PROCEEDINGS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

# The evolutionary basis of human social learning

T. J. H. Morgan, L. E. Rendell, M. Ehn, W. Hoppitt and K. N. Laland

*Proc. R. Soc. B* 2012 **279**, 653-662 first published online 27 July 2011
doi: 10.1098/rspb.2011.1172

PROCEEDINGS OF THE ROYAL SOCIETY B

*Proc. R. Soc. B* (2012) **279**, 653–662
doi:10.1098/rspb.2011.1172
*Published online* 27 July 2011

# The evolutionary basis of human social learning

**T. J. H. Morgan[1], L. E. Rendell[1], M. Ehn[2], W. Hoppitt[1] and K. N. Laland[1,]***

[1]*Centre for Social Learning and Cognitive Evolution, School of Biology, University of St Andrews, Bute Medical Building, St Andrews, Fife KY16 9TS, UK*
[2]*The Centre for the Study of Cultural Evolution, Stockholm University, Stockholm, Sweden*

Humans are characterized by an extreme dependence on culturally transmitted information. Such dependence requires the complex integration of social and asocial information to generate effective learning and decision making. Recent formal theory predicts that natural selection should favour adaptive learning strategies, but relevant empirical work is scarce and rarely examines multiple strategies or tasks. We tested nine hypotheses derived from theoretical models, running a series of experiments investigating factors affecting when and how humans use social information, and whether such behaviour is adaptive, across several computer-based tasks. The number of demonstrators, consensus among demonstrators, confidence of subjects, task difficulty, number of sessions, cost of asocial learning, subject performance and demonstrator performance all influenced subjects' use of social information, and did so adaptively. Our analysis provides strong support for the hypothesis that human social learning is regulated by adaptive learning rules.

**Keywords:** social learning; asocial learning; social learning strategy; copying; conformity; consensus

## 1. INTRODUCTION

Rules that govern the use of social information are variously referred to as 'social learning strategies' [1], 'transmission biases' [2,3] and 'trust' [4]. Theory suggests that individuals ought to be selective with respect to when and whom they copy [2,5], and that natural selection will favour the deployment of adaptive social learning strategies that guide individual reliance on social information [1,2,6]. Social learning strategies have been primarily examined through theoretical work using population genetic and game theory models [2,5,7–14]. Such rules are also receiving attention from researchers in a wide variety of academic disciplines with interests in the experimental analysis of social learning, cultural transmission and cultural evolution [15–24]. However, there remains comparatively little empirical data on human social learning with which to test the hypotheses generated by evolutionary models.

One relatively well-studied class of rules are frequency-dependent strategies, such as conformity and 'anti-conformity' [2,13,14,18,25], which involve individuals selectively adopting traits based on how common they are. Following Boyd & Richerson [2, p. 206], we define conformist frequency-dependent copying as the *disproportionately* likely adoption of the most common variant. Theoretical work on conformity has produced mixed results; some analyses suggest that conformity readily evolves under a broad range of conditions, including temporally and spatially variable environments [2,9], while other models conclude that conformity should be selected against because it hinders cumulative culture [25]. Empirical evidence of conformity has proved elusive [17,18,25,26], and some work has suggested that changes in frequency may be more salient than absolute frequencies [27].

Another class of social learning strategies is pay-off-based rules, where copying depends on the return to the observed individual [10,14]. Game-theoretic analyses have indicated that strategies where an individual's use of social information was proportional either to their own pay-off, the pay-off to demonstrators, or the difference between the two can be particularly effective [10,11]. There is good evidence that humans and other animals are sensitive to such information and do use it to direct social learning [19,20,28–30]. Other types of strategy are less studied, but nonetheless, there is evidence from human populations that adaptive beliefs are transmitted via prestige [31] and kinship biases [32].

There is, of course, a long-standing interest among social psychologists in when individuals will adopt the decisions of others [33–40]. Social impact theory clearly relates to social learning strategies, proposes a psychological mechanism and has been extended to consider its effect upon population-level belief patterns [37,41]. However, such work typically focuses on the adoption of arbitrary or incorrect group decisions [42], and by doing so limits consideration of the evolutionary, population-level consequences of such behaviour, and of whether the use of social information leads to adaptive behaviour. Conversely, we aim to understand not only how different factors affect decision making, but also their impact upon individual performance, leading to functional explanations for the evolution of decision-making rules [43].

---

* Author for correspondence (knl1@st-andrews.ac.uk).

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2011.1172 or via http://rspb.royalsocietypublishing.org.

*Received* 3 June 2011
*Accepted* 4 July 2011

A limitation of previous research into social learning strategies is the implicit assumption that individuals only employ one strategy in a given context [1], with models rarely considering more than one strategy, and experiments designed in such a way that subjects cannot use multiple strategies simultaneously. Furthermore, empirical work is typically limited to a single experimental task, raising questions about the generality of observations. Finally, there is a paucity of empirical data on whether the strategies people use are employed adaptively. Here, we present four experiments in which adult human subjects were required to solve computer-based problems by using asocial and/or social information. In total, we employed six tasks and two methods of information presentation and investigated the effect of nine different factors, often presented simultaneously, on subject reliance on social information use. This corresponds to our testing nine specific hypotheses derived from the cultural evolution literature [2,9,10,44]. Factors considered include: the number of demonstrators (+), demonstrator consensus (+), subject confidence (−), task difficulty (+), the cost of asocial learning (+), task familiarity (−), demonstrator (+) and subject (−) performance, and their difference (+); where the + and − signs signify predictions for positive or negative relationships with social information use. Our use of multiple tasks allows us to examine whether social learning strategies are deployed consistently across diverse contexts and sensory modalities, while investigating numerous factors allows us to test whether subjects are limited to using a single strategy at a time. Furthermore, by setting social information use in a task-solving context, we are able to investigate the adaptiveness of subjects' behaviour by measuring subjects' success in the tasks. Thus, the work presented here aims to provide a comprehensive empirical test of the adaptive learning strategies predicted by evolutionary models, to provide new data concerning pay-off and frequency-dependent social learning and to extend existing work by examining the simultaneous use of multiple strategies.

## 2. METHODS

### (a) *General methods*

Across four experiments, subjects took part in computer-based binary choice tasks, using asocial and/or social information to guide decision making. Asocial information gave subjects access to the task itself, whereas social information presented subjects with the decisions of a number of demonstrator individuals. Experimental sessions lasted for 60 min. Subjects were paid £5 for taking part, plus a bonus of up to £5 dependent on their performance.

#### (i) *Subjects and apparatus*

In total, 99 subjects took part in experiment 1, 57 in experiment 2, 38 in experiment 3 and 61 in experiment 4. Subjects ages ranged from 18 to 58 (mean = 22, s.d. = 4). Eighty three were male, 172 were female and all but nine were students of the University of St Andrews. Full details are given in the electronic supplementary material.

