Conflict and Strategy in Collective Computation

Eleanor Brush [*][†], **David Krakauer** [†][‡], **and Jessica Flack** [†][‡]

[*]Princeton University, Princeton, NJ, USA,[†]Wisconsin Institute for Discovery, University of Wisconsin, Madison, USA, and [‡]Santa Fe Institute, Santa Fe, USA

Function in biological systems emerges from the behavior of tens (e.g. animal social groups) to millions of components (e.g. neural systems), which have imperfect information and only partially-aligned interests. Components make pairwise decisions and the combined decisions produce a system-level output. The roles of conflict and strategy in such collective computations are poorly understood. Leaky-integrator models have been used to study neural pairwise decision-making. Here we extend a leaky-integrator model (LIM) to study pairwise decision-making under conflict and error in animal social groups. Our model system is a macaque society. The decision at the pairwise level is whether to emit a subordination signal. The output of the collective computation is the distribution of social power (DSP). We study how properties (waiting time, error rate) of the decision to signal and the strength of conflicts of interest influence decision-making strategies and how these strategies influence the collective output. We find that conflicts of interest in the decision process can improve the average error rate of all decisions being made. We then identify a global property of the decision network that is informative about the individuals' underlying values, indicating that the collective computation is nontrivial. Finally, we find that the shape of the DSP can be controlled by changing the costs of waiting for a decision. The successful use of the LIM in the neural and social contexts suggests general principles of collective computation due to decision-making tradeoffs common across substrates and scales.

collective computation, noisy learning, leaky integrator, decision, social network, consensus, power

In many biological systems, functional patterns emerge from the interactions between individual components making decisions under uncertainty. This includes the decision-making behavior of an animal that emerges from the firing decisions of billions of neurons; social structures, like the distribution of power, arising from the status-signaling decisions in chimpanzee and some macaque social groups; the collective motion of fish schools emerging from the velocity and alignment decisions of individual fish; and the toxins produced by quorum sensing bacteria once the bacteria have aggregated at sufficient density, arising from individual cells' decisions to produce a signaling molecule (Table 1). In each of these examples the components make decisions by accumulating information extracted from noisy environments. Their joint behavior produces an aggregate-level pattern with fitness consequences for the components and the collective. This two part process, which has now been described in a number of systems, constitutes a collective computation.

An open question is how components should choose their decision-making strategies when there are conflicts of interest between components, perceptual errors, and noisy inputs, in order to collectively compute outputs with positive payoffs. This requires understanding (1) how the strength of the conflicts of interest and the importance given to properties of the decision, including waiting time and accuracy, determine what strategies should be used, (2) how the decisions of the components combine to produce the computation, and (3) how decision-making strategies impact the collective computation.

A variety of models, including the sequential probability ratio test (SPRT) and the leaky-integrator model (LIM), have been developed to study how components choose among alternatives in a noisy environment. For example, the LIM has been used to describe the firing of neurons during a motion coherence task in which a subject must decide whether it is seeing dots moving left or right. Both the SPRT and the LIM keep track of the amount of accumulated evidence supporting alternative choices. The LIM has the advantage over the SPRT of allowing for memory loss, but application of the LIM to explain, for example, neural firing, has been largely phenomenological. (More details on the SPRT are provided in the Supplemental Information.) Here we develop a LIM by deriving stochastic differential equations that mechanistically specify how information is accumulated by components and used in decision-making. We use published empirical and computational results from work on collective computation in a well-studied model system to justify the form of our equations. The model system is a captive macaque society (*Macaca nemestrina*, N=48) that is characterized by social learning at the individual level, social structures that arise from nonlinear processes and feed back to influence individual behavior, frequent non-kin interactions and multiplayer conflict interactions (see Appendix for more details) [5–9, 13]. We then extend the LIM in two ways: we introduce a game-theoretic component and we study a network of pairwise decisions generated by our stochastic model to explore how pairwise interactions combine to produce a collective output and how the output is influenced by the components' strategies.

Model

Model System. In our model system, a component is an individual monkey and the decision it makes is whether or not to emit a silent-bared teeth display, signaling agreement to the subordinate role in its relationship with another monkey. The decision to signal depends on the perceived magnitude of the asymmetry in their fighting abilities. A monkey emits the subordination signal when it perceives the cost of continued aggression to be greater than the cost of subordination, in other words, when it perceives the asymmetry to be large and in the other monkey's favor. Encoded in the directed network of subordination signals is the output of the collective computation: the distribution of social power (DSP). Social power is operationalized as the degree of agreement in the group that an individual is capable of successfully using force during

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fights. The DSP is known in this system to affect interaction and conflict-management cost. For example, heavy-tailed distributions make otherwise costly conflict-management strategies, like policing, accessible, at least to individuals who sit in the tail. The DSP is obtained by quantifying consensus in the network about a node's capacity to use force successfully. Consensus can be measured using several algorithms that return consensus scores for each individual. These algorithms can be viewed as alternative hypotheses for how power is computed in the system. (Details are provided below in the Section "Collective Computation".) We study how the strength of the input to the decision process (the asymmetry in fighting ability), the strength of the conflict of interest between animals, and the importance of different properties of the decision to signal (waiting time, error rate) influence what decision-making strategies the animals should use and how these decision-level properties impact the shape of the DSP.

