Corrections

APPLIED PHYSICAL SCIENCES, BIOPHYSICS AND COMPUTATIONAL BIOLOGY

The authors note that they omitted a reference to an article by Dumont et al. The complete reference appears below.


ECOLOGY

The authors note that on page 20509, left column, first full paragraph, line 15, “α = (log(a) + log(1/0.95 − 1))/log(s)” should instead appear as “α = (log(a) − log(1/0.95 − 1))/log(s)”. This typographical error does not affect the calculations or conclusions of the article.

PHARMACOLOGY

The authors note that the author name Pallavi Mhsake should instead appear as Pallavi Mhaske. The corrected author line appears below. The online version has been corrected.

APPLIED BIOLOGICAL SCIENCES

The authors note that the author name Jennifer Danniels should instead appear as Jennifer Daniels. The corrected author line appears below. The online version has been corrected.

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PHARMACOLOGY

The authors note that the author name Pallavi Mhsake should instead appear as Pallavi Mhaske. The corrected author line appears below. The online version has been corrected.

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A common rule for decision making in animal collectives across species

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A diversity of decision-making systems has been observed in animal collectives. In some species, choices depend on the differences of the numbers of animals that have chosen each of the available options, whereas in other species on the relative differences (a behavior known as Weber’s law), or follow more complex rules. We here show that this diversity of decision systems corresponds to a single rule of decision making in collectives. We first obtained a decision rule based on Bayesian estimation that uses the information provided by the behaviors of the other individuals to improve the estimation of the structure of the world. We then tested this rule in decision experiments using zebrafish (Danio rerio), and in existing rich datasets of argentine ants (Linepithema humile) and sticklebacks (Gasterosteus aculeatus), showing that a unified model across species can quantitatively explain the diversity of decision systems. Further, these results show that the different counting systems used by animals, including humans, can emerge from the common principle of using social information to make good decisions.

Results

We studied how the behaviors of others should be taken into account to improve the estimations of the structure of the world and make decisions in animal collectives. For a situation with two identical options to choose from (Fig. 1A), we looked for the probability that one option, say x, is a good option given that n₁ and n₂ animals have already chosen options x and y, respectively. We used Bayesian theory to find an approximated analytic expression for this probability as (SI Text)

\[ P(x \text{ is good}) = \frac{1}{1 + a s^{-\left(n_1 - n_2\right)}}. \]

Parameter a measures the quality of nonsocial information available to the deciding individual, and s measures how reliably an individual that has chosen x indicates to the deciding individual that x is a good option. According to Eq. 1, the higher the number of individuals that chose option x, n₁, the higher the probability that option x is good for the deciding individual, and more so the higher the reliability s of the information from the individuals that already chose x. However, each individual that chooses y decreases the probability that x is a good option. Parameter k measures the relative impact of these two opposing effects. Individuals need to decide based on the estimated probabilities in Eq. 1. A common decision rule in animals, from insects to humans, is probability matching, according to which the probability of choosing a behavior is proportional to the estimated probability (35–44),

\[ P_x = \frac{P(x \text{ is good})}{P(x \text{ is good}) + P(y \text{ is good})}. \]

This rule is known to be optimal when there is competition for resources (39, 40) and when the estimated probabilities change in time (41–44). Probability matching in Eq. 2, together with the estimation in Eq. 1, gives that the probability of choosing x is

\[ P_x = \left( 1 + \frac{1 + a s^{-\left(n_1 - n_2\right)}}{1 + a s^{-\left(n_1 - n_2\right)}} \right)^{-1}, \]

and \( P_y = 1 - P_x \) is the probability of choosing y. The main implications of Eq. 3 are apparent in its plot (Fig. 1B). First, decision making in collectives is predicted to be different for low and high numbers of individuals. For low numbers, there is a fast

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transition between preferring one side over the other, whereas for high numbers the transition has an intermediate region with no preference in which the probability has a plateau of value of one-half. There is a clear separation between the low- and high-numbers regimes at the point $\tau = \log(a)/(\log(s) (1-k))$ in which the plateau starts (Fig. 1B; SI Text). Second, in the high-numbers regime, the isoprobability curves are straight lines of slope $k$. We can use this slope to classify three very different scenarios we found to correspond to different experimental datasets: $k = 0$, $0 < k < 1$, and $k = 1$ (Fig. 1C).