Subjects took part in experiments in batches of 1–11 individuals. All subjects had access to a computer and were separated by large screens such that they could not see other subjects. Subjects were provided with headphones such that they could listen to any required sounds without disturbing other participants.

#### (ii) *Procedure*

On arrival, the experimenter read subjects a briefing and gave them the opportunity to ask any questions. The experimenter then went to an adjoining room and remotely started the experiment programme on the subjects' computers. The connecting door was kept open so that the experimenter could hear if any subjects communicated, but no instances of between-subject communication were observed. When all subjects had completed the experiment, the experimenter returned to debrief the subjects who were then free to collect payment and leave. The briefing and debriefing script for each experiment are presented in the electronic supplementary material.

#### (iii) *General design*

The four experiments were designed to repeatedly test numerous factors in a range of contexts and involved two methods of information presentation, six tasks and three sources of social information. We first describe these general design components and then present details and results of each experiment. Each experiment was designed without knowledge of the results of any others. Thus, they can be viewed as independent attempts to address a set of related questions about human social learning. We, therefore, discuss the results together, rather than each in turn, as many results were repeated across experiments. Since several results were replicated across multiple tasks, this gives confidence in the generality of our findings.

#### (iv) *Methods of information presentation*

We termed the first method of information presentation the linear protocol. Here, subjects received asocial and then social information (or vice-versa). After receiving each type of information, subjects were required to make a decision and rate their confidence in their decision on a 7-point Likert scale [45]. Subjects were considered to have used social information if their final decision (following social information) differed from their initial decision (following asocial information), given that the majority of demonstrators disagreed with the subject. Here, asocial information was 'free' and the duration of the task stimulus was fixed.

In the second protocol, termed the parallel protocol, subjects were given the choice of either social or asocial information, before which they were informed of specifics of the trial (detailed below). After receiving their chosen source of information, subjects were required to make a single decision. Subjects were considered to have used social information when they chose to view social over asocial information. Here, asocial information was costly, and subjects determined the duration or number of presentations of the task stimulus.

#### (v) *The tasks*

*Foraging task*

This task involved selecting the more profitable of two virtual foraging sites and was designed to mimic the procedures deployed in published animal experiments [46–48]. Subjects received 20 visual presentations of a number of apples at the two sites, 10 at each. The true values of the sites were either 8 v. 4, 6 v. 2 or vice-versa. The number of apples shown in each presentation was independently drawn from a Poisson distribution centred on the true value of the site (e.g. an image of 12 apples at the right-hand site with a true value of 8), however, further uncertainty was introduced by drawing the number of apples from the value of the other site for 1 of the 10 presentations at each site. The apple presentations were given in a random order and each lasted 500 ms.

*Mental-rotation task*

Subjects were required to decide whether two shapes were the same shape seen from different angles or different shapes (see the electronic supplementary material for example). This task was based on that used by Shepard & Metzler [49], and allows trials of different difficulty to be generated. In each trial, subjects received a single visual presentation of an image of two shapes, the duration of which varied across experiments.

*Length-estimation task*

Subjects were required to decide which of two irregular lines was longest (see the electronic supplementary material for example). In each trial, subjects received a single visual presentation of an image of two lines, the duration of which varied as detailed below. This task was chosen as it is hard to solve through visual observation alone and so all responses will be associated with some degree of uncertainty.

*Audio tasks*

Subjects were required to decide which of two tones was (i) higher in pitch (the 'pitch task'), (ii) greater in intensity (the 'intensity task'), or (iii) whether a single tone was increasing or decreasing in pitch (the 'pitch-modulation task'). These tasks provided a test of the sensory multimodality of learning strategies. Subjects had access to button(s) that played the relevant tone(s) and could play them as many times as they wished, but incurred a cost per playing, detailed below, that reduced their bonus payment.

#### (vi) *Types of social information*

The decisions of others were presented using two tiles labelled with the possible answers. A demonstrator's decision was represented by the relevant tile flashing for 350 ms. This information was either from a battery of previous subject responses (battery), from other subjects taking part in the same experimental session (live) or was generated by us. When social information was manipulated, we employed a conditional information lottery [50] to ensure subjects would treat the information as genuine without being deceived. Under this procedure, a minority of trials used genuine (battery) social information and only performance on these trials affected payment. Subjects were informed of this, but not of which trials used genuine information. Under this protocol, subjects have been shown to treat all information as genuine [50]. Subject feedback following the experiment was used to identify subjects who had failed to understand this procedure and their data were excluded from the analysis.

#### (vii) *General analyses*

Unless otherwise stated, we analysed the data using generalized linear mixed models with a Bernoulli error structure and logit link function. We used Markov Chain Monte Carlo methods [51,52] to fit the models in WINBUGS 1.4 [53] and to generate credible intervals for each parameter. All models included a baseline constant, standardized variables (see below for details) and a random subject effect. Minimal adequate models (detailed in the electronic supplementary material) were constructed by backwards elimination, removing variables for which the 95% central credible interval included 0 from a model containing all predictors and second-order interactions. Parameter values were estimated using a sample of at least 3000 iterations, after a suitable burn-in period and thinning to remove autocorrelations. Effects are reported on the logit scale. Preliminary analyses (detailed in the electronic supplementary material) were carried out to establish whether factors should be modelled as linear or categorical.

Unless otherwise stated, all graphs show the median of posterior samples from the fitted models, as estimates of parameter values. Plots of the posterior parameter estimates are preferred to raw data because they directly illustrate the marginal effect sizes associated with a given predictor while controlling for the effects of other predictors. See figure 1*a*,*b* for a comparison of the raw data and model estimates.

### (b) *Experiment 1*

#### (i) *Design*

Subjects completed 10 trials using the foraging task, linear protocol and manipulated social information, presented in a random order. We manipulated (i) the number of demonstrators and (ii) the level of consensus in the social information they provided, such that social information consisted of either 4 v. 0, 5 v. 3, 6 v. 2, 7 v. 5 or 8 v. 4 demonstrators. For 48 of the subjects, the order of information presentation was reversed (i.e. social first) to investigate commitment effects.

#### (ii) *Analyses*

We modelled the probability of social information use for subjects given asocial information first as a function of demonstrator number, demonstrator consensus (the proportion of demonstrators choosing the majority option, scaled to range between 0 and 1) and subject confidence in their initial decision. To investigate whether the use of social information was adaptive, we modelled the effect of subject confidence on the probability that a subject's initial, asocial, decision was correct.

To investigate how the order of information presentation affected our results, we pooled data from all subjects and modelled whether social information was used differently dependent on the order of information presentation.

