Both information and social cohesion determine collective decisions in animal groups

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During consensus decision making, individuals in groups balance personal information (based on their own past experiences) with social information (based on the behavior of other individuals), allowing the group to reach a single collective choice. Previous studies of consensus decision making processes have focused on the informational aspects of behavioral choice, assuming that individuals make choices based solely on their likelihood of being beneficial (e.g., rewarded). However, decisions by both humans and non-human animals systematically violate such expectations. Furthermore, the typical experimental paradigm of assessing binary decisions, those between two mutually exclusive options, confounds two aspects common to most group decisions: minimizing uncertainty (through the use of personal and social information) and maintaining group cohesion (for example, to reduce predation risk). Here we experimentally disassociate cohesion-based decisions from information-based decisions using a three-choice paradigm and demonstrate that both factors are crucial to understanding the collective decision making of schooling fish. In addition, we demonstrate how multiple informational dimensions (here color and stripe orientation) are integrated within groups to achieve consensus, even though no individual is explicitly aware of, or has a unique preference for, the consensus option. Balancing of personal information and social cues by individuals in key frontal positions in the group is shown to be essential for such group-level capabilities. Our results demonstrate the importance of integrating informational with other social considerations when explaining the collective capabilities of group-living animals.

collective intelligence | golden shiner | behaviour | Bayesian

Understanding the mechanisms of social influence and collective intelligence is a key challenge in contemporary science (1–5) and is essential for achieving progress in a variety of fields ranging from the organization of gregarious and social organisms (6–8) to the dynamics of information exchange in human societies (1–4). In animal groups, effective distributed decision making occurs across a range of taxa and environmental contexts (7, 9–17), making them an excellent model in which to study the evolved capabilities of collectives. Individuals in groups must balance personal information, accumulated from their own past experiences, with potentially conflicting social information, gleaned from the behavior of conspecifics. Additionally, achieving a single consensus choice is often crucial to maintaining group cohesion, and individuals that make a dissenting choice may find themselves isolated, increasing their risk of predation (18). Thus, additional social considerations—such as attempting to minimize the risk of isolation—may bias individual decisions away from what might be predicted from purely informational considerations (19–22). Both humans (23–25) and nonhuman animals (26–31) have been shown to make such biased decisions, which are not based solely on their information about the quality of their options.

Previous investigations of how group-living organisms balance personal and social information have typically involved assessing solitary individuals making decisions between two mutually exclusive options (9–16, 22, 32, 33), one indicated by their personal information and one by social cues (previous choices made by others, which they observed). Because individuals are tested in isolation, considerations based on social cohesion are eliminated

or equalized (i.e., both choices contain no conspecifics at the time of testing; refs. 10–13). The two-choice paradigm has also been employed to investigate decisions made by groups of individuals (9, 14–16), but here the tendencies to maintain group cohesion and to maximize information acquisition will both indicate the same choice and these factors are therefore confounded in the resulting data. For example, copying the choice made by the majority of previous individuals both maximally reduces the risk of isolation and is the option most favored by social information. It is currently unclear to what degree consensus decisions are based on maximizing cohesion or minimizing uncertainty, raising questions about the interpretation of the results of many models of collective decision making (19–22).

Furthermore, although many studies have considered how groups choose between mutually exclusive options, in many environments the information held by different members of a group may be complementary, such that some possible courses of collective action reconcile most members' personal and social preferences. If personal information is informative (i.e., following personal information tends to lead to "better" outcomes) then groups that effectively integrate the personal information of their members will, probabilistically, make better collective decisions than groups that do not. Additionally, groups that can integrate their members' preferences are more likely to remain cohesive.

To reveal how grouping animals integrate personal and social information, and to explicitly disassociate information-based and cohesion-based considerations, we trained separate groups of golden shiner fish (*Notemigonus crysoleucas*) to exhibit different, but complementary, preferences using a three-choice design (Fig. 1 and Fig. S1). Sixteen groups of 16 fish each were trained to associate either floor color (group A) or wall-stripe orientation (group B) with a food reward. In test trials we created mixed groups, consisting of equal numbers of fish from groups A and B, which made decisions among three possible arm choices: one that had only the rewarded floor color (color arm), one with only the rewarded type of wall striping (stripe arm), and one option that contained the rewarded color and stripe stimuli for both groups (consensus arm; *Methods* and Movie S1).

