

Discrete modes of social information processing predict individual behavior of fish in a group

Roy Harpaz^a, Gašper Tkačik^b, and Elad Schneidman^{a,c,1}

^aDepartment of Neurobiology, Weizmann Institute of Science, Rehovot 76100, Israel; ^bInstitute of Science and Technology Austria, A-3400 Klosterneuburg, Austria; and ^cCenter for Neural Science, New York University, New York, NY 10012

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Individual computations and social interactions underlying collective behavior in groups of animals are of great ethological, behavioral, and theoretical interest. While complex individual behaviors have successfully been parsed into small dictionaries of stereotyped behavioral modes, studies of collective behavior largely ignored these findings; instead, their focus was on inferring single, mode-independent social interaction rules that reproduced macroscopic and often qualitative features of group behavior. Here, we bring these two approaches together to predict individual swimming patterns of adult zebrafish in a group. We show that fish alternate between an “active” mode, in which they are sensitive to the swimming patterns of conspecifics, and a “passive” mode, where they ignore them. Using a model that accounts for these two modes explicitly, we predict behaviors of individual fish with high accuracy, outperforming previous approaches that assumed a single continuous computation by individuals and simple metric or topological weighing of neighbors’ behavior. At the group level, switching between active and passive modes is uncorrelated among fish, but correlated directional swimming behavior still emerges. Our quantitative approach for studying complex, multi-modal individual behavior jointly with emergent group behavior is readily extensible to additional behavioral modes and their neural correlates as well as to other species.

collective behavior | information processing | zebrafish | behavioral modeling | social interactions

Group behavior has been studied in a wide range of species—bacteria (1), insects (2–4), fish (5–11), birds (12–15), and mammals (16–19)—seeking the design principles of collective information processing, decision making, and movement. Theoretical models have suggested possible classes of computations and interaction rules that generate complex collective behavior, qualitatively replicating macroscopic features of behavior observed in real animal groups (20–26), and also have algorithmic, behavioral, and economic implications (27, 28). The ability to record the movement patterns of animals in a group with high temporal and spatial precision for long periods (9, 12, 14, 16, 29, 30) allows for direct exploration of individual traits and interactions between group members. Such attempts have considered topological vs. metric relations between conspecifics (14), effective social “forces” depending on the distance between individuals (5, 6), inference of functional interactions based on maximum entropy models of observed directional correlations (13), hierarchical spatial ordering (12, 31, 32), and active signaling (33, 34).

Because individual behavior is complex, most studies have focused on modeling various statistics of the group, like polarization or moments of the distribution of interindividual distances (7, 14, 35–37). These approaches, however, do not necessarily give a clear or a unique solution for the underlying interactions between individuals (38). Furthermore, in many cases, the suggested models were nonphysiological in terms of response times or temporal causality; ignored physical constraints, such as momentum and friction; or omitted the role of nonsocial sensory information. Somewhat surprisingly, most models of individual behavior in a group assume that animals continuously update their movement

based on the location or velocity of their neighbors (20–24, 37). However, characterization of movement patterns of individual zebrafish larva, *Caenorhabditis elegans*, and *Drosophila*, for example, suggests that a relatively small set of distinct stereotyped “modes” underlies complex individual behavior (39–41).

Here, we incorporated the concept of discrete behavioral modes in individual animals into a mathematical framework for animal motion in an interacting group. We studied individual behavior in groups of adult zebrafish in a large arena using high spatiotemporal individual tracking under different behavioral contexts. Adult zebrafish live in nature in groups of 4–20 fish, either in still waters or in running rivers (42), and exhibit social behaviors and shoaling tendencies both in the wild and in the laboratory (8, 42). We analyzed the behavior of individuals in the group and identified distinct behavioral modes, which were used to build a highly accurate mathematical model of swimming behavior of individual fish in a group. The model was based on the sensory and social information that was available to each animal and took into account spatial and temporal biophysical constraints. Importantly, we evaluated the models in terms of their power to predict the trajectories of individual fish rather than statistical averages over the whole group (43, 44) and analyzed how behavioral modes of individuals relate to emergent collective behavior of the group.