Stochastic differential equations. We first derive a stochastic model describing decisions made about or between pairs of components. In the decision-making literature, the stochastic differential equations (SDEs) used to model noisy decision processes are usually presented without any mechanistic justification. In contrast, the Langevin equations used to describe the dynamics of the concentrations of solutes can be derived from a mechanistic description of chemical reactions [11]. By following the mathematical derivation of the SDEs in chemical systems given by Gillespie [11], we can derive the SDEs used in the leaky integrator model. In our model system, each component is a monkey accumulating evidence about its ability relative to another monkey by keeping track of the fights it has won and lost. We could use the same derivation to reach a set of SDEs describing the firing rates of neural populations responding to left and right motion in the visual field, the system to which the LIM has been applied most frequently. More details about this system are provided in the Supplemental Information.

In our model system, for a given pair of monkeys A and B, A has a decision variable, X_1, indicating the evidence that it has accumulated about its ability relative to B, and similarly B has a decision variable, X_2. In the absence of new information, the decision variables leak back towards 0 with rate ℓ. (A table of all variables used in the text is given in Table 2.) If there is no input, then over a period of length τ each decision variable decreases as $X_i(t + \tau) = (1 - \ell\tau)X_i(t)$.

If there is input from the environment, each decision variable incorporates the new evidence. Specifically, X_1 increases by an amount b when monkey A wins a fight against monkey B and decreases by b when it loses, and conversely for X_2. To calculate the variables at time $t+\tau$, we count how many times each type of input occurred in the time since t and add the changes resulting from these events to the background leaky estimate:

$$X_1(t + \tau) = (1 - \ell\tau)X_1(t) + b \times \# \text{ of times } A \text{ wins in } [t, t+\tau]$$
$$- b \times \# \text{ of times } B \text{ wins in } [t, t+\tau]$$
$$X_2(t + \tau) = (1 - \ell\tau)X_2(t) - b \times \# \text{ of times } A \text{ wins in } [t, t+\tau]$$
$$+ b \times \# \text{ of times } B \text{ wins in } [t, t+\tau].$$

There are stochastic factors affecting how many times each type of event occurs. Our first assumption is that the rates at which the inputs (fights) occur is constant over time. We can thus describe the number of each type of event with a Poisson random variable, N_A and N_B, giving

$$X_1(t + \tau) = (1 - \ell\tau)X_1(t) + bN_A - bN_B$$
$$X_1(t + \tau) = (1 - \ell\tau)X_2(t) - bN_A + bN_B.$$

If fights happen at a rate r and A wins with probability c and loses with probability $1 - c$, then the expectation of N_A and N_B in a period of length τ are, respectively, τrc and $\tau r(1-c)$. In our model system, c is related to the strength of the asymmetry in the monkeys' abilities: if A is stronger then it is more likely to win and $c > 0.5$. In the neural case, c is related to the "coherence" of the visual stimulus. A value of c close to 0 or 1 means that the decision is easier to make than when c is close to 0.5.

If enough events happen in the period of time from t to $t + \tau$ then we can approximate the Poisson random variables with normal random variables with mean and variance equal to the mean of the Poisson random variables. Our second assumption, then, is that the period of time of length τ is long enough to make this approximation. Let Z_A and Z_B, be independent standard Normal random variables, i.e. with mean 0 and standard deviation 1, giving

$$X_1(t + \tau) = (1 - \ell\tau)X_1(t) + b\left(\tau rc + \sqrt{\tau rc}Z_A\right)$$
$$- b\left(\tau r(1 - c) + \sqrt{\tau r(1-c)}Z_B\right)$$
$$X_2(t + \tau) = (1 - \ell\tau)X_2(t) - b\left(\tau rc + \sqrt{\tau rc}Z_A\right)$$
$$+ b\left(\tau r(1 - c) + \sqrt{\tau r(1-c)}Z_B\right).$$

Finally, as we make the period of time shorter and shorter, making τ infinitesimally small, these equations become stochastic differential equations,

$$dX_1 = (-\ell X_1(t) + br(2c - 1))\, dt + b\sqrt{rc}dW_A t$$
$$- b\sqrt{r(1 - c)}dW_B t$$
$$dX_2 = (-\ell X_2(t) - br(2c - 1))\, dt - b\sqrt{rc}dW_A t$$
$$+ b\sqrt{r(1 - c)}dW_B t,$$

where dW_A and dW_B are independent Wiener processes, respectively, the wins monkey A and the wins for monkey B. The assumptions about the timescales on which inputs occur are reasonable in the social system, and the successful application of this type of model to neural populations implies they are not unreasonable in that system.