Individuals' initial arm choices were ranked (rank 1 = first fish to choose, rank 16 = last to choose; Fig. S2) and compared to their personal information (i.e., whether or not they chose an arm they had been rewarded at during training) and to social cues [i.e., which arm(s) the fish that had already chosen were in, determined either by directly observing previous choices or simply by counting, or some simpler proxy of counting (34), the number of fish currently in each arm]. We denote the arm containing the largest number of fish at any individual's decision

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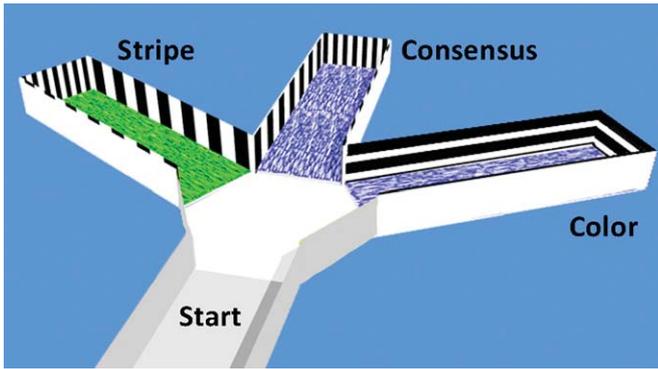
Fig. 1. Schematic of the test environment with the start and choice arms labeled. The color (blue floor, horizontal stripes) and stripe (green floor, vertical stripes) arms contained only the rewarded stimuli for groups A (blue floors) or B (vertical stripes), respectively; the consensus arm contained the rewarded stimuli for both groups (blue floors and vertical stripes). The relative location of each arm (to the left, right, or center of the start arm) was randomized across tests (*Methods*).

time as the "majority arm" and consider this both the arm indicated by social information and also the choice that maximizes group cohesion, because it permits that individual to remain with the largest part of the group. By presenting each individual with three choices, two of which conform to its trained preference, we are able to directly investigate how individuals weigh (personal and social) informational considerations against a general propensity to maintain cohesion (such as to reduce predation risk) when making decisions.

If fish in groups can combine their personal information, and thus exhibit collective integration of information, we would expect mixed groups to spend the majority of their time in the consensus arm—the only arm preferred by all individuals. If individuals are not able to combine information, but do exhibit social cohesion, they should tend to remain together and choose collectively, but randomly, among the options. If they neither exhibit social cohesion nor utilize social cues to obtain information about their environment they may choose based solely on their personal preferences, causing the groups to split, with members choosing among, or dividing their time between, their two preferred arms.

