent by A players (in MU)			Amount sent by B players who received 10 MU			Amount sent by B players who received 30 MU		
Firstborn	11.1	[9.4–12.8]	(79)	14.9	[12.6–17.1]	(54)	36.7	[29.3–44.0]	(45)
Non firstborn	14.8	[13.1–16.6]	(117)	21.0	[17.4–24.8]	(58)	47.0	[40.8–53.2]	(64)
Middleborn	15.0	[11.0–18.9]	(26)	27.0	[6.0–48.0]	(5)	54.4	[41.8–68.2]	(17)
Lastborn	14.8	[12.4–17.3]	(60)	17.7	[14.0–21.8]	(33)	46.4	[38.8–54.5]	(32)
Only child	14.6	[11.1–18.3]	(31)	25.0	[19.0–31.8]	(20)	39.7	[27.4–52.7]	(15)

MU: monetary units. 95% confidence intervals are given in brackets. Sample sizes are in parentheses.

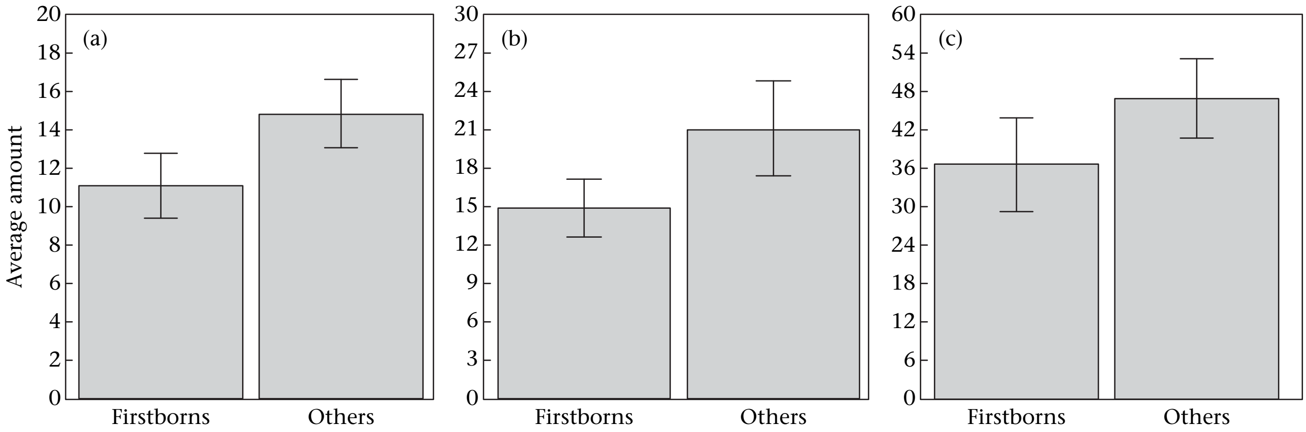

Figure 2. Firstborn effect on trust and reciprocity in the investment game. (a) Average amount (monetary units) sent by A players. Average amount sent back from B players when they received 10 monetary units (b) or 30 monetary units (c). Error bars represent the 95% confidence intervals of the means.

$N = 102$, $P = 0.54$), but sibship size was (for $x_F = 10$: -2.0, $N = 112$, $P = 0.16$; for $x_F = 30$: 6.4, $N = 109$, $P = 0.017$). However, birth order still significantly influenced y within each sibship size category (e.g. test DO for first- versus lastborn in families of two siblings: $F = 12$, $N = 111$, $P < 0.001$). In addition, sibship size still significantly influenced y within each birth order category (e.g. regression coefficient when $x_F = 30$ for firstborns: 15.0, $N = 45$, $P < 0.001$). Hence, birth order and the number of siblings independently affected y, although they could also interact.

For B players, birth order was the personal characteristic that explained most of the deviance in the probability of sending back to A players an amount of money larger than the median of the distribution of y (Table 1). Consistent with the randomization test, firstborn status decreased this probability: the odds that a laterborn or an only child sent an amount larger than the median of y is 3.2 (CI: 1.3–7.8) times higher than the corresponding odds for a firstborn. Obviously, x_F explained a large part of the deviance, and all other covariates were not significant. Overall, ca. 47% of the total deviance was explained by the model.

DISCUSSION

Birth Order Effects on Trust and Reciprocity

Status as a first-, middle-, lastborn or only child accounted for interindividual differences in behaviour as measured by the investment game. Siblings seemed to develop distinct cooperation strategies based on their birth order, which had long-term effects on cooperation between unrelated individuals in adulthood. These results constitute some of the first experimental evidence that birth order differences established within the family can persist in adult behaviour among nonkin. More precisely, this study reveals a significant behavioural difference between firstborns and other children.

