

# Social Learning and Associative Processes: A Synthesis

Noam Miller  
Wilfrid Laurier University

Social learning is often considered different from asocial learning in both its characteristics and mechanisms. I presented pigeons with a concurrent discrimination task in which they received artificial social information, consisting of simple shapes that distributed themselves between two options similarly to how conspecifics might. Subjects in some conditions combined personal information about the two options with this social-like information, but subjects in conditions in which personal information was very reliable ignored the social cues, much like cases in which animals only choose to copy choices of others under certain conditions. I present a modification of a popular associative model of individual learning that can replicate these results, despite not distinguishing between social and asocial cues. The model suggests that the adaptive use of social information does not require the assumption of specifically social learning strategies, but may be driven by the overshadowing of less reliable asocial cues by more reliable social cues.

*Keywords:* social learning strategies, associative model, Rescorla-Wagner, pigeon

*Supplemental materials:* <http://dx.doi.org/10.1037/xan0000167.supp>

Social learning, the ability to acquire information about the environment by observing the behaviors of others, has been demonstrated in a wide range of species (Shettleworth, 2010) and given rise to a large body of theory on its costs (Giraldeau, Valone, & Templeton, 2002) and benefits (Hoppitt & Laland, 2011). However, as noted by Heyes (2012), there has not been a correspondingly extensive study of the cognitive mechanisms of social learning. Behavioral ecologists studying social effects on behavior have mostly addressed the effects of group living (Krause & Ruxton, 2002) and emphasized, for example, how social influence varies with group size (e.g., Perez-Escudero & de Polavieja, 2011). Experiments on a range of species from fish (Pike & Laland, 2010; Sumpter, Krause, James, Couzin, & Ward, 2008) to humans (Bikhchandani, Hirshleifer, & Welch, 1992) have shown that larger groups tend to be more informative and therefore have a greater effect on individual choice. This effect has been largely absent from discussions of social learning, as few psychological studies have used more than a single demonstrator (with a few notable exceptions: Asch, 1956; Beck & Galef, 1989; Lefebvre & Giraldeau, 1994).

In both the psychological and ecological traditions, however, it has often been assumed that social learning operates via separate mech-

anisms from asocial (or individual) learning (Heyes, 2012). For example, it has been suggested that animals follow social learning strategies, such as only copying the choices of conspecifics when they are dissatisfied with their own success rate, or when their own preference conflicts with that of the majority (Laland, 2004). This view has recently been challenged (Heyes, 2012; Heyes & Pearce, 2015), raising the question as to whether social learning may engage the same mechanisms that drive asocial learning—specifically, that social learning is a form of associative learning in which cues happen to emanate from one or more conspecifics rather than from the environment (e.g., Wilkinson, Kuenstner, Mueller, & Huber, 2010).

Here, I attempt to test the suggestion that social and asocial cues enter into learning in the same way both empirically and theoretically. I first present experimental evidence that asocial learning in pigeons can produce the same pattern of results as social learning, if asocial cues “behave” similarly to social cues. I then present an associative model that can reproduce these findings and may shed some light on the mechanisms of social learning.

Social learning experiments cannot, for the most part, be simulated using existing formulations of associative learning models because social cues are inherently different from asocial cues in two important ways. In a group, there are often several individuals demonstrating each of a number of different behavioral choices at any one time. For example, a meerkat deciding whether or not to leave a foraging patch may observe several conspecifics that are already moving away from the patch and several others that are not (Bousquet, Sumpter, & Manser, 2011). Social cues, unlike most asocial cues, can therefore indicate several behavioral options at the same time, to different degrees. This is comparable to situations in which the same cue is present at more than one of a set of choices (as in, e.g., relative validity paradigms; Wagner, Logan, Haberlandt, & Price, 1968) but can also vary in intensity. In addition, choices demonstrated by larger subgroups are often more likely to be

---

This article was published Online First February 19, 2018.

This research was supported by a grant from the Natural Sciences and Engineering Research Council of Canada. I thank Ariana Strandburg-Peshkin, Albert Kao, and Colin Twomey for helpful discussions; Angelo Santi for providing the experimental subjects; Kelley Putzu for animal care; and Ramy Ayoub, Kaitlin Petter, and other members of the Collective Cognition Lab for assistance running the experiment.

Data are available at <https://osf.io/u49wa/>

Correspondence concerning this article should be addressed to Noam Miller, Department of Psychology, Wilfrid Laurier University, 75 University Avenue West, Waterloo, Ontario N2L 3C5, Canada. E-mail: [nmiller@wlu.ca](mailto:nmiller@wlu.ca)

