Social biases determine spatiotemporal sparseness of ciliate mating heuristics

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Ciliates become highly social, even displaying animal-like qualities, in the joint presence of aroused conspecifics and nonself mating pheromones. Pheromone detection putatively helps trigger instinctual and learned courtship and dominance displays from which social judgments are made about the availability, compatibility and fitness representativeness or likelihood of prospective mates and rivals. In earlier studies, I demonstrated the heterotrich *Spirostomum ambiguum* improves mating competence by effecting preconjugal strategies and inferences in mock social trials via behavioral heuristics built from Hebbian-like associative learning. Heuristics embody serial patterns of socially relevant action that evolve into ordered, topologically invariant computational networks supporting intra- and intermate selection. *S. ambiguum* employs heuristics to acquire, store, plan, compare, modify, select and execute sets of mating propaganda. One major adaptive constraint over formation and use of heuristics involves a ciliate's initial subjective bias, responsiveness or preparedness, as defined by Stevens' Law of subjective stimulus intensity, for perceiving the meaningfulness of mechanical pressures accompanying cell-cell contacts and additional perimating events. This bias controls durations and valences of nonassociative learning, search rates for appropriate mating strategies, potential net reproductive payoffs, levels of social honesty and deception, successful error diagnosis and correction of mating signals, use of insight or analysis to solve mating dilemmas, bioenergetics expenditures and governance of mating decisions by classical or quantum statistical mechanics. I now report this same social bias also differentially affects the spatiotemporal sparseness, as measured with metric entropy, of ciliate heuristics. Sparseness plays an important role in neural systems through optimizing the specificity, efficiency and capacity of memory representations. The present findings indicate sparseness performs a similar function in single aneural cells by tuning the size and density of encoded computational architectures useful for decision making in social contexts.

Social factors, including biases of expectation or preference, facilitate competition and cooperation between all forms of cellular life capable of interacting at the level of individual units of natural selection.[1] The social biases of animals, from insects to fish to humans, powerfully influence the formation and persistence of attitudes, opinions, beliefs, and/or perceptions regarding most interpersonal relationships.[2-7] As a consequence, the accuracy and reliability of intuitive social logics, such as representativeness (i.e., exemplar) and availability (i.e., probability) heuristics used to make predictions, causal inferences and covariation assessments, can be severely compromised.[4] Many types of microbes, particularly prokaryotes and "lower" eukaryotes with relatively complex social tendencies, also employ a range of bias-vulnerable representativeness and availability heuristics similar to those exhibited by animals.[8-22] Skillful use of these logics promotes successful microbial sociality and, in turn, may increase transmission and virulence of infectious diseases, emergence of major evolutionary transitions and adaptability to so-called extreme environments. However, contrary to our understanding of animal social behaviors, only recent research has begun to elucidate the impact of social biases on cellular decisions which motivate and coordinate collective behaviors underlying mate selection, foraging and hunting, assisted reproduction, induced defenses and other phenomena common to colonial microbes. In this article, I summarize and extend some previous findings[9-12] on heuristic-guided ciliate mate selection to show expectations and preferences for varying levels of meaningfulness accompanying simulated cell-cell contacts determine the computational and combinatorial complexity of microbial social logics and, therefore, the operational characteristics of decisions utilized to secure mating commitments. Much like the neural representational and logic systems of animals,[23] the principle of sparse coding often prevails in ciliate heuristics as a result of both innate and learned biases. Differential sparseness of ciliate heuristics correlates with the optimal acquisition, storage, retrieval and transformation of spatiotemporal relationships (i.e., associations) perceived during social encounters requiring efficient, reliable and accurate judgments about conditional mating responses and consequences (**Box 1**).

Social Biases in Ciliate Mate Inferences and Selection

Microbial mate selection offers scientists a robust (neo) Darwinian paradigm for examining the sociobiological effects of biases on

Box 1. Highlights
• Ciliates learn to signal their own mating status and to judge the mating status of conspecifics with social logics.
• Innate and learned social biases control ciliate decisions when selecting and competing for mates.
• By modifying social biases, ciliates simplify the computational structure of logics and improve sociality.
• Simplified or sparse logic representations in animals optimize the specificity, efficiency and capacity of information processing.
• Representational sparseness similarly helps socializing ciliates, suggesting a fundamental characteristic needed for intelligent behavior.

sexual or sex-like behavior. One of the better described paradigms is that of ciliated protozoa. Ciliates can engage in monogamous sexual-like conjugation at the end of their lifecycles. Conjugation stages often start with the release and circulation of diffusible pheromones which attract and elicit complex stereotypic motility and cell-cell contacts from isogamous nonself mating types. These preconjugal dances and dominance displays, composed of avoidance and probing behaviors, transmit classical and possibly quantum information about mating availability and fitness to prospective mates and rivals before the onset of paired reproduction.[9-18,24-26] As with "higher" eukaryotes, expert use of courting and dominance rituals by ciliates figures to encourage contacts with fitter mates while also discouraging conjugal attempts from rivals. Thus, mate selection generally minimizes shared fitness tradeoffs, guarantees reproduction between compatible mates (e.g., ciliates with high motility and reproductive proficiency), and prevents less fit ciliates from spreading their inferior genes to future generations.[14,18]