Results

Social Integration of Personal Information During Collective Decision Making. Mixed groups (those containing individuals from groups A and B) are most likely to choose the consensus arm in our experimental trials [paired-sample t tests, consensus vs. color or stripe, both $t(47) > 3.8$, $P < 0.001$; color vs. stripe, $t(47) = 0.33$, $P = 0.742$; Fig. 2*A*]. However, this is not sufficient to test for effective integration of information by group members; because all the fish in the mixed groups were trained to prefer the consensus arm and only half of the fish were trained to prefer each of the other two arms, a distribution of arm choices biased toward the consensus arm could have resulted from each fish's choosing solely based on its trained preferences (its personal information) and not being influenced by the preferences of others. If this were the case, however, mixed groups would tend to split by training group (A or B) and thus we would find smaller numbers of fish in each of the three arms than if the mixed group made an integrated collective decision. A comparison of the distribution of first choices of reward arms to the distribution that would have resulted were fish choosing based only on their personal information (Fig. 2*C*; *SI Text*
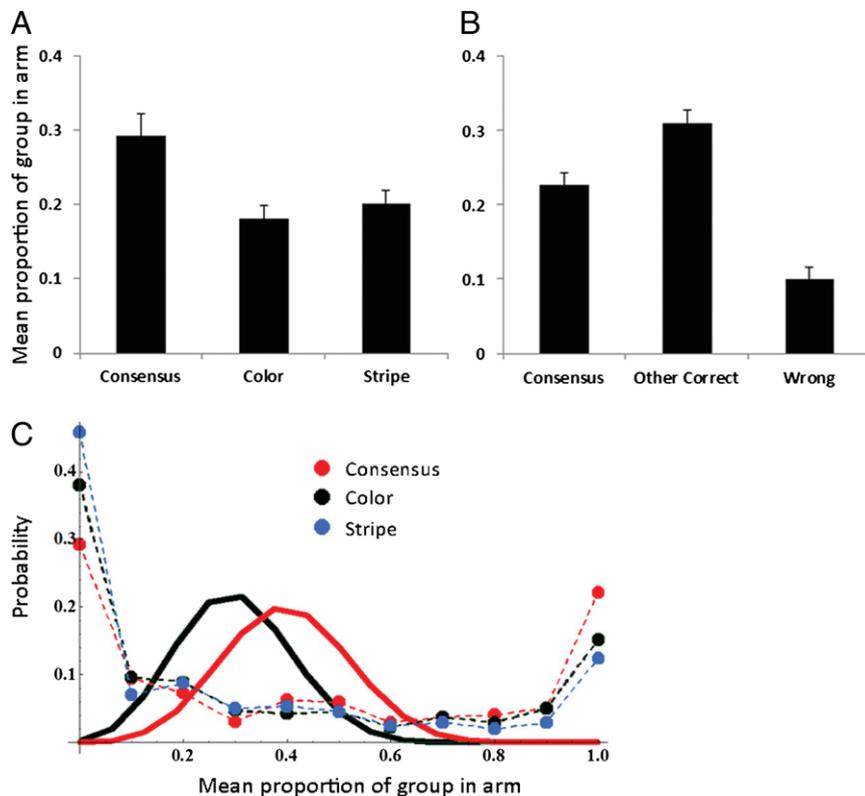

Fig. 2. Distributions of reward arm residency during tests. Arm choice distributions for the entire duration of mixed tests (*A*) and unmixed control tests (*B*). Error bars represent ± standard error (= $\sigma / \sqrt{N}$). (*C*) Comparison of data distributions of initial arm choice in mixed tests (dotted lines) to the theoretical distributions expected if fish ignored social information (solid lines; the predictions for the color and stripe arms overlap). Details are given in the text.

shows derivation of theoretical distributions) demonstrates that shiners achieved consensus, remaining together as a single group, on about half of the trials, more than expected if they were ignoring social information (Kolmogorov–Smirnov test, all $D > 0.397$, all $P < 0.0001$; ref. 14 includes a similar analysis). In other words, the distributions of the fish in the reward arms (dotted lines in Fig. 2C) are U-shaped, indicating that groups do tend to remain cohesive. If the fish ignored social cues we would not expect their choices to correlate and their choice distributions would be binomial (solid lines in Fig. 2C). Fig. 2A further shows that these collective choices were more often directed at the consensus arm than either of the other two arms.

Thus, schooling fish can effectively integrate congruent personal information, even though no one individual is explicitly aware of, or has a unique preference for, the consensus option. In our unmixed control tests, which were identical to the mixed test trials but included only fish from a single training group (A or B), fish preferred both the consensus arm and their other rewarded arm (the color arm for group A and the stripe arm for group B) to their unrewarded arm [both $t(31) > 4.8$, $P < 0.001$] and actually displayed a smaller but still significant preference for their other rewarded arm over the consensus arm [$t(31) = 3.54$, $P < 0.002$; Fig. 2B]. That this preference was reversed in the mixed trials, in which groups were composed of individuals from both training groups, is further evidence that consensus decisions result from effective integration of personal and social information within groups.

Role of Position Within the Group on the Integration of Personal Information and Social Cues. A further property evident in the decision making of our fish is that individuals that are relatively close to the front of the group ("early followers") are particularly important for the group's integration of personal information and social cues. This is due to the way in which ordered (sequential) collective decisions are made. The order of the fish in the shoal, from front to back, rarely changes between their leaving the start arm and entering one of the reward arms (Fig. S2A) and the choice an individual makes is predicted with a high degree of accuracy by which reward arm it is heading toward, even when it is still relatively far from the arm's entrance (Fig. S2B). The first fish to make a choice among arms in each mixed group (rank 1) selected one of its two preferred arms on 78% of trials. In all later ranks, personal information and the direction indicated by social cues (the choice made by the majority of

earlier ranks) may either be congruent (i.e., both indicate the same arm) or in conflict (each indicates a different arm).

