Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion

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Coordination among social animals requires rapid and efficient transfer of information among individuals, which may depend crucially on the underlying structure of the communication network. Establishing the decision-making circuits and networks that give rise to individual behavior has been a central goal of neuroscience. However, the analogous problem of determining the structure of the communication network among organisms that gives rise to coordinated collective behavior, such as is exhibited by schooling fish and flocking birds, has remained almost entirely neglected. Here, we study collective evasion maneuvers, manifested through rapid waves, or cascades, of behavioral change (a ubiquitous behavior among taxa) in schooling fish (*Notemigonus crysoleucas*). We automatically track the positions and body postures, calculate visual fields of all individuals in schools of ~150 fish, and determine the functional mapping between socially generated sensory input and motor response during collective evasion. We find that individuals use simple, robust measures to assess behavioral changes in neighbors, and that the resulting networks by which behavior propagates throughout groups are complex, being weighted, directed, and heterogeneous. By studying these interaction networks, we reveal the (complex, fractional) nature of social contagion and establish that individuals with relatively few, but strongly connected, neighbors are both most socially influential and most susceptible to social influence. Furthermore, we demonstrate that we can predict complex cascades of behavioral change at their moment of initiation, before they actually occur. Consequently, despite the intrinsic stochasticity of individual behavior, establishing the hidden communication networks in large self-organized groups facilitates a quantitative understanding of behavioral contagion.

swarm | behavioral epidemic | alarm | escape waves | social influence

The social transmission of behavioral change is central to collective animal behavior. For many mobile groups, such as schooling fish and flocking birds, social contagion can be fast, resulting in dramatic waves of response (1 6). Such waves are evident in particular when individuals are under threat of attack from predators (1). Despite the ubiquity and importance of behavioral contagion, and the fact that survival depends on how individual interactions scale to collective properties (2), we still know very little about the sensory basis and mechanism of such coordinated collective response.

In the early 20th century, Edmund Selous proposed that rapid waves of turning in large flocks of birds resulted from a direct transference of thoughts among animals: "They must think collectively, all at the same time... a flash out of so many brains" (3). By the mid 1950s, however, attention had turned from telepathy to synchrony arising from the rapid transmission of local behavioral response to neighbors, with some of the first experimental studies of cascading behavioral change undertaken by Dimitrii Radakov (4). Radakov (4) hand traced the paths of each fish, frame by frame, revealing that the speed of the "wave of agitation" could propagate much faster than the maximum swim speed of individuals. Using similar methodology, Treherne and Foster (5) studied rapid waves of escape response in marine skaters, describing what they saw as "the Trafalgar effect" in reference to the speed of communication, via signaling flags, among ships in the British Navy's fleet at the battle of Trafalgar in 1805. Signals observable at a distance allowed information to travel much faster than the ships could move themselves. Since these studies, similar behavioral cascades have been found in many other organisms (2, 6 8).

Describing general "macroscopic" properties, such as the speed or direction of behavioral waves, is relatively straightforward. Revealing the nature of social interactions by which information propagates among individuals, however, has proven much more difficult. In many situations, such as when a predator attacks a group (1) or when artificial stimuli are used, it is not possible to differentiate between the propagation of behavior via social contagion and the propagation of behavior resulting from direct response to the stimulus, or some combination of both. For example, the sound of an object dropped into the water (9) creates a near instantaneous acoustic cue typically available to all individuals. This problem is further exacerbated by the fact that response latency associated with direct behavioral response increases with distance to the stimulus (10); thus, the null expectation for asocial response by members of a group to a stimulus would be a fast wave of response (appearing to travel via contagion) from the stimulus outward.

Significance

We know little about the nature of the evolved interaction networks that give rise to the rapid coordinated collective response exhibited by many group-living organisms. Here, we study collective evasion in schooling fish using computational techniques to reconstruct the scene from the perspective of the organisms themselves. This method allows us to establish how the complex social scene is translated into behavioral response at the level of individuals and to visualize, and analyze, the resulting complex communication network as behavioral change spreads rapidly through groups. Thus, we can map, for any moment in time, the extent to which each individual is socially influential during collective evasion and predict the magnitude of such behavioral epidemics before they actually occur.