#### (iii) *Results*

Subjects were increasingly likely to adopt a conflicting majority decision with decreasing confidence in their own decision (subject confidence 95% credible interval (CI): $(-0.8737, -0.1308)$, median $= -0.4809$; figure 1*e*), increasing demonstrator consensus (CI: (1.226, 4.011), median $=$ 2.497; figure 1*c*) and increasing numbers of demonstrators (CI: (0.0007, 0.2332), median $= 0.1128$; figure 1*d*). There were no interactions. Subject confidence predicted whether a subject was right or wrong, with low confidence predicting an incorrect answer (CI: (0.1883, 0.8387), median $=$ 0.4988; figure 1*e*). There was no effect of information presentation order (social/asocial first) on social information use (CI: $(-0.4924, 0.4901)$, median $= 0.01072$).

### (c) *Experiment 2*

#### (i) *Design*

Subjects completed 24 trials using the mental-rotation task, linear protocol and manipulated social information, presented in a random order. The shape images were presented for a fixed time of 4 s. We manipulated (i) the number of demonstrators and (ii) the level of consensus in the social information as in experiment 1.

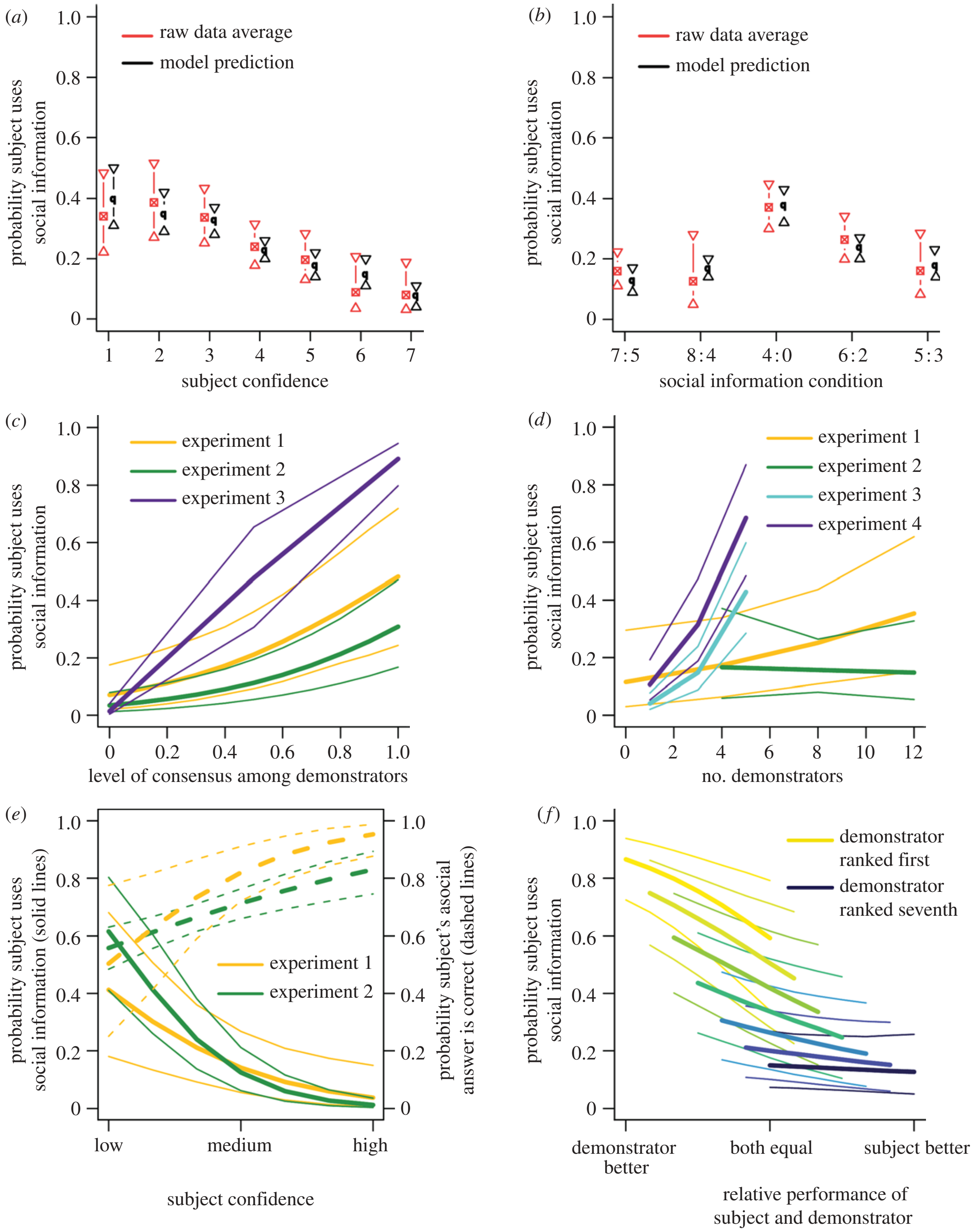

Figure 1. (*a*,*b*) A comparison of the raw data (red, average and Wilson confidence interval) and model predictions (black, median and 95% central credible interval) for (*a*) subject confidence and (*b*) the different social information conditions (where 7 : 5 means seven demonstrators make one decision while five make the other). The model closely matches the raw data, the narrower intervals for model estimates highlight the increase in precision offered by the model. (*c*) Median (thick lines) and 95% credible intervals (thin lines) for the probability that a subject uses social information depending on demonstrator consensus in experiments 1 and 2 (modelled as linear) and 4 (modelled as categorical). (*d*) The probability that subjects use social information increases with the number of demonstrators in three of four experiments, with more pronounced effects in experiments 3 and 4, which used the parallel protocol. (*e*) In experiments 1 and 2 the probability that a subject uses social information decreases with subject confidence in their own judgement based on asocial information (solid lines), while the probability that subject is correct increases (dashed lines). (*f*) The probability a subject copies a demonstrator depends on their relative performance and the absolute performance of the demonstrator. (experiment 4). Subjects respond differently to high performing demonstrators dependent on their own success, however, all subjects are equally unlikely to copy a poorly performing demonstrator.

### (ii) *Analyses*

We modelled social information use as a function of the number of demonstrators, demonstrator consensus and subject confidence in their initial decision. We modelled the probability that a subject's initial decision was correct as a function of their confidence in that decision.

We investigated conformity in two ways, neither of which limited the data to cases where the social information disagreed with the subject's initial decision. First, we modelled the probability a subject would change their decision. All predictors from the main analysis were included except demonstrator consensus, which was replaced with demonstrator disagreement (the proportion of demonstrators that disagreed with the subject's initial choice). Second, we modelled the probability that a subject's final decision would be that the shapes matched. Predictors used were the number of demonstrators, the proportion of demonstrators reporting a match (modelled separately as linear and categorical, see the electronic supplementary material for the reason), the subject's initial decision, their confidence in it, whether the shapes actually matched or not, and a random effect for each question.