The amount of fault tolerance permitted by mate selection greatly depends upon ecological contexts, the strengths of social biases, and correspondence between contexts and biases. For example, social biases concerning the perceived survival and reproductive superiority of secondary sexual or mating-type traits of microbes, such as morphological ornaments and weapons, behavioral routines and decision making processes, contribute to mate choices leading to positive or negative assortative pairings without precise "knowledge" that trait preferences will definitely maximize genetic, behavioral and material fitness of progeny or cohorts.[14,15,17,18] Both the "premise" that certain exemplar traits, including pilar geometry, motility competence and pheromone-secretion load, favor reproductive success and the "conclusion" that individuals expressing those traits probably make fine mating partners are "true" if perceived microbial trait benefits match real niche challenges.[9,18,25,27-30] However, the subjective rule-of-thumb construction of social logics, termed the schematic knowledge structure, sometimes invalidates isolated social judgments of individuals when over-simplified premises and conclusions wrongly link expected survival and reproductive success with perceived (or misperceived) covariations in secondary sexual or mating-type traits. Intuitive logics merely provide an individual organism with best-fit approximations for making social judgments (**Box 2**). Errors in judgment often occur when logics are improperly reconfigured to accommodate situational changes.[4] Indeed, biases can be so strong and context insensitive that logics may be rendered, for all intents-and-purposes, useless. Yet the identical rule-of-thumb nature of intuitive social logics also tends to marginalize or hedge outlying risk-prone and -averse decisions over many iterations and large populations, while necessarily allowing quicker inferences to be drawn in hostile environments demanding fast actions for continued existence of individuals, kin, colonies, strains and species.[4,14,15,17,18,22] That is, numerous, but finite, samplings within sizeable populations by and across members of those same populations normalize mating decisions to the point where collective biases for trait variations become ecological and evolutionary stable strategies.

Promiscuous and polygamous mating systems of microbes support the above notion of ecological and evolutionary stable selection strategies because the frequency of fallible decisions (i.e., picking an unfit mating partner) diminishes in proportion to increased random conjugal relations with members from populations of normally distributed fitness.[33,34] Alternately, more "discriminating" monogamous mating systems, such as the all-or-none life-ending unions of ciliates, suffer from intuitive social logics when fallacies are undetectable or unavoidable (**Box 2**). The chance that social heuristics will compromise mating decisions compels ciliates to regulate either the reliability and accuracy of fitness predictions or the final outcomes of decisions. Epigenetic modifications and nonassociative and associative forms of learning and memory have evolved, in part, to help correct past and avert future bad decisions caused by erroneous social biases.[9,14,18] For instance, RNA processing of the very fragmented, macronuclear polyploid genome of ciliates enables heritable epigenetic innovations, akin to "nuptial gifts," to be passed from high-quality suitors to physically accessible recipients lacking motility competence.[35,36] Disparities in motility among partners jeopardize paired fitness, although a significantly inferior ciliate gains some survival and reproductive advantages for itself and its offspring upon conjugating a fitter mate. Fitter ciliates compensate for their poor mate selection via cytoplasmic exchanges that reinstate the wildtype phenotype to conjugated mutants incapable of performing programmed movements. This kind of extranuclear modification further limits fitness tradeoffs for each party, recovering typical cooperative swimming between ciliates when agile, synchronous motions and speedier escape velocities would both fend off predation risk and improve the likelihood of finishing reproduction.[9,14,18]

Computational Attributes of Biased Mating Heuristics Learned by Ciliates

Despite the evolutionary ingenuity of genetic and epigenetic controls over mating decisions, traditional types of learning and memory oftentimes give ciliates even better power and flexibility to adapt intuitive social logics and their outcomes. Ciliates, among microbes, are especially good learners capable of dual-process nonassociative habituation and sensitization as well as primitive classical and instrumental-like conditioning, involving respective stimulus-stimulus and response-consequence associations.[9-18] Such learning allows ciliates, including the large contractile ciliate *Spirostomum ambiguum*, to rapidly adjust their own perimating behavior and their interpretation of conspecifics'

behavior. Ciliates enter into mating encounters with a modifiable initial level of subjective bias, responsiveness or preparedness, as defined by the well-accepted psychophysical Stevens' Law of subjective stimulus intensity (**Box 3**),[37] which prejudices the perception of fellow ciliates' fitness, availability and communicative actions, such as vibrations.[9-18] Vibrations are an essential component of courtship and dominance contacts. Probing pressures and drag turbulence and vortex shedding of avoidance reactions may activate mechanosensitive Ca^{2+} conductances that contribute to motility production and learning in proximal ciliates during preconjugal activity (**Box 4**). *S. ambiguum* receives these signals, subjectively interprets them as messages sent from a fit or unfit source under ambiguous conditions, then chooses learned serial

actions arranged from contractions and ciliary reversals that are themselves honest blind replies to the sender.