When personal information and social cues were congruent, fish chose the arm selected by the majority of earlier ranks 85% ($\pm$ 0.07%) of the time (Fig. 3A, red circles). However, when personal information and social cues conflicted, individuals' choices depended on their rank: Early followers, consisting of ranks 2–5, approximately (Fig. 3A, shaded area), were less likely to choose the majority arm ($64 \pm 0.16\%$) and more likely to choose one of their trained arms ($36 \pm 0.16\%$; Fig. 3A, blue circles); "late followers" (rank > 5, approximately), however, chose the majority arm about 80% of the time, regardless of whether it was an arm they preferred ($77 \pm 0.11\%$) or not ($82 \pm 0.07\%$). In such mixed groups early followers, by ignoring or confirming the choices of earlier ranks, give rise to the global preference for the consensus arm. In addition, when social cues and personal information coincided, early followers strongly favored the majority arm over their other preferred arm, disambiguating those two choices for later ranks. Later followers made little or no contribution to the group's decision, suggesting that the influence of social cues on late followers was greater than it was for early followers, inhibiting them from expressing their personal preferences.

In unmixed control tests, the lead fish selected one of its preferred arms on 84% of trials. Later ranks exhibited a pattern of choices similar to that in the mixed tests discussed above (Fig. 3B), although there were far fewer cases in which social and personal information conflicted (Fig. 3B, blue circles), because all the fish in each test had identical personal preferences (Fig. S3).

Isolation-Averse Bayesian Model of Decision Making. To quantify the respective roles in collective decision making of information (both personal and social) and other factors that bias groups in favor of social cohesion (such as minimizing predation risk), we first adapt a recent Bayesian approach (19, 20) to explore the degree to which our data can be accounted for purely by optimal combination of personal and social information. In the pure Bayesian model each individual compares every reward arm, Y, to all other arms, m, and makes a probabilistic choice based on the likelihood that each arm is "correct" based on available personal and social information. Personal information is encoded as $a_{my} = P(m+)/P(Y+)$, where $P(x+)$ is the likelihood that arm x is rewarded, based on that individual's trained preferences (19). In our data, lead fish (rank 1) choose one of their two
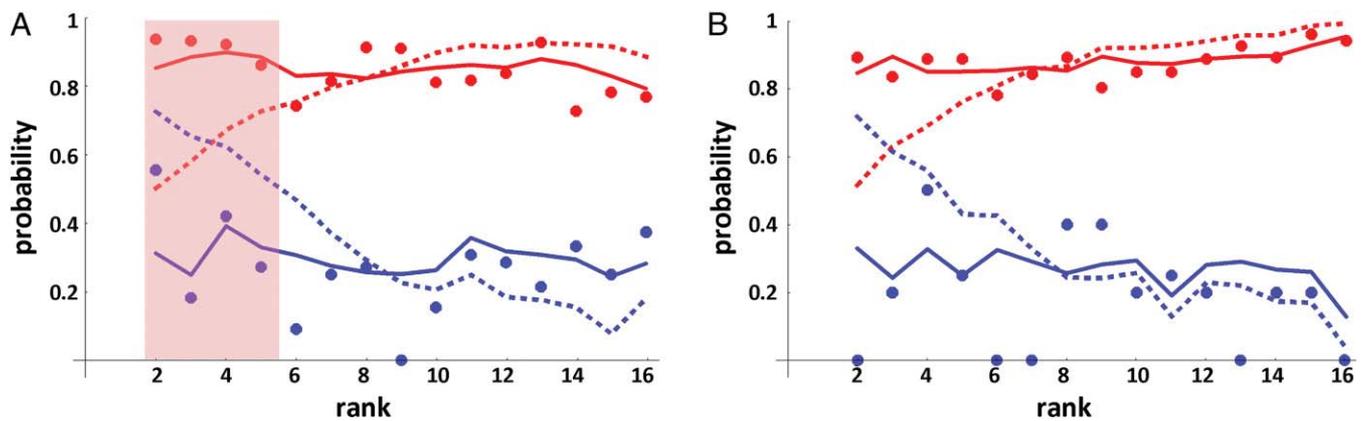