In previous studies, therefore, it has not been possible to isolate the social component of rapid collective response. Although simulations can qualitatively reproduce phenomena reminiscent of such waves (6, 11), the underlying assumptions made may be incorrect. For example, a predominant paradigm has been to consider individuals as "self propelled particles," which (inspired by collective processes in physical systems) interact with neighbors through social "forces" (12 15). In such models, it is usually assumed that they do so with neighbors within a fixed distance [a "metric range" (12, 13)] or with a fixed number of near neighbors regardless of their distance [a "topological range" (15)]. These assumptions, although mathematically convenient, do not necessarily represent what is convenient, or appropriate, for neural sensing and decision making. Furthermore, it has been shown that these representations poorly reflect the sensory information used during social response in schooling golden shiner fish (16), the focal species of the present work.

A major challenge in the study of collective animal behavior is that the pathways of communication are not directly observable. In the study of isolated organisms, it has long been realized that mapping the physical and functional connectivity of neural networks is essential to developing a quantitative and predictive science of how individual behavior is generated. By contrast, in the study of mobile animal groups, the analogous issue of determining the structure of the sensory networks by which interactions, and the resulting group behavior, are mediated remains to be explored. The structure and heterogeneity of networks are known to have a profound impact on contagious processes in general, from spreading neural electrical activity (17), innovations (18), disease (19), or power grid (20) failure. In all such scenarios, predicting the magnitude of contagion and identifying influential nodes (either in terms of their capacity to instigate or inhibit widespread contagion) are crucial.

Several measures have become prominent predictors of influence in networks, including an individual's degree (number of connections) (21) and betweenness centrality (the number of shortest paths that pass through a focal individual) (22). In the study of contagious disease, those individuals who have a large number of social contacts (a high degree), yet whose contacts do not form a tight clique [i.e., have a low clustering coefficient (19)], have the capacity to be "superspreaders," allowing infection to spread extensively (23). Although disease transmission and social contagion are similar in some respects, there are important differences. Whereas disease transmission can follow contact with a single infected individual (simple contagion), in many social processes, behavioral change depends on reinforcement via multiple contacts [complex contagion (24)].

Here, we focus on studying rapid waves of behavioral change in the context of collective evasion, using strongly schooling fish (golden shiners) as an experimental study system. To uncover the process by which this behavioral change spreads, we exploit the fact that shiners, like other fish, exhibit "fast start" behavior when they perceive an aversive stimulus (e.g., via the visual, acoustic, or mechanosensory system) (25), and occasionally do so in the absence of any external stimulus. Studying fast start evasion resulting from spontaneous startle events, instead of presenting a stimulus visible to multiple individuals, offers us the opportunity to identify the initiator of escape waves unambiguously and to avoid confounding social and asocial factors.

Because fast start is mediated by a reflex circuit involving a pair of giant neurons, the Mauthner cells (26), it may be expected that individual fish would be unable to establish the causal factor for escape in others (i.e., whether it resulted from a real threat or not). We first test this hypothesis by comparing evasion response resulting from spontaneous startles with evasion response resulting from an experimentally controlled alarming mechanosensory stimulus, and find no difference in response. This result suggests that when responding to fast start

behavior, golden shiners do not differentiate between threat induced and spontaneous startles, and is consistent with previous experiments on birds (27), and also with theoretical predictions suggesting that the risk of predation makes it simply too costly for vulnerable organisms, like golden shiners, to wait to determine if the escape motion of others is associated with real danger (28).

To investigate the mechanism of transmission of evasion behavior, we performed a detailed analysis of 138 spontaneous evasion maneuvers in schools of 150 ± 4 freely swimming fish (body length of ≈ 4.5 5 cm, spontaneous evasion experiments minimally interfered with schooling behavior). Due to the importance of visual cues in this species (16, 29), we reconstruct a planar representation of each fish's visual field using ray casting to approximate the pathways of light onto the retina, based on automated estimation of the body posture and eye position of each individual (*SI Appendix*). This representation reveals the underlying visual information available to each fish. Because we can determine unambiguously the initiator and first responder (the first and second individuals to startle) of any behavioral cascade, and only social cues are present, we can investigate the nature of social contagion in this system by asking what sensory information is predictive of whether or not an individual will be the first to respond.