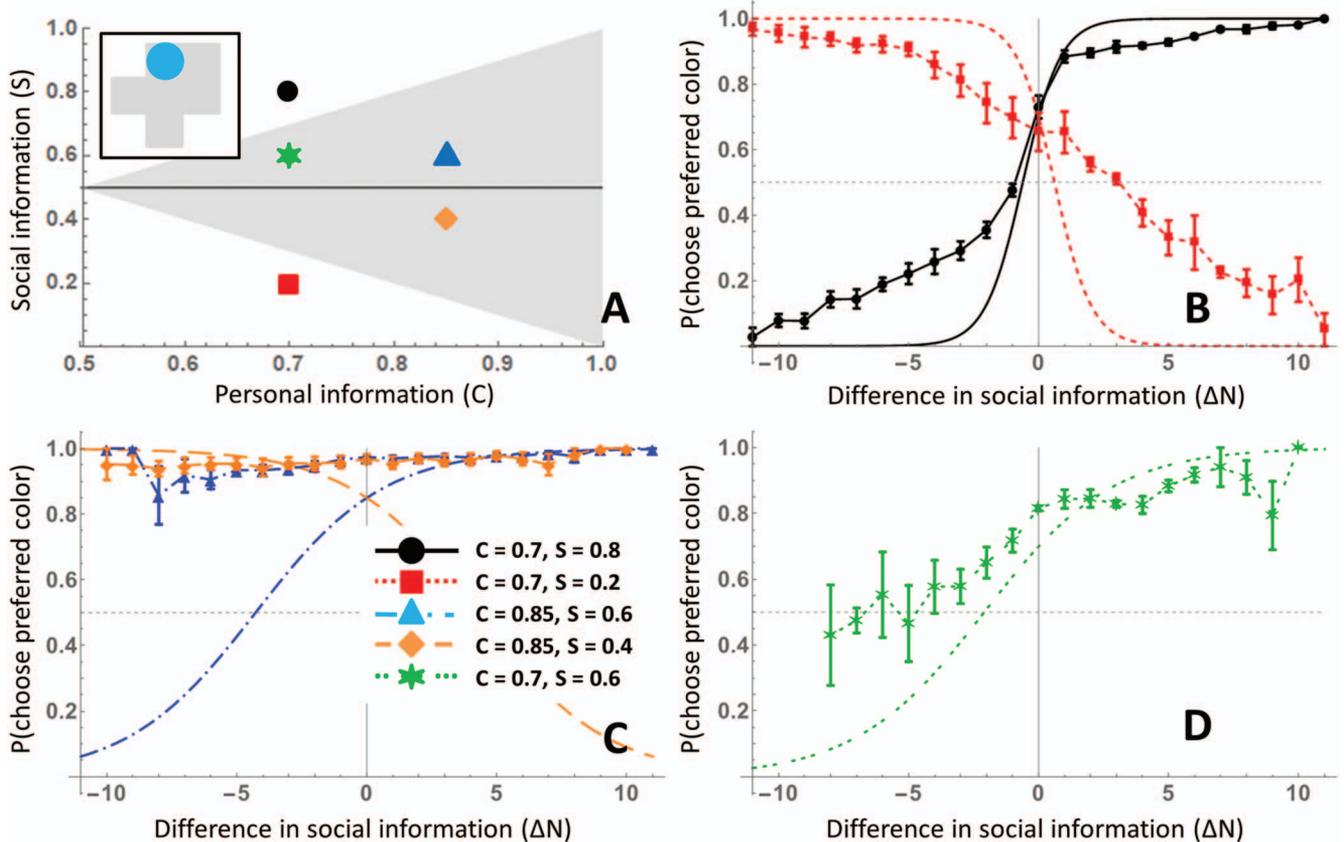
correct (especially if the decisions made by the demonstrators are independent of each other; Kao & Couzin, 2014; Perez-Escudero & de Polavieja, 2011). In associative terms, the contingency of a social cue with a reward will often correlate with its magnitude or intensity. I present a simple modification to a well-known associative learning model that permits such cues to be incorporated and show that this model can produce “social-like” learning, despite not distinguishing between social and asocial cues.

### Experiment

A key feature of social decision making is that different numbers of conspecifics may be concurrently demonstrating each behavioral choice (e.g., Sumpter et al., 2008). To simulate this, I presented pigeons in an operant box with an artificial social cue—a varying number of gray squares—which behaved like a social cue, in that each square independently “chose” one of two options to associate with, only one of which was rewarded. Each gray square had a fixed probability of choosing the correct option. Pigeons were also given personal informa-

tion about each option: One possible stimulus color (green or blue) was more likely to be rewarded than the other. This was intended to simulate a choice situation in which a number of conspecifics (gray squares) have already chosen between two options (the green and blue circles), presumably based on their own personal information.

Birds were divided into five groups, in which the reliability of personal information (denoted “C”) and the accuracy of the gray squares (denoted “S”) were varied (Figure 1A):  $C = 0.7, S = 0.8$ ;  $C = 0.7, S = 0.6$ ;  $C = 0.7, S = 0.2$ ;  $C = 0.85, S = 0.6$ ; and  $C = 0.85, S = 0.4$ . For the two groups for which  $S < 0.5$  (Figure 1A, red square and orange diamond), the gray squares were more likely to associate with the incorrect option than the correct one. The squares are equally informative in such cases, but it is their absence that reliably correlates with reward. For three of the five groups, personal (color) information was more reliable than social (gray squares) information (Figure 1A, shaded area). However, by Condorcet’s jury theorem (Condorcet, 1785), the reliability of social information increases with group size, such that a suffi-



**Figure 1.** (A) Parameter values for the experimental groups. Values of C (reliability of color information; x-axis) and S (reliability of “social” information; y-axis) for the five experimental groups are plotted. The gray shaded area is where personal information is more reliable than social information. The inset shows a sample stimulus, this one with  $N = 5$  gray squares. (B–D) Experimental results (lines with symbols) and theoretical probabilities (without symbols) for each experimental group. Data are plotted as the proportion of trials on which subjects selected their preferred (more often rewarded) color as a function of  $\Delta N$ , the difference between the number of squares at the preferred and nonpreferred color options. Error bars indicate  $\pm SEM$ . See the online article for the color version of this figure.

ciently large majority (or minority when  $S < 0.5$ ) of gray squares at one option should outweigh personal information in these groups.

Because the behavior of the social cue in this experiment is determined by a simple algorithm—each square has a fixed probability,  $S$ , of choosing correctly on any given trial—it is possible to calculate, on each trial, the probability that each stimulus is correct. From this, it is possible to derive the optimal choice behavior for the subjects, which is simply to choose whichever stimulus is more likely to be correct on that trial. Note that this requires the subject have accurate representations of the values of  $C$  and  $S$  and be able to precisely identify the number (or area) of gray squares at each option, all of which is unlikely. In the Appendix, I derive the probability that an option is correct as a function of its color and the number of gray squares.

## Method

### Subjects

Subjects were 19 adult homing pigeons (*Columba livia*). An additional three birds were excluded from the experiment, as they consistently failed to complete their training sessions. Each of the five experimental groups contained four subjects, except for the  $C = 0.7$ ,  $S = 0.6$  group, which had three subjects. All of the birds had previously participated in unrelated operant box experiments on interval timing but were naïve to all the cues used in the current experiment. Birds were individually housed and, on days when they were not participating in the experiment, allowed into a flight pen in groups of three to four. For the duration of the experiment, birds were food-restricted to between 80% and 85% of their free-feeding weight. Birds were fed Purina Pigeon Chow after each experimental session to maintain their reduced body weights. All animal procedures were approved by the Wilfrid Laurier University Animal Care Committee.

### Apparatus

Birds were tested individually in operant boxes constructed of clear Plexiglas (30 × 40 × 37 cm high). The boxes had a mesh floor and, along the wall opposite the door, a touch frame (Keytec Inc., PPMT-IR) attached to a 15-in. LCD monitor. Each box had two grain hoppers (Coulbourn Instruments, H14-10R) attached near the touchscreen on opposite sides of the box (so birds could be rewarded on either side), containing a mix of seeds. Each hopper had a small light that illuminated when the hopper was active. Each operant box also had a house-light mounted on the top of the box. Two computer speakers were placed to the sides of each box and played white noise throughout the session. The house-light and hoppers for each box were connected to a dedicated PC via a custom interface. The monitor and speakers for each box connected to the same PC. Each PC was running in-house software that displayed stimuli on the screen, recorded the birds' responses, and activated the house-light and hoppers as needed. A webcam was attached to each PC so that the bird could be observed during the trial from outside the room. The room lights were turned off during experimental sessions.