### (iii) *Results*

As in experiment 1, subjects were increasingly likely to switch to a conflicting majority decision as demonstrator consensus increased (CI: (1.633, 3.413), median = 2.512; figure 1*c*) and with decreasing confidence in their initial choice (CI: (−1.086, −0.5561), median = −0.8142; figure 1*e*). However, there was no effect of the number of demonstrators (CI: (−0.2128, 0.1384), median = −0.0168; figure 1*d*). Low subject confidence again predicted an incorrect answer (CI: (0.1125, 0.338), median = 0.226; figure 1*e*).

The first conformity analysis showed that subjects were increasingly likely to change their initial decision as the proportion of demonstrators that disagreed with them increased (CI: (4.042, 6.438), median = 5.123). There was an interaction between demonstrator number and disagreement (CI: (0.1743, 0.7608), median = 0.4415), producing an S-shaped curve when demonstrator number was high and subject confidence was low (figure 2*a*,*b*).

The second conformity analysis found the likelihood a subject's final decision was that the shapes matched covaried with the proportion of demonstrators reporting a match (CI: (6.558, 10.45), median = 8.296; figure 2*d*), an effect that increased with the number of demonstrators (i.e. a proportion × number interaction, CI: (0.3373, 1.017), median = 0.6625, 'proportion' modelled as linear). There was another interaction between a subject's initial decision and their confidence in that decision (initial decision CI: (5.897, 7.902), median = 5.795; confidence CI: (−0.2669, 0.005424), median = −0.1295, interaction CI: (0.4234, 0.9641), median = 0.6881). Subjects were also more likely to decide the shapes matched if they genuinely did (CI: (0.02914, 0.848), median = 0.4322, if not CI: (−0.7708, −0.1283), median = −0.4418). With proportion modelled as categorical results were qualitatively the same, but moderate consensus among the demonstrators had a disproportionate impact (figure 2*c*) and interactions between proportion and other factors could not be investigated.

## (d) ***Experiment 3***

### (i) *Design*

Subjects completed 60 trials using the parallel protocol and battery social information. The trials were arranged into four groups of 15, the first and third using the mental-rotation task and the second and fourth the length-estimation task. This structure was adopted to avoid subjects becoming bored and not attending to trials. The order of trials within each group was randomized for each subject.

Prior to choosing between the two sources of information, subjects were informed of question difficulty ('very easy', 'easy', 'moderate', 'hard' or 'very hard') and the number of demonstrators (1, 3 or 5). For the mental-rotation task, difficulty was calculated as the proportion of previous subjects that got the question wrong (as an objective measure of task difficulty—the angle of rotation—failed to predict performance), while for the length-estimation task, it was proportional to the similarity in length of the lines.

Subjects who chose asocial information were free to examine the relevant image indefinitely, but at a cost proportional to the time spent observing that reduced their possible bonus payment. Subjects were informed of the cost incurred after each trial. Social information was free.

### (ii) *Analyses*

We modelled the probability that an individual would choose to view social information as a function of demonstrator number, task difficulty, session number and previous costs incurred using asocial information. To investigate whether the use of social information was adaptive, we modelled the pay-off of subjects on trials where they used asocial information (using a normal error structure). The predictors were task difficulty, trial group and task.

### (iii) *Results*

Subjects were more likely to choose to view social information on harder than easier trials (CI: (0.2518, 0.4402), median = 0.3463) and when they had incurred greater than lesser costs on the previous trial (CI: (0.02067, 0.1391), median = 0.07678). No effect of task was found (CI: (−0.444, 0.1752), median = −0.1349; see the electronic supplementary material for discussion of the effects of different tasks). There was an interaction between the trial group and the number of demonstrators (demonstrator number CI: (0.4586, 0.6316), median = 0.5488; figure 1*d*; trial group CI: (−0.3137, −0.05748), median = −0.1836, interaction CI: (0.02559, 0.1694), median = 0.09607). While subjects increasingly chose social information as the number of demonstrators increased, over groups of trials subjects became less likely to choose social information when there was only one (CI: (−0.5963, −0.1454), median = −0.3714) or three (CI: (−0.3036, −0.05188), median = −0.1765) demonstrators, but not when there were five (CI: (−0.1364, 0.1647), median = 0.01801).

Subject pay-off when using asocial information increased over groups of trials (CI: (0.4195, 0.7898), median = 0.6073) and was negatively related with question difficulty in trials using the length-estimation task (CI: (−0.3879, −0.01722), median = −0.1982), but not those using the mental-rotation task (CI: (−0.04259, 0.329), median = 0.1392).

## (e) ***Experiment 4***

### (i) *Methods*

Subjects completed 45 trials using the parallel protocol arranged into three groups of 15 that deployed the pitch task, intensity task and pitch modulation task, respectively. Three tasks were in a single session to help maintain subject attention across the experiment. The first two trial groups used battery social information, and within each group, trial order was randomized for each subject. The third trial group used live social information and so subjects were required to complete individual trials simultaneously; trial order was, however, randomized between batches of subjects. If a subject chose to copy an individual who was copying