Since W_A and W_B are independent of each other, we can further simplify by combining them into one process W:

$$dX_1 = (-\ell X_1(t) + br(2c - 1))\, dt + b\sqrt{r}dW_t$$
$$dX_2 = (-\ell X_2(t) - br(2c - 1))\, dt - b\sqrt{r}dW_t.$$

We assume that $X_1(0) = X_2(0) = 0$. The sensitivity of our model to initial conditions is discussed in the Supplemental Information. In Table 2, we list the inputs, outputs, and variables of the decision model and how they should be interpreted in the social and neural systems.

Note that the two decision variables experience the same noise, which is due to the randomness in fight outcomes. In our model system, this is a reasonable assumption since both monkeys should come to the same conclusion about whether a fight has been won or lost. However, in neural systems or other social systems in which the evidence requires interpretation, there may be additional noise sources for each individual due to their independent assessments of the evidence, which can be modeled with independent Wiener processes, as in [1, 2, 4, 10].

Reaching a decision. There are two ways to use the decision variables X_1 and X_2 to make a decision. If the difference in the variables can be observed, it indicates the relative strength of the amounts of evidence for each option. If we write $Y = X_1 - X_2$, the pair should decide on X_1 when Y

is large and positive and on X_2 when Y is large and negative. Therefore, we set two thresholds, T_1 and T_2, such that, if $Y > T_1$, the decision is that A has higher ability and, if $Y < -T_2$, the decision is that B has higher ability. However, it may be the case that the difference in the variables cannot be observed. In this case, the decision depends on whether X_1 or X_2 hits a threshold first. Again, we set two thresholds, T_1 and T_2, and, if $X_2 < -T_2$, the decision is that A has higher ability and, if the $X_1 < -T_1$, the decision is that B has higher ability.

For neural systems, the two stochastic equations describing the activity of two neural populations integrating environmental evidence are often reduced to a one-dimensional equation describing the difference in the activity levels, Y [1, 2, 4]. The reduced model is easier to analyze, but it assumes a neural mechanism for calculating the difference in activity rates and there is no empirical basis for this. In social systems like our model system, the one-dimensional simplification implies a third party evaluating the difference in the evidence each animal has accumulated, but it is more realistic to assume that a decision, i.e. the emission of a signal from one of the two animals, is only reached when one of the two animals' decision variables goes below its threshold. Because the two-dimensional process is more appropriate for the social system (and perhaps the neural system as well), we use the two-dimensional system in our analyses.

In the Supplemental Information and in Supplemental Figure S1, we show that, with our choice of initial conditions $X_1(0) = X_2(0) = 0$, the two-dimensional and one-dimensional processes are actually equivalent. We also show that, if $X_1(0) - X_2(0)$ is not zero, then the error rates of the two processes are *nearly* equal. If the two decision variables experience independent sources of noise, as in the models of neural decision-making in [1, 2, 4] and in the model of social decision-making in [10], then the two processes will still perform comparably. The fact that the existence of a third-party decider only negligibly affects the model output means that the results of our model should apply in either case and it highlights the similarity between the social and neural systems.

Utility of decision. A "good" decision is one that reaches the correct output quickly, i.e. the expected time until a decision is reached (decision time, DT) and the probability that an incorrect decision is made (error rate, ER) are low. However, it is impossible to minimize both simultaneously, since waiting longer and accumulating more evidence makes the decision more accurate. We also allow for individuals to have preferences for the outcome of the decision, independent of correctness. Each component involved in the decision prefers a different outcome and wants to maximize the probability that the preferred outcome is reached (probability of decision preference being chosen, DP_i). To describe the tradeoffs between error rate, decision time, and preference, we quantify the utility of the decision process by introducing three weights, w_1, w_2, and w_3 such that $w_1 + w_2 + w_3 = 1$. These weights describe how the three quantities are prioritized. For individual i, we define

$$U_i = w_1 \text{ER} + w_2 \text{DT} + w_3(1 - \text{DP}_i).$$

The decision is better if U_i is lower. In the social system, w_2 can be interpreted as the cost of fighting since when w_2 is higher, the time spent fighting until a decision is reached is more costly. It is impossible for both components to maximize DP_i, so w_3 indicates the strength of the conflict of interests between components. In the social system, w_3 captures the benefit from being the dominant animal in a pair and the ex-

tent to which the weaker animal perceives the subordination contract to be more costly than continued fighting. We show in the Supplemental Information that each of the decision properties, ER, DT, and DP, satisfies a partial differential equation that depends on the decision thresholds and the parameters of the model.