### Procedure

In all stages of the experiment, birds ran one session per day, 6 days a week. At all stages, trials were separated by a  $45 \pm 10$ -s intertrial interval (ITI), during which the screen was blank and the house-light was on.

**Autoshaping.** For the first 2 days of the experiment, all birds were given autoshaping sessions. On each trial, a white circle appeared in the center of the screen. Pecking at the circle or within 2 cm of it led to immediate reward. If no peck was detected, reward was delivered after the circle had been on the screen for 6 s. Rewards were activation of one randomly selected hopper for 4 s. The stimulus remained on the screen during the reward. Birds completed 50 trials per session.

**Continuous reinforcement.** Birds were next given 4 days of continuous reinforcement training. On each trial, one randomly selected stimulus from the experiment was displayed on the screen. Stimuli could be either a small white triangle in the center of the screen (later used as the start stimulus) or one of the experimental stimuli (see Stimulus Construction). For the first 2 days, a peck to any part of the stimulus or within 2 cm of it led to immediate reward (4 s of activation of a hopper on the same side as the stimulus, or a randomly selected hopper if the stimulus was centered). The stimulus remained on the screen during the reward period. For the third and fourth days, only pecks to the central colored circle of the stimulus or within 2 cm of it were rewarded. The stimulus remained on the screen until pecked or the session ended. Birds were given either 120 trials or 2 hr per session, whichever came first. Birds that did not complete at least 250 trials over the 4 days were given additional sessions.

**Training.** At the start of each trial, a small white triangle was presented at the center of the screen. A single peck to this stimulus started the trial. Following this, on each trial, two stimuli were presented on opposite sides of the screen (see Stimulus Construction). On each trial, one stimulus was deemed correct. Birds were required to peck the stimulus for 3 s to select it. Selecting the correct stimulus led to reward (the hopper on that side was activated for 4 s), followed by the ITI. Selecting the incorrect stimulus immediately terminated the trial and started the ITI. The stimulus remained on the screen until selected or the session ended. Birds were given either 120 trials or 2 hr per session, whichever came first. Each subject was assigned a preferred color (blue or green, counterbalanced across subjects within each group), which was more often correct, with probability  $C$  ( $C$  varied between groups but was always  $>0.5$ ). Birds continued in the experiment until they had completed a minimum of 3,500 trials of this phase, which took  $51 \pm 13$  sessions. Two subjects only completed approximately 2,000 trials (in 17 and 27 sessions); their data were retained.

### Stimulus Construction

On each trial, one colored circle was selected as the correct option for that trial, based on the value of  $C$  for that subject. One circle was displayed on either side of the screen, selected at random for each trial, inscribed in a gray square. Each circle was surrounded by a variable number of gray squares, such that the total number of squares around both stimuli was between 1 and 12 (excluding the squares behind the central circles), selected at random from a uniform distribution. Each gray square had a fixed probability,  $S$ , of being attached to the correct stimulus for that trial (whether or not that happened to be the subject's preferred

color). Squares' choices were independent of each other. Squares were placed around each circle by an algorithm that ensured they were clustered into a single shape (i.e., each square had to share at least one side with another square). Within these constraints, squares were placed at random so that the overall shape of the stimulus was unlikely to be repeated. Gray squares had no borders, so that the entire stimulus appeared as a gray blob, with the green or blue circle at its (approximate) center (Figure 1A, inset). Subjects probably did not count the squares (or perceive them as separate), but the number of squares correlated perfectly with the overall area of gray in the stimulus.

## Data Analysis

The program running the operant boxes recorded all the details of the stimuli for that trial (the side on which each color was presented, the number of gray squares around each circle, and the rewarded option) and the choice made by the subject on that trial. Data were saved to a separate text file for each session of each subject. These files were read into *Mathematica* (Version 10.4, Wolfram Research) for all statistical analyses. A significance level of 0.01 was used for all statistical tests.

## Results

All subjects learned the task and quickly reached a performance plateau (success rates on last 10 sessions:  $C = 0.7, S = 0.8, 0.823 \pm 0.012$ ;  $C = 0.7, S = 0.2, 0.756 \pm 0.038$ ;  $C = 0.85, S = 0.6, 0.806 \pm 0.033$ ;  $C = 0.85, S = 0.4, 0.819 \pm 0.022$ ;  $C = 0.7, S = 0.6, 0.655 \pm 0.013$ ). Success rates varied significantly between groups (one-way ANOVA:  $F[4, 14] = 23.18, p < .0001, \eta^2 = 0.869$ ; Bonferroni post hoc pairwise comparisons showed that Group  $C = 0.7, S = 0.6$  was significantly different from all the other groups).

Figure 1 (B-D) shows the performance data for each group, along with the theoretical probabilities that the preferred color was correct for each condition (see Appendix). The data are displayed as a function of  $\Delta N$ , the difference between the number of gray squares around the preferred-color option and the number around the non preferred-color option (when  $\Delta N > 0$ , there are more gray squares around the preferred-color option). As the figure shows, birds in some groups adjusted their choice of their preferred color as a function of the information provided by the gray squares (Figure 1B, D). However, in two conditions, in which color information was particularly reliable ( $C = 0.85$ ; Figure 1C), birds appear to have ignored the gray squares and almost always chosen the option bearing their preferred color. Note that these birds could have increased their success rate had they taken into consideration the information conveyed by the distribution of the gray squares. For example, for the  $C = 0.85, S = 0.6$  group (Figure 1C), if there were five more gray squares at the nonpreferred than the preferred color option (i.e.,  $\Delta N = -5$ ), the nonpreferred color option was more likely to be correct (57%). Larger differences should have biased birds' choices even more. Even more strikingly, birds in the other three groups appear to match their choice probabilities to the theoretical likelihood of each option being correct (though they tend to undermatch). Birds in the two  $C = 0.85$  groups show no matching at all, suggesting that they are employing a different strategy altogether than the birds in the other groups.

Differences in response function between the groups were tested by fitting linear functions to each group's choice data (see Table 1).