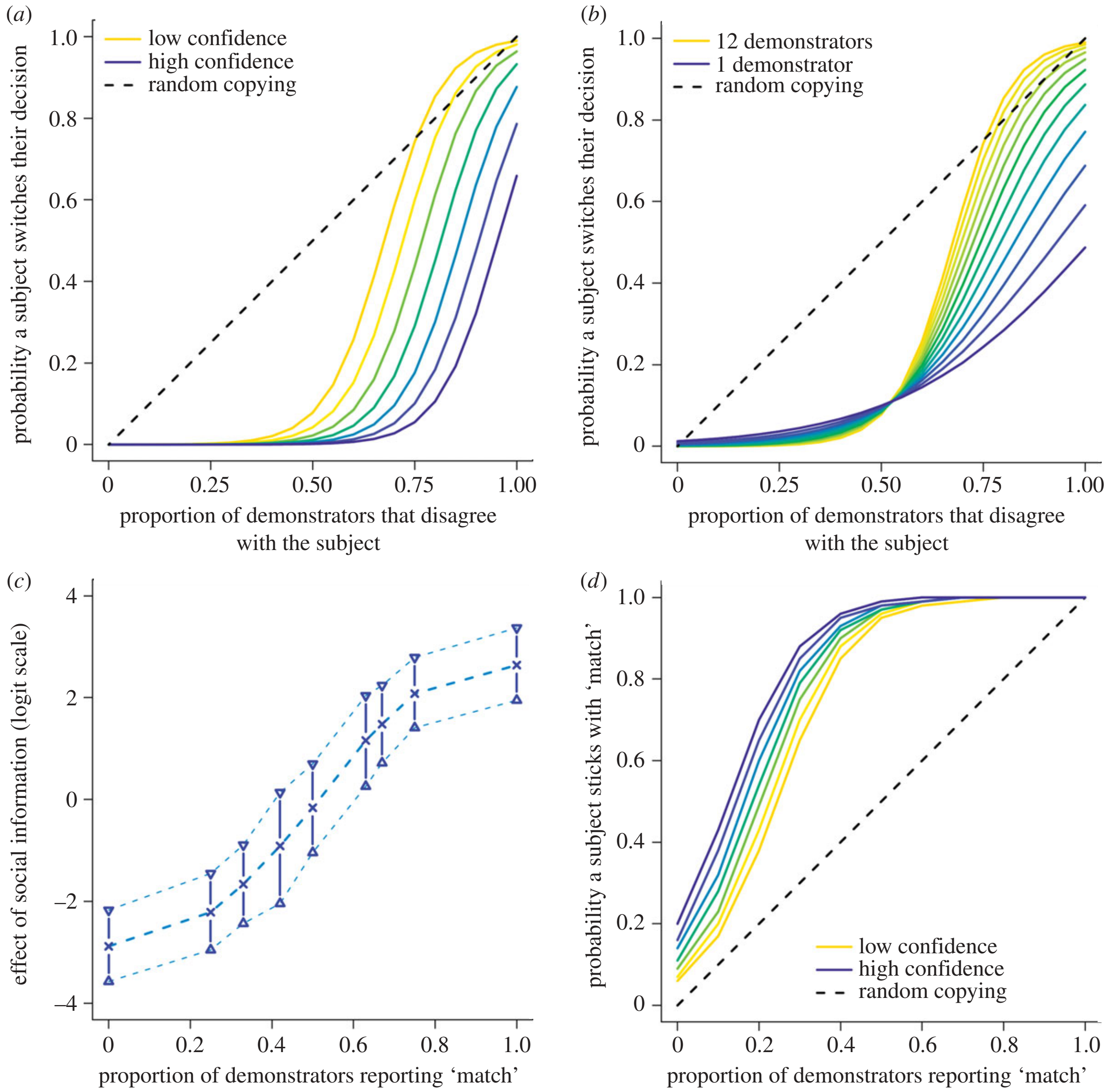

Figure 2. (*a*,*b*). The proportion of demonstrators that disagree with the subject's initial, asocial, choice strongly affects the probability that subjects will change their decision. (*a*) Decreases in subject's confidence based on asocial information (number of demonstrators = 12), and (*b*) increases in demonstrator number (subject confidence = low) increases the likelihood of a switch following conflicting social information. Subject behaviour, when uncertain and given many demonstrators, is conformist in that subjects are disproportionately likely to switch their decision when faced with a strong opposing majority. The black dashed lines portray the expected result of random copying. (*c*,*d*). The proportion of demonstrators reporting the shapes match strongly affects the probability that subjects' final decision will be that the shapes match. (*c*) In line with a conformist response to social information, when unconstrained (i.e. modelled as categorical), intermediate levels of consensus have a disproportionately large effect on decision making. The $y$-axis is the change to the linear predictor of the model, on which a change of magnitude four could alter the probability a subject decides the shapes match by as much as 76%. Accordingly, without other influences, social information is likely to have a dramatic effect on subject behaviour. (*d*) Subject behaviour, however, is also strongly affected by prior information and their confidence in it (the lines shown are for cases where subjects already believe that the shapes match). Thus, although subject behaviour may not be conformist, their response to the social information alone was conformist. The black dashed line portrays the expected result of random copying.

someone themselves, the subject received only a message informing them of this, and therefore had to guess.

Prior to choosing a source of information, in the pitch trials, subjects were informed of the number of demonstrators available (1, 3 or 5) and the cost incurred each time they played a tone (10, 20 or 30% of maximum pay-off). In the intensity trials, subjects were informed of the degree (but not direction) of consensus among the demonstrators (0, 0.5 or 1), while the cost to listen to the tones was held constant and subjects were informed at the end of each trial of the cost incurred. In the pitch-modulation task, subjects were ranked on their performance, assayed by summing their pay-off across all pitch-modulation trials irrespective of the source of information, and were informed of their own rank and the rank of their single potential demonstrator at the start of each trial.

### (ii) *Analyses*

For each of the three tasks, we modelled the probability that an individual would choose social information. In the pitch task, predictors were demonstrator number and the cost to play the sounds, in the intensity task, they were demonstrator consensus and costs incurred when using asocial information previously, and in the pitch-modulation task, they were subject rank, demonstrator rank and the difference between the two. To investigate whether the use of social information was adaptive, we investigated the effect of subject rank on the probability that a subject's asocial decision was correct.

(iii) *Results*

The likelihood of subjects choosing social information covaried positively with the consensus among demonstrators (figure 1*c*), the number of demonstrators (CI: (0.5161, 0.7778), median = 0.6428; figure 1*d*) and the cost to play the sounds (CI: (0.792, 1.279), median = 1.025). Costs incurred on the previous question had no effect (CI: (−0.1883, 0.4168), median = 0.1084) and neither did subject rank (CI: (−0.03578, 0.1501), median = 0.0557). There was a positive interaction between demonstrator rank and the difference between demonstrator and subject rank (demonstrator rank CI: (−0.4843, −0.2249), median = −0.3533, rank difference CI: (−0.1713, 0.04723), median = −0.06232, interaction CI: (0.001068, 0.05605), median = 0.03588; figure 1*f*)—successful demonstrators were most likely to be copied, particularly when offered to a poorly performing subject. A subject's rank predicted their asocial performance (CI: (−0.2099, −0.04212), median = −0.1255), showing that higher ranking demonstrators offered higher quality information.

## 3. DISCUSSION

Our experiments show that several factors simultaneously influence human social information use, consistent with a number of social learning strategies, and that such behaviour leads to adaptive decision making. The findings provide confirmatory support for all nine hypotheses derived from evolutionary models [2,9,10,44].

Three of four experiments found that the rate of copying increased with the number of demonstrators (figure 1*d*). As majority decisions of larger groups are known to be more likely to be correct than those of smaller groups [54], this tendency is likely to prove adaptive. The impact of demonstrator number was enhanced when subjects chose between social and asocial information, as opposed to receiving both in sequence. This difference cannot be attributed to a commitment effect [55], where subjects stick with an earlier decision, as reversing the order of information presentation had no effect on social-information use. It may be that the linear protocol weakens the effect by limiting the analysis to instances where subjects disagree with the social information that they receive. However, it is also possible that the effect is enhanced in experiments using the parallel protocol as when subjects were informed of demonstrator number they were unaware of the consensus among them (in experiments using the linear protocol subjects knew of both) and hence number was all that subjects had to go on.

Demonstrator consensus strongly affected the rate of copying. In all cases, subjects were more likely to copy as consensus increased (figure 1*c*). Such behaviour is expected to be adaptive as we show using probability theory that the greater the consensus, the more likely that the majority opinion is correct, provided individuals make independent decisions and perform above chance levels (see the electronic supplementary material for formal proof). This effect is enhanced in larger groups, providing further support for the adaptiveness of copying larger groups of demonstrators.