This approach allows us to study how individuals translate sensory information to motor response (evasion) and, consequently, to reveal the social cues that inform individual decision making in this behavioral context. Knowing these cues then allows us to reconstruct quantitative interaction networks by which evasion behavior propagates across groups. We address a key question: From the structural properties of the network alone, is it possible to predict whether a given individual's startle will result in a behavioral cascade, and of what magnitude? We also reveal the general nature of this contagion process and the relationship between spatial position and social influence, and susceptibility to social influence, in large, mobile animal groups.

Results and Discussion

We studied free swimming groups of juvenile golden shiners (*Notemigonus crysoleucas*), a widespread species of freshwater fish that swims close to the water surface (30) and whose schooling behavior is well characterized by vision (16) [in this species, the lateral line is thought to contribute minimally to schooling (31, 32)]. Like many juvenile fish (33), shiners experience very high mortality due to predation; abundance is limited by predation rather than food availability (34). Under our experimental conditions, which minimize external visual and acoustic cues (*SI Appendix*), we find that shiners occasionally exhibit spontaneous fast starts in the absence of any apparent cue. Spontaneous fast starts may arise from spontaneous discharge, or so called "synaptic noise," in the reflex escape circuit (35), or from the reflex system being triggered somehow in only a single individual, such as by ripples on the surface of the water. Such startles are rare, occurring, on average, approximately once every 3.3 h per individual (*SI Appendix*), and they are easily identifiable due to a sudden acceleration well outside the norm associated with general schooling behavior (Fig. 1*A* and *SI Appendix*, Fig. S1).

We find no evidence that golden shiners differentiate between fast starts arising from an induced alarming stimulus (sudden mechanosensory stimulation; *SI Appendix*, Fig. S2) and those fast starts that arise spontaneously (*SI Appendix*, Fig. S3). Following initiation, evasion behavior can propagate quickly (approximately twice the maximum swim speed of any individual; Fig. 1*D* and *SI Appendix*, Fig. S1*B*) within groups, away from the point of initiation (and thus rapidly away from any potential threat).

Such waves of evasion can spread extensively (Fig. 1*A*) or may rapidly die out, resulting in a broad distribution of cascade magnitudes (number of responding individuals), a property shared with other spreading processes [e.g., neural activity (36), human communication (37)], and with propagation speeds that
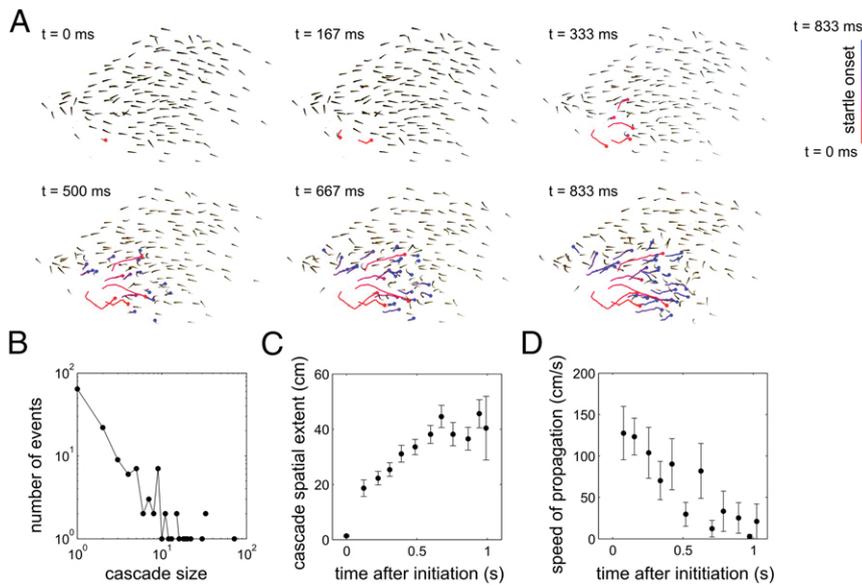
Fig. 1. Collective evasion. (*A*) Six sequential frames 167 ms apart of an escape response cascade in schooling fish, with a school size of 154 fish; color indicates the time of startle initiation, with lines showing the trajectory of startled individuals. (*B*) Distribution of observed cascade sizes on a log log scale. (*C*) Spatial extent of behavioral cascades: the average distance between initiator position and the position of individuals that responded time *t* after initiation. (*D*) Average speed of cascade wave prop agation, calculated as the change in the spatial extent of the cascade per second, averaged over all cascade events. Data points in *C* and *D* show the mean, with error bars for ± the SE.