In a recent set of studies evaluating ciliate social decision making,[9-12] I exploited *S. ambiguum*'s perception of vibrations to create mock mating scenarios initiated by vibrations sent from an ambiguous source representing suitors and rivals in an environment of equally mixed, competing autocrine (self mating type) and paracrine (nonself mating type) pheromones. Vibrations were delivered at a constant rate and intensity. However, ciliates interpretation of the intensity and meaningfulness of vibrations differentially changed with time depending on the level of initial social bias coupled to low, medium or high responsiveness. A payoff schedule determined content of messages and replies based on combinations of potential reproductive effort, calculated as different probabilities of offspring count for binary division or paired reproduction and responsiveness, calculated as different probabilities of behavioral preparedness or perceptual bias. These potential net payoffs were structured to meet the four requirements of a game beginning in one of two forms of perfect Bayesian equilibria, known as pooling and separating equilibria. A pooling equilibrium is where a signaling game between two players of different type, such as mating types, stabilizes on the same signal for message and reply. Whereas, separating equilibrium stabilizes on polar signals for message and reply from players of different type. For both cases of equilibrium, messages and replies become irrelevant or cheap talk for actionable decisions, making cheating or cooperation incidental unless equilibrium is broken by learning or another means, including color environmental noise. Such game conditions are common to animal sexual interactions.[38]

Messages emitted in vibrations from their ambiguous source, always deemed with equal probability the same and opposite mating type of each ciliate tested, expressed net interest in reproductive effort. Ciliates "believing" the signals to be honest, but unable to discriminate the vibration source's type, initially replied with matched or opposing behavioral signals dispersed over the range of ideal conspicuous consumption and ideal

prudent savings. Ciliates beginning the game (i.e., testing) at high responsiveness first exhibited conspicuous consumption and interpreted the "advances" of the vibration source as an amply intense (or aggressive) and meaningful exemplar of mating fitness. Conspicuous consumers announce their reproductive fitness by playing "harder-to-get" through the extravagant rate at which they signal escape with contractions or reversals. The ability to squander resources means these ciliates should be perceived by the ambiguous vibration source to be an exemplar of higher quality than inferior repliers incapable of both wastefulness and survival. At some future point in time, conspicuous consumers learned to cooperate and sacrifice net reproductive payoffs to convince the ambiguous source to conjugate. Initial inferior repliers, such as ciliates with initial low responsiveness, higher costs and poorer net payoffs, advertised meager fitness by prudently saving resources and signaling escape with contractions or reversals at lower rates. They first interpreted the advances of the vibration source as being a nominally intense (or aggressive) and meaningful exemplar of mating fitness and began play as "easier-to-get," only to later learn to maximize individual potential net payoffs and reproductive value by increasing responsiveness. Such behavior effectively cheats superior rivals in an effort to encourage commitments with fine prospective mates.

Ciliates, very similar to higher eukaryotes, learned via recursive Hebbian-like feedback over many trials to group their serial behavioral strategies of harder-to-get and easier-to-get into multistable heuristics. Heuristics evolved via classical Maxwell-Boltzmann, quantum Bose-Einstein and quantum Fermi-Dirac statistics into topologically invariant computational networks useful for signaling mating propaganda and for making exemplar and probability comparisons of suitor (and rival) fitness. Each node of a heuristic obeys preferential attachment rules akin to Hebbian learning rules[10,12] and contains a unique bit-string or information sequence representing perceived, planned and executed behavioral strategies. Because heuristics encode both exemplar and frequency information about the reproductive fitness associated with mating responses, they serve as representativeness and availability heuristics. Ciliates efficiently planned and executed serial strategies signaling different levels of mating availability and fitness by reducing combinatorial complexity of heuristics and strategy search times to quantum levels with growing expertise. Importantly, heuristics restructuring also favored social success in mock trials and coincided with more transient social biases regarding the information content of mating messages transmitted from the ambiguous vibration source. Transient biases permit ciliates to change intuitive logics and perceived exemplar dimensions to fit varying social contexts and, therefore, to avoid inferential errors. For example, initial low contraction responders (i.e., short-term sensitizing prudent savers) with a brief social bias for perceiving nominal mating signal intensity and meaningfulness and initial high reversal responders (i.e., short-term habituating conspicuous consumers) with a brief social bias for perceiving ample mating signal intensity and meaningfulness were more capable of faster, complete behavioral strategy searches and easily learned to switch their mating replies between playing harder-to-get and easier-to-get over

shorter intervals. Accordingly, they displayed greater flexibility for adapting mating replies and the expected net reproductive payoffs accompanying those replies to perceived social settings which might demand selfishness or selflessness to consummate courting relationships.