Subject confidence in their own judgement had a negative effect on the probability that they would use social information (figure 1*e*). This finding is consistent with experimental work using non-human animals, which reports a *copy-when-uncertain* rule in rats and nine-spined sticklebacks [48,56,57]. This behaviour was adaptive, in the sense that it increased subject pay-off, as subject confidence genuinely predicted whether subjects were correct or not (figure 1*e*). Incorrect subjects typically expressed lower confidence than correct subjects, and so were more likely to use social information and change their answer to the correct choice.

We also found evidence consistent with a *copy-when-asocial-learning-is-costly* strategy [2]. In the third experiment, subjects using asocial information received lower pay-offs on harder than easier questions, however, subjects were also more likely to use social information when informed the upcoming question was difficult compared with easy and so used social information to avoid costly asocial information. Similarly, subjects in the third experiment were also more likely to choose social information after previously incurring high than low costs using asocial information. Finally, in the fourth experiment, subjects chose to use social information more frequently when the cost to listen to the sounds was high compared with when it was low.

There was a drop in social information use across trial groups in experiment 3, with a corresponding increase in asocial performance, showing that this was an adaptive response. With practice, subjects apparently became increasingly confident in their own abilities and subsequently decreased their reliance on social information. We also observed an interaction with demonstrator number, such that social information use decreased when there were three or less demonstrators, but remained steady when there were five. Subjects appeared aware of the risks of reliance on a small number of demonstrators [54] and selectively refined their use of social information accordingly as their own skill improved.

In experiment 4, subjects' performance rank did not affect the likelihood of copying, but demonstrators' performance did (figure 1*f*). This is strikingly consistent with the pattern of pay-off-based copying observed in nine-spined sticklebacks [29], which also copied in proportion to the success of the demonstrator, regardless of their own success. Thus, humans and fishes alike behave in accordance with 'proportional observation' [10]. Selectively copying higher performing demonstrators is likely to be adaptive, since such individuals are more likely to demonstrate behaviour associated with high returns [1,2]. In our experiment, subjects' performance rank did indeed predict their asocial performance, so top-ranking individuals were genuinely more skilled at the task and had not copied their way to the top. Subjects were also sensitive to the demonstrator's performance relative to their own and were even more likely to copy when being outperformed than otherwise. However, all subjects were equally unlikely to copy poorly performing demonstrators, irrespective of their own performance. Thus, information from strongly performing demonstrators was most valuable to poorly performing subjects such that behaviour matched 'proportional observation' with conditional 'proportional imitation' [10].

Subjects were sensitive to the frequencies of the two options in the demonstrators' decisions (figure 2). The observed relationships suggest the conditional deployment of a conformist social learning strategy [2,9] dependent on the number of demonstrators as well as the subject's confidence in their own judgement. Conformity results in the disproportionate adoption of popular traits at the expense of rare traits, producing an S-shaped relationship between trait frequency and probability of adoption. We found an S-shaped curve only when there were many demonstrators, and subjects express low confidences (figure 2*a*,*b*). Furthermore, formal models set the threshold for disproportionate copying at 0.5 [2], however in all cases, our results show a higher threshold. However, the formal models assume individuals choose between two variants without prior information, which was not the case under the linear protocol. Indeed, the effect of social information alone matches closely with conformity as its impact is symmetric, and moderate levels of consensus have a disproportionately large influence (figure 2*c*). Thus, our data are consistent with a conformist use of social information, but as subject's behaviour is the result of both social and asocial influences, the resultant behaviour may not be conformist, depending on the magnitude of the asocial influence (figure 2*d*).

The rarity of conditions under which conformist behaviour is realized suggests a bias towards asocial over social information. Increased subject confidence strengthens this bias, making subjects more willing to go against the consensus (figure 2*a*). Such behavioural flexibility may explain the contradictory findings of previous work. For example, data from the Asch experiments found that subjects copied at lower rates than predicted [18]; we suggest the simplicity of the task used probably leads to high subject confidence in asocial information, shifting the curve to a point where conformist behaviour would not be realized. We predict that, even against unanimous social information, subjects may be unlikely to copy on tasks that they believe they can readily solve asocially and that even on difficult tasks, subjects may not use social information if there are few demonstrators. Accordingly, we anticipate that conformist behaviour will depend on demonstrator number as well as the characteristics of the task.

A bias for asocial over social information has been documented elsewhere [48,58,59] and various explanations have been proposed for it. These include that (i) people have a distrust of socially acquired information, (ii) asocially acquired information has a greater learning impact, and (iii) people have prosocial tendencies that lead them to produce information [58]. We offer three further suggestions; that (iv) the tasks thus far deployed have been sufficiently simple that subjects have considerable confidence in their own judgement, (v) the low cost of making an incorrect answer favoured asocial information as, although potentially the poorer source of information, subjects found it more enjoyable (several individuals from our experiment reported finding 'having-a-go' rewarding), and (vi) that such a bias is the product of a mixed population of 'conformists' (who readily use social information) and 'mavericks'(who resist social information) [18,60]. With regards to the latter, although our analysis finds subjects rely on social information to different extents, we do not find evidence of discrete personality types, instead subjects form a continuum ranging from conformist to 'maverick' behaviour.

In summary, our experiments provide conditional or strong support for the deployment of several social learning strategies predicted by the theoretical cultural evolution literature, including conformity, pay-off-based copying, *copy-when-asocial-learning-is-costly* and *copy-when-uncertain* [1,2,9–11,14]. We also show a strong influence of demonstrator consensus on the likelihood of taking advice. Importantly, these various influences appear to operate simultaneously, and interact to produce behaviour leading to effective decision making and higher pay-offs. These results are not incompatible with the notion that social learning may sometimes have maladaptive consequences [61], but nonetheless illustrate the adaptive aspects of cultural transmission necessary for it to have been favoured by selection. It is apparent that formal evolutionary models provide a framework for predicting the conditions that are likely to produce a reliance on social information on which maladaptive cultural traits can occasionally ride [2]. We see no reason to suggest that these learning biases must themselves be unlearned or under tight genetic control. Rather, we maintain, as is common in the evolutionary game theory literature, that even if the strategies were learned, culturally or otherwise, they can still fruitfully be investigated as though controlled by a simple genetic system, and can still be considered evolved [1,62]. The success of this approach is born out in the effectiveness of the cultural evolution theory in predicting human copying behaviour. Nonetheless, it remains an important topic for future studies to identify the mechanisms underlying implementation of these functional rules.

Ethical approval for this study was given by the University Teaching and Research Ethics Committee of the University of St Andrews (approval reference BL5 881).