For $k = 0$, the animals at one option do not impact negatively on the estimated quality of the other option; this can take place, for example, when animals at one option do not seem to have information about the other option. An important prediction for this case is that for high numbers of animals there is a large plateau of probability one-half of choosing each of the two options (Fig. 1C, Left). To have a significantly higher probability of choosing one option, say $x$, it is then needed not only that $n_x > n_y$, but also to be outside of the large plateau, which means that very few animals have chosen the other option $y$, $n_y < \tau$. A second prediction is that there is a finite number of animals that need to be distinguished; to see this, consider that the probability that option $x$ is a good one (Eq. 1) for $k = 0$ increases monotonically with $n_x$ and converges to 1. The number of animals $n_x$ needed to reach a high probability of 0.95 is given by $a = (\log(a) + \log(1/(0.95 - 1))/\log(s))$ (Fig. S1). Beyond $a$ the probability changes very little, thus in practice it is not necessary to count beyond that number. For a wide range of parameters $a$ and $s$, $a$ has low values, corresponding to counting up to a low number of animals (Fig. S1).

We have found that wild-type zebrafish (*D. rerio*) in a two-choice setup used for tests of sociability (45, 46) make choices that quantitatively correspond to the predictions of the $k = 0$ case. The setup has three chambers separated by transparent walls; a central chamber with the zebrafish we monitor, and two lateral chambers with different numbers of zebrafish acting as social stimuli (Fig. 2A; Materials and Methods). An interesting feature of this setup is that it measures the behavior of a single individual when presented with social stimuli, allowing a direct test of the individual decision rule in Eq. 3. Specifically, we measured the probability that the focal fish chooses each of the two options for a range of configurations (Fig. 2B; each dot is the mean of typically $n = 15$ animals). We found that these experimental results correspond to Eq. 3 for $a = 11.2$, $s = 5$, and $k = 0$ (Fig. 2B, blue surface) with a robust fit (Fig. S2). To make a more quantitative comparison between theory and experiment, we highlighted several lines on the theoretical surface, using different colors to indicate different numbers of fish at option $y$. Fig. 2C compares the probability values for these five lines with the experimental data, showing a close match. The model offers both a quantitative fit to data and a simple explanation of the experimental result. Fish do not choose directly according to the number of other fish, but to how these numbers indicate that a place is a good option, giving a rule of “counting up to 3.”

The close match between experimental data and the decision-making model supports that zebrafish behavior corresponds to probabilistic estimations about the quality of sites using social information. However, the processing steps made by the fish brain need not have a one-to-one correspondence with the computational steps in the theory. Instead, a likely option is that zebrafish use simple behavioral rules that approximate good estimations. We found mechanistic models with simple probabilistic attraction rules for individual fish that approximate well the decision-making model and the data (Figs. S3 and S4).

The second case we consider has parameter $k$ in the range from 0 to 1. For this range, the estimation that $a$ is a good option increases with how many animals have already chosen $x$ and decreases,
although at a slower rate, with how many have chosen option y. This situation might be common, for example, in food search. Animals choosing one option can indicate that there is a food source in that direction, but also that there might not be a food source at the other option. In this case, the probability of choosing x has a plateau in which both options are equally likely, but increasing the number of animals that have chosen x, n_x, reaches a transition region of rapid increase in probability (Fig. 1B). This transition region follows a straight line of slope k in the probability plot (Fig. 1B). This line obeys for high number of animals that n_y ≈ k n_x. This is a Weber law (23, 24), according to which the just-noticeable difference between two groups is proportional to the total number of individuals. Indeed, if we substitute n_x ≈ k n_y into ΔN/N ≡ (n_x - n_y)/(n_x + n_y) we obtain a constant of value k ≈ (k - 1)/(k + 1). A second prediction of the model is that decisions should deviate from Weber behavior at low numbers (below the transition point τ in Fig. 1B).

