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Social learning and the demise of costly cooperation in humans

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Humans have a sophisticated ability to learn from others, termed social learning, which has allowed us to spread over the planet, construct complex societies, and travel to the moon. It has been hypothesized that social learning has played a pivotal role in making human societies cooperative, by favouring cooperation even when it is not favoured by genetical selection. However, this hypothesis lacks direct experimental testing, and the opposite prediction has also been made, that social learning disfavours cooperation. We experimentally tested how different aspects of social learning affect the level of cooperation in public-goods games. We found that: (i) social information never increased cooperation and usually led to decreased cooperation; (ii) cooperation was lowest when individuals could observe how successful individuals behaved; and (iii) cooperation declined because individuals preferred to copy successful individuals, who cooperated less, rather than copy common behaviours. Overall, these results suggest that individuals use social information to try and improve their own success, and that this can lead to lower levels of cooperation.

1. Introduction

> 'Consider the luxurious dress, hair and behaviour of leaders and people. See how you have wanted to copy the pagan [Viking] way of cutting hair and beards. Are not these the people whose terror threatens us, yet you want to copy their hair?
> —Alcuin of York, 793 AD [1, p. 19]

The social transmission of behavioural traits (cultural evolution) has been hypothesized as an explanation for the high level of cooperation in human societies [2–12]. The problem of cooperation is to explain why individuals would help others when this could reduce the relative fitness of the cooperator. Models of genetical evolution have shown that cooperation can be selected if it increases the inclusive fitness of the cooperator in the long term, such as when there is reciprocal helping between individuals or if cooperation is directed towards relatives that share cooperative genes [13,14]. However, human cooperation arguably occurs in large groups of unrelated individuals, where these explanations of cooperation might not apply [15,16]. Cultural evolution provides a potential explanation, because if cooperative behaviours are learned socially from others (social learning), then cooperation can spread within groups, and cooperative groups can outcompete relatively uncooperative groups [3–10,16].

The extent to which cultural evolution favours higher levels of cooperation is controversial [17–30]. First, theory suggests that the outcome of cultural evolution depends critically upon the mechanisms by which individuals obtain and use social information. Cultural evolution can either favour or disfavour cooperation depending on whether individuals copy common behaviours, successful groups, or successful individuals [5,6,10–12,17,19,24,31,32]. Second, from an empirical perspective, it is unclear how humans obtain social information about the extent to which others cooperate, and how they respond to such information. There is only limited experimental evidence that these potential learning mechanisms apply to costly social behaviours, work in the predicted ways, and/or lead to different levels of cooperation between groups over time [33–36].