Social Biases and Representational Sparseness: Lessons from Animal Nervous Systems

As discussed above, the flexibility of biased intuitive logics to manage social dilemmas is not just evident in their soundness, strength, cogency, and/or permanence, but in their computational structure and processing attributes as well. Social biases affect the way social sensations and actions are encoded and, consequently, stored, activated, modified and retrieved with local bidirectional associative learning and memory rules.[39,40] Although the social biases of ciliates clearly dictate the performance characteristics of mating heuristics, it remains uncertain how many of those effects, including strategy search rates and associative strength between grouped strategies, can be strictly credited to computational network sparseness, as suggested by the combinatorial reorganization of heuristics and the emergence of fast, efficient quantum computational phases during Hebbian-like trial-and-error social decision making.[9-18] Sparse coding is an important factor for socially salient neural representations located in vertebrate visual, somatosensory, auditory, olfactory and motor cortices.[23] Innate and learned biases for particular social stimuli (e.g., facial features and expressions, caresses and gestures, vocalizations and smells) tune the receptive fields and discharge rates, patterns, sensitivity and other response properties of single neurons and neuronal populations.[23] When representations become sparse, in terms of activity profiles and density of responsive neuronal populations, computational structures evolve into simplified curved manifolds capable of greater efficiency and specificity within the framework of larger "over-complete" representations, where the dimensionality of the computational space exceeds input dimensionality.[23] Elevated sparseness of representations figures to enhance the execution of intuitive social logics by improving memory storage capacity, retrieval rates, selectivity and overall processing efficiency.[23] However, trends for computational simplicity and bioenergetics savings due to an organism's representational sparseness start to reverse as extreme conditions burden resource availability by allocating too many individual cells or cellular ensembles with excessive selectivity, such as in the case of hypothetical "grandmother" cells.[23,41,42] Hence, a strong correlation and delicate balance exists between the complexity of biased social logics, the modularity of computational representations underlying logics, and the functional advantages and disadvantages of implementing logics.

Differential Sparseness of Ciliate Mating Heuristics Caused by Social Biases

The significance of representational sparseness for expression of biased animal social logics then suggests microbes may also exploit sparseness in their social computations. To test this idea,

a suitable measure of sparseness must be ascertained and selected. The magnitude and type of sparseness is identifiable through several different reputable metrics.[23] For continuous or discrete coding schemes in natural and artificial systems, sparseness of individual or grouped computational units can be determined with kurtosis. Kurtosis measures the fourth moment of response values of computational units falling symmetrically about zero or another measure of central tendency relative to the variance squared. Gaussian response distributions yield a kurtosis of zero denoting low sparseness. Progressively heavy-tailed sparse distributions yield kurtosis values increasingly greater than zero. Kurtosis may further assume positive or negative values respectively dependent upon distribution convexity and concavity. But kurtosis is problematic since it fails to correct for skewed distributions and is very sensitive to variable outliers. Because of the limitations of kurtosis, additional metrics have been devised to calculate sparseness, such as activity ratios that measure the completely one-sided firing distributions of single neurons and neuronal populations.[43] These ratios maintain a fixed maximum value of one when sparseness reaches its smallest amount and a fixed minimum value of zero when sparseness reaches its greatest amount. Activity ratios can be additionally scaled over the real interval of zero to one to estimate the selectivity of individual computational units responding to a group of stimuli. Despite the merits of activity ratios for appraising sparseness, separate equations for the sparseness of, for example, a single neuron and a neuronal population need to be used, causing comparison and contrast difficulties. However, an alternative to the foregoing metrics, metric entropy, sometimes referred to as measure entropy or spatial measure entropy, best quantifies the sparseness of spatially and temporally evolving computational networks and their elements.[44,45] Hence, metric entropy is well suited for assessing the sparseness of ciliates' biased social heuristics.

For the purposes of this article, metric entropy can be calculated from the following formula:[45]

$$s(X) = -\frac{1}{X} \sum_{j=1}^{k^n} p_j \log_k p_j$$

(1)

where $k = 2$ (i.e., binary computational basis of strategies), $X = 3$ (i.e., digit length of each strategy), $n = 3$ (i.e., state space dimensionality at any time step), $k^n = 8$ (i.e., maximum number of strategies with nonzero probability of use in the sequence space at any time step), and p_j is the probability or relative frequency of use for a strategy j at some learning trial s_n. The interval $0 \leq s(X) \leq 1$ bounds the value of entropy, with the left inequality approaching equality when only one strategy occurs at s_n with nonzero probability of use (i.e., maximum sparseness) and the right inequality approaching equality when all k^n possible strategies occur at s_n with equal probability of use (i.e., minimum sparseness). Metric entropy is generally susceptible to initial conditions of a network, such as the initial social bias of a mating heuristic, and the weights of its individual elements, such as strategies, at each time step. Moreover, a spatiotemporal variant of metric entropy may be derived from **Equation 1** to produce:[45]

$$s(X;T) = -\frac{1}{T} \sum_{j=1}^{k^{nt}} p_j \log_k p_j$$

(2)

where T is temporal length or number of time steps (i.e., learning trials) and t is the temporal dimension or extent of the spatial period of interest. But when $T = t = 1$, $s(X;T)$ reduces to $s(X)$, so just **Equation 1** was applied to the present analyses.