decelerate over time (Fig. 1*D* and *SI Appendix*, Fig. S3). Con sequently, predicting the magnitude of behavioral cascades is challenging. Furthermore, we find that variability in the ini tiator's behavioral response does not influence the nature of contagion (the influence of the initiator cannot, for example, be attributed to its maximum speed, turning rate, or turning accel eration; *SI Appendix*), emphasizing the need to consider explic itly the sensory information available to potential responders, which may observe the initiator differently due to their different relative positions throughout the group.

Functional Mapping Between Sensory Input and Behavioral Change.

To reveal the hidden pathways of interaction, we must first es tablish a functional mapping between sensory input and the rele vant behavioral output (escape response). To obtain this mapping, we considered only the first responder to the initiator of a behav ioral cascade, for which we have the clearest causal relationship. As expected (16), visual contact (Movie S1) is a strong predictor of response, with fish being unlikely to respond if the initiator is oc cluded from view, regardless of their proximity (logistic regression: likelihood ratio test of visual model compared with null model, $P < 0.0001$; *SI Appendix*).

To determine which properties of visible neighbors are used in decision making by the first responder, we considered a broad set of both absolute and comparative features of the neighborhood (38). Absolute features depend only on the relationship between the observer and the initiator but are invariant to other visible neighbors. Absolute features include metric (or Euclidean) dis tance to visible neighbors, as well as their angular position and area subtended on the retina (Fig. 2*A*; a complete list is provided in *SI Appendix*, Table S1). Comparative features, on the other hand, do contain implicit information regarding multiple visual neigh bors, and include properties such as topological distance, ranked angular area, and relative metric distance (Fig. 2*B* and *SI Appendix*, Table S1). Log transformed predictors were also considered, be cause many sensory systems operate on logarithmic scales to in crease dynamic range, and thus response sensitivity, as reflected by the well known Weber Fechner law (39).

Two approaches were used to find the combination of features that best predict the identities of the first responders in the data. First, we used multimodel inference based on exhaustive (i.e., not stepwise) evaluation of all feature subsets, where we computed a logistic regression (generalized linear model, with a logistic link function) for every possible combination of features and compared

their performance. We selected the features that consistently appeared in top performing models, instead of just selecting the single best model (40) (*SI Appendix*, Fig. S7). Second, we used an L_1 regularized logistic regression (41) of all features (*SI Appendix*, Fig. S10).

We selected the two most predictive features of behavioral response for inclusion in the model, where we exclude other features because of low feature relevance, or because they con tain similar information as features with higher relevance (details on feature selection are provided in *SI Appendix*). The two model selection methods found consistent results, with small differ ences due to the nonexhaustive search used by the L_1 regulari zation method. The two most predictive features were (*i*) the logarithm of the metric distance to visible neighbors (Fig. 2*C*) and (*ii*) the ranking of the initiator, with respect to others, in
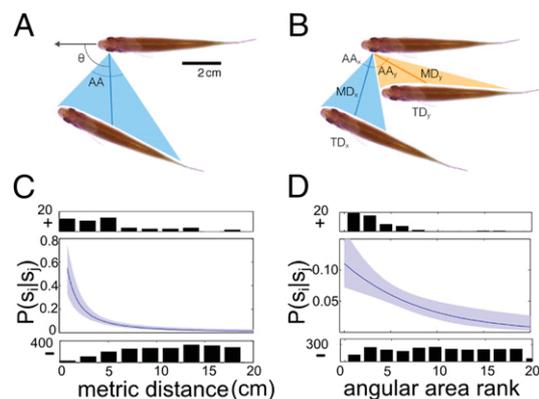