Table 1  
*Regression Results*

| Group                               | Intercept [95% CI]       | Slope [95% CI]           | $R^2$       |
|-------------------------------------|--------------------------|--------------------------|-------------|
| $C = .7, S = .8$                    | .581 [.529, .633]        | .054 [.046, .061]        | .906        |
| $C = .7, S = .2$                    | .606 [.577, .633]        | -.045 [-.049, -.04]      | .958        |
| <b><math>C = .85, S = .6</math></b> | <b>.962 [.948, .975]</b> | <b>.003 [.001, .005]</b> | <b>.325</b> |
| <b><math>C = .85, S = .4</math></b> | <b>.963 [.958, .967]</b> | <b>.002 [.001, .003]</b> | <b>.655</b> |
| $C = .7, S = .6$                    | .703 [.67, .737]         | .031 [.025, .037]        | .878        |

Note. Best-fit parameters (intercept and slope) for the linear regression performed on each group's response function, along with 95% confidence intervals (CIs), and  $R^2$  for each regression. The rows for the two groups for which  $C = .85$ —that appeared to mostly ignore social information—are bolded.

Though the slopes of the regression lines for all groups were significantly different from zero (ANOVA;  $C = 0.7, S = 0.8, F[1, 21] = 202.14, p < .0001, \eta^2 = 0.906$ ;  $C = 0.7, S = 0.2, F[1, 21] = 483.26, p < .0001, \eta^2 = 0.958$ ;  $C = 0.85, S = 0.6, F[1, 20] = 9.63, p = .0056, \eta^2 = 0.325$ ;  $C = 0.85, S = 0.4, F[1, 19] = 36.06, p < .0001, \eta^2 = 0.655$ ;  $C = 0.7, S = 0.6, F[1, 18] = 129.73, p < .0001, \eta^2 = 0.878$ ), those for the groups in which  $C = 0.85$  were more than an order of magnitude smaller than those for the other three groups (Table 1, bolded rows), suggesting that subjects in groups in which  $C = 0.85$  adjusted their responses as a function of social information much less than subjects in the other groups.

The intercept of the regression line serves as a prediction of the birds' reliance on personal information, as it occurs when there is no differential social information (the number of gray squares at the two options is the same). If animals are probability matching, the probability of choosing the preferred color at the intercept should equal  $C$ . Birds in the two groups for which  $C = 0.85$  tended to overmatch (Table 1; both intercepts are around 0.96), whereas birds in the other groups mostly undermatched. This result is further evidence that birds in the  $C = 0.85$  groups are almost entirely relying on their personal information.

For two of the groups,  $S < 0.5$ , meaning that, for these subjects, increasing numbers of gray squares at an option make that option *less* likely to be correct. These conditions were included to establish whether pigeons show an innate preference for more of a cue. This question is of interest because, in situations containing true social cues, larger groups are usually more likely to be correct (assuming that each demonstrator's reliability is  $> 0.5$ ; Condorcut, 1785). To see whether the birds treated antireliable social information differently, the regression lines for Groups  $C = 0.7, S = 0.8$  and  $C = 0.7, S = 0.2$  were compared (the data for the latter group were first reflected about the y-axis). If social cues can be used equally easily whatever the sign of their correlation with reward, both these conditions are informationally identical. There was no significant difference between the response functions of the two groups (ANOVA, between-groups comparison only:  $F[1, 43] = 0.63, p = .43, \eta^2 = 0.0012$ ).

Finally, the current data shed some light on how group size might affect decision making. In most models of collective choice (e.g., Pérez-Escudero & de Polavieja, 2011), it is assumed that the influence of social information depends on the difference between the number of demonstrators at each option, commonly denoted  $\Delta N$ . Though it can be demonstrated that using this measure to modulate social influence is optimal (Pérez-Escudero & de Polav-

iejka, 2011), this does not necessarily mean that animals use social cues in this way. On the contrary, it is likely that animals sense or use cues that vary in magnitude, like social cues, as a function of their relative proportions rather than absolute differences. To test this hypothesis, I examined the proportion of choices to their preferred color made by the pigeons both as a function of  $\Delta N$  and as a function of  $\Delta N/\Sigma N$ , that is, the proportion of the social cue that was at the preferred color. Figures S1 and S2 of the online supplemental materials show the choice data for two of the experimental groups by both measures. If birds are using one measure over the other, then their choices, when plotted against that measure, should be less variable than when plotted against the alternative measure. A comparison of the aggregated variances across all birds suggests that they are either perceiving or using the relative proportion of the social cue present at each option rather than the absolute difference in amount of social cue (Figure S3; two-sample Kolmogorov–Smirnov test,  $D = 0.108$ ,  $p = .027$ ).

### Model

The data presented above appear to show pigeons following a social learning strategy similar to “copy when dissatisfied” (Laland, 2004). When personal information is a sufficiently good cue ( $C = 0.85$ ), they ignore social information. However, it is extremely unlikely that the birds perceive the small, two-dimensional, clumped gray squares as actual conspecifics, suggesting that their behavior may be driven by asocial learning processes. To test this idea, I next construct an associative model that simulates the experiment. The model is based on a well-known framework that accurately describes many forms of individual learning (Miller & Shettleworth, 2007, 2008; Rescorla & Wagner, 1972). Note that although I only simulate a single agent choosing between two options in the presence of existing social information—to match my experimental data—it is easy to expand the model to simulate situations in which several agents in a group choose consecutively between any number of options (e.g., Kao, Miller, Torney, Hartnett, & Couzin, 2014; Miller, Garnier, Hartnett, & Couzin, 2013).

In the model, an agent is required to make multiple consecutive decisions between two options,  $x$  and  $y$ . One option,  $y$ , is consistently more likely to be rewarded, with probability  $C$  (as in the experiment). Only one option is correct on each trial, so that option  $x$  is rewarded with probability  $1 - C$ . Each option is identifiable by a single cue (e.g., its color) and the agent represents each cue by a variable,  $V$ , whose value is the strength of that cue’s association with reward (Rescorla & Wagner, 1972). There are some number of “conspicifics” already at each option,  $n_x$  and  $n_y$ , providing social information that is represented as one additional variable,  $V_s$ . The agent’s representation of its information can thus be written as  $\{V_x, V_y, V_s\}$ . Note that no distinction is made in the model between social and asocial cues.

Agents learn in the same way as in previous associative models of operant choice (Kao et al., 2014; Miller & Shettleworth, 2007). All associative strengths start at zero and are updated each time the agent makes a choice. After each choice, the strengths of all cues present at the chosen option change by

$$\Delta V_q = \alpha_q(\lambda - \Sigma V), \quad (1)$$

where  $\alpha_q$  is the salience of Cue  $q$ ,  $\lambda$  represents the reward received ( $\lambda = 1$  for correct choices and  $0$  for incorrect choices), and  $\Sigma V$  is

the sum of the associative strengths of all the cues present at the chosen option (Rescorla & Wagner, 1972).