In models of animal conflict and dominance relationships, it is often assumed that both animals prefer to be dominant, regardless of whether they are actually stronger [10, 12]. However, a subordination signal from a weaker to a stronger animal may lead to a more stable and affiliative relationship [6], so error rate, as well as decision preferences, need to be considered in our model system. Conversely, in models of neural decision making, error rate, rather than decision preference, is usually assumed to be the decision property driving decision-making strategies [1]. Our model connects these bodies of work by allowing for both error rate *and* decision preference to affect the components' strategies.

Nash equilibrium thresholds. In a group of individuals, each with a value a_i, the difficulty with which the pair (i, j) makes a decision increases with the difference in value. Specifically, $c_{ij} = \frac{\exp(a_i - a_j)}{\exp(a_i - a_j) + 1}$. In the social system, the value a_i reflects an animal's fighting ability. In the neural system, the value a_i is high if the property (e.g. left motion) a neural population responds to is abundant in the visual stimulus. We assume each individual has the same decision threshold for all the decisions processes with each of its peers and, given those thresholds, each individual i has a utility U_{ij} from its decision process with individual j and a total utility given by the average of these, $\langle U_{ij} \rangle_j$. For each set of values $\{a_1, \ldots, a_N\}$, we find the Nash equilibrium thresholds $\{T_1, \ldots, T_N\}$ such that no individual has an incentive to choose another threshold to improve its utility. (For further discussion of Nash equilibria, see the Supplemental Information). Since the Nash thresholds depend on the values $\{a_1, \ldots, a_N\}$, we repeatedly draw a set of values from a uniform distribution and find the Nash thresholds for each set. Then, for each rank $i = 1, \ldots, N$, we find the average Nash threshold for an individual with the ith highest ability. Our procedure for finding the Nash equilibrium thresholds and a discussion of how these thresholds might be reached is provided in the Supplemental Information.

Collective computation. In both the neural system and the social system, the decision can also be thought of as an opinion. In the neural system, when the neural population evaluating the difference in activity levels of upstream populations fires, it can be viewed as the opinion of the decider population that the relative 'value' of one upstream population is higher than another. In our model system, when one monkey emits the subordination signal, it communicates its opinion that the receiver is capable of using force. In each case, the opinions in favor of one of each pair of components form a directed network and the collective opinion or degree of consensus in the group about the value of a given component is encoded in this network. In the social case, a monkey's social power is given by the degree of consensus about its ability to use force successfully and the distribution of these consensus scores across the group is the distribution of social power (DSP) [3, 5].

The integration of the opinions about or between each pair of components into a set of consensus scores is the collective computation. There are a number of algorithms that can be used to compute these consensus scores [3, 5]. Here we ask which consensus algorithm is most informative about the components' values. To do this, we use the algorithms to compute a DSP from networks generated by our model of

decision-making and ask which model-generated DSP is most informative about the underlying values.

The simplest algorithm is the unweighted in-degree of a node, i.e. the number of opinions in favor of each individual. If these opinions have different strengths, we can also consider the weighted in-degree of a node, which is a finer measure. The third is the entropy of the distribution of the weights of the opinions about each individual, which gives a coarse measurement of the uniformity of all of the opinions in the group about a focal individual. The fourth is the eigenvector centrality of the network, which measures how central each node is in the global structure of the network. For more details see [3]. Using many random sets of values $\{a_1, \ldots, a_n\}$ to generate Nash thresholds $\{T_1, \ldots, T_N\}$ and then a directed network, we find the mutual information between the consensus scores from the networks and the values, for each consensus algorithm. (Details on mutual information are provided in the Supplemental Information.) We also find the average skewness of the set of consensus scores given by each algorithm.

To create a directed network, for each set of values $\{a_1, \ldots, a_N\}$ and Nash thresholds $\{T_1, \ldots, T_N\}$, we find the probability that each pair will reach either outcome and the expected time it will take to make a decision. We draw the direction of decision between each pair according to these probabilities, using the convention that a decision is sent from i to j if the decision is in favor of j. In our model system, once a monkey decides to emit the subordination signal, it will continue to emit the signal to the receiver until their relationship switches. In general, if a component can accumulate evidence and make a decision quickly, it will be more certain and have a stronger opinion than if it made the decision more slowly. To describe the accumulation of signals over time and to allow for opinions of different strengths, at each point in time t, we define the weight of the edge from i to j to be

$$\begin{array}{ll} 0 & \text{if the decision is in favor of } i \text{ or } DT_{ij} > t \\ t - DT_{ij} & \text{if the decision is in favor of } j \text{ and } DT_{ij} < t. \end{array}$$

A schematic of the whole model, starting with components' values and ending with the collective computation, is provided in Supplemental Figure S2.