Fig. 2. Sensory basis of social contagion. (*A*) Illustration of the angular position relative to heading (θ) and angular area (AA) estimation for a neighboring fish. (*B*) Metric distance (MD), topological distance (TD), and ranked angular area for two neighboring fish. (*C*) Probability of an indi vidual's response as a function of the top predictor, log(metric distance), holding ranked angular area constant. (*D*) Probability of an individual's re sponse as a function of the second predictor, ranked angular area, holding log(metric distance) constant. In *C* and *D*, the solid blue line is the fit of the model with the top two feature variables to the first responder data, whereas the shaded blue area represents 95% confidence intervals. Histo grams above are distributions of first responders in the data, whereas his tograms below are distributions of nonresponders.

terms of the angular area subtended on the retina (Fig. 2D and *SI Appendix*, Fig. S7). This model can be formulated as a probability of response, $P(i|j)$, in fish i, given that fish j has startled:

$$P(i|j) = \left(1 + exp\left(-\beta_1 - \beta_2 LMD - \beta_3 AR\right)\right)^{-1}, \qquad [1]$$

where β_1, β_2, and β_3 are the model coefficients fit to the data (0.302, −1.421, and −0.126, respectively); *LMD* is the log of the metric distance between fish i and fish j; and *AR* is the ranked angular area of fish j subtended on the eye of fish i.

The logarithm of the metric distance is a scale dependent absolute feature; the initiator of a startle behavior is much more likely to trigger evasion in an observer if it is not occluded, and in close proximity (Fig. 2C). Ranked angular area is a scale independent and comparative feature in which an individual's neighbors are ranked by their visual size: the area they subtend on the retina of the observing focal fish, such that the neighbor with the largest angular area observed by a given individual will have an $AR = 1$, the neighbor with the second largest angular area will have an $AR = 2$, and so on (Fig. 2D). Ranking in this way encodes implicit information about other neighbors, and so facilitates inhibition. For example, if an initiator has a relatively low rank (i.e., there are many individuals that subtend higher areas on the retina that do not respond), the focal individual is inhibited from responding. This ranking does not imply counting, and is consistent with the computation of preattentive features of relative stimulus conspicuity, or salience (42).

Reconstruction and Analysis of the Quantitative Interaction Network. This mapping between sensory input and behavioral response, constructed based only on the behavior of first responders, allows us to build a hypothetical network predictive of how behavior will spread through the group. Here, the weight of an edge between individuals i and j, $w_{ij} = P(i|j)$, is the probability of a behavioral response by individual i if individual j exhibits behavioral change.

Because neither visibility nor the ranked angular area is a symmetrical property (w_{ij} need not equal w_{ji}), social connectivity is both directed and weighted (*SI Appendix*). A visualization of this network just before an initiation event is shown in Fig. 3A, where a magnified view of a subset of the group highlights the weighted, directed interconnectivity (Fig. 3B). Although we consider just the static network immediately preceding startle initiation (because we want to predict events before they occur), an example of how these networks change over time is shown in Movie S2. Because the strength of connections between individuals depends, in part, on distance, these networks are relatively lattice like in structure with few strong, but many weak, long range connections (*SI Appendix*, Fig. S9).

Predicting Behavioral Cascades and the Relationship Between Spatial Position and Social Influence in Groups. A central focus is whether we can predict, immediately preceding the event, whether a change of behavior by any single individual will propagate extensively, thus profoundly influencing group behavior (Fig. 1B). As discussed previously, variability in the motion characteristics of the initiator do not explain influence (*SI Appendix*). By contrast, however, the local structural properties of the complex interaction network we have identified are highly informative. Unlike predictions arising from epidemiological contagion, we find that those individuals with a highly interconnected local neighborhood, as quantified by the local, weighted, directed clustering coefficient (43), have the greatest ability to effect behavioral change through the group, (generalized linear model fit: likelihood ratio test, $P < 0.0001$; Fig. 3C).