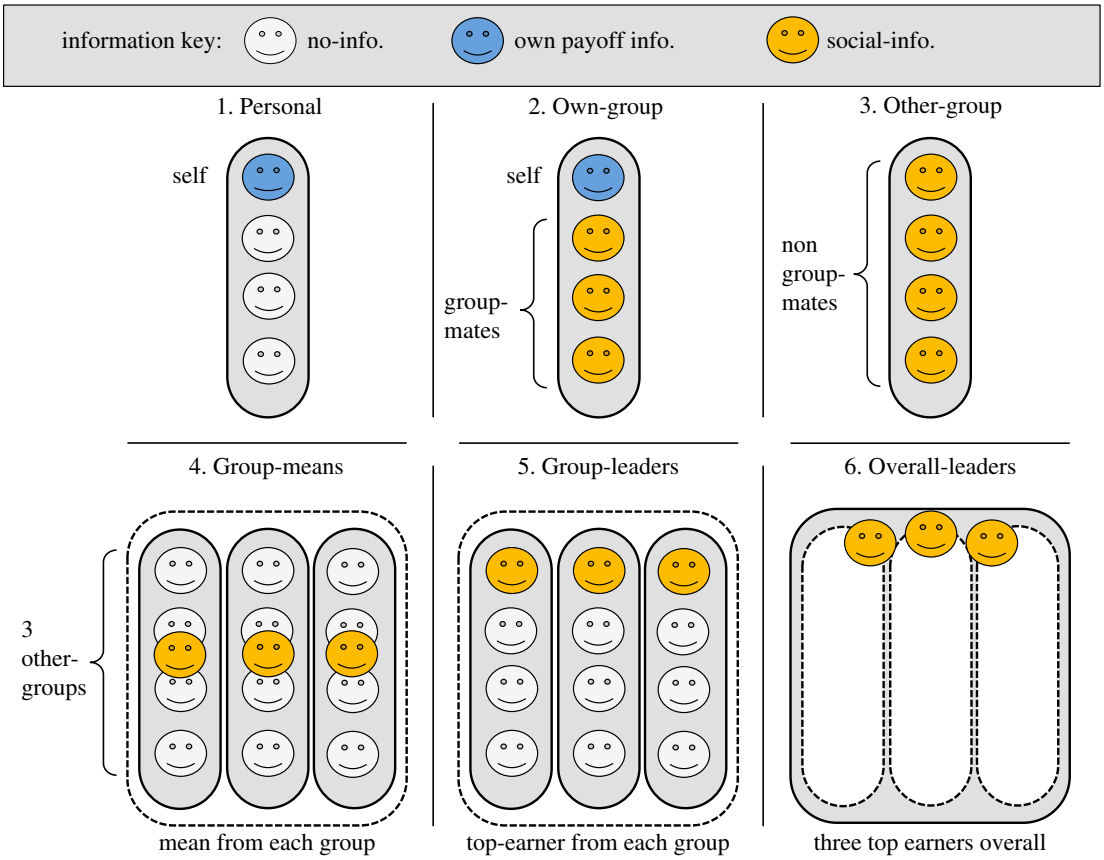

Figure 1. Our experimental design. Shown are the sources of information that players received in each treatment. All players received the same sources of information within each treatment. Treatments 1 and 2 were controls for responses to own payoffs (Personal, $n = 4 \times 12$) or the decisions of groupmates (Own-group, $n = 4 \times 12$). In treatments 3–6 we controlled for within-group effects by only providing social information about behaviour in another group (Other-group, $n = 4 \times 12$) or other groups (Group-means, Group-leaders, Overall-leaders, $n = 4 \times 12$ in each). In each of treatments 3–6, 24 of the 48 participants also received information about the concurrent payoffs for the behaviours they observed. Individuals in treatment 3 were observing the individuals in treatment 2. Individuals in treatments 4–6 were observing individuals/groups in treatments 1–3.

We experimentally tested how different social learning mechanisms influence cooperation in humans. Our general method was to experimentally vary the sources of social information available to individuals, and to test whether this led to changes in their level of cooperation over time. We used a repeated public-goods game, with constant groups, where individuals could choose to pay a cost to benefit everyone else in their group. This game resembles many natural situations, where cooperation provides a benefit to the group, but there is an individual incentive to not cooperate. In addition, previous studies have found geographical variation in how people play the game, which could potentially fuel cultural evolution [15,22,37,38].

A problem with investigating social learning in the public-goods game is that the typical experimental design would confound social learning with other factors. Individuals are often told how much they earn (personal payoff), and the behaviour of their groupmates. The first problem here is that individuals might be altering their own level of cooperation to influence the behaviour of their group-mates [16,34,39–42]. The second problem is that individuals could use their earnings to learn about the behaviour of their groupmates, of if they are uncertain, about how best to play the game [43–45].

We separated social learning from these confounding factors by only providing individuals with information about behaviours within other groups, groups that had no payoff consequences for the individual concerned (figure 1). Specifically, we gave feedback after each round on either: (i) the individual behaviour of all four individuals in another group ('Other-group' treatment); (ii) the average behaviour in each of three other groups ('Group-means'); (iii) the behaviour of the most successful individual within each of these same three other groups ('Group-leaders'); or (iv) the behaviour of the three most successful individuals overall from these same three groups, regardless of which particular group they came from ('Overall-leaders') [46]. To investigate how social learning was influenced by knowledge of financial gains, we also provided half of the players in each treatment with information about the corresponding earnings for these behaviours. In all of these treatments, the social information was only ever transmitted between groups in one direction, and so there was no way that individuals could influence the behaviour of their group-mates nor the individuals their group-mates observed [13,47–49].

An advantage of our treatments is that they allow us to investigate different mechanisms of social learning one at a time. For example, when individuals observe the behaviour of the most successful individuals (Overall-leaders treatment) they could potentially copy the highest earning individual, but they lack information on what was the most common behaviour. Likewise, when they observe the average behaviour across groups (Group-means treatment) they could potentially copy common behaviours (conformity bias), but they lack information on the success of different individuals. If individuals copy successful behaviours [10,36], then, depending on treatment, our participants could select to