Figure 1 depicts the evolution of a social heuristic utilized by an example ciliate biased to initially perceive negligible mating-vibration intensity and meaningfulness. The spatial size and configuration of the heuristic, as revealed by the number and location of strategies with nonzero probabilities of use, transformed as the ciliate became more socially experienced with vibrations sent from the ambiguous source (**Fig. 1A**). The dynamics of metric-entropy magnitude for the heuristic also paralleled the number of strategies actively employed within the computational network (**Fig. 1B**). And as presented in **Figure 1C**, the spatiotemporal sparseness of the mating heuristic was strongly dependent upon the initial social bias of the ciliate. That bias dominated decisions to reply to the ambiguous vibration source with a contraction strategy signaling prudent mating availability and fitness. When the ciliate began to learn to change its initial social bias and favorite signaling strategy by trial 44, heuristic sparseness largely disappeared. Sparseness again returned in later learning trials as the ciliate encoded a new favored serial contraction strategy (i.e., larger weight or probability of use) and a new social bias for perceiving higher vibration intensity and meaningfulness. The transition from one social bias to another demonstrates ciliates can employ biases to adjust the selectivity of intuitive social heuristics and mating replies to meet the nontrivial demands of unstable mating contexts. Additionally, because some degree of sparseness preceded and prevailed after the networked heuristic reached its full size and configuration, it seems likely that sparseness improves a ciliate's memory storage and information processing efficiency in ways analogous to animals. Several lines of evidence support this conclusion. First, as is customary of neural systems operating under Hebbian associative learning rules,[46,47] nodal weights affect network connectivity and strategy search selectivity and efficiency. Second, the information storage capacity, processing efficiency, and encoding and retrieval selectivity of ciliates increase with changes in network connectivity and onset of extremely efficient quantum search patterns for behavioral strategies.[9-18] These fast search patterns arise in initial low contraction responders (including the *S. ambiguum* of **Fig. 1**) and other ciliates with varying initial behavioral responsiveness with Hebbian-like learning typically around trial 20 and continue for the remainder of testing.