Results

Conflicts of interest. We start with a pair of individuals, i.e. a group of size two, to build intuition for how the optimization weights affect the Nash equilibrium thresholds. If the error rate of the decision is important ($w_1 = 1$), the Nash strategies are for the weaker individual to set his threshold as low as possible and the stronger animal to set his threshold as high as possible. This will, with high probability, lead to the weaker animal signaling, which is the correct outcome. When only decision preference matters and there is a strong conflict of interest between the individuals ($w_3 = 1$), the Nash strategies are for both to set their threshold high since each prefers to wait for the other to signal and there is no incentive for the individuals to stop accumulating evidence. As the importance of decision time increases, the Nash thresholds of both individuals decrease in order to reach the decision more quickly (Figure 1). The error rate with which a pair using Nash thresholds can reach a decision is lowest when only error rate matters ($w_1 = 1$) and increases as either decision time or decision preference becomes more important (Figure 1).

In a group with more than two individuals, the Nash thresholds respond to the optimization weights in a similar way: when error rate is most important, the Nash strategies are for strong animals to have high thresholds and weak animals to have low thresholds, whereas, when decision preference is most important, the Nash strategies are for all animals to have high thresholds (Figure 2). There is, however, a significant change brought about by introducing more components: as long as there are non-zero waiting costs, the average error rate of all decisions, and particularly those made by low-valued animals, in a group using Nash thresholds *decreases* as decision preference becomes more important (Figure 2).

If a low-valued individual could improve its error rate by raising its threshold, it would do so when error rate is important. Instead, it is the higher-valued individuals' raising their thresholds that improves the error rate of the low-valued individuals. If a higher-valued individual raises its threshold, it increases its decision times with *all* individuals, increases the error rate of its decisions with the individuals *above* it, and decreases the error rate of its decisions with the individuals *below* it. When only error rate and decision time matter, the net effect is to increase $\langle U_{ij} \rangle_j$, and the individual has no incentive to incur this cost. Increasing the weight given to decision preference provides the incentive for higher-valued individuals to raise their thresholds and consequently for the lower-valued individuals to raise their thresholds, resulting in an improvement in the error rates of decisions made by low-valued components. The increase in the accuracy of decisions by low-valued components outweighs the decrease in accuracy in decisions by high-valued components, resulting in an increase in the average error rate of *all* decisions. (We analyzed a group of $N = 20$ individuals. In Supplemental Figure S3, we show that our results are robust to increasing group size.)

Waiting time . Pairs with similar and high values always take as long or longer to make a decision than any other pairs do (Figure 2). When waiting costs are low, pairs with different values also take a fairly long time. At intermediate costs, most pairs can reach a decision quite quickly, except those who have similar and high abilities. When waiting costs are high, all pairs reach decisions quickly.

Algorithms. For each consensus algorithm, the mutual information between the DSP and the underlying distribution of fighting abilities increases as the average error rate decreases (Supplemental Figure S4). Hence the information content of the consensus scores produced by every algorithm is maintained or improved when decision preference is prioritized over error rate, for any group with more than two components.

We first consider the information content of the algorithms applied to fully developed networks. When waiting costs are low, the "finer" consensus algorithms—weighted in-degree and eigenvector centrality—outperform the "coarser" algorithms—in-degree and entropy—because, in these circumstances, the edges of the decision network tend to be accurate and the finer measures make use of more information in the network. When decision preference is the most important and there are no waiting costs ($w_2 = 0$, w_1 low), a high-valued component will sometimes err in its decision with a low-valued component. This type of error gives the low-valued component an inappropriately high eigenvector centrality score, whereas its weighted in-degree is still quite low, so that weighted in-degree outperforms eigenvector centrality under these circumstances. Otherwise, eigenvector centrality is the the most informative when waiting costs are low (Figure 3). When waiting costs are higher, unweighted in-degree and entropy are more informative then eigenvector centrality, but only by a very small margin. A more detailed discussion of the advantages of different algorithms under different conditions is provided in the Supplemental Information.

When we look at how the information content of the consensus scores change as the network is developing, we find that the information content of the scores produced by eigenvector centrality increase as more edges are formed (Figure 3). The information content of the other algorithms may surpass eigenvector centrality when the network becomes fully formed, but their information content sometimes decreases as incorrect decisions are added to the decision network. Eigenvector centrality has the advantages of never losing information content and consistently performing well on networks that are not fully formed.

Aggregate-level output properties. For each measure of consensus in the decision network, we find the average skewness of the distribution of consensus scores of a group using Nash thresholds, as a function of the optimization weights. We find that, for all measures, skewness is maximized at intermediate waiting costs and does not depend strongly on the tradeoff between error rate and preference (Figure 4). (Example distributions are shown in Supplemental Figure S5 and results for all algorithms are shown in Supplemental Figure S6.) More details on this pattern are provided in the Supplemental Information.