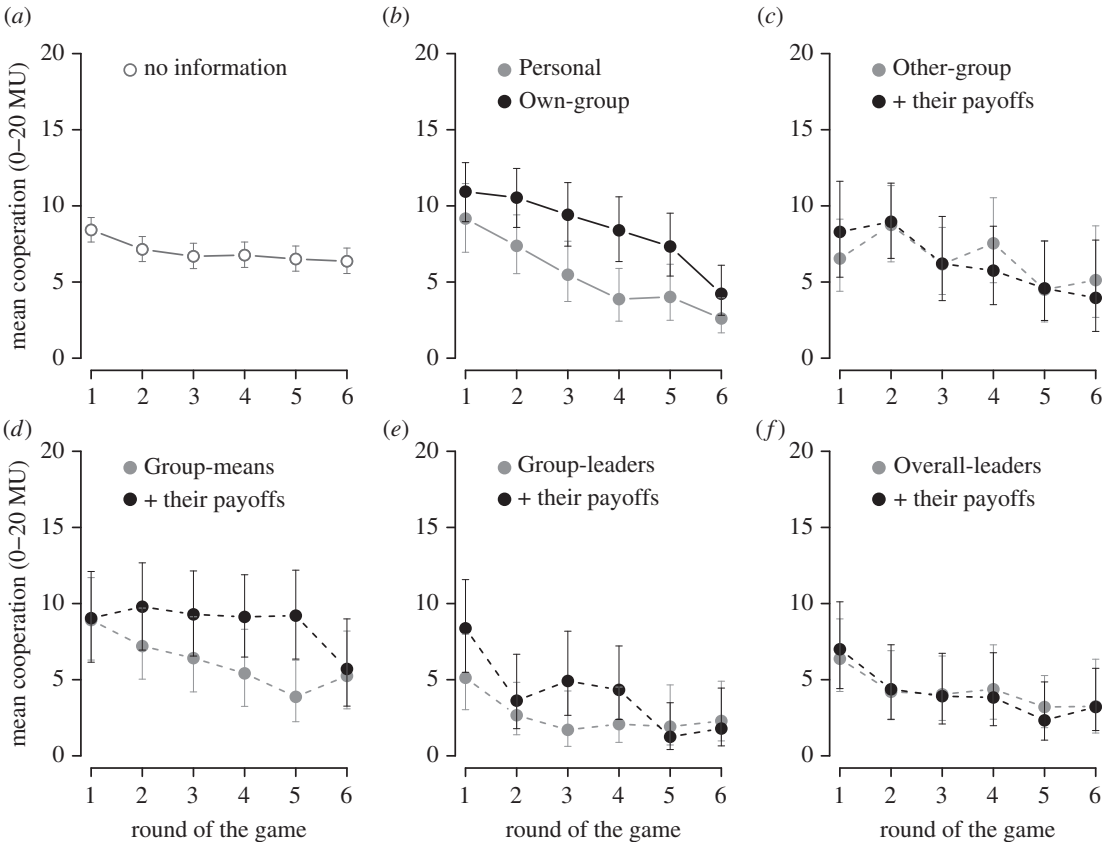

Figure 2. (*a–f*) Social learning and mean cooperation. Shown is the mean level of cooperation (0–20 MU) per round of the game for each treatment outlined in figure 1. Within each plot, the black circles show the effect of providing more information than in the grey circles and lines. Empty circles refer to when we provided no information (*a*). Solid lines refer to within-group effects (*b*). Dashed lines refer to social learning treatments (*c–f*). Error bars show 95% confidence intervals. In all but one treatment, social learning leads to a significant decline in the level of cooperation. The exception is when we showed individuals the mean cooperation, along with the concurrent payoffs, in three other groups, in which case cooperation remained relatively constant (*d*, Group-means + their payoffs).

copy behaviours on the basis of within-group success (Group-leaders), among-group success (Group-means with payoffs), or overall success, i.e. a function of both within- and among-group success (Overall-leaders) [46].

Finally, to enable a comparison between the effects of social learning, personal-learning and the within group-effects that we discussed above, our final two treatments were controls, where we only gave individuals information about their own group [18,50]. In one treatment we only gave them information about their own payoffs, to allow learning from changes in personal success ('Personal' treatment), and in the other treatment we gave them information about both their own payoffs, and the behaviour of other individuals in their group, as is typically done in the public-goods game literature ('Own-group' treatment; figure 1).