This work was supported by an ERC Advanced Investigator grant (EVOCULTURE, Ref: 232823) and EU Framework 6 grant (NESTPATH, CULTAPTATION, Ref: 043434) to K.N.L.

## REFERENCES

1 Laland, K. N. 2004 Social learning strategies. *Learn. Behav.* **32**, 4–14. (doi:10.3758/BF03196002)

2 Boyd, R. & Richerson, P. J. 1985 *Culture and the evolutionary process.* Chicago, IL: University of Chicago Press.

3 Henrich, J. 2001 Cultural transmission and the diffusion of innovations: adoption dynamics indicate that biased cultural transmission is the predominate force in behavioral change. *Am. Anthropol.* **103**, 992–1013. (doi:10.1525/aa.2001.103.4.992)

4 Harris, P. L. 2007 Trust. *Dev. Sci.* **10**, 135–138. (doi:10.1111/j.1467-7687.2007.00575.x)

5 Rogers, A. R. 1988 Does biology constrain culture. *Am. Anthropol.* **90**, 819–831. (doi:10.1525/aa.1988.90.4.02a00030)

6 Henrich, J. & McElreath, R. 2003 The evolution of cultural evolution. *Evol. Anthropol.* **12**, 123–135. (doi:10.1002/Evan.10110)

7 Cavalli-Sforza, L. L. & Feldman, M. W. 1981 Cultural transmission and evolution: a quantitative approach. *Monogr. Popul. Biol.* **16**, 1–388.

8 Feldman, M. W., Aoki, K. & Kumm, J. 1996 Individual versus social learning: evolutionary analysis in a fluctuating environment. *Anthropol. Sci.* **104**, 209–231.

9 Henrich, J. & Boyd, R. 1998 The evolution of conformist transmission and the emergence of between-group differences. *Evol. Hum. Behav.* **19**, 215–241. (doi:10.1016/S1090-5138(98)00018-X)

10 Schlag, K. H. 1998 Why imitate, and if so, how? A boundedly rational approach to multi-armed bandits. *J. Econ. Theory* **78**, 130–156. (doi:10.1006/jeth.1997.2347)

11 Schlag, K. H. 1999 Which one should I imitate? *J. Math. Econ.* **31**, 493–522. (doi:10.1016/S0304-4068(97)00068-2)

12 Enquist, M., Eriksson, K. & Ghirlanda, S. 2007 Critical social learning: a solution to Rogers's paradox of nonadaptive culture. *Am. Anthropol.* **109**, 727–734. (doi:10.1525/Aa.2007.109.4.727)

13 Wakano, J. Y. & Aoki, K. 2007 Do social learning and conformist bias coevolve? Henrich and Boyd revisited. *Theor. Popul. Biol.* **72**, 504–512. (doi:10.1016/j.tpb.2007.04.003)

14 Kendal, J., Giraldeau, L. A. & Laland, K. 2009 The evolution of social learning rules: payoff-biased and frequency-dependent biased transmission. *J. Theor. Biol.* **260**, 210–219. (doi:10.1016/j.jtbi.2009.05.029)

15 Kameda, T. & Nakanishi, D. 2003 Does social/cultural learning increase human adaptability? Rogers's question revisited. *Evol. Hum. Behav.* **24**, 242–260. (doi:10.1016/S1090-5138(03)00015-1)

16 Kameda, T. & Nakanishi, D. 2002 Cost-benefit analysis of social/cultural learning in a nonstationary uncertain environment: an evolutionary simulation and an experiment with human subjects. *Evol. Hum. Behav.* **23**, 373–393. (doi:10.PiiS1090-5138(02)00101-0)

17 McElreath, R., Lubell, M., Richerson, P. J., Waring, T. M., Baum, W., Edsten, E., Efferson, C. & Paciotti, B. 2005 Applying evolutionary models to the laboratory study of social learning. *Evol. Hum. Behav.* **26**, 483–508. (doi:10.1016/j.evolhumbehav.2005.04.003)

18 Efferson, C., Lalive, R., Richerson, P. J., McElreath, R. & Lubell, M. 2008 Conformists and mavericks: the empirics of frequency-dependent cultural transmission. *Evol. Hum. Behav.* **29**, 56–64. (doi:10.1016/j.evolhumbehav.2007.08.003)

19 Mesoudi, A. & O'Brien, M. J. 2008 The cultural transmission of Great Basin projectile-point technology. I. An experimental simulation. *Am. Antiquity* **73**, 3–28.

20 Caldwell, C. A. & Millen, A. E. 2008 Experimental models for testing hypotheses about cumulative cultural evolution. *Evol. Hum. Behav.* **29**, 165–171. (doi:10.1016/j.evolhumbehav.2007.12.001)

21 Caldwell, C. A. & Millen, A. E. 2009 Social learning mechanisms and cumulative cultural evolution: is imitation necessary? *Psychol. Sci.* **20**, 1478–1483. (doi:10.1111/j.1467-9280.2009.02469.x)

22 Dindo, M., Whiten, A. & de Waal, F. B. M. 2009 In-group conformity sustains different foraging traditions in Capuchin monkeys (*Cebus apella*). *PLoS ONE* **4**, e7858. (doi:10.1371/Journal.Pone.0007858)

23 Horner, V., Proctor, D., Bonnie, K. E., Whiten, A. & de Waal, F. B. M. 2010 Prestige affects cultural learning in chimpanzees. *PLoS ONE* **5**, e10625. (doi:10.1371/journal.pone.0010625)

24 Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M. & Laland, K. N. 2011 Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends Cogn. Sci.* **15**, 68–76. (doi:10.1016/j.tics.2010.12.002)

25 Eriksson, K., Enquist, M. & Ghirlanda, S. 2007 Critical points in current theory of conformist social learning. *J. Evol. Psychol.* **5**, 67–87. (doi:10.1556/JEP.2007.1009)

26 Eriksson, K. & Coultas, J. C. 2009 Are people really conformist-biased? An empirical test and a new mathematical model. *J. Evol. Psychol.* **7**, 5–21. (doi:10.1556/JEP.7.2009.1.3)

27 Toelch, U., Bruce, M. J., Meeus, M. T. H. & Reader, S. M. 2010 Humans copy rapidly increasing choices in a multiarmed bandit problem. *Evol. Hum. Behav.* **31**, 326–333. (doi:10.1016/j.evolhumbehav.2010.03.002)

28 Mesoudi, A. 2008 An experimental simulation of the 'copy-successful-individuals' cultural learning strategy: adaptive landscapes, producer-scrounger dynamics, and informational access costs. *Evol. Hum. Behav.* **29**, 350–363. (doi:10.1016/j.evolhumbehav.2008.04.005)

29 Pike, T. W., Kendal, J. R., Rendell, L. E. & Laland, K. N. 2010 Learning by proportional observation in a species of fish. *Behav. Ecol.* **21**, 570–575. (doi:10.1093/beheco/arq025)