Fig. 3. Reward arm choice probabilities as a function of choice rank. Probability of choosing the majority arm when it was also a preferred arm (i.e., one of the two arms rewarded during training; red circles) or of choosing either preferred arm when the majority arm was the nonpreferred arm (blue circles) at different choice ranks in the mixed (A) and unmixed control (B) tests. Early followers (ranks 2–5) are shaded. Lines represent model predictions of the data for the pure Bayesian (dashed lines; $s = 1.51$ for mixed and 1.59 for unmixed data) and isolation-averse Bayesian (solid lines; $s = 1.15$ for mixed and 1.2 for unmixed data, $\alpha = 0.93$ for mixed and 0.92 for unmixed data) models.

preferred arms approximately 80% of the time (78% in mixed trials, 84% in unmixed control trials), so we set $P(x+) = 0.4$ for preferred arms and therefore $P(x+) = 0.2$ for the nonpreferred arm. As a result, $a_{my} = 1$ when comparing two preferred arms (i.e., personal information does not discriminate between these arms).

Social information, in the pure Bayesian model, is assumed not only to depend on which is the majority arm but also on the absolute number of fish in each arm, n_Y, such that larger majorities have a greater effect on choice than small majorities (19). Social information is further weighted by a single free parameter, s, which represents the reliability of the social information (19). The probability of choosing an arm Y, $P(Y)$, is equal to the estimated probability of that arm's being rewarded, based on both personal and social information, which we denote $P(Y_{Corr})$ and is given by

$$P(Y) = P(Y_{Corr}) = \left(\sum_{m=1}^{M} a_{mY} s^{-(n_Y - n_m)} \right)^{-1}. \quad [1]$$

Following a choice, the values of n_m for all arms m are updated before the next individual chooses. We fit this model to our data and find that the best-fit value of s is 1.51 for our mixed and 1.59 for our unmixed data (Fig. S4A and Fig. 3, dashed lines).

The pure Bayesian model determines only how likely each option is to be correct and then distributes its choices proportionally to that likelihood. Although this model seems to provide a good fit to previous collective decision making data from stickleback fish (19, 20) and zebrafish (20) (although we note that those experiments involved a two-choice paradigm), we find that it systematically underestimates early followers' (approximately ranks 2–5) choices of the majority arm when it is also a preferred arm. When choosing between their two preferred arms, early followers choose the arm that has more conspecifics in it 91% (± 0.04%) of the time (Fig. 3, red circles). However, according to the pure Bayesian model, early followers in this situation have only weak social information indicating the majority arm over their other preferred arm and so should choose both arms almost equally (Fig. 3, red dashed line).

A parsimonious explanation for this discrepancy is that the fish in our experiments are not acting solely based on informational considerations. By failing to include the various other mechanisms that contribute to social cohesion, purely informational approaches, such as the model presented above, neglect important ecological considerations. To test this hypothesis we develop a model that integrates information-based choices with an aversion to isolation, representing the other factors that tend toward group cohesion. We represent the aversion to any option Y by the function $\alpha/(n_Y + 1)$, where α characterizes the degree of aversion to isolation that an individual expresses. The probability of selecting an arm purely based on considerations of social cohesion is therefore proportional to the number of individuals inhabiting it, which could be considered a simple operational definition of isolation aversion. This gives rise to the following isolation-averse Bayesian model:

$$P(Y) = \frac{P(Y_{Corr})\left(1 - \dfrac{\alpha}{n_Y + 1}\right)}{\sum\limits_{m=1}^{M} P(m_{Corr})\left(1 - \dfrac{\alpha}{n_m + 1}\right)}, \quad [2]$$

where $P(Y_{Corr})$ is given by Eq. 1. Note that if $\alpha = 0$, individuals have no aversion to isolation and the model reduces to the pure Bayesian model (Eq. 1). This is because the sum in the denominator, which becomes $\sum_{m=1}^{M} P(m_{Corr})$, will always = 1, giving $P(Y) = P(Y_{Corr})$; if $\alpha = 1$, individuals never select an empty arm

(i.e., an arm that no previous ranks chose). Fitting Eq. 2 to our data (Fig. 3, solid lines), we find the best fit at $s = 1.15$, $\alpha = 0.93$ for the mixed data and $s = 1.2$, $\alpha = 0.92$ for the unmixed data, implying that our fish are highly averse to isolation (Fig. S4 B and C). The isolation-averse Bayesian model provides a significantly better fit to our data than the pure Bayesian model [models were compared using the Bayesian Information Criterion (BIC), which penalizes models with additional parameters; lower BIC scores imply a better fit. Mixed tests: pure Bayesian 930.4, isolation-averse Bayesian 792.7; unmixed control tests: pure Bayesian 535.6, isolation-averse Bayesian 475.7].