2. Material and methods

We conducted 12 sessions each with 24 participants ($n = 288$) in six groups of four, one group for each treatment (Personal, Own-group, Other-group, Group-means, Group-leaders, Overall-leaders). We gave all players the same initial instructions, and then first measured how their baseline level of cooperation changed over time when no information was available about either their own success, or the behaviour of other individuals (No-information treatment) [51,52]. We then randomly assigned groups of four individuals to each of our six treatments described above (four social learning treatments and two controls), randomly assigning two players per social learning treatment to also receive information about the concurrent payoffs for the behaviours they observed (figures 1 and 2). This provides eight separate tests of how social learning affects cooperation over time (four treatments, either with/without payoff information, figure 2*c–f*). Individuals in the Other-group treatment were observing the behaviour of individuals in the Own-group treatment. Individuals in the Group-means, Group-leaders, and Overall-leaders treatments were observing behaviour sampled from the Personal, Own-group, and Other-group treatments. The treatment names are for reference only. The instructions used 'neutral' language (electronic supplementary material, Methods).

The instructions, control questions and experimental game were conducted using Z-TREE [53] and all decisions were made anonymously through a computer interface with partitions separating participants. We presented instructions both on screen in full and a summary version on paper for each player to use as a reminder during the experiment. Instructions and control questions and cost-benefit parameters were copied as directly as possible from references [54,55] (electronic supplementary material, Methods). Experiments were conducted at the Centre for Experimental Social Science (CESS), Nuffield College, University of Oxford and CESS recruited all participants using ORSEE [56].

3. Results and discussion

(a) Baseline cooperation

When we provided individuals with 'no information' at all, either about their own performance, or the behaviour or success of any other individuals, we found that the level of

cooperation was relatively stable, with players contributing approximately 35% of their endowment to the cooperative group project (7.0 ± 0.17 s.e.m. of 20 monetary units (MU), median = 5 MU, mode = 0 MU). There was a very small but significant decline in cooperation over time (generalized linear mixed model (GzLMM) with binomial logit-link: $F_{1,1373} = 45.7$, $p < 0.001$, $\beta = -0.12 \pm 0.018$ 95% CI) (figure 2*a*).

(b) Social learning and cooperation

We found that providing social information did not increase the level of cooperation in any of our social learning treatments (figure 2*c–f*). When we only provided information on behaviour, and not payoffs, cooperation significantly declined in all four treatments. Specifically, cooperation declined when we gave information about; the behaviour of individuals in another group (Other-group, GzLMM: $F_{1,113} = 6.2$, $p = 0.014$, $\beta = -0.16 \pm 0.063$; figure 2*c*); the mean behaviour in three other groups (Group-means, GzLMM: $F_{1,116} = 24.0$, $p < 0.001$, $\beta = -0.27 \pm 0.056$; figure 2*d*); the behaviour of the individuals who each had the largest payoff in three other groups (Group-leaders, GzLMM: $F_{1,119} = 13.7$, $p < 0.001$, $\beta = -0.27 \pm 0.074$; figure 2*e*); and the behaviour of the three most successful individuals overall (Overall-leaders, GzLMM: $F_{1,116} = 8.6$, $p = 0.004$, $\beta = -0.19 \pm 0.066$, figure 2*f*).

When we also provided information on the relevant payoffs, cooperation significantly declined in three of the four treatments (GzLMM: Other-group, $F_{1,114} = 32.5$, $p < 0.001$, $\beta = -0.38 \pm 0.067$; Group-leaders, $F_{1,120} = 33.6$, $p < 0.001$, $\beta = -0.49 \pm 0.084$; Overall-leaders, $F_{1,117} = 22.5$, $p < 0.001$, $\beta = -0.31 \pm 0.066$). The only exception was the Group-means treatment, where we gave information about the mean behaviour and earnings in three other groups (figure 2*d*). In this treatment, the level of cooperation did not significantly change over the first five periods (GzLMM: $F_{1,90} = 0.02$, $p = 0.88$, $\beta = -0.01 \pm 0.069$) although there was a significant decline in the final round (GzLMM: $F_{1,19} = 5.3$, $p = 0.032$, $\beta = -0.9 \pm 0.400$).

Overall, our results suggest that in almost all cases, social learning from other groups leads to the demise of costly cooperation. In the final round, after five rounds of social learning, the median contribution was 0% (0 MU) for five treatments and below 15% (3 MU) in all eight treatments (electronic supplementary material, figure S1). We suggest two potential reasons for this pattern. First, motivated by a desire to copy common behaviours, individuals could be using the social information to conform with the average/typical behaviour of other players (conformity bias) [11]. Second, individuals could be using the social information to learn which levels of cooperation lead to higher payoffs, and one way to do this is to copy successful individuals (payoff-biased transmission and/or prestige-bias) [32]. We investigated these hypotheses by comparing the relative rates of decline in cooperation across our different social learning treatments.