We have found that decisions made by the Argentine ant (L. humilis) correspond to the case 0 < k < 1. Ants’ choices to turn left and right have been recorded by Perna et al. (24), and we find that they have choice probabilities well described by Eq. 3, except that experimental probabilities do not reach values as close to 0 or 1 as the theory. This difference might be due simply to the fact that ants are not always making turn decisions based on pheromones, but responding to other factors, such as roughness of terrain or collisions with other ants. We therefore considered that ants choose at random with a given probability and otherwise make a decision according to Eq. 3 (Eq. 4). This modification only introduces an overall rescaling in the probabilities, so all structural features described below are present in Eq. 3 (Fig. S5). We obtain a good correspondence with data for high (Fig. 3A) and low numbers of animals (Fig. 3B) with a fit that is robust (Fig. S6). The experimental data are smoother than the theory, without a central plateau, but still with a close correspondence, as also shown in the following analysis. According to Weber’s law, isoprobability curves should be horizontal lines in the ΔN/N ≡ (n_x - n_y)/(n_x + n_y) vs. N ≡ n_x + n_y plane, and this is true both for the theory and experiments for high numbers of total animals N (Fig. 3C). The advantage of this plot is that it magnifies the region of low N, where the data deviate from Weber's law similarly to the theoretical prediction. A further quantitative analysis revealing the close correspondence between theory and data are shown in Fig. 3D. We performed a linear fit to the experimental probability along the lines of constant n_x + n_y depicted in Fig. 3D. Inset. The slope of each linear fit was then plotted against the total number of animals N (Fig. 3D, blue dots). The experimental data has a very close correspondence with the theoretical values in this plot (Fig. 3D, red line). For a high number of animals, both theory and data show Weber behavior, corresponding in this logarithmic plot to a straight line with slope −1 (Fig. 3D, black line) (24). Interestingly, for low numbers of animals, the theoretical prediction of a deviation from Weber behavior corresponds to the data.

The last case we consider has k = 1, for which Eq. 3 depends only on the variable ΔN ≡ n_x - n_y. This situation could take place when there is a high probability that only one of the options is good, and those animals choosing x indicate that x may be the good one in a similar way that those choosing y may indicate that y might not be the good one. We have previously shown (22) that the simple decision rule P_x = 1/(1 + a s^{-ΔN}) explains well a large dataset of collective decisions in sticklebacks, G. aculeatus (25, 26). In these experiments, animal groups were made to choose in two-choice setups with different combinations of social and nonsocial information (Fig. 4A, Far Left). Interestingly, Eq. 3 has the simple rule P_x = 1/(1 + a s^{-ΔN}) as a particular case for k = 1 (SI Text). Indeed, all experimental results (blue histograms in Fig. 4A and Fig. S7) are fit using Eq. 3 with parameters s = 2.5, k = 1 (Fig. 4A, red lines). Additionally, for low numbers of animals (up to τ in Fig. 1B), an approximated ΔN rule can also be found for any value of k but with different values of the nonsocial reliability parameter a (SI Text). Therefore, the stickleback data can be fit with any value of k (green and blue lines in Fig. 4A and Fig. S7 for k = 0.5 and k = 0, respectively), with robust fits (Fig. S8). The reason why in this case k can have any value is that its main effect is to control the slope of the boundaries of the plateau of probability 0.5, which is not present in the experimentally explored region of the stickleback dataset (Fig. 4B, white triangle). Still, all these fits
also the diversity in number discrimination schemes used in collective decisions, including counting up to a given number of animals, counting the difference of animals choosing among options, \( \Delta N \), or the relative difference, \( \Delta N/N \), as well as observed deviations from these ideal cases and the existence of different counting regimes for high and low numbers as observed in many species, including humans (47, 48). A single mathematical rule contains all these cases and can be used as a first-principles approach to quantitatively study decisions in animal collectives.