Above, we noted that the imperative associated with social cues seems greater for late followers than for early followers, causing the late followers to rely more on such cues even when they conflict with their personal information. Our model indicates that the key parameter affecting the influence of social information is the size of the majority in a given arm, Δn. Exploring the space of Δn as a function of choice rank reveals in greater detail how groups of fish in our experiment combine information (Fig. 4). Early followers experience a small Δn and therefore give similar weight to personal and social information, even if their personal information conflicts with the choice of earlier ranks, remaining relatively free to "express" their personal preferences. As long as Δn remains close to 0, in both model and data, individuals are approximately equally likely to choose one of their preferred options or to choose the majority arm (green region in Fig. 4). However, when Δn is large, even in relatively early ranks, the pull exerted by social information becomes too strong to resist (the s term in Eq. 1 dominates) and individuals mostly choose the majority arm, as in cases of informational cascades (35).

Because the preferences of the individuals in our experiment are at least partially correlated, it is rare for Δn to remain small (implying an even distribution of the fish between at least two arms) in later ranks, due to the tendency for fish to come to consensus, and thus both model and data rarely reach the region of parameter space between the arms of the "V" in Fig. 4 (low Δn, high rank). In our experimental data, we find that the decision regarding which arm the group chose was usually determined by the time the eighth rank chose, indicating that only the front half of the group participated in collectively determining the group's choice.

Discussion

The cohesiveness of animal groups has been commented on and documented for a wide range of avian, fish, insect, and mammalian species (e.g., 18, 36–41). Group cohesion is beneficial for a number of reasons. Being in a (larger) group decreases individuals' risk of predation both through dilution (8, 42) and improved predator detection (via the many-eyes effect; refs. 18, 42) and dense, polarized groups may lead to predator confusion (8, 43, 44), further reducing predation risk and encouraging cohesiveness. Groups may also be able to collectively hunt larger (18) or aggregating (45) prey. Finally, other individuals (conspecific or heterospecific) may constitute an additional source of indirect information about the environment.

Previous studies of collective decision making have not made clear whether individuals copy the choices made by others because they are using the information provided by those choices or because of other factors that drive social cohesion, such as minimizing predation risk. We dissociated these two types of choice copying by creating situations in which individuals were faced with a situation in which their personal information was either incongruent with the predominant choice made by others (when the majority arm was a nonpreferred arm) or when their personal information and social cues were congruent (when the majority arm was one of the two arms they preferred based on personal information). In the first case, when choosing between personal information and social cues, early followers weighted the
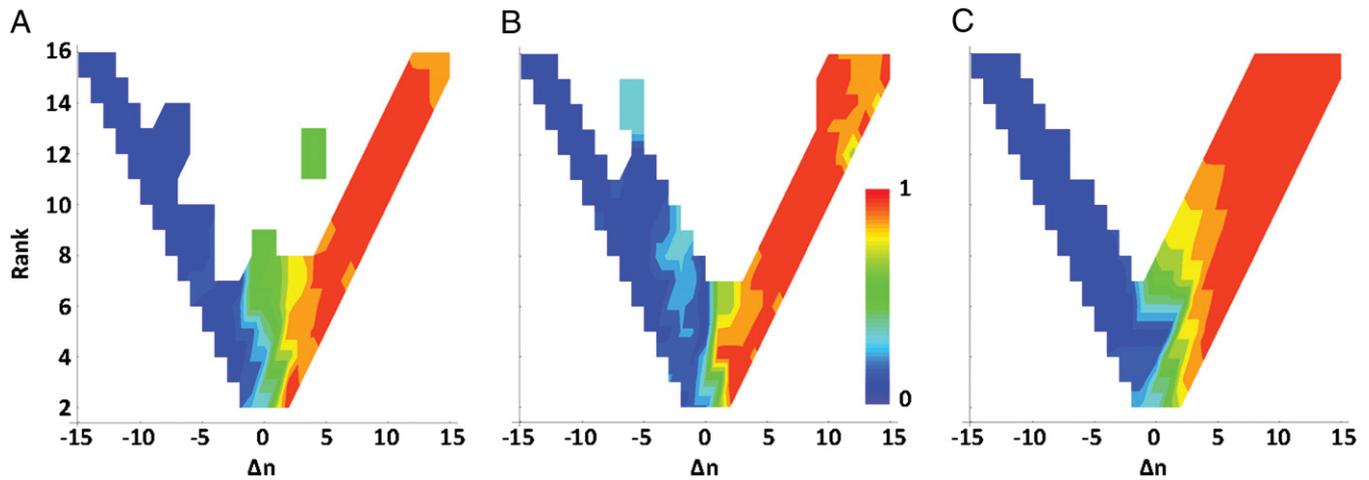
Fig. 4. Density maps of the probability of choosing an arm as a function of choice rank and the size of the majority in that arm, Δn. (*A*) mixed test data; (*B*) unmixed control data; (*C*) isolation-averse Bayesian model simulation data (average of 5,000 runs); all for choices of the consensus arm. White areas indicate no data. Note that here $\Delta n = n(\text{consensus arm}) - Max[n(\text{color arm}), n(\text{stripe arm})]$.