Agents next use what they have learned to make a choice on each trial, choosing an option proportionally to the total associative strength of all the cues present there. The probability that Option  $y$  is chosen is as follows:

$$P(Y) = 1 / e^{b(\Sigma V_x - \Sigma V_y)}, \quad (2)$$

where  $b$  is a scaling parameter that determines the steepness of the choice function, and  $\Sigma V_x$  and  $\Sigma V_y$  are the total associative strengths of all the cues at options  $x$  and  $y$ , respectively. This procedure assumes that agents probability match (the proportion of choices to an option tracks how likely that option is to be rewarded; Pérez-Escudero & de Polavieja, 2011).

However, as noted above, social cues are not simply present or absent at a given option. There can be different numbers of individuals demonstrating each option, and this will affect how reliable the social information is. In other words, social cues are *partial* cues, and the intensity or proportion of the cue present correlates with its reward contingency. I assume that the intensity of a cue affects learning in two ways. First, the experience of partial cues depends on their intensity; the calculation of  $\Sigma V$  is altered to reflect that. Second, when updating  $V$ , stronger cues are learned faster.

Note that although the idea of partial cues derives from the distribution of social cues, there is no reason why asocial cues could not also sometimes function as partial cues (indeed, the gray squares in the experiment reported above behave in exactly such a manner). For example, the strength of an odor might correlate with the likelihood that it predicts a food reward. A somewhat similar situation occurs in some studies of metacognition (e.g., Foote & Crystal, 2007), and I note that such experiments can be successfully simulated by the current model, in a similar way to that proposed by Le Pelley (2012). I therefore do not limit partiality to social cues but apply the modification of the learning equations to all cues. However, in the experiment simulated here, nonsocial cues will always either be completely absent or completely present.

I express the intensity of a partial cue, denoted  $\theta$ , by the proportion of its maximal possible value that is present ( $0 \leq \theta \leq 1$ ). So, in the current simulation, the partiality coefficient for the social cue at Option  $y$ ,  $\theta_{s,y} = n_y / N$ , where  $N$  is the maximal total number of conspecifics. The calculation of the summed associative strength at either option is modified to reflect the proportion of each cue present there. For option  $y$ , for example, this would be as follows:

$$\Sigma V_y = \sum_q \theta_{q,y} V_q \quad (3)$$

Additionally, the equation for updating the associative strength of a cue now also depends on the proportion of that cue present. Thus, for Cue  $q$  at Option  $y$ , Equation 1 becomes

$$\Delta V_q = \theta_{q,y} \alpha_q (\lambda - \Sigma V_y). \quad (4)$$

Simulations were run under the same values of  $C$  and  $S$  as the experiment, to reproduce the experimental results. The saliences of all cues in all conditions were set to 0.15. The value of  $b$  (in Equation 2) was set to 5 for all conditions. In each simulation, the maximal possible intensity of the social cue,  $N$ , was set to 12, as in the experiment. Each simulation was run for 300 time steps, and the data

from the first 100 time steps were discarded. Each simulation was repeated 100 times and the repetitions averaged together. Figure 2A-C shows the simulation results, arranged as in Figure 1B-D.

Though the model is intended only as a qualitative description of the data, and is not fit to the data in any way, the simulation results are very similar to the experimental data (Figure 2D). It is clear that the model reproduces the main result in the experimental data: Groups for which  $C = 0.85$  ignore social information while the other groups probability match (the model, like the pigeons, undermatches).

Figure 3 shows the associative strengths for the three cues in the model ( $x$ ,  $y$ , and  $s$ ) for each set of parameter values and helps explain the model results. For groups in which personal information is much more reliable than social information ( $C \gg S$ ), Cue  $y$ , which indicates the preferred-color option, gains associative strength quickly and overshadows Cue  $s$ , the social cue. For groups in which  $C$  is not as large, Cue  $s$  is able to compete with Cue  $y$  and the agents learn that social information, in sufficiently large quantities, can be more informative than personal information. This is true even if  $S < C$  (as in the  $C = 0.7, S = 0.6$  group). Thus, the model demonstrates that the effects observed in the experimental

data need not be driven by social learning strategies but may be the result of more reliable cues overshadowing less reliable cues, in accordance with well-established principles of asocial learning (Rescorla & Wagner, 1972).

## Discussion

Theories of collective decision making and social learning often assume that social cues are treated differently from asocial cues. By creating simple visual cues that distributed themselves between behavioral choices like conspecifics, I generated artificial social cues. Pigeons presented with these cues, together with personal information about which of two options was more likely to be rewarded, produced similar behavior to that found in collective choice situations. Pigeons, under some conditions, adaptively weighted the two kinds of information, relying more on the social cues as the proportion at one option increased. Under other conditions, when personal information was much more reliable than social information, pigeons appeared to ignore social information completely, despite being potentially able to perform better had they incorporated it. Similar data have been con-