According to evolutionary psychologists, birth order effects result from sibling competition for parental investment (Sulloway 1996), together with an unequal distribution of investment among siblings by the parents (Hertwig et al. 2002). Hence, interindividual variation in cooperation partly results from sibling competition.

Firstborns appeared to be less trustful and reciprocate less than laterborn and only children. The absence of behavioural differences between laterborn and only children suggests that birth order differences could result from a decrease in cooperative behaviour by firstborns rather than an increase by laterborn children through cooperation coalitions. Therefore, it seems unlikely that the higher level of cooperation of laterborn children results from their higher dependence towards parental investment or from enforced cooperation within the family. Rather, shifting from only child to firstborn status following the birth of a younger sibling seems to lead the eldest child to reduce his/her cooperative behaviour. None the less, the fact that differences between amounts sent by firstborns and only children during the experiment were only marginally significant precludes any definitive conclusion. Importantly, the differences between firstborns and laterborn children for trust and reciprocity hold whether or not only children were considered in the analysis (data not shown).

Previous psychological works on birth order differences in cooperativeness, based on subjective assessments of personality, are inconsistent, although a meta-analytical amalgamation of existing data from four different studies in which effect sizes are available indicates a small but significant trend in the same direction as the results found here (F. J. Sulloway, personal communication, based on an analysis of 10 studies in Paulhus et al. 1999; Jefferson et al. 1998; Sulloway 2001). However, these studies were based on self- or peer-reported measures of cooperativeness, rather than on objective and quantitative measures of cooperative behaviours, such as those provided by economic games. In addition, detection of such effects, which only explain a small part of the behavioural variation, requires a sufficient sample size and adequate statistical tools. We observed this negative effect of firstborn status on cooperativeness in two different samples of students (A and B players). In each sample, the statistical support for this effect was strong ($P < 0.005$) for the corresponding cooperation components (trust or reciprocity). Thus, the present result seems to be robust, although cross-cultural comparisons are needed to assess its generality.

The importance of familial environment in human cooperation could appear somewhat weak, since most of the variance remained unexplained. None the less, firstborn status had the highest explanatory power compared to the other individual characteristics considered. In addition, part of the variance in cooperative behaviour among individuals has a genetic basis, and only the nongenetic part of the variance can be explained by factors such as birth order and other familial characteristics. Rushton (1986) found that around 50% of the variance in cooperativeness is associated with genetic effects, leaving 50% to nongenetic effects. Further estimation of the genetic contribution to the variance in cooperative behaviour is required, and this should use economic games rather than self-reporting (as in Rushton 1986). This is a necessary step in assessing the explanatory power of familial traits on the behavioural variability observed, and consequently in estimating precisely the relevance of these traits for evolutionary explanations.

Consequences for Methodological Issues in Future Studies

Our results highlight the interest of using experiments rather than subjective measures of personality, since we revealed an important influence of birth order on trust and reciprocity, while many psychological studies reported no effect despite using larger samples. In addition, our analyses also reveal two problems related to the use of students in empirical work on cooperation. First, as in many studies based on university samples (Altus 1966; Rohde et al. 2003), firstborns are overrepresented compared to lastborn children. Parental resource depletion and different abilities of siblings are the classical explanations for this phenomenon (Blake 1981; Downey 2001; Zajonc 2001; Hertwig et al. 2002). The existence of a firstborn effect on cooperation, in conjunction with the unbalanced representation of birth orders, could potentially lead to biased estimates of cooperation levels in studies involving student samples but neglecting birth order effects. Second, as most students are highly dependent on parental financial support (at least in France), sibling competition could affect their behaviours more than in economically independent adults. This could affect cross-cultural studies, where industrialized societies are generally represented by a student population and traditional societies are represented by a nonstudent population (e.g. Henrich 2000).

Cooperation Towards Nonkin Individuals

Although in our experimental design the subjects played the investment game with nonkin individuals using nonparental resources, they behaved differently depending on their position in the family. Two main mechanisms could be involved: an allocation trade-off between cooperation within and outside the family, or a by-product of how cooperative behaviours were selected to be adaptive inside the family.