(c) Using social information

We found that information about the most successful players strongly influenced behaviour, in ways that suggest individuals are using social information to try and improve their personal payoffs. First, when individuals knew they were observing the behaviour of the highest-earners (Group-leaders and Overall-leaders treatments combined, figure 2*e,f*), this led to significantly less cooperation on average than when we showed samples of common behaviours (Other-group and Group-means treatments combined, figure 2*c,d*) (GzLMM: $F_{1,160} = 25.3$, $p < 0.001$, estimated mean cooperation = 9% and 27% respectively).

Second, when we provided individuals with samples of common behaviours (Other-group and Group-means treatments), their responses differed if we also showed the concurrent payoffs. Specifically, the information about concurrent payoffs led to individuals making responses more inline with the income maximizing behaviour for the units (individuals or groups) being compared. Thus, when we showed individuals how payoffs differed for individuals within the same group (Other-group), showing that cooperation is personally costly, cooperation arguably declined faster (GzLMM interaction between period and whether payoffs shown: $F_{1,227} = 5.1$, $p = 0.025$, difference in $\beta = -0.21 \pm 0.092$, electronic supplementary material). Similarly, when we showed individuals how payoffs differed for different groups (Group-means), showing that members of more cooperative groups earned more, cooperation declined slower over the first five periods (GzLMM: $F_{1,181} = 13.4$, $p < 0.001$, difference in $\beta = 0.37 \pm 0.101$).

By contrast, we found mixed support for the hypothesis that individuals were using the social information to copy common behaviours (conformity bias). Contradictory to this conformity hypothesis, as discussed above, when we showed the relevant payoff information for different behaviours, responses differed. In the Other-group and Group-means treatments, providing payoffs provides no extra information about the frequency of different behaviours, and so should have no influence on individuals who are merely trying to conform.

Potentially consistent with the conformity hypothesis, we found that providing information only about the behaviour of others (Other-group and Group-means treatments) without any payoff information still led to an eventual decrease in cooperation (as reported above). However, when individuals could only observe the behaviour, and not the corresponding payoffs, of individuals in another group (Other-group), the decline in cooperation was not evident during the first four to five periods (GzLMM on first four rounds: $F_{1,65} = 0.01$, $p = 0.911$; on first five rounds: $F_{1,89} = 3.84$, $p = 0.053$; figure 2*c*). Indeed, over all six periods, the levels of cooperation in the Other-group treatment remained statistically unchanged from when we provided them with no information (No-information) (GzLMM comparing within-participants between treatments: $F_{1,232} = 1.5$, $p = 0.225$, $\beta = 0.19 \pm 0.157$, electronic supplementary material, Results). Thus it is unclear if these players were trying to match the behaviour of others (normative conformity), or updating their beliefs about how best to play the game (informational conformity), or were merely ignoring the social information [57]. Therefore, to circumvent this problem of multiple explanations, and to investigate directly if individuals are motivated to copy either common or successful behaviours, we examined the mechanisms that drive individual variation in the level of cooperation.

(d) Mechanisms of social learning

We explicitly tested if individuals were using social information to copy either common or successful behaviours. We did this by testing if our players adjusted their level of cooperation towards behaviours that are either more common, or more successful.

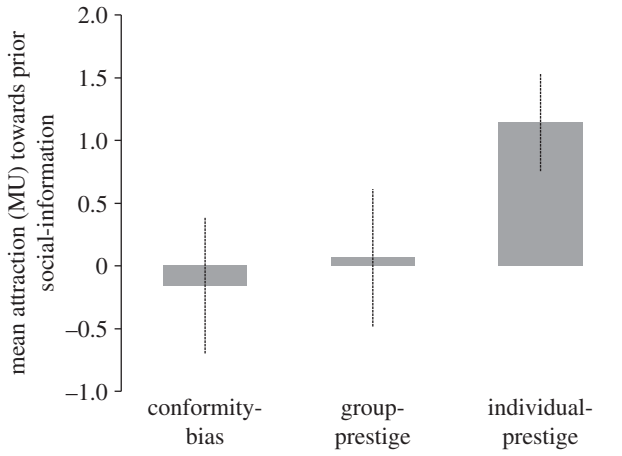

Figure 3. Mechanisms of social learning. Shown is the extent to which individuals adjust their behaviour towards different types of social information. The types of social information are: modal behaviour in the Other-group treatment (conformity-bias, $n = 180$ observations on 48 individuals); highest-earning group in the Group-means shown with payoffs treatment (group-prestige, $n = 120$ observations on 24 individuals); highest-earning individual in each of the Group-leaders and Overall-leaders treatments when payoffs were shown (individual prestige, $n = 240$ observations on 48 individuals). Error bars show 95% confidence intervals. On average, individuals adjusted their level of cooperation to be more similar, in absolute terms, to that of successful individuals, and not towards common behaviours or that in successful groups.