One important ingredient of our theory is the use of probability matching (Eq. 2); for symmetric decisions, it implies a functional form of the type \( P_x = \frac{f(x)}{f(x) + f(y)} \). Our model in Eq. 3 is a particular case of this function, with \( f(x, y) = \frac{y}{\sqrt{x^2 + y^2}} \) derived from an approximation to Bayesian estimation. Interestingly, many previous approaches derive from the form \( P_x = \frac{f(x)}{f(x) + f(y)} \) (21, 22, 27, 28), which is also a particular case of \( P_x = \frac{f(x)}{f(x) + f(y)} + f(y) \), and therefore compatible with probability matching. In other cases, the basic form \( P_x = \frac{f(x)}{f(x) + f(y)} \) has been modified by adding constant terms (29, 30) or an extra function (25), as \( P_x = \frac{f(x)}{f(x) + f(k)} \), with \( k \) a constant when animals have access to a single choice (31, 32, 34). Weber behavior can also be seen as a particular case. It has been previously described using a function (24) that can be expressed as \( f(x, y) = 1/2 + \delta(n_x - n_y)/(n_x + n_y) \), with \( \delta \) between 0 and 1/2. This function obeys \( f(x, y) = f(x, x) = 1 \), so in this case \( P_x = f(x, x) \), following Weber behavior.

These previous functions are very useful when applied to particular datasets because they may use few parameters in these conditions. In particular, our previous model (22), a particular case of Eq. 3 (SI Text), used only one parameter in the symmetric experiments with sticklebacks, and a model with two parameters described the ants dataset (24). However, these two models cannot fit the three datasets or even two of them (Fig. S9 A and D and S10). For the zebrafish data in Fig. 2, none of the previously proposed functions (21, 22, 24, 27–29) give a good fit of the plateau in the data (Fig. S9). Our approach has been developed to be applied in very different species and conditions, here tested for three large datasets in three different species. One important factor in this ability to describe different datasets is that our basic function \( f(x, y) \) has a term \( s^{-k(n_x - n_y)} \) that captures how the estimated quality of an option depends not only on the animals choosing that option but also on the animals choosing the other option. These two sources of information are balanced by parameter \( k \), and different datasets are found to correspond to different balances \( k \).

Previous functions describing ant foraging include a constant term that represents a threshold of pheromone concentration below which ants do not react (24, 27, 28). In this way, these functions can describe the deviation from Weber’s law at low pheromone concentration (24). In our case, the theory naturally shows this behavior as one more particular case of the predicted difference between a low and high number of animals. Comparing the two approaches, it is interesting to consider that the behavior for low numbers that is predicted from estimation theory can be achieved in ants using a threshold of pheromone concentration.

An advantage of our approach is that the form of the function \( f(x, y) \) is derived for any type of setup simply from estimation given non-social sensory data and the behaviors of others (SI Text). For example, we predict for a symmetric setup with \( N \) options a generalization of Eq. 1 of the form

\[
P(x \text{ is good}) = \frac{1}{1 + M \delta s^{-k(n_x - n_y)}}
\]

with \( M = \sum_{n_x} n_x \) the total number of animals choosing any option except \( x \) (see Eq. S10 for the more general case of asymmetric choices).

A further advantage is that the parameters \( a \), \( s \), and \( k \) are not only fitting parameters but have expressions, Eqs. S4, S9, and...
S16, respectively, which give additional predictions. For example, the social reliability parameter is given by

\[ s = \frac{P(y|x,C)}{P(y|X,C)} \]

with \( \beta \) a given animal behavior. This expression means that the social reliability parameter \( s \) is higher for a behavior \( \beta \) that is produced with high probability when \( x \) is a good option, and with very low probability when it is not a good option. Among all behaviors, those with higher \( s \) allow an individual to obtain a higher probability that option \( x \) is a good one (Eq. 1), so we expect them to have a larger effect on collective decision making.