In simple contagion processes, such as most epidemiological contagion, multiple connections between neighbors (i.e., a high clustering coefficient) create redundancies in the network that reduce the extent of propagation. However, in complex contagious processes, these multiple ties can provide a reinforcement effect, helping the response to propagate further (44). In contrast to
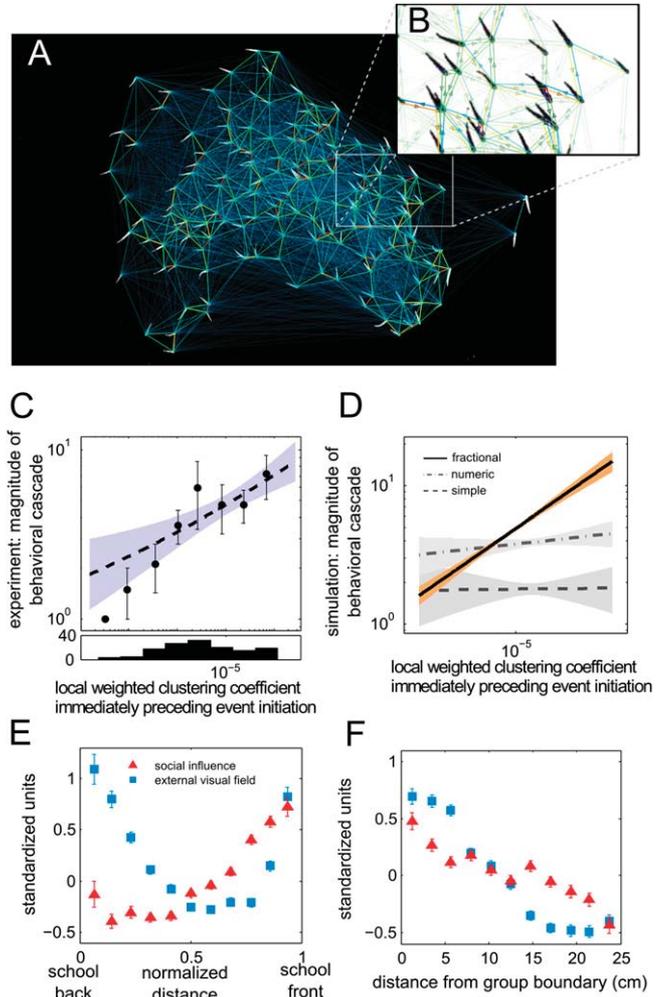

Fig. 3. Local weighted clustering coefficient in interaction networks predicts the magnitude of behavioral cascades. (A) Interaction network, where link weights are determined as a function of the log metric distance and ranked angular area. (B) Directedness of the network. Although many links are reciprocal (green), there also exist connections that are much stronger in one direction than the other (yellow/blue). (C) Relationship between weighted directed clustering coefficient of the initiator at the time of cascade initiation and the magnitude of the behavioral cascade, where the black dots show the mean value of all cascade sizes falling in each bin and the error bars show the SE. Data are divided into eight logarithmically spaced bins. The dotted line and blue shaded region represent the best generalized linear model fit to the data with a log link function and the 95% confidence interval. The histogram below is the distribution of initiator weighted directed clustering coefficients. (D) Relationship between simulated cascade size and local weighted clustering coefficient for three contagion models (fractional, solid line; numerical, dashed dotted line; simple, dashed line). Solid and dotted lines are regression fits to the simulated data, whereas shaded regions are 95% confidence intervals. Here, we use the best fit parameters from each model and simulate behavioral cascades on all nodes in 20 different fish configurations. Model details are provided in *SI Appendix*. (E) Social influence (red triangles, approximated by weighted directed clustering coefficient) and visual field that extends outside the group (blue squares), plotted against normalized distance from school back to school front, in polarized fish groups (*SI Appendix*). (F) Same as in E, plotted against distance from group boundary, again calculated for polarized groups. Units in E and F are standardized such that the mean is 0 and SD is 1.

analyses of social contagion for online social networks, such as Twitter and Facebook (45, 46), individuals' proximity to the core of the network is not predictive of social influence (generalized linear model fit with weighted k core: likelihood ratio test, $P = 0.18$; *SI Appendix*, Table S2). In addition, individuals with a high betweenness centrality are less likely to be influential (*SI Appendix*).