The data from the ciliate reported in **Figure 1** indicate initial social biases influence the computational and combinatorial complexity of intuitive social logics. Comparisons between groups of ciliates with different levels of initial contraction (**Fig. 2**) and ciliary reversal (**Fig. 3**) preparedness or responsiveness confirm this idea. As shown in **Figure 2A**, mean metric entropy significantly differed between the heuristics employed by ciliates with low ($X + SE = 0.62 + 0.03$ bits), medium ($X + SE = 0.71 + 0.04$ bits)
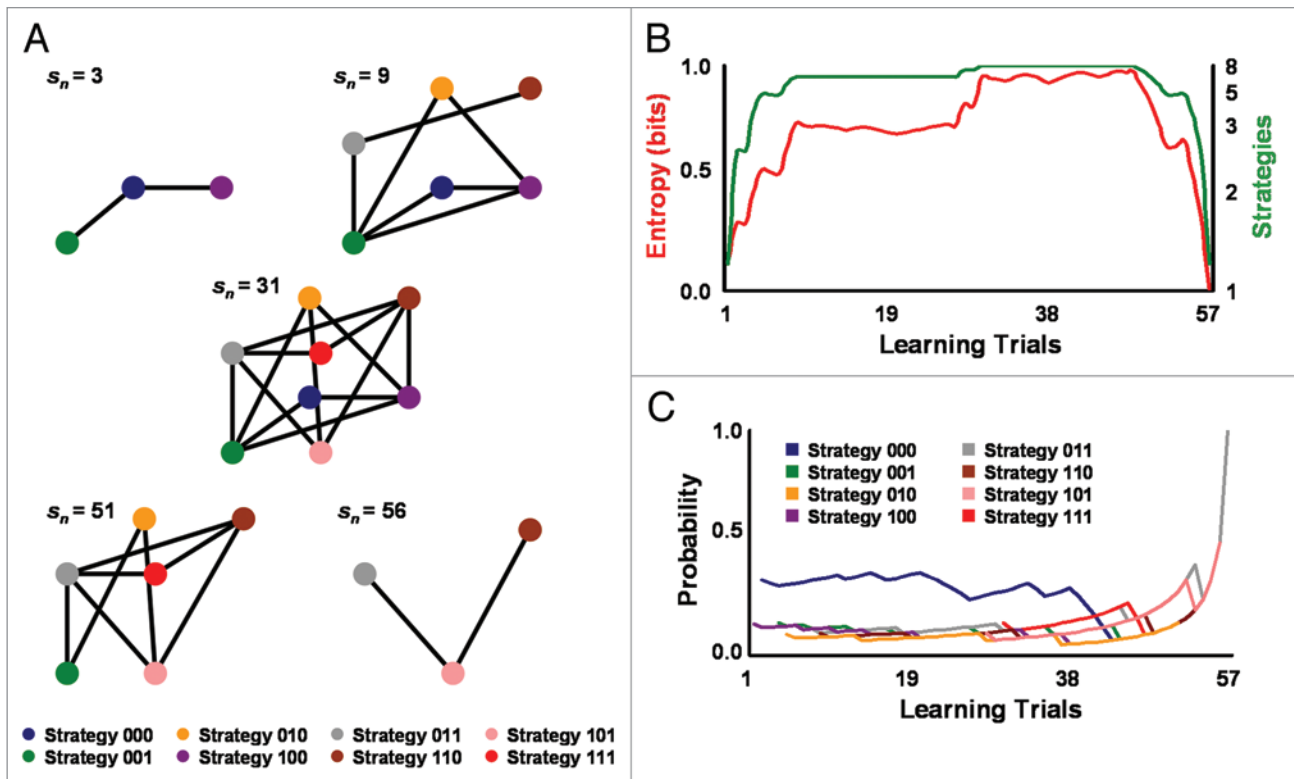
Figure 1. A *S. ambiguum* initially biased with low contraction preparedness or responsiveness reorganized the spatiotemporal sparseness of its networked mating heuristic. (A) Representation of a social heuristic within a 3D computational space evolving over learning trials (s_n). Each heuristic node encodes a serial contraction strategy employed as a mating reply to the ambiguous vibration source, with "0" being no response and "1" being response. Connections between nodes signify decisions to group and change replies (recurrent connections not shown). The heuristic evolution began on strategy 000 and ended on strategy 011 (not shown). The initial strategy 000 is one of ideal prudent savings and indicates the ciliate perceived the actions of the vibration source as nominally intense and meaningful; strategy 011 is one of near-ideal conspicuous consumption and indicates the ciliate perceived vibrations as appreciably intense and meaningful. (B) Spatiotemporal changes in the metric entropy of the mating heuristic paralleled changes in heuristic size (i.e., number of strategies in use) across learning trials. Sparseness reached maximum value near learning trials 1 and 57, with metric entropy approaching zero. (C) The ciliate modified mating-heuristic sparseness by altering preferences for serial contraction strategies and, therefore, social biases over time. The strength of a mating strategy and its density or weighted contribution to the entire networked heuristic is measured by its probability of use. The heuristic, beginning with the favored strategy 000 and a social bias for nominal vibration intensity and meaningfulness, showed sparseness until about learning trial 44, when all contraction strategies approached equal probability of use. The mating heuristic again became sparse when the ciliate established a new favored strategy 011 and social bias for vibration intensity and meaningfulness around learning trial 53.