Discussion

In some situations, conflicts of interest between members of a group can sow discord and lead to gridlock. Only by considering a group with more than two components do we find the surprising result that strengthening the conflicts of interest between components can improve the accuracy of a collective computation. When we observe a collective phenomenon in nature, it might lead us to think that the components of the system are working together to produce that output. Our result shows that not only can a collective computation be performed despite conflicts of interest, but it can even by facilitated by them. We know of no models of neural decision-making that allow for conflicts of interest between neural populations, but our results suggests that we might expect to find such conflicts since they could improve the accuracy of their collective output, i.e. the brain's decision. Our finding also suggests that if we were to try to design a system with which to perform collective computation, it might be advantageous to introduce conflicts of interest between its components.

While there is no measure of consensus that produces the most informative scores across the possible optimization weights, eigenvector centrality emerges as a generally good way to measure consensus, especially while the decision network is forming. In previous work, we found that eigenvector centrality produced consensus scores that were informative about components' functional behavior in our macaque model system, as well as in a physicist collaboration network, which suggests that the components—the macaques or the physicists—are using eigenvector centrality, or an approximation thereof, to decide how to behave with respect to their peers. This agrees with our finding that it is an informative measure to use. Since this is the most computationally intensive measure we consider, this shows that the collective computation is a nontrivial one. The need of the components in a system to make estimates of the distribution of consensus scores in their group might select for components more capable of approximating such a complex measure.

In our model system, we observe a right-skewed distribution of power, which allows the very few individuals in the right tail to police the aggressive interactions between other members of the group [3, 5, 8]. Hence an important question is how this property can be tuned or controlled. If skewness in the DSP results from skewness in the distribution of fighting abilities, the animals would not be able to control the skewness of the DSP. If, on the other hand, the skewness results from changing fighting costs, as we find in our model, the animals might be able to tune these costs to construct a beneficial DSP. In a spatially explicitly simulation model of a macaque social group, the "aggressiveness" of the animals was found to affect the shape of the dominance hierarchy [12]. While the mechanisms of that model are quite different, our results are consistent with their finding that changing the underlying distribution of fighting abilities is not required to change the distribution of dominance or power. More details on the implications for understanding variation in the skewness of DSP across macaque species are provided in the Supplemental Information.

While our finding that the consensus measure the monkeys seem to be using in our model system is generally the most informative one suggests a coarse agreement between our model and the data, there are discrepancies between the decisions times our model predicts and those observed in the data. In our data, we observe that pairs of animals with high abilities reach agreements about their relative dominance, but that pairs of animals with low abilities sometimes do not reach such agreements (Flack, unpublished data). In our model, decisions between pairs who have similar and high abilities always take as long or longer than decisions between any other pairs. This indicates that our simple model is missing a level of social complexity that could explain this empirical pattern.

There are (at least) two modifications to the model that we expect would produce results closer to the empirical observations. First, in the model, the rates at which animals fight each other do not depend on the abilities of the animals. However, it is likely that animals with lower abilities are less mobile and encounter their peers at a lower rate than animals with higher abilities who are more free to range throughout the group. In the model, this heterogeneity in encounter rate would make the decisions between animals with low encounter rates take longer. Second, in the model, all animals value preference, error rate, and waiting costs equally. However, it is likely that the benefits from receiving a subordination signal from a partner and the costs of fighting depend on both animals' abilities. If animals with low ability do not value an agreement with other animals with similar abilities, there would be less incentive for them to reach an agreement. These types of heterogeneity would make our model more biologically realistic when applied to the social system, but without them it is general enough to be applied to a number of systems in which collective computations are being performed.

Our noisy learning model can be applied to two different biological systems, one social and one neural, and our model reduces to previously studied "war of attrition" games in the game theory literature when the abilities of the two individuals are equal. Conflict and strategy are not usually ascribed to the neural model, and the war of attrition is not usually thought of as a process through which the pair of competitors reaches a decision about an external truth. However, the similarities between these three frameworks—social decision making, neural decision making, and game theory—suggest that there are common principles of decision making through conflict that are applicable to a number of systems. Our work is a first step toward unifying these different frameworks and better understanding the importance of conflict and strategy in collective computation.