Results

To study individual computations and interactions underlying group behavior in zebrafish, we tracked individuals in groups of 2, 3, 6, and 12 adult fish for up to 1 h at a time in a large circular arena with shallow waters constituting an effective 2D environment (Fig. 1A, *SI Materials and Methods*, Fig. S1A, and *Movie S1*). We sampled the trajectory of the center of mass of each fish i in the group, denoted as $\bar{x}_i(t)$, with high spatial and temporal resolution

Significance

The way that individuals interact and coordinate their motion in a group is fundamental to the nature of individual and group behavior. Here, we inferred interaction rules that govern individual swimming behavior of adult zebrafish in a group. We show that fish alternate between apparent “active” and “passive” behavioral modes, which we describe using mode-dependent spatiotemporal models of social and sensory computation. This modeling framework closely matches the behavior of individual fish in a group, surpassing previously suggested models that use a universal, ongoing computation. We conclude that group behavior depends on both the computation used by the fish and their current behavioral mode and that the way that fish alternate between modes can shape collective behavior of the group.

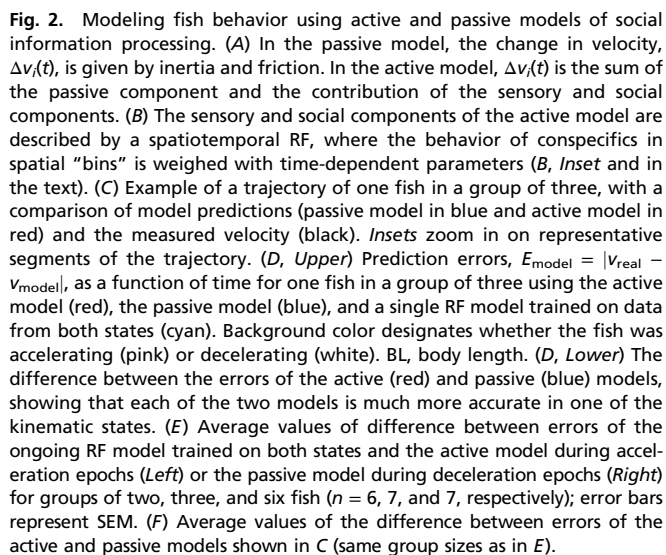
Author contributions: R.H., G.T., and E.S. designed research, performed research, analyzed data, and wrote the paper.

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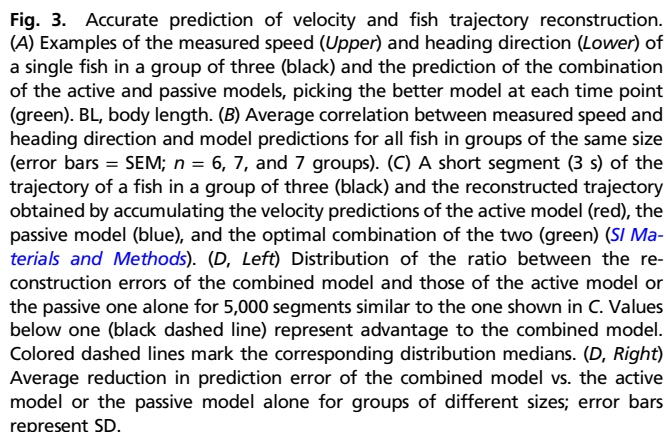
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¹To whom correspondence should be addressed. Email: elad.schneidman@weizmann.ac.il.

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Since we do not have access to the internal state of information processing of the fish, we asked how well we could explain fish behavior if we were to pick the best model for each time point (the one that gives the lowest error compared with the real velocity). This combined model (Movie S3) gives an excellent fit to the data both in terms of the speed (Fig. 3A, Upper) and the heading direction of swimming (Fig. 3A, Lower). Over all groups, the correlations between the real and the estimated velocity of the fish were ~ 0.97 for direction and ~ 0.94 for speed on test data (Fig. 3B). To further illustrate the importance of the two interleaved modes for describing individual behavior, we compared the accumulated effect of the errors in predicting the instantaneous velocity vectors that each of the models makes. Fig. 3C shows the “reconstructed” swimming trajectory of a fish in a group that would result from summing over the instantaneous velocity predictions of each model to obtain a complete trajectory segment (SI Materials and Methods). Repeating this analysis for 5,000 3-s-long segments of a group of three fish, we found that combining the active and passive models gave much more accurate reconstructions than either model alone (Fig. 3D, Left and Fig. S3C). The reconstruction errors over trajectory segments for all groups of three fish were lower by $37 \pm 5\%$ compared with the passive model alone and $19 \pm 11\%$