Specifically, we examined changes in the absolute difference between the cooperation of our focal players and the social information they observed [35]. We used absolute differences to avoid the problem of regression to the mean, which we return to later [58].

In general, when we provided information on the highest-earners, individuals significantly adjusted their contributions to be more similar to those highest earners. In the most extreme case, when we provided information about the behaviour and earnings of the highest-earning individuals (Group-leaders & Overall-leaders), we found that, on average, players moved their behaviour 1.2 ± 0.20 MU closer to (became more similar to) the highest-earning example (linear mixed model (LMM) test if intercept different to 0: $t = 5.8$, $p < 0.001$; figure 3). This attraction to the behaviour of the most successful individual is consistent with payoff-biased transmission, and could also be consistent with prestige bias, if we assume that prestige is directed to the most successful individual(s) [10]. Furthermore, across all four social learning treatments combined, this attraction towards the highest-earning example was consistently greater when payoffs were shown (LMM testing effect of showing payoffs, controlling for treatment: $F_{1,173} = 4.8$, $p = 0.030$, difference in $\beta = 0.41 \pm 0.188$; electronic supplementary material, figure S2). Individuals may condition their cooperation on the behaviour of others, and thus withdraw their cooperation in response to observing non-cooperators [55]. As non-cooperators will tend to be relatively high-earners in our experiment, this could then explain attraction towards high-earners. However the greater attraction to the behaviour of high-earners when payoffs were shown confirms individuals were not simply conditionally withdrawing cooperation in response to the presence of non-cooperators. Instead our overall results support the hypothesis that individuals are using social information to try and improve their personal payoffs. Consequently, costly cooperation decreases. However, in contexts where cooperation leads to personal success, such social learning might facilitate cooperation.

By contrast, we found no evidence that individuals modify their behaviour to be more similar to the most common behaviour within a group (the mode), or to the average behaviour (the mean), either within or across groups. Specifically, when we showed individuals the distribution of behaviours within another group (Other-group), their subsequent contributions moved no closer to the modal behaviour (mean attraction $= -0.2 \pm 0.27$ MU; LMM test of intercept: $t = -0.6$, $p = 0.556$; figure 3). This was true even for cases where the mode was cooperative (more than 0 MU), instead the subsequent contributions actually moved significantly away from the mode (mean attraction $= -0.6 \pm 0.25$ MU; LMM test of intercept: $t = -2.4$, $p = 0.018$). Likewise, individuals showed no significant attraction to the mean of the social information when we showed them the behaviour of four other individuals (Other-group: mean attraction $= -0.3 \pm 0.16$ MU; LMM test of intercept: $t = -1.9$, $p = 0.064$), or the behaviour of three other groups (Group-means: mean attraction $= 0.2 \pm 0.15$ MU; LMM test of intercept: $t = 1.4$, $p = 0.152$; electronic supplementary material, figure S3).

In addition, we found no support for imitating successful groups (group-prestige) [8,10]. Specifically, when we showed our players the average behaviour and earnings of three other groups (Group-means) we found that their subsequent contributions moved no closer to the highest earning group (mean attraction $= 0.06 \pm 0.26$ MU; LMM test of intercept: $t = 0.2$, $p = 0.812$; figure 3). Consequently, our overall results are inconsistent with conformity bias, and group-prestige, but are consistent with payoff-biased transmission via prestige-bias towards successful individuals. This suggests that a psychology to copy the successful is primarily applied to successful individuals rather than to groups. But if individuals do not imitate more successful groups, then why did showing the earnings of different groups halt the otherwise observed decline in cooperation? This aggregate result is consistent with group prestige. However, it could also arise if some individuals, when observing that more cooperative groups earn more money, reasoned that contributions to the public good were personally profitable. Either way, being able to observe and compare the success of different groups may favour cooperation, providing individuals do not focus upon the success of different individuals.