two approximately equally and often chose one of their preferred arms even if it was empty (and therefore potentially dangerous). In other words, a small number of conspecifics in a nonpreferred arm (a relatively weak social cue) was not sufficient to completely determine an individual's choice. However, when choosing between two equally preferred arms, in terms of personal information, individuals almost always chose the arm that had the larger number of conspecifics in it, even if that number was too small to determine their choice in the earlier, conflict situation. Thus, when personal information provides no guidance (both arms are equally preferred), individuals choose the option that maximizes group cohesion far more often than would be predicted based purely on the social information they have.

We also demonstrate that schooling fish are able to effectively combine complementary information about the location of a food reward. Individuals at the front of the group, leaders and early followers, whose social cues are dependent on the choices of only a few others, choose primarily based on their own personal preferences. If early followers "confirm" each other's choices, the size, and therefore authority, of the majority choosing a particular option quickly becomes such that later individuals blindly follow their decision, even if it conflicts with their personal information (as in the model of ref. 35). However, if early ranks "contradict" each other, there will be no clear majority and individuals that choose later still express their personal preferences. Thus, any indecision by the lead ranks effectively "polls" the opinions of later ranks to reach a decision. If there is a potential consensus choice for the group (i.e., one option that the majority of individuals can agree on), as there was in our experiment, a large fraction of the group will eventually achieve it in most cases.

Our results suggest that this form of collective intelligence will tend to be most effective when information is evenly spread (spatially) throughout the group. If a sufficient number of lead individuals have the same personal preferences, then the group will not be able to combine this information with any complementary information held by individuals further back in the group, because the size of the majority for one option (the option preferred by the leaders) will be sufficiently large to inhibit further expression of personal preferences. In other words, the effectiveness of information integration depends on a diversity of information in the early ranks (Fig. S5*A*). In our experiments we found that groups were self-structured to be well mixed, with neither training group more likely to appear at any given rank (Fig. S5*B*).

The mechanism of collective intelligence demonstrated here does not require individuals to be aware of the diversity of information in the group. In our unmixed control tests, in which all the individuals had identical preferences, individuals weighted personal and social information and social cohesion similarly to individuals in mixed trials (Fig. 3; both of the models we tested fit these data best with almost the same parameter values used for the mixed test data, Fig. S4). Thus, at the level of individual interaction rules, individuals in mixed and control groups behave in the same way. However, in both our model and the data, the global distributions of choices that result from these interaction rules (Fig. 2 *A* and *B*) are very different in the two cases: Mixed groups effectively select the consensus arm whereas control groups do not. Thus, the collective intelligence exhibited by groups emerges naturally from diversity of information and from the simple interaction rules used by individuals.