compared with the active model alone, with similar results for groups of two and six fish (Fig. 3D, *Right*) ($P < 0.005$ for all group sizes and for both comparisons, t test for matched samples). While this combined model is an upper bound on the performance of any mix of the active and passive models, similar performance gains are retained in a model where the active and passive models are chosen according to the kinematic state of the fish (Fig. S3).

A significant part of the high correlation between model predictions and the data originates from the autocorrelation of individual swimming behavior. This is especially true in deceleration epochs, where the correlation between the measured $\vec{v}_i(t)$ and prediction based on $\Delta\vec{v}_i^{\text{passive}}(t)$ was 0.986 ± 0.002 (low prediction error values in Fig. S24). We, therefore, focused on the change in velocity that is not explained by autocorrelation and friction: Fig. 4A shows the change in velocity that is not explained by the passive component, which we denote as $\Delta\vec{u}_i(t) = \Delta\vec{v}_i(t) - \Delta\vec{v}_i^{\text{passive}}(t)$. Clearly, in the deceleration epochs, removing the passive component leaves very little change to explain. In the acceleration epochs, the correlation between $\Delta\vec{u}_i(t)$ and the prediction of $\Delta\vec{v}_i^{\text{RF}}(t)$ was ~ 0.5 . When we examined the social or sensory contributions to the RF model in isolation, the prediction performance was significantly lower than when both were included (Fig. 4B) ($P < 0.0005$ for all group sizes, t test for matched samples), with small differences between group sizes (Fig. S44). The nonadditivity of social information and nonsocial sensory information reflects the redundancy between them. In this setup, it is impossible to discern whether fish “read” sensory information about the environment from their own senses or from the behavior of other fish. We note that the relation between $\Delta\vec{v}_i$ and the predictions of the models did not indicate a need for a nonlinear extension of the RF

model (Fig. S4C) [compare with linear–nonlinear models in neuroscience (46)]. Predicting the entire acceleration epoch using a similar RF model from the sensory and social information at the beginning of the epoch performed significantly worse (*SI Materials and Methods* and Fig. S5).

Our RF model outperformed common models of collective movement in predicting $\Delta\vec{u}_i$, even when the parameters of these competing models were optimized for our data (*SI Materials and Methods*): we predicted $\Delta\vec{u}_i(t) \sim 8 \pm 2.5\%$ better on average than a “zonal model” (23) and $\sim 11.3 \pm 4\%$ better than a “topological model” (14) (Fig. 4C) ($P < 0.05$ for all group sizes and both model comparisons, t test for matched samples). The advantage of the RF model was even more pronounced when prediction was based only on social information (Fig. S4B). We found similar advantages of the RF model over the zonal and topological models when studying groups of 12 fish (Fig. S4D), but these larger groups do not stay in a cohesive structure for long periods of time (Fig. S4E), effectively breaking up into smaller subgroups.

To characterize the spatiotemporal effects of social and sensory information on the movement decisions of a focal fish, we compared the weight maps of the RF models under two different behavioral contexts—fish swimming freely in the arena as described above and fish who were trained to seek food that is randomly scattered in the arena (*SI Materials and Methods*). Inhomogeneity in the RF map reflects the effects of the relative distance and relative angle of neighbors on the focal fish (Fig. 5A): social effects are strongest in front of the fish and weaker behind it. The weights of the nonsocial information show the opposite structure, with walls directly to the side of the fish having the strongest effect on its behavior. Overall, the effects of neighbors are weaker for longer temporal delays but retain their positive sign, whereas the effect of the wall decreases faster with time (Fig. 5A, *Center*) and then switches sign. Interestingly, the way that fish integrate information from their surroundings changes with the behavioral context (Fig. 5B): the effects of arena walls are weaker in food-searching fish, and the effects of fish positioned directly behind the focal fish are positive and stronger (Fig. S6A and B shows statistically significant differences between weight maps). In addition, during food searching, fish in groups (unlike solitary fish) show longer acceleration epochs compared with freely swimming ones (Fig. S6C).