Appendix: Model System

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Appendix: Testing the algorithms and notion of "correctness"

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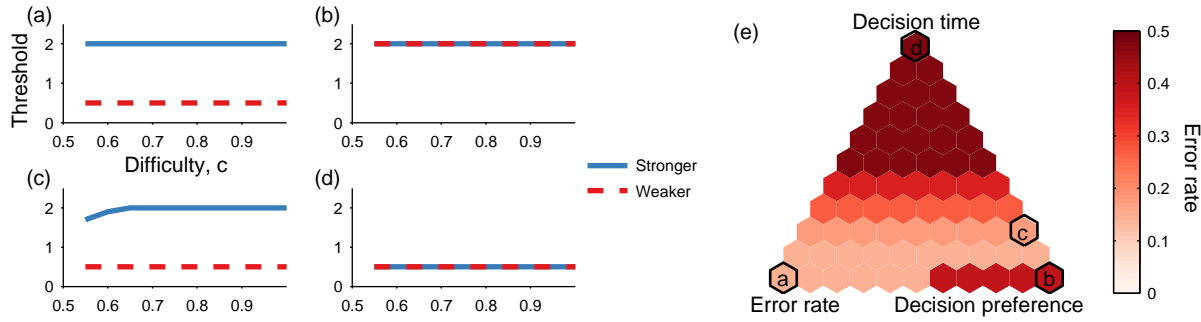
Fig. 1. Nash thresholds depend on the optimization weights. The error rate of a pair using Nash equilibrium thresholds increases as the weight given to either decision time or decision preference increases. In (a)-(d) the lines show the Nash equilibrium thresholds for a pair of animals as a function of the difficulty of the decision (c). The optimization weights for each panel are indicated in the simplex with the corresponding letter. In (e) the color indicates the error rate of a decision made by a pair making a difficult decision ($c = .55$) using Nash equilibrium thresholds, as a function of the optimization weights, w_1, w_2, w_3. In the lower left corner of the simplex, only error rate matters ($w_1 = 1$). In the upper corner, only decision time matters ($w_2 = 1$). In the lower right corner, only preference matters ($w_3 = 1$). Parameters: $w_1 = 1$, $w_2 = 0$, $w_3 = 0$ (a), $w_1 = 0$, $w_2 = 0$, $w_3 = 1$ (b), $w_1 = 0$, $w_2 = 0.2$, $w_3 = 0.8$ (c), $w_1 = 0$, $w_2 = 0$, $w_3 = 1$ (d), $b = 1$, $r = 1$, $\ell = 0.1$ in all panels.
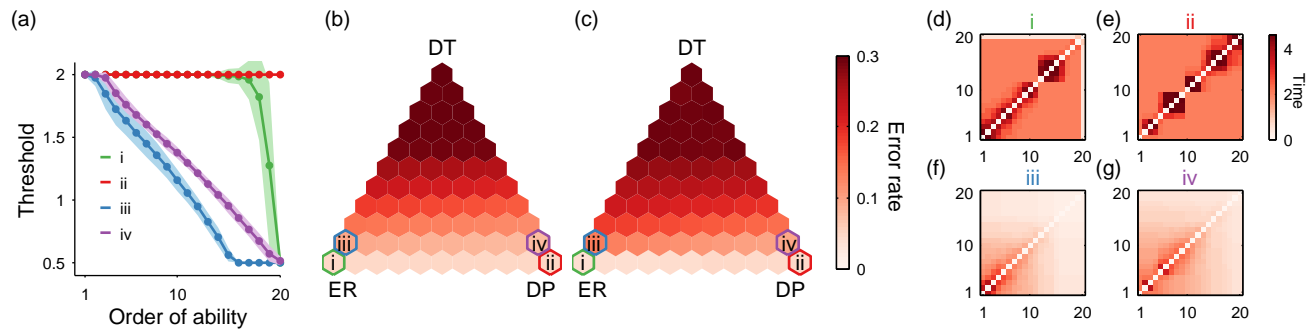