Familial interactions may still be important in adulthood and may influence the tendency to cooperate with nonrelatives. In this situation, there would be an allocation trade-off between cooperation within or outside the family. Owing to resource limitations such as time and energy, forming any cooperative alliance within the family would lower the probability of making another cooperative alliance outside the family. In this scenario, our results suggest that firstborns tend to favour cooperation within the family, and that laterborn children, who cooperate more with nonkin, are less prone to cooperate with their siblings (only children represent an extreme situation because they can uniquely interact with nonkin children during childhood). This is supported by studies of familial attachment: for instance, firstborns feel closer to their parents and other relatives than laterborn children (Salmon & Daly 1998). In addition, our study showed a nonsignificant trend for middleborn children to be the most trustful towards nonkin and to reciprocate the most. This is consistent with the fact that middleborn children are described as feeling the closest to unrelated individuals (Salmon & Daly 1998). It follows that they would be the least cooperative with their siblings. Indeed, Salmon (2003) showed, using questionnaires, that middleborn children seem less prone to help family members in need.

An alternative view is to consider that cooperation outside the family is independent of cooperation inside the family. In this scenario, no birth order effect is expected unless cooperative behaviour towards nonkin individuals is a by-product of intrafamilial cooperation. Cooperative skills may be shaped during childhood in interactions with siblings, and may not be plastic enough to become completely independent of this past environment in adulthood. In this situation, adults would cooperate with unrelated individuals using rules initially designed to be optimal within the family, even though they are potentially irrelevant outside. The fact that birth order seems to have a long-lasting impact on many personality traits measured in adults (Sulloway 1995) provides support for this hypothesis. Among possible proximal mechanisms, the endocrine system is likely to be involved. The familial environment has long-term effects on the blood concentrations of hormones such as cortisol and testosterone (Flinn & England 1997; Alvergne et al. 2008). In addition, these hormones have been found to influence behaviour in economic games (Burnham 2007; Apicella et al. 2008; Coates & Herbert 2008).

Implications for the Evolution of Human Cooperation

The role of sibling competition in determining adult cooperation may provide some indirect insights into the evolutionary puzzle of human cooperation. Within the family, kin selection and direct and indirect reciprocity promote cooperative behaviours. The allocation trade-off and constrained plasticity scenarios both imply that human adults keep cooperating according to family-related determinants, even when interacting with unrelated individuals. The importance of birth order is probably just one illustration of the impact of familial structure and familial interactions on cooperation. Therefore, the extended dependence of offspring on parental investment is an important factor to consider when investigating the evolution of cooperation among humans. For instance, studying the influence of parental strategies on offspring cooperativeness could bring some additional light on the evolution of human cooperation. In this regard, replicating the present study in populations that differ in wealth inheritance practices (e.g. primogeniture, egalitarian, ultimogeniture) would be of particular interest.

Obviously, cooperative actions depend on many personality traits and behavioural tendencies. In the present study we investigated only two components of cooperation, namely trust and reciprocity, as measured in the investment game. Therefore, economic games measuring other aspects of cooperation need also to be performed as well as experiments in natural situations and in other cultural contexts before definitive conclusions can be drawn.

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APPENDIX

The variance structure between factor categories was analysed with a version of Levene's test (Levene 1960) using randomizations (Conover et al. 1981) as suggested by Manly (2007) for situations of strong departure from normality. Following Brown & Forsythe (1974), residuals were computed using the median rather than the mean to perform Levene's tests. Both the residuals of the amount sent by A players (x) within birth order categories and the residuals of the amount sent back by B players (y) within x_F and birth order modalities presented strong evidence for heteroscedasticity (Levene's test in its randomization version: for A players: $W = 4.0$, $N = 196$, $P = 0.01$; for B players: $W = 9.4$, $N = 221$, $P = 0.0001$).

Owing to the large heteroscedasticity in the data sets, specific tests were performed for the mean analysis. For A players, we used the two best tests designed for one-factor analysis described by Manly: test 3 (Manly 1995) and test DO (Manly & Francis 1999). Test 3 involved transforming raw data to keep mean differences between factor categories while removing variance differences. A classic one-way ANOVA was then applied on the transformed data, and the significance was determined by comparing the F statistic with its randomization distribution. Test DO is also based on a classic ANOVA but adopts an alternative strategy: raw data are not transformed but variance heteroscedasticity is reintroduced into each randomization set (see Manly & Francis 1999 for details). For B players, only test DO was used because the statistical accuracy of test 3 is reduced when two factors are present (Manly & Francis 1999).

Post hoc analysis was based on pairwise comparisons of all four birth order categories, followed by grouping categories that did not differ significantly according to the previous tests 3 and DO.

To analyse the possible bias from parental ages at birth and the number of siblings, coefficients of the linear regressions on the amount sent (x for A players and y for B players) were computed independently as a function of each of these two variables. The significance levels of these coefficients were obtained by comparing them with their randomization distributions under the null hypothesis.

Significance in all randomization tests was assessed by comparing the observed value of the statistic with 9999 randomization sets. All statistical analyses were implemented in the language R (R.2.9.1, R Development Core Team, Vienna, Austria).