30 Apesteguia, J., Huck, S. & Oechssler, J. 2007 Imitation: theory and experimental evidence. *J. Econ. Theory* **136**, 217–235. (doi:10.1016/j.jet.2006.07.006)

31 Henrich, J. & Gil-White, F. J. 2001 The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evol. Hum. Behav.* **22**, 165–196. (doi:10.1016/S1090-5138(00)00071-4)

32 Henrich, J. & Henrich, N. 2010 The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. *Proc. R. Soc. B* **277**, 3715–3724. (doi:10.1098/rspb.2010.1191)

33 Bond, R. 2005 Group size and conformity. *Group Process. Interg.* **8**, 331–354. (doi:10.1177/1368430205056464)

34 Bond, R. & Smith, P. B. 1996 Culture and conformity: a meta-analysis of studies using Asch's (1952b, 1956) line judgment task. *Psychol. Bull.* **119**, 111–137. (doi:10.1037/0033-2909.119.1.111)

35 Latane, B. 1981 The psychology of social impact. *Am. Psychol.* **36**, 343–356. (doi:10.1037/0003-066X.36.4.343)

36 Latane, B. & Wolf, S. 1981 The social impact of majorities and minorities. *Psychol. Rev.* **88**, 438–453. (doi:10.1037/0033-295X.88.5.438)

37 Nowak, A., Szamrej, J. & Latane, B. 1990 From private attitude to public-opinion: a dynamic theory of social impact. *Psychol. Rev.* **97**, 362–376. (doi:10.1037/0033-295X.97.3.362)

38 Coultas, J. C. 2004 When in Rome ... an evolutionary perspective on conformity. *Group Process. Interg.* **7**, 317–331. (doi:10.1177/1368430204046141)

39 Tanford, S. & Penrod, S. 1984 Social-influence model: a formal integration of research on majority and minority influence processes. *Psychol. Bull.* **95**, 189–225. (doi:10.1037/0033-2909.95.2.189)

40 Mullen, B. 1985 Strength and immediacy of sources: a meta-analytic evaluation of the forgotten elements of social impact theory. *J. Pers. Soc. Psychol.* **48**, 1458–1466. (doi:10.1037/0022-3514.48.6.1458)

41 Latané, B. 1996 Dynamic social impact: the creation of culture by communication. *J. Commun.* **46**, 13–25. (doi:10.1111/j.1460-2466.1996.tb01501.x)

42 Asch, S. E. 1955 Opinions and social pressure. *Sci. Am.* **193**, 31–35. (doi:10.1038/scientificamerican1155-31)

43 Mesoudi, A. 2009 How cultural evolutionary theory can inform social psychology and vice versa. *Psychol. Rev.* **116**, 929–952. (doi:10.1037/0017062)

44 Boyd, R. & Richerson, P. J. 1988 An evolutionary model of social learning: the effects of spatial and temporal variation. In *Social learning: psychological and biological perspectives* (eds T. R. Zentall & B. G. Galef), pp. 29–48. Mahwah, NJ: Lawrence Erlbaum.

45 Likert, R. 1932 A technique for the measurement of attitudes. *Arch. Psychol.* **140**, 1–55.

46 Coolen, I., Van Bergen, Y., Day, R. L. & Laland, K. N. 2003 Species difference in adaptive use of public information in sticklebacks. *Proc. R. Soc. Lond. B* **270**, 2413–2419. (doi:10.1098/rspb.2003.2525)

47 Coolen, I., Ward, A. J. W., Hart, P. J. B. & Laland, K. N. 2005 Foraging nine-spined sticklebacks prefer to rely on public information over simpler social cues. *Behav. Ecol.* **16**, 865–870. (doi:10.1093/beheco/ari064)

48 Van Bergen, Y., Coolen, I. & Laland, K. N. 2004 Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proc. R. Soc. Lond. B* **271**, 957–962. (doi:10.1098/rspb.2004.2684)

49 Shepard, R. N. & Metzler, J. 1971 Mental rotation of 3-dimensional objects. *Science* **171**, 701–703. (doi:10.1126/science.171.3972.701)

50 Bardsley, N. 2000 Control without deception: individual behaviour in free-riding experiments revisited. *Exp. Econ.* **3**, 215–240. (doi:10.1023/a:1011420500828)

51 Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J. S. S. 2009 Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135. (doi:10.1016/j.tree.2008.10.008)

52 Kruschke, J. K. 2010 What to believe: Bayesian methods for data analysis. *Trends Cogn. Sci.* **14**, 293–300. (doi:10.1016/j.tics.2010.05.001)

53 Lunn, D. J., Thomas, A., Best, N. & Spiegelhalter, D. 2000 WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. *Stat. Comput.* **10**, 325–337. (doi:10.1023/A:1008929526011)

54 King, A. J. & Cowlishaw, G. 2007 When to use social information: the advantage of large group size in individual decision making. *Biol. Lett.* **3**, 137–139. (doi:10.1098/rsbl.2007.0017)

55 Brody, N. 1965 The effect of commitment to correct and incorrect decisions on confidence in a sequential decision-task. *Am. J. Psychol.* **78**, 251–256. (doi:10.2307/1420497)

56 Galef, B. G., Dudley, K. E. & Whiskin, E. E. 2008 Social learning of food preferences in 'dissatisfied' and 'uncertain' Norway rats. *Anim. Behav.* **75**, 631–637. (doi:10.1016/j.anbehav.2007.06.024)

57 Kendal, R. L., Coolen, I., Van Bergen, Y. & Laland, K. N. 2005 Trade-offs in the adaptive use of social and asocial learning. *Adv. Stud. Behav.* **35**, 333–379. (doi:10.1016/S0065-3454(05)35008-X)

58 Eriksson, K. & Strimling, P. 2009 Biases for acquiring information individually rather than socially. *J. Evol. Psychol.* **7**, 309–329. (doi:10.1556/JEP.7.2009.4.4)

59 Weizsacker, G. 2010 Do we follow others when we should? A simple test of rational expectations. *Am. Econ. Rev.* **100**, 2340–2360. (doi:10.1257/aer.100.5.2340)

60 Mesoudi, A. In press. An experimental comparison of human social learning strategies: payoff-biased social learning is adaptive but underused. *Evol. Hum. Behav.* (doi:10.1016/j.evolhumbehav.2010.12.001)

61 Tanaka, M. M., Kendal, J. R. & Laland, K. N. 2009 From traditional medicine to witchcraft: why medical treatments are not always efficacious. *PLoS ONE* **4**, e5192. (doi:10.1371/Journal.Pone.0005192)

62 Grafen, A. 1984 Natural selection, kin selection and group selection. In *Behavioural ecology*, 2nd edn (eds J. R. Krebs & N. B. Davies), pp. 62–84. Oxford, UK: Blackwell.