What does switching between the two modes of information processing at the individual level imply for the behavior of the group? Fig. 6A and B shows an example of the swimming velocities of three fish decomposed into the speed $s_i(t)$ (Fig. 6A) and the direction of swimming $\theta(\vec{d}_i)$ (Fig. 6B). We asked what the temporal relations were between kinematic states in pairs of fish in the group by seeking the time lag that would maximize the correlation for short movement segments (1-s long) for each fish pair (using ref. 47 to verify the identity of tracked individuals) (*SI Materials and Methods*). The distribution of the time of maximal correlation (τ_{max}) was indistinguishable from the expectation of fish changing states independently (Fig. 6C), and correlation values also did not differ from what was expected by chance (Fig. S74). Such independent transitions between behavioral modes of individual fish could give the group a way to sample the sensory space in a distributed and interleaved manner, with no temporal processing gaps, without the need for scheduling. In contrast, similar analyses identified significant correlations between swimming directions in pairs of fish (Fig. S74) and a corresponding significant peak in the distribution of temporal lags, suggesting causal relationships (Fig. 6D). The independence of kinematic states among fish with correlated swimming direction was apparent also at the level of the group from the distribution of synchronized states among the fish: namely, the probability to find k of the N fish in the group to be accelerating synchronously (Fig. 6E) and the probability of k fish swimming in a similar direction (Fig. 6F). For synchronous accelerations, the probability distribution was symmetric and matched

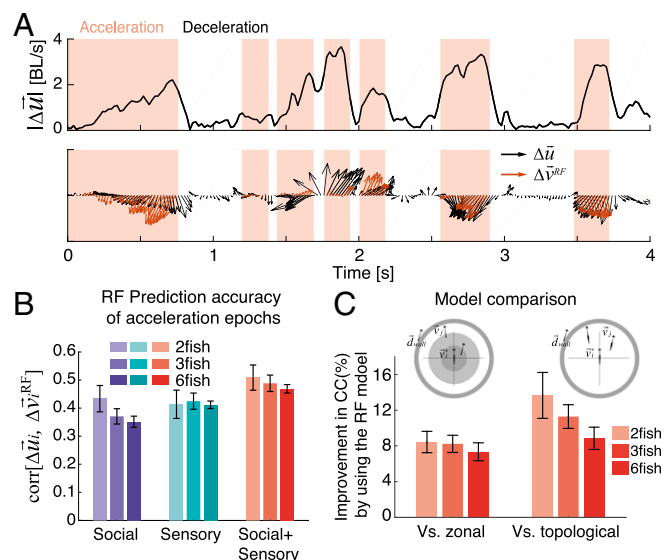
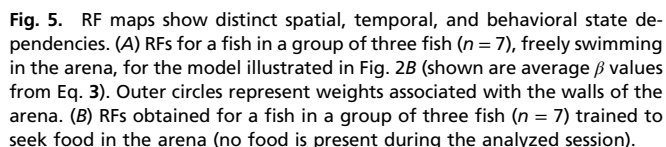


Fig. 4. Active movement changes are accurately predicted by the RF model using both social and sensory information. (A, *Upper*) An example of $|\Delta\vec{u}_i(t)|$, the magnitude of the measured change in velocity after subtracting the passive component (in the text) of a single fish in a group of three over 4 s; background colors mark acceleration epochs (pink) and deceleration epochs (white). BL, body length. (A, *Lower*) Comparison of the measured $\Delta\vec{u}_i(t)$ and the prediction obtained using the RF model (red arrows) in the acceleration epochs. (B) Prediction accuracy of $\Delta\vec{u}_i(t)$ by RF models that use only the social information component, only the sensory information component, or both components of Eq. 3 for different group sizes (error bars represent SEM; $n = 6, 7$, and 7 groups). (C) Improvement in predicting $\Delta\vec{u}_i(t)$ in acceleration epochs by the RF model relative to