Another advantage of an approach based on a theory of estimation is that generalizations of the theoretical expressions can be envisaged deriving models using fewer assumptions. For example, including dependencies in the behaviors of the other individuals and explicit space and time variables should be natural extensions of the theory.

Materials and Methods

Experimental Protocol for Zebrafish. All procedures met with European Economic Community (EEC) guidelines for animal experiments under Directive 86/609/EEC. Experimental procedures were approved by the Bioethics Sub-committee of Consejo Superior de Investigaciones Científicas. We used wild-type adult zebrafish, D. rerio, of both sexes. Fish were acclimatized to the setup water for 1 d before the experiments (Fig. S11). At 1 h before the experiment, each fish was isolated and fed to ensure uniform nutritional status across individuals. A focal fish entered the setup and swam freely in a central chamber between two social chambers with different number of fish and separated from the choice chamber by glass. Once a fish had been recorded for 5 min it could be placed in one of the lateral chambers as a social stimulus for another fish. The fish in the lateral chambers were interchanged between trials to randomize trials to ensure uniformity, and standardized. The central chamber of the setup was washed between trials to remove odor traces. We computed the probability \( p_s \) as the fraction of time the focal fish spent on the black region close to one of the social chambers, \( x \). This fraction of time converges to \( p_s \) for a fish that makes repeated decisions choosing \( x \) (with probability \( p_s \)). A total of 238 fish were tested only once. To test the effect of previous experience, another 233 trials were performed with fish that were tested several times. We found no significant difference between the two groups in the mean times spent at each side (Fig. S12), so all data were pooled for Fig. 2.

Model with Noise Added to the Decision Rule. The model in Eq. 3 has a good agreement with data from experiments using the Argentine ant, L. humile (24), except that experimental probabilities do not reach values as close to 0 or 1 as the theory. To account for the experimental data, we made a simple modification of the model by assuming that the ant has some probability \( p_{rand} \) of making the decision at random motivated by unknown factors. Then, with probability \((1 − p_{rand})\), the ant makes the decision according to Eq. 3. Therefore, the probability of turning toward \( x \) is

\[ P_x = \frac{p_{rand}}{2} + (1 − p_{rand}) \left( 1 + \frac{1}{1 + a r (s_x)} \right)^{-1} \]

The parameters that best fit the data are \( a = 2.5, s = 1.07, k = 0.53, \) and \( p_{rand} = 0.39 \). This same model can be applied to the zebrafish and stickleback datasets, but in these cases the best fit is obtained for \( p_{rand} = 0 \) which corresponds to Eq. 3.

Analysis of the Ants Dataset. Both the raw dataset and preprocessing routines were provided by Perna et al. (24), and we used their data assuming no evaporation of pheromone (this assumption does not change the results significantly). We calculated from the data the probability of turning right or left, not a continuous angle, to compare directly to our predicted probabilities. To reduce the noise in the experimental maps of Fig. 3, we symmetrized the data so that the probability shown at point \((n_x, n_y)\) is obtained as \( (P_x(n_x,n_y) + 1 − P_x(n_y,n_x))/2 \).

Experimental data from Perna et al. (24) measures a quantity that is proportional to the number of ants previously at the left/right side of the deciding ant, not directly the numbers, so the number of ants \((n_x, n_y)\) used in the plots are related to the actual number of ants that count for the decision \((n_x_{true}, n_y_{true})\). The relation means that the model still applies but with \( s = s_{true} \), where \( s_{true} \) is the actual value of the reliability parameter.

Asymmetric models. For the case of sticklebacks deciding in the presence of a predator (Fig. 4A, Middle), we derived the more general asymmetric version of Eq. 1, Eq. S22 (Figs. S13 and S14). We also derived Eq. S23 for the case with two different types of replicas (Fig. 4A, Bottom).

Fitting Procedures. To fit the model’s parameters to the data, we performed 2D exhaustive searches in the space of parameters. For functions with more than two parameters, we performed the search successively with all possible pairs of parameters. In these cases we repeated the fit several times starting from different initial conditions, always getting the same final result.

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