Our results were robust to how we analysed the data. Our above results remain qualitatively unchanged if we investigated proportional changes in the absolute difference between cooperation and the social information examples (electronic supplementary material, Results and discussion). Another alternative is to examine the frequency of exact matching, between a player's subsequent contribution and the examples from the prior-social information. By comparing our Group-means and Group-leaders treatments we could test if players were more likely to match typical or successful behaviours while controlling for the source of information, as both treatments simultaneously observed the same three groups. This also allowed us to estimate the frequency of unintended matching by 'chance', by comparing how often players observing typical behaviours matched successful behaviours and vice versa. We found that players who observed the highest-earning individuals in each group (Group-leaders treatment) matched one, or the mean ± 1 MU of these three

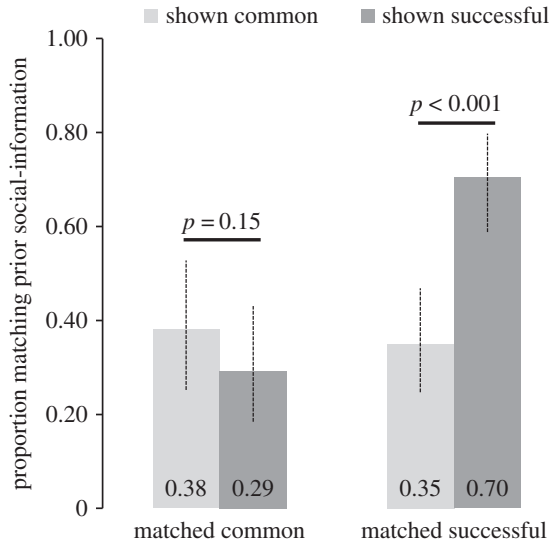

Figure 4. Imitating successful versus common behaviours. Shown are the frequencies of exact matching between the cooperation of individuals and different types of social information. The types of social information are: the mean level of cooperation within each of three groups (common behaviours) and the individual level of cooperation for the highest-earning individual in each of three groups (successful behaviours). Values are the estimated marginal means from the GzLMM model controlling for individual, and thus differ slightly from the raw values reported in the main text. Error bars show 95% confidence intervals. When individuals could observe successful behaviours (the behaviour of the highest-earning individuals) they were significantly more likely to match them than we would have expected from chance ($n = 48$). By contrast, when they could observe common behaviours (the mean behaviour in each of three groups) they were no more likely to match them than we would have expected by chance ($n = 48$).

examples, 70% of the time, significantly more likely than the 36% by 'chance' (GzLMM with binary-logit link: $F_{1,94} = 19.8$, $p < 0.001$, $\beta = 1.42 \pm 0.319$; figure 4, electronic supplementary material). Again, this result is consistent with payoff-biased transmission via prestige-bias towards successful individuals. By contrast we found that individuals who observed the average behaviour in the same three groups (Group-means treatment) only matched one, or the mean of the three examples, 40% of the time, which was not significantly more likely than the 32% by 'chance' (GzLMM: $F_{1,94} = 2.1$, $p = 0.150$, $\beta = 0.37 \pm 0.258$; figure 4, electronic supplementary material). This lack of a result is inconsistent with a mechanism of conformity bias towards group typical behaviours.

(e) Learning about people or about payoffs

A potential alternative hypothesis is that individuals were using the social information to learn about the likely behaviour of other individuals rather than about how to play the game. The logic here is that when individuals received information about the behaviour of others, they reasoned that it was indicative of how their groupmates would play next. They then adjusted their own cooperation in an attempt to condition it on what they believed to be the likely cooperation of their own groupmates [55]. Alternatively, we have argued that individuals were using the social information to learn how personal payoffs vary with the level of cooperation. To test between these competing explanations, we also made individuals play the same game but with computerized groupmates that played randomly, both before ($n = 288$) and after ($n = 216$) playing the above games with humans. If individuals use social information to conform to the behaviour of other people then the different social learning treatments should have no effect on their subsequent behaviour with computers playing randomly. However if individuals use social information to improve their personal payoffs, then the different social learning treatments will affect their subsequent cooperation with computers if they try to maximize their earnings.

In support of the latter interpretation, we found that individual cooperation with computers significantly depended on what type of social information individuals received in prior games with humans. Specifically, those individuals that could observe that lower contributions lead to more individual success cooperated significantly less with computers (3.4 ± 0.63 MU, Other-group with payoffs, Group-leaders, Overall-leaders) than those that received samples of social information pertaining to common behaviours (6.2 ± 0.92 MU, Other-group without payoffs, Group-means) (GzLMM: $F_{1,135} = 5.9$, $p = 0.016$; electronic supplementary material, Results).