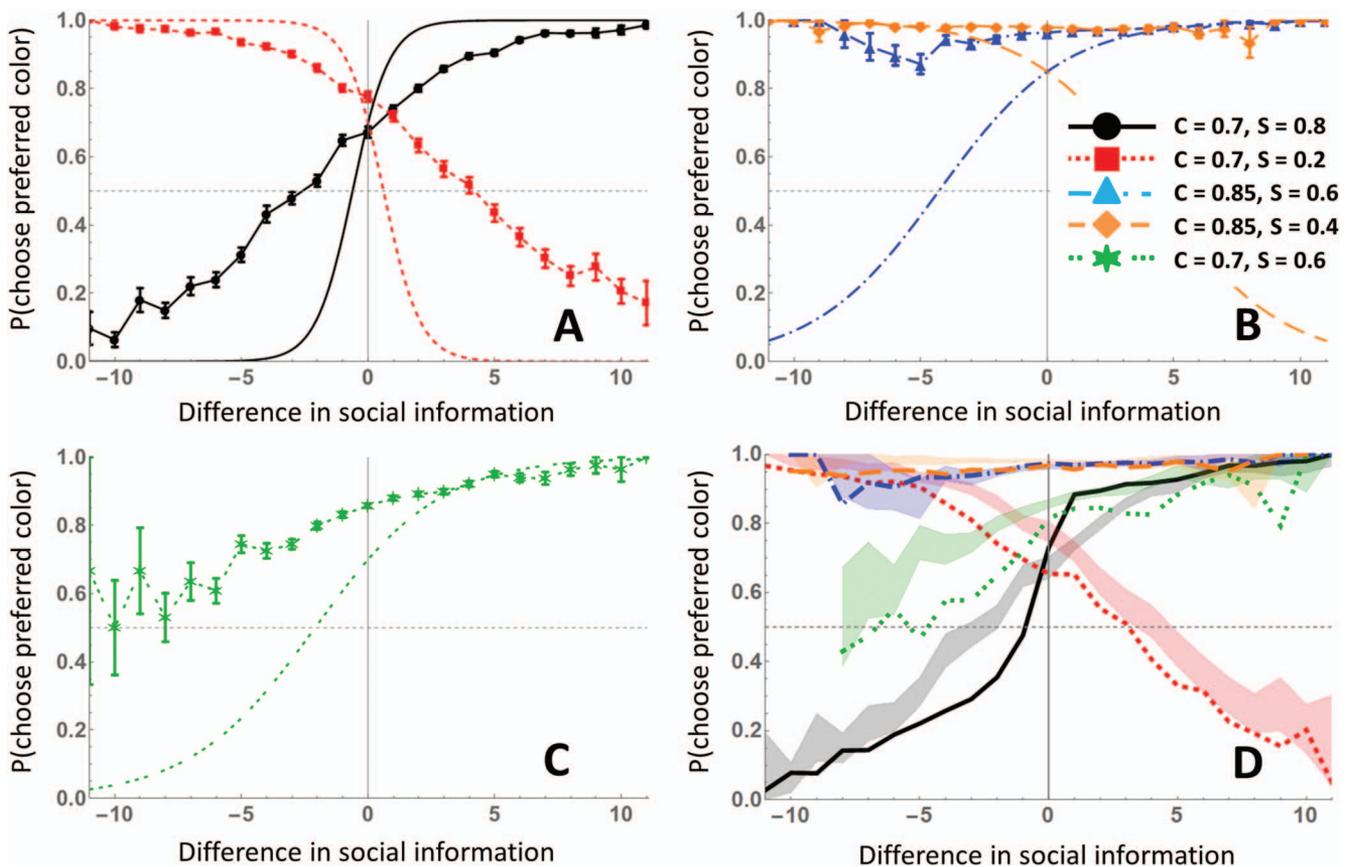
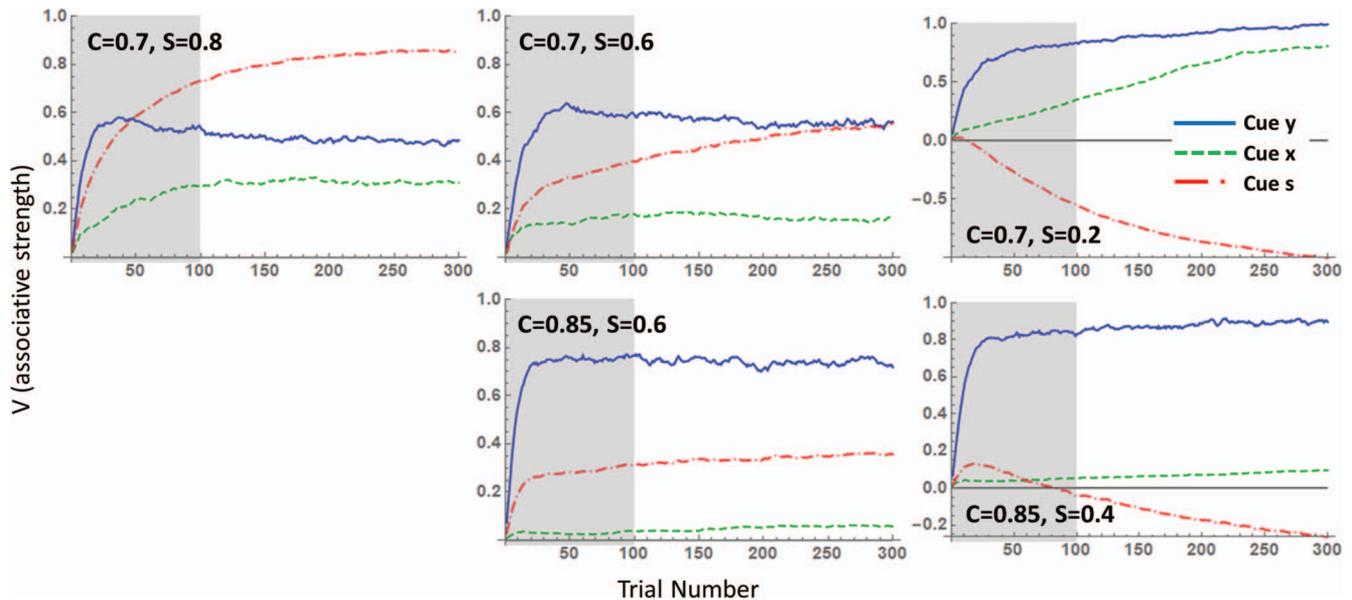


Figure 2. Simulation results. (A–C) Results of the learning model (lines with symbols) and theoretical probabilities (just lines) for each set of parameters. Data are plotted as the proportion of trials on which model agents selected their preferred (more often rewarded) option as a function of the difference in the amount of social cue at each option. Data are from the last 200 (of 300) trials and are averages of 100 simulation runs for each set of parameter values. Error bars indicate  $\pm SEM$ . (D) Comparison of the model and experimental data. Lines show the experimental data (as in Figure 1); shaded areas show 95% confidence intervals for the corresponding models. See the online article for the color version of this figure.



*Figure 3.* Associative strengths in the model. Each panel shows the associative strengths of the three cues ( $y$ ,  $x$ , and  $s$ ) over the 300 trials of the simulation, for each set of parameters. Parameter values for  $C$  and  $S$  are noted on each panel. Data are averages of 100 runs for each set of parameters. Shaded areas show the first 100 trials, which were excluded from the analysis. See the online article for the color version of this figure.

sidered evidence for the use of social learning strategies such as “copy when dissatisfied” or “copy when asocial learning is costly” (Laland, 2004). However, it is unlikely that the pigeons perceived the social cues, which were gray blobs on a screen, as actual conspecifics. This raises the possibility that social cues enter into learning in the same way as asocial cues and are subject to the same learning rules.