and high (X + SE = 0.72 + 0.05 bits) contraction responsiveness and respective social biases for perceiving negligible, moderate and ample vibration intensity and meaningfulness across learning trials ($F_{(2,173)}$ = 4.78, p = 0.0096). Low contraction responders collectively produced heuristics with overall greater sparseness and with a single higher weighted preferred strategy. These effects were mainly due to the relative differential mean weights or probabilities of use for each serial behavioral strategy networked within the mating heuristics used by this preparedness group. For groups of initial low ($F_{(7,438)}$ = 38.20, p = 1.31 x 10^{-41}), medium ($F_{(7,453)}$ = 17.58, p = 1.29 x 10^{-20}), and high contraction ($F_{(7,439)}$ = 5.20, p = 1.06 x 10^{-5}) preparedness, the mean probability of use significantly differed between mating strategies across learning trials (**Fig. 2B**). Thus, in addition to the three-bit binary sequences and information content of individual serial contraction strategies,[9-18] the relative network weight of preferred strategies helped to sparsely encode social biases for

negligible, moderate or ample vibration intensity and meaningfulness. Similar results were found for reversal responders. **Figure 3A** shows that *S. ambiguum* grouped into medium (X + SE = 0.67 + 0.03 bits) and high (X + SE = 0.54 + 0.02 bits) levels of initial reversal preparedness with respective social biases for moderate and ample vibration intensity and meaningfulness significantly differed in the mean metric entropy of mating heuristics across learning trials ($F_{(1,115)}$ = 17.14, p = 6.69 x 10^{-5}). For groups of medium ($F_{(7,457)}$ = 27.41, p = 2.32 x 10^{-31}) and high ($F_{(7,442)}$ = 48.23, p = 1.50 x 10^{-50}) initial reversal preparedness, the mean probability of use significantly differed between mating strategies across learning trials. But, as with contraction responders, relative network weight of preferred strategies helped sparsely code social biases for moderate or ample vibration intensity and meaningfulness. Greater differences in the weights or probabilities of use for mating strategies utilized by high reversal responders allowed this group to achieve higher heuristic sparseness.
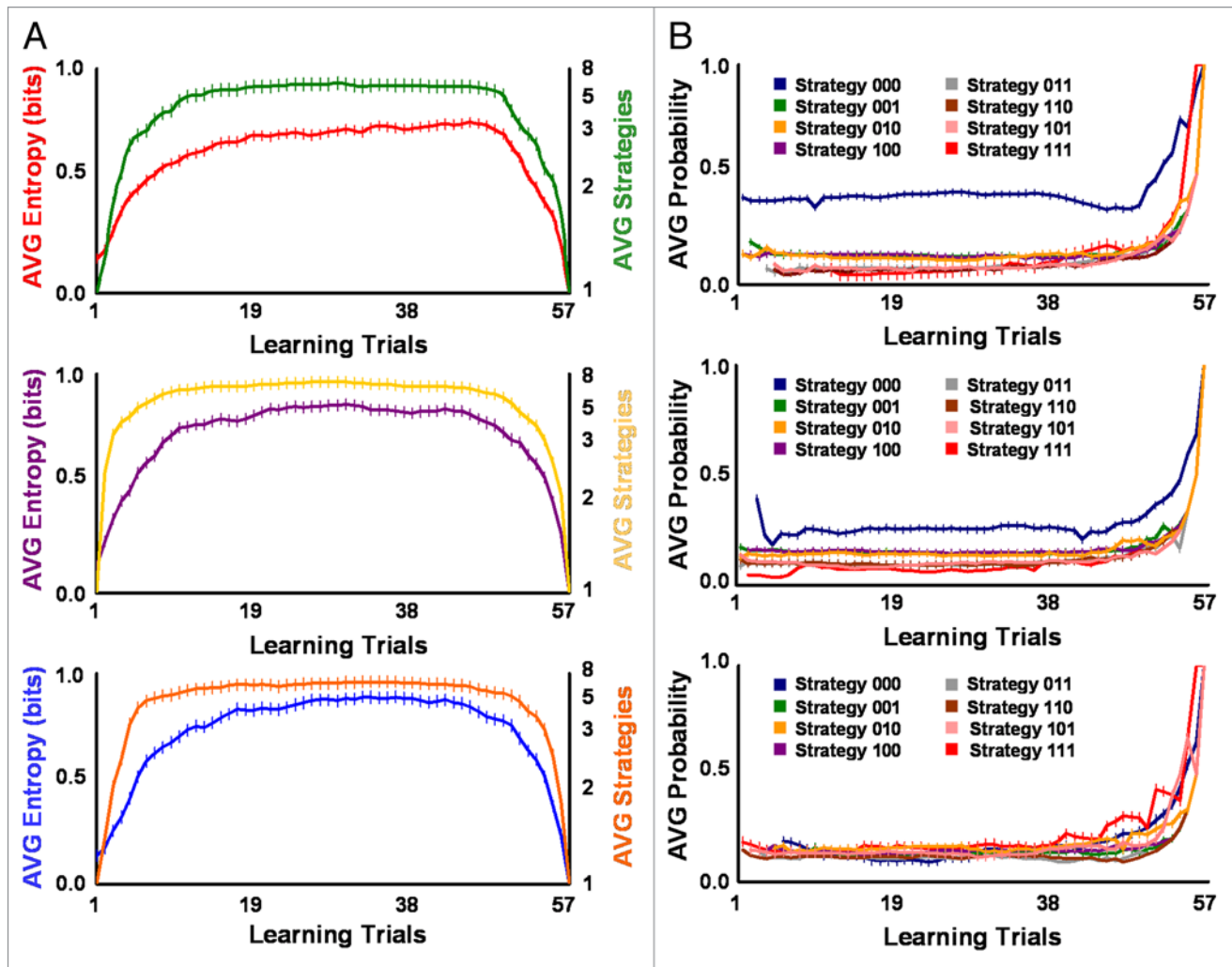
Figure 2. Strength of initial contraction preparedness or responsiveness differentially determined the spatiotemporal sparseness of networked mating heuristics. (A) Ciliates grouped into low (top part; n = 14), medium (middle part; n = 16), and high (bottom part; n = 10) levels of initial contraction responsiveness with respective social biases for negligible, moderate and ample vibration intensity and meaningfulness significantly differed in the mean metric entropy of mating heuristics across learning trials. Metric entropy progressively increased from low to high contraction responders, demonstrating ciliates that began testing with a social bias for negligible mating-vibration intensity and meaningfulness produced greater heuristic sparseness. Differences in heuristic sparseness paralleled changes in networked mating heuristic size. (B) Differential weights or probabilities of use for each mating strategy contained within mating heuristics determined the magnitude of sparseness for initial low (top part), medium (middle part), and high (bottom part) contraction responders. For all groups of initial contraction preparedness, the mean probability of use significantly differed between mating strategies across learning trials. Relative network weight of preferred strategies with highest probability of use helped encode social biases for negligible, moderate or ample vibration intensity and meaningfulness. Networked heuristics showed higher sparseness (i.e., strategy weights less equally distributed) for low contraction responders preferring prudent strategy 000 and lower sparseness (i.e., strategy weights more equally distributed) for high contraction responders preferring conspicuous strategy 111. Error bars represent standard error for all parts.