(f) Alternative tests for conformity bias

Our results contradict the conclusion of several previous studies, which suggested that players modify their cooperation to be more similar to the common behaviour of others (conformity bias) [33,34,39,55,59–61]. One reason for the discrepancy may be that our players were responding to the behaviour of individuals in other groups, rather than their groupmates, and the psychology of learning and cooperation may rely on different mechanisms for in-group and out-group members [62]. Another reason is that some of these previous studies analysed their data in ways that can potentially lead to misinterpretation [59–61].

Studies that test if showing players the behaviour of others makes relatively low cooperators subsequently increase their level of cooperation, and vice versa, are particularly problematic [59–61]. This is because such a pattern of behaviour is expected even by chance, through a phenomenon known as 'regression to the mean' [58]. If the behaviour of individuals is varying, even randomly, then on average, individuals who initially cooperate at relatively 'high' or 'low' values will subsequently cooperate at values closer to the mean. We were able to explicitly test whether this problem occurs in public-goods games, by examining the data from our No-information treatment. Here, we found that players who cooperated less than their groupmates significantly increased their subsequent level of cooperation on average and vice versa, even though they had no information so could not possibly have been responding to the cooperation of others (LMM: $F_{1,330} = 54.2$, $p < 0.001$, $\beta = -0.11 \pm 0.015$; electronic supplementary material, figure S4). By contrast, this problem of regression to the mean did not occur when we used the method of analysing absolute differences to test if individuals shifted their behaviour towards the behaviour of groupmates (mean attraction to the average behaviour of groupmates $= -0.03 \pm 0.07$ MU, LMM test of intercept: $t = -0.5$, $p = 0.636$; electronic supplementary material, Results).

Other studies have regressed individual contributions upon the prior contributions of groupmates [39]. A potential problem with this design is that personal payoffs and the contributions of groupmates are positively correlated, and hence confounded. Consequently, even if individuals are just adjusting their

behaviour in response to their own payoffs, this could lead to a correlation between changes in their behaviour and the behaviour of others [43–45]. We were able to test for this potential problem by comparing behaviour in our two control treatments, where we informed individuals of only their payoffs (Personal treatment), or their payoffs and also the decisions of their groupmates (Own-group treatment). We found that individual contributions were just as positively correlated with the prior mean contribution of their group-mates, even when we did not directly inform them about how their group-mates behaved (GzLMM: cooperation~treatment*groupmates' previous average contribution, $F_{1,460} = 0.2$, $p = 0.652$, $\beta = 0.10 \pm 0.029$; difference $= -0.019 \pm 0.043$; electronic supplementary material, tables S1 and S2). However it is possible that individuals use knowledge of their payoffs to infer the cooperation of their groupmates. We discuss other problems with previous conclusions, such as whether detailed within group information favours or disfavours cooperation [33], the role of confusion [55,63] and confounding effects of group psychology [34,59,62,64,65], in our electronic supplementary material.

4. Conclusion

We found that when players could learn by observing individuals from other groups, levels of costly cooperation never increased, and usually decreased (figure 2*c–f*). When we examined why this occurred, it appears to be because individuals copy the behaviour of more successful individuals, who tend to be cooperating at relatively low rates. By contrast, we found no evidence that individuals copied common behaviours, or the behaviour of more successful groups (figures 3 and 4). Our results are consistent with studies showing that individuals copy successful behaviours when faced with unfamiliar environments, and cooperate less in social dilemmas when additional payoff information is available [36,43,66–69]. Our results suggest that social learning is used as a mechanism to increase the personal success of individuals, by paying attention to successful individuals [35]. Our results come from a study of small groups, however cooperation through social learning in larger groups is predicted to be even less likely to evolve and be maintained [70]. More generally, our conclusion is consistent with the idea that natural selection will favour social learning mechanisms that are adaptive [5,10,20,71,72]. Major tasks for the future are to determine how and why individuals use different learning mechanisms in different situations [18,73–76], what explains individual variation in the use of social learning mechanisms [77–80] and how the behaviour of those being copied will evolve [12].

Data accessibility. Data available from the Dryad Digital Repository: (http://dx.doi.org/10.5061/dryad.10g95) [81].

Authors' contributions. M.N.B.-C. conceived, designed, programmed, conducted, analysed and wrote the study; C.E.M. conceived, designed, conducted, analysed and wrote the study; S.A.W. conceived, designed, analysed and wrote the study.

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