There is one inherent difference between most social cues and asocial cues: Social cues are partial cues. Groups may demonstrate more than one option at a time, and the reliability of a social cue correlates with the relative sizes of each subgroup. By modifying existing standard models of associative learning to incorporate partial cues, I am able to reproduce the experimental data accurately. The model suggests that, in those groups in which subjects did not use social information, social cues were overshadowed by the much more reliable personal information. This does not require that animals are able to adaptively select a strategy for different social situations but relies only on well-validated mechanisms of learning (Rescorla & Wagner, 1972).

It is quite possible that my experimental results have no bearing on social learning at all. The stimuli used in the study are only “social” in the sense that they distributed themselves between the subject’s options such that larger groups were more likely to associate with the correct option, as most social groups do. The gray squares were connected into a single gray blob—so the birds may have been using the area of gray rather than the number of squares—further distinguishing the cues from the multimodal experience of actual conspecifics. Social cues are known to be perceived and processed very differently from asocial cues, and are likely weighted more strongly (e.g., Galef, 1993). The conclusion that the birds did not perceive the gray squares in my experiment as social cues is strengthened by the finding that they learned to use them just as well when they were more likely to be incorrect than correct (i.e., when  $S < 0.5$ ). These data

might, then, merely represent an example of how pigeons learn (or do not learn) to use partial cues—cues whose contingency varies with their magnitude. The experimental and simulation results in this article might shed no light on the use of social learning strategies, as the cues used are insufficiently similar to real social cues. Nonetheless, it is possible to reframe in a similar way many studies of collective choice that show, for example, that social information is adaptively used as a function of its age or reliability (van Bergen, Coolen, & Laland, 2004). The model presented here is able to reproduce the results of many of these studies without assuming that animals distinguish between social and asocial cues. By this theory, information is information, irrespective of its source. The experimental and simulation data presented here thus constitute an alternative explanation—one that is almost certainly too simple—for how social information enters into learning. The advantage of this view is that it does not require the animal to have any cognitive skills apart from associative learning.

The artificial social cues used in the experiment and model here also differ from real social cues in that the subjects had no previous experience with them and (most likely) no innate response to them. Animals that live in groups will have a lot of experience of social interactions, such that they are unlikely to enter into any given situation with no existing association between social cues and reward. In other words, setting the associative strengths of social cues at zero at the start of the simulations is likely an accurate way to simulate the experiment but may not correspond to how real social cues are used. Similarly, it is likely that most group-living animals innately orient toward social cues, meaning that the salience of social cues is almost certainly higher than that of most asocial cues. To partially test how these effects might alter my conclusions, I reran the simulations with the salience of social cues increased (Figure S4 of the online supplemental materials;  $\alpha_s = 0.5$ ), with the initial associative strength of

social cues increased (Figure S5;  $V_s[0] = 0.4$ ), and with both the salience and initial associative strength increased (Figure S6;  $\alpha_s = 0.5$ ,  $V_s[0] = 0.4$ ). In all three cases, the results were qualitatively the same as those reported above.

In summary, when presented with asocial cues to a reward that distributed themselves similarly to social cues, pigeons generate performance that is similar to that seen in many studies of collective choice. Specifically, birds for which personal cues were much more informative than social cues ignored social information, similar to data suggesting the use of a social learning strategy. An associative model of learning that does not discriminate between social and asocial cues was able to reproduce these results, suggesting that very reliable personal information overshadows social information and prevents its use. This result may be added to a recent list (Heyes & Pearce, 2015) of associative explanations for social learning phenomena.

## References

- Asch, S. E. (1956). Studies of independence and conformity: I. A minority of one against a unanimous majority. *Psychological Monographs: General and Applied*, 70, 1–70. <http://dx.doi.org/10.1037/h0093718>
- Beck, M., & Galef, B. G. (1989). Social influences on the selection of a protein-sufficient diet by Norway rats (*Rattus norvegicus*). *Journal of Comparative Psychology*, 103, 132–139. <http://dx.doi.org/10.1037/0735-7036.103.2.132>
- Bikhchandani, S., Hirshleifer, D., & Welch, I. (1992). A theory of fads, custom, and cultural change as informational cascades. *Journal of Political Economy*, 100, 992–1026. <http://dx.doi.org/10.1086/261849>
- Bousquet, C. A. H., Sumpter, D. J. T., & Manser, M. B. (2011). Moving calls: A vocal mechanism underlying quorum decisions in cohesive groups. *Proceedings of the Royal Society B. Biological Sciences*, 278, 1482–1488. <http://dx.doi.org/10.1098/rspb.2010.1739>
- Condorcet, M. (1785). *Essai sur l'application de l'analyse à la probabilité des décisions rendues à la pluralité des voix* [Essay on the application of analysis to the probability of majority decisions]. Paris, France: Imprimerie Royale.
- Footo, A. L., & Crystal, J. D. (2007). Metacognition in the rat. *Current Biology*, 17, 551–555. <http://dx.doi.org/10.1016/j.cub.2007.01.061>
- Galef, B. G., Jr. (1993). Functions of social learning about food: A causal analysis of effects of diet novelty on preference transmission. *Animal Behaviour*, 46, 257–265. <http://dx.doi.org/10.1006/anbe.1993.1187>
- Giraldeau, L.-A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 357, 1559–1566. <http://dx.doi.org/10.1098/rstb.2002.1065>
- Heyes, C. (2012). What's social about social learning? *Journal of Comparative Psychology*, 126, 193–202. <http://dx.doi.org/10.1037/a0025180>
- Heyes, C., & Pearce, J. M. (2015). Not-so-social learning strategies. *Proceedings of the Royal Society B. Biological Sciences*, 282, 20141709. <http://dx.doi.org/10.1098/rspb.2014.1709>
- Hoppitt, W., & Laland, K. N. (2011). *Social learning: An introduction to mechanisms, methods, and models*. Princeton, NJ: Princeton University Press.
- Kao, A. B., & Couzin, I. D. (2014). Decision accuracy in complex environments is often maximized by small group sizes. *Proceedings of the Royal Society B. Biological Sciences*, 281, 20133305. <http://dx.doi.org/10.1098/rspb.2013.3305>
- Kao, A. B., Miller, N., Torney, C., Hartnett, A., & Couzin, I. D. (2014). Collective learning and optimal consensus decisions in social animal groups. *PLoS Computational Biology*, 10, e1003762. <http://dx.doi.org/10.1371/journal.pcbi.1003762>
- Krause, J., & Ruxton, G. D. (2002). *Living in groups*. New York, NY: Oxford University Press.
- Laland, K. N. (2004). Social learning strategies. *Learning & Behavior*, 32, 4–14. <http://dx.doi.org/10.3758/BF03196002>
- Lefebvre, L., & Giraldeau, L.-A. (1994). Cultural transmission in pigeons is affected by the number of tutors and bystanders present. *Animal Behaviour*, 47, 331–337. <http://dx.doi.org/10.1006/anbe.1994.1046>
- Le Pelley, M. E. (2012). Metacognitive monkeys or associative animals? Simple reinforcement learning explains uncertainty in nonhuman animals. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 38, 686–708. <http://dx.doi.org/10.1037/a0026478>
- Miller, N., Garnier, S., Hartnett, A. T., & Couzin, I. D. (2013). Both information and social cohesion determine collective decisions in animal groups. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 5263–5268. <http://dx.doi.org/10.1073/pnas.1217513110>
- Miller, N. Y., & Shettleworth, S. J. (2007). Learning about environmental geometry: An associative model. *Journal of Experimental Psychology: Animal Behavior Processes*, 33, 191–212. <http://dx.doi.org/10.1037/0097-7403.33.3.191>
- Miller, N. Y., & Shettleworth, S. J. (2008). An associative model of geometry learning: A modified choice rule. *Journal of Experimental Psychology: Animal Behavior Processes*, 34, 419–422. <http://dx.doi.org/10.1037/0097-7403.34.3.419>
- Pérez-Escudero, A., & de Polavieja, G. G. (2011). Collective animal behavior from Bayesian estimation and probability matching. *PLoS Computational Biology*, 7, e1002282. <http://dx.doi.org/10.1371/journal.pcbi.1002282>
- Pike, T. W., & Laland, K. N. (2010). Conformist learning in nine-spined sticklebacks' foraging decisions. *Biology Letters*, 6, 466–468. <http://dx.doi.org/10.1098/rsbl.2009.1014>
- Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory* (pp. 64–99). New York, NY: Appleton-Century-Crofts.
- Shettleworth, S. J. (2010). *Cognition, evolution, and behavior*. New York, NY: Oxford University Press.
- Sumpter, D. J. T., Krause, J., James, R., Couzin, I. D., & Ward, A. J. W. (2008). Consensus decision making by fish. *Current Biology*, 18, 1773–1777. <http://dx.doi.org/10.1016/j.cub.2008.09.064>
- van Bergen, Y., Coolen, I., & Laland, K. N. (2004). Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society B. Biological Sciences*, 271, 957–962. <http://dx.doi.org/10.1098/rspb.2004.2684>
- Wagner, A. R., Logan, F. A., Haberlandt, K., & Price, T. (1968). Stimulus selection in animal discrimination learning. *Journal of Experimental Psychology*, 76, 171–180. <http://dx.doi.org/10.1037/h0025414>
- Wilkinson, A., Kuenstner, K., Mueller, J., & Huber, L. (2010). Social learning in a non-social reptile (*Geochelone carbonaria*). *Biology Letters*, 6, 614–616. <http://dx.doi.org/10.1098/rsbl.2010.0092>