Methods

Subjects. Subjects were 256 adult golden shiners (*Notemigonus crysoleucas*), obtained from Anderson Minnow Farms. Fish were housed in 10-gallon stock tanks for at least 2 wk prior to the start of experiments. All fish were injected with either green or red subcutaneous fluorescent elastomer tags (Northwest Marine Technology) to identify their training group and were given 4 d to recover from the tagging before the start of experiments. Fish were deprived of food for 24 h prior to the start of the experiments and were fed only during training trials until the end of the experiment. Groups of fish to be tested together were housed together. All experimental procedures were approved by the Princeton University Institutional Animal Care and Use Committee.

Apparatus. Experiments were conducted in an aquatic six-arm radial maze (Fig. S1; arm width, 20 cm; arm length, 28 cm; maze height, 15 cm) placed inside a 210- × 120-cm tank filled with aged tap water to a depth of 10 cm. The entire tank was placed inside a tent of white fabric that was lit from the sides by eight fluorescent lamps, aimed at the roof of the tent. A camera (Sony EX1) was mounted on the ceiling with its lens positioned in the center of the roof of the tent. The water in the tank was aerated and kept at a temperature of 20 (± 2) °C and a salinity of 900 ± 50 µS. At the end of each arm of the radial maze a floating feeding ring was attached in which floating food pellets (Tropical Micro Pellets; Hikari) could be placed. Transparencies were attached to the bottom and sides of each arm to serve as training stimuli. Floor transparencies were either blue or green and wall transparencies had either vertical or horizontal stripes printed on them. Unused arms were blocked off with removable plastic doors. The start arm had a door that could be remotely raised from outside the tent.

Procedure. Fish were trained in groups of 16 with different groups (A or B) trained separately. Group A were trained to find a food reward at the ends of arms that had a particular floor color (e.g., food was present in blue-floored arms but not green-floored arms); group B was rewarded in arms with stripes of a certain orientation on the walls (e.g., food was present in arms with vertically striped walls but not in arms with horizontal stripes). On each training trial, two reward arms of the maze were accessible, one to the left and one to the right of the start arm.

Test trials were of two types: For mixed test trials, the group of subjects consisted of 8 fish from each training group (A and B); for unmixed control tests, the group consisted of 16 fish from a single training group (A or B), as in the training trials. On all test trials (mixed and unmixed), three arms were accessible, to the left, right, and directly across from the start arm. The three accessible arms were a consensus arm, which contained both the rewarded color and stripe orientation (e.g., a blue floor and vertically striped walls); a color arm, which had only the rewarded color (e.g., a blue floor and horizontally striped walls); and a stripe arm, which had only the rewarded stripe orientation (e.g., a green floor and vertically striped walls; Fig. 1).

The absolute locations of the start and reward arms were randomized across trials, as was the relative location of the correct reward arm (to the left or right of the start arm). Fish received four trials per day every day for 10 d. One mixed-group test trial was interspersed with the training trials on days 5, 7, and 10. Unmixed control tests were given on days 3 and 9. The identity of the discriminative cue that indicated the rewarded arm was randomized between groups.

At the beginning of each day, all the fish were netted from their housing tanks into buckets. For each trial, a group of 16 fish were netted from their bucket and released into the start arm of the maze for 2 min before the start-arm door was raised. On training trials, one arm was baited with 0.03 g of floating food pellets. After 5 min, or after the fish had consumed the food,

the fish were gently netted out of the maze and back into their holding bucket. Fish were given at least 45 min between trials. On test trials, no food was present in any of the arms and the trial lasted for 10 min. All trials were filmed.

Data Analysis. Videos of all test trials (mixed and unmixed) were analyzed using a custom MATLAB (R2011b; MathWorks) script that counted the number of fish in each arm and in the center of the maze once per second for the entire 10 min of the trial. In addition, the beginning of each trial—from the opening of the start arm door until all the fish had made their first choice—was tracked using the MTrackJ plugin for ImageJ (http://rsbweb.nih.gov/ij). A fish was considered to have made a choice at the first frame of video in which its snout was inside any reward arm. The trajectory of each fish was linked to that individual's group identity (A or B), identified from the video by tag color. Trajectories and counting data were further analyzed in Mathematica (v. 7.0; Wolfram Technologies). All statistics were also calculated in Mathematica.

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