Fig. 2. The error rate of a group using Nash thresholds decreases as the weight given to decision preference increases, as long as there are non-zero waiting costs. In (a) the points show the average Nash thresholds as a function of position in the group for different optimization weights, where 1 is the strongest individual and 20 is the weakest. The shaded region shows the average plus or minus the standard deviation across 1000 draws of values. The optimization weights for each panel are indicated in the simplex with the corresponding letter. The color in the simplices indicates, in (b), the average error rate of the whole group, and, in (c), the average error rate of the decisions made by individuals in the bottom quartile of the group, as a function of the optimization weights, w_1, w_2, w_3. In the lower left corner of the simplex, only error rate matters ($w_1 = 1$). In the upper corner, only decision time matters ($w_2 = 1$). In the lower right corner, only preference matters ($w_3 = 1$). In (d)-(g) the color indicates the expected time it takes each pair of components to reach a decision in a group using Nash thresholds. Parameters: $w_1 = 1$, $w_2 = 0$, $w_3 = 0$ (i), $w_1 = 0$, $w_2 = 0$, $w_3 = 1$ (ii), $w_1 = 0.9$, $w_2 = 0.1$, $w_3 = 0$ (iii), $w_1 = 0$, $w_2 = 0.1$, $w_3 = 0.9$ (iv), $N = 20$, $b = 1$, $r = 1$, $\ell = 0.1$ in all panels.
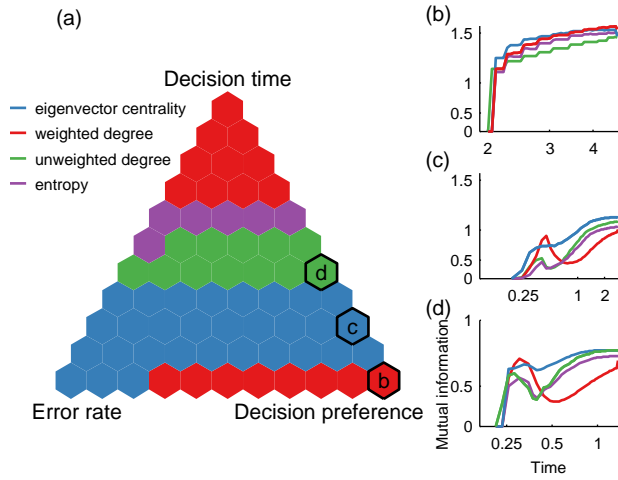
Fig. 3. The best measure of consensus in the decision network depends on the average error rate and the types of errors being made. In (a) the color indicates the most informative consensus measure to apply to a network constructed by a group using Nash thresholds, as a function of the optimization weights. In the lower left corner of the simplex, only error rate matters ($w_1 = 1$). In the upper corner, only decision time matters ($w_2 = 1$). In the lower right corner, only preference matters ($w_3 = 1$). In (b)-(d) we show how the mutual information of each consensus formalism changes over time as the network forms. The optimization weights for each panel are indicated in the simplex with the corresponding letter. Parameters: $w_1 = 0$, $w_2 = 0$, $w_3 = 1$ (c), $w_1 = 0$, $w_2 = 0.2$, $w_3 = 0.8$ (d), $w_1 = 0$, $w_2 = 0.4$, $w_3 = 0.6$ (e), $N = 20$, $b = 1$, $r = 1$, $\ell = 0.1$ in all panels.
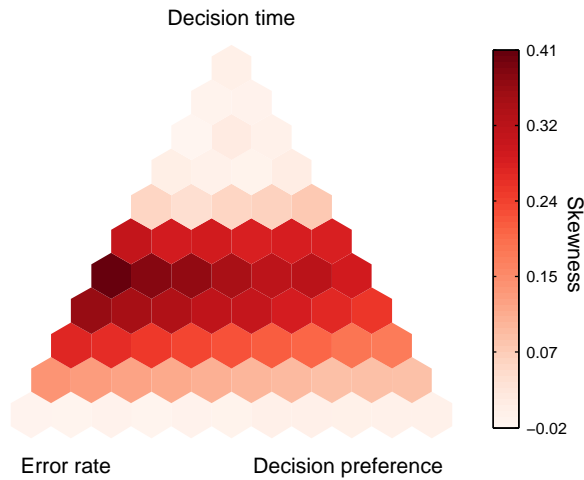

Fig. 4. The average skewness of the distribution of unweighted in-degree is maximized at intermediate waiting costs. The color indicates the average skewness of the distribution of a group using Nash thresholds, as a function of the optimization weights, w_1, w_2, w_3. In the lower left corner of the simplex, only error rate matters ($w_1 = 1$). In the upper corner, only decision time matters ($w_2 = 1$). In the lower right corner, only preference matters ($w_3 = 1$). Parameters: $N = 20$, $b = 1$, $r = 1$, $\ell = 0.1$.

Table 1. Examples of collective computation. A collective computation can occur when a group of components, each of which gathers information and makes a decision in a noisy environment, produces an output that depends in a complex non-linear way on the individuals' decisions. This phenomenon is found in many biological systems.

System	Information	Component	Component decision	Collective computation
brain	moving dots	neural population	to stop firing	decision of the brain
social group	fights won or lost	monkey	to emit a subordination signal	power structure
quorum sensing	signaling molecule	bacteria	to produce signaling molecule	production of toxin
flock movement	environment	bird	where to fly and how quickly	flock movement

Table 2. Variables in the model and their interpretations in neural and social systems.

Variable	Definition	Neural	Social
a	value	degree to which the property a neural population responds to is present in the environment	fighting ability
b	change due to new evidence		
c	strength of input	coherence of dots	probability of stronger animal winning
ℓ	leak rate		
r	interaction rate		
T_1, T_2	decision thresholds		
w_1	error rate weight	reward from being "correct"	reward from being "correct"
w_2	decision time weight	penalty for taking a long time	costs of fighting
w_3	probability of preference weight		benefit from receiving signal
X_1, X_2	decision variables	firing rates of neural populations	evidence accumulated about relative dominance