## Appendix

### Deriving the Optimal Choice Behavior

In the experiment I report, stimuli consist of a colored circle surrounded by one to 12 gray squares. Each subject has a “preferred” color, which is more often correct, with probability  $C$  ( $>0.5$ ). Each gray square has a fixed probability,  $S$ , of being associated with the rewarded option on that trial (independently of whether or not that is the subject’s preferred color). Given this, it is possible to derive the probability that any given stimulus is correct. Note that this requires that the birds know  $C$  and  $S$ , and be able to accurately estimate the number (or area) of the gray squares at each option, which is unlikely. Nonetheless, the optimal behavior serves as a benchmark against which subjects’ actual choices can be compared.

I denote the two color stimuli  $x$  and  $y$ , and assume that Stimulus  $y$  bears the more often rewarded color. I denote the probability that Option  $y$  is correct,  $Y$ .  $Y$  depends on personal information (about the color; denoted  $A$ ) and on “social” information (given by the gray squares; denoted  $G$ ).

Following Perez-Escudero and de Polavieja (2011),

$$P(Y|A, G) = \frac{P(G|Y, A)P(Y|A)}{P(G|X, A)P(X|A) + P(G|Y, A)P(Y|A)}, \quad (\text{A1})$$

where  $X$  is the probability that stimulus  $x$  is correct. This can be simplified as

$$P(Y|A, G) = \frac{1}{1 + \left[ \frac{P(X|A)}{P(Y|A)} \right] \left[ \frac{P(G|X, A)}{P(G|Y, A)} \right]}. \quad (\text{A2})$$

If the subject knows that Cue  $y$  is more often rewarded, then its personal information,  $A$ , indicates  $Y$ , and therefore  $P(Y|A) = C$  and  $P(X|A) = 1 - C$ .

Social information consists of the number of gray squares that “chose” each of the two options,  $y$  and  $x$ :  $n_y$  and  $n_x$ . Each square has a fixed probability of being correct,  $S$ , and squares make their

decisions independently of each other. Therefore, the probability of getting a particular distribution of social information,  $G$ , is given by

$$P(G|Y, A) = \binom{N}{n_y} S^{n_y} (1 - S)^{n_x}, \quad (\text{A3})$$

$$P(G|X, A) = \binom{N}{n_y} (1 - S)^{n_y} S^{n_x}, \quad (\text{A4})$$

where  $N = n_x + n_y$  is the total number of gray squares. Note that Equations A3 and A4 do not depend on  $C$ . In other words, the information used by the gray squares to choose an option is different from the color of that option (i.e., gray squares have a fixed probability of choosing *correctly*, not of choosing the more-often rewarded color). This is comparable to models of collective choice in which the correlation between the personal information of group members is (close to) zero (Kao et al., 2014).

From Equations A3 and A4,

$$\frac{P(G|X, A)}{P(G|Y, A)} = S^{\Delta N} (1 - S)^{-\Delta N}, \quad (\text{A5})$$

where  $\Delta N = n_x - n_y$ . Substituting into Equation A2, I find the following:

$$P(Y|A, G) = \frac{1}{1 + \left[ \frac{1 - C}{C} \right] \left[ S^{\Delta N} (1 - S)^{-\Delta N} \right]}. \quad (\text{A6})$$

As noted by Perez-Escudero and de Polavieja (2011),  $P(Y)$  here depends only on  $\Delta N$ , not on absolute values of either  $n_y$  or  $n_x$ . Figure 1 in the main text shows Equation A6 for each experimental group.

Received October 20, 2017

Revision received December 29, 2017

Accepted January 2, 2018 ■