Because interaction networks are directed, there is a subtle, but relevant, distinction between influence and susceptibility to influence. From an initiator's perspective, a higher local weighted clustering coefficient represents a more susceptible neighborhood; that is, once the alarm reaches at least one neighbor, more individuals in the neighborhood will observe multiple alarms, and thus will be more likely to respond. From a potential responder's perspective, a response is more likely in the focal individual (it is more susceptible) if it is strongly connected to the initiator (short path length) and if it has neighbors that are strongly connected to each other (high clustering coefficient).

The mechanism by which shortest paths function is simple to understand: Shortest paths represent the most probable paths for the propagation of behavioral change. In fact, we find that even when controlling for metric distance, the shortest path length retains significant power for predicting responders (logistic regression; df $= 2, N = 5502, P < 0.0001$). We also find that a strong interconnection among an individual's neighbors (high clustering coefficient) increases the probability of response beyond the first responder (*SI Appendix*, Fig. S19B) due to the fact that multiple pathways allow for reinforcement of observations, increasing the likelihood of behavioral change. We find that it is specifically the structural properties of the interaction network, more so than other correlated variables [e.g., number of visible neighbors, local density, weighted out degree, proximity to the edge of the group (*SI Appendix*)], that account for individual social influence and susceptibility within groups (*SI Appendix*, Fig. S18).

Mapping influence in spatial terms reveals that it is those individuals near the front and side periphery of groups that are both most capable of propagating, and the most sensitive to, social cues (Fig. 3 *E* and *F*). In addition, such individuals have the most access to visual cues outside the group (Fig. 3 *E* and *F*; details are provided in *SI Appendix*), suggesting that they may play a particularly important role in obtaining and propagating information about potential threats. The spatial structure of the group also explains why the centrality measures described above are not good predictors of social influence in our study. Individuals with high centrality tend to be located near the group center, where they are more inhibited from responding (thus inhibiting the cascade) because they tend to have a large number of nonresponding neighbors.

Nature of the Contagion Process. Considerations of social influence and susceptibility to social influence (as described above) both suggest that redundant paths are important for amplification of behavioral change, and that an individual's activation probability increases with reinforcement from others but is inhibited when there exist a large number of visible neighbors that have not responded. To investigate further the nature of this contagious process and to explore why we see a strong positive relationship between clustering coefficient and influence, as well as to better understand the relationship between spatial position and social influence, we simulate three types of contagion on the fish sensory interaction networks: (*i*) a simple contagion, where response probability depends only on the link weight connecting the focal individual (node) to the active (startled) node; (*ii*) a numerical threshold response, where the response probability of the focal node depends on the absolute number of observed active nodes; and (*iii*) a fractional threshold response, where the response probability depends on the fraction of observed active neighbors (simulation details are provided in *SI Appendix*).

All three of these models have been used in different contexts: in the propagation of disease on networks [simple contagion

(47)]; in the study of self organized criticality [numerical contagion (48)]; and in examining the origin of large, rare cascades in random networks [fractional contagion (49)]. Both the numerical threshold and fractional threshold are models of complex contagion, meaning that propagation becomes more likely when multiple responses are observed, in contrast to simple contagion, where propagation only depends on the link connecting two nodes. Only in the fractional threshold model, however, is inhibition from inactive neighbors accounted for, because having more nonresponding neighbors lowers the probability of response in this case.

We simulate transmission events on each of our experimentally derived networks, which start from the same initiators (nodes) as in our data (optimizing over 5,000 sets of parameter values, with 50 replicate simulations for each set of parameter values on each network). We compare this simulated transmission with our experimental data in two ways: (*i*) We ask how well the simulation predicts the magnitude of the behavioral cascade, and (*ii*) we ask how well it predicts the actual identities of responders. We compare the performance (maximum likelihood) of each candidate contagion model, along with the performance on randomized versions of the network (*SI Appendix*). We use these models on the randomized identity networks as a baseline with which to compare model performances using the real responder identities (*SI Appendix*).