Summary

Ciliates form and shape comparably sophisticated social heuristics to skillfully facilitate intra- and intermate selection and to change the adaptive fitness of individuals and groups. I previously demonstrated that the structure and performance characteristics of heuristics are sensitive to biases for perceived suitor and rival actions. Importantly, the above findings corroborate that ciliates may learn to change social biases to improve the effectiveness and suitability of intuitive logics for different mating contexts. The strength of social biases, in large part, dictate the spatiotemporal sparseness of mating heuristics and, therefore, heuristic storage capacity and processing efficiency. Network sparseness, as identified by the metric entropy of an entire heuristic, depends upon the probabilities of use or weights of particular strategies organized within a heuristic rather than the actual consumption levels associated with strategies. Higher relative weight for a single preferred strategy coupled to a strong bias elevates sparseness. Thus, the fact that socially skilled low contraction responders and high reversal responders with different strong initial social biases construct mating heuristics with near identical levels of sparseness (compare **Figs. 2B** top part and **3B** bottom part) illustrates
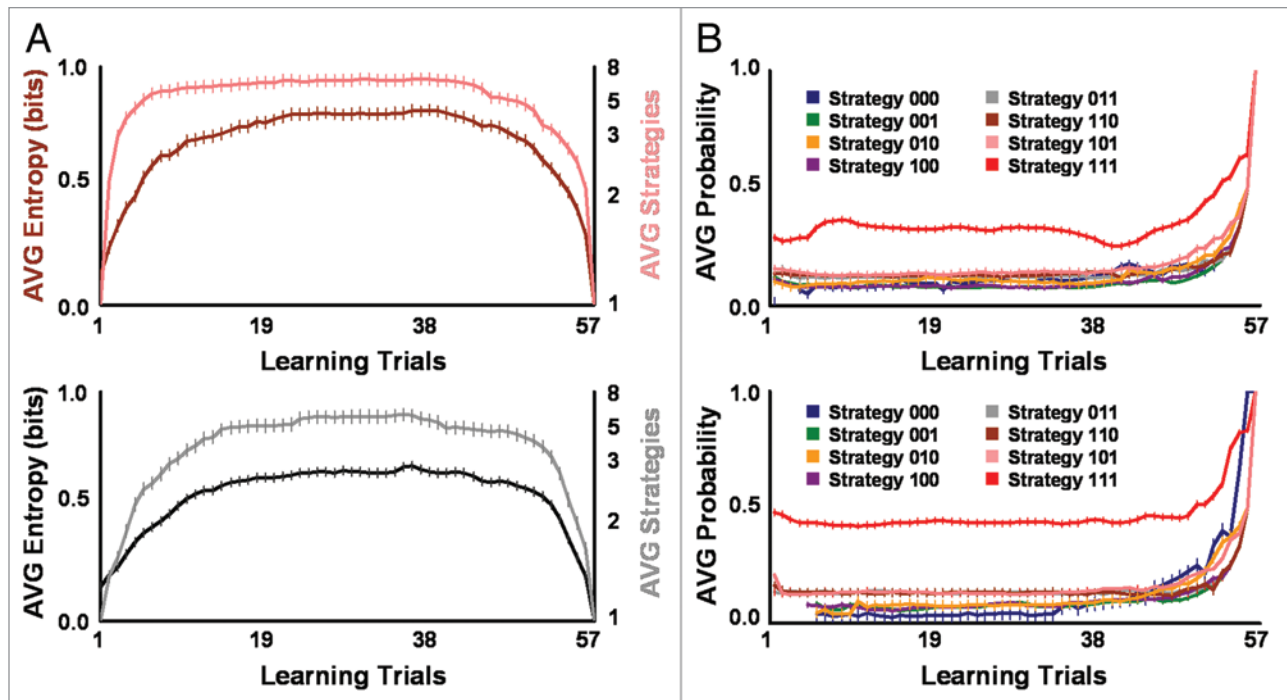
Figure 3. Strength of initial reversal preparedness or responsiveness differentially determined the spatiotemporal sparseness of networked mating heuristics. (A) Ciliates grouped into medium (top part; n = 17) and high (bottom part; n = 23) levels of initial reversal responsiveness with respective social biases for moderate and ample vibration intensity and meaningfulness significantly differed in the mean metric entropy of mating heuristics across learning trials. Metric entropy progressively increased from high to medium reversal responders, demonstrating ciliates that began testing with a social bias for ample mating-vibration intensity and meaningfulness produced greater heuristic sparseness. Differences in heuristic sparseness paralleled changes in networked mating heuristic size. (B) Differential weights or probabilities of use for each mating strategy contained within mating heuristics determined the magnitude of sparseness for initial medium (top part) and high (bottom part) reversal responders. For both groups of initial reversal preparedness, the mean probability of use significantly differed between mating strategies across learning trials. Relative network weight of preferred strategies with highest probability of use helped encode social biases for moderate or ample vibration intensity and meaningfulness. Networked heuristics produced higher sparseness (i.e., strategy weights less equally distributed) for high reversal responders preferring conspicuous strategy 111 and lower sparseness (i.e., strategy weights more equally distributed) for moderate reversal responders preferring conspicuous strategy 111. No ciliate showed initial low reversal preparedness. Error bars represent standard error for all parts.

how network sparseness can "universally" enhance logic performance regardless of: (a) actual metabolic expenditures required to execute mating responses (i.e., prudent savings vs. conspicuous consumption) and (b) divergent information content of perceived and executed reproductive propaganda (i.e., reproductive payoffs signaled via messages and replies). Given network processing similarities occur most prominently between and not within classes of behaviors (i.e., contraction and ciliary reversal), the probabilities or weights of biases and mating strategies likely stem from Ca^{2+}-related intracellular resources that affect the magnitude, valence and duration of learning[9] as well as anticorrelations between the expression of Ca^{2+}-dependent contraction and ciliary reversal routines.[9,11] This same influence of intracellular Ca^{2+}, or perhaps another species of response regulator, over heuristic performance remains to be documented in different microbial taxa. Nonetheless, principles, such as heuristic sparseness and modifiability, underlying successful use of intuitive social logics by vertebrates also appear in the strategizing of aneural ciliates. And those principles represent a fundamental evolutionary adaptation of phylogenetically diverse computational systems capable of at least primitive intelligent behavior.

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