We find that the transmission of behavior in our fish schools is best described by a fractional contagion process (Fig. 3D and *SI Appendix*, Figs. S21 S25). The fractional threshold model also has the strongest relationship with the local clustering coefficient, in which we find that the most influential nodes are those nodes with high clustering coefficients (holding out degree and local density constant), a relationship we observed in our data (Fig. 3C). The alternative processes of contagion (simple and numerical) cannot account for the experimental relationship between network properties and social influence (Fig. 3D and *SI Appendix*, Fig. S25B).

The fractional nature of contagion also accounts for the relationship between spatial position and influence (Fig. 3 *E* and *F*). Individuals near the front and side edges of the group tend to have fewer visible neighbors than those individuals near the group center (those individuals with high centrality). For a fractional contagion process, the activity of a small number of neighbors near such peripheral individuals can therefore have a relatively large effect. The barrier to startling is lowered still more by the fact that neighbors of these peripheral individuals tend to have more interconnections than do neighbors of more central nodes (Fig. 3F), leading to higher levels of reinforcement via observation of multiple fast start evasion maneuvers.

Conclusions

We demonstrate here that it is possible to reconstruct quantitative interaction networks based on the sensory information used by organisms in mobile groups when making movement decisions. Unlike abstracted representations of connectivity, such as when it is assumed that individuals in close proximity are "connected" in a social network, the strength of connections here (Fig. 3 *A* and *B*) actually represents the probability of responding to others, should they change behavioral state. Individual fish use simple, likely fast to compute (42), measures to assess behavioral change, which would give the social behavior robustness in the face of factors, such as changing light conditions or turbidity, compared with other possible visual measures. Fish appear not to regulate their response based on the exact nature of fast starts (i.e., they tend to perceive others as having either responded, or not responded, in a binary manner), possibly because it is too time consuming to make a more complex assessment and/or because a fast start is inherently ambiguous, typically being a reflex response (26). Consequently, as has been predicted theoretically (28), false alarms may be an inevitable corollary of adaptive collective response in a dangerous and uncertain world. Previous observations of animal groups have found

false alarms to be common, often accounting for a large proportion of overall alarms (50 53).

Analysis of the local structural properties of the interaction networks within schools proves to be highly informative, allowing us to understand, and thus to predict, how behavioral change is transmitted through groups. We reveal the vital role of strong in terconnection among an individual's neighbors (high local cluster ing coefficient). This local property of the network increases the probability of response due to the fact that multiple pathways allow for reinforcement of observations, increasing the likelihood of be havioral change. Such properties would not be observed for simple contagion, and our experimental data, as well as our simulations, provide strong evidence for behavioral transitions spreading as complex fractional contagion.

We find that individuals near the leading and side edges of the group tend to be the most socially influential, and most susceptible to social influence. In addition, individuals in such positions have best access to visual cues outside the group. This positioning may counteract costs associated with their proximity to the group boundary, such as increased exposure to the risks of predation, and may help explain why some predators preferentially attack highly coordinated groups from their rear (2).

Thus, despite the inherently probabilistic nature of individual behavior, revealing the structure of sensory networks of interaction allows us to identify which individuals in a group are the most influential, and to predict cascades of behavioral change at their moment of initiation. This analysis demonstrates that a precise and quantitative understanding of collective behavior in large, self or ganized animal groups can be achieved if the hidden pathways of communication are effectively revealed.

Materials and Methods

Approximately 1,000 juvenile golden shiners (*Notemigonus crysoleucas*) sub sampled in groups of 150 ± 4 individuals at a time were recorded freely schooling in a 2.1 × 1.2 m tank in 4.5 5 cm of water at 16 °C for 53 minutes. Spontaneous startle cascades were identified in videos after recording. Details of experimental methods, multimodel inference, fish tracking, visual field re construction, startle classification, network analysis, and cascade simulations on experimentally derived networks are provided in *SI Appendix*.

All experiments were conducted in accordance with federal and state regulations and were approved by the Princeton University Institutional Animal Care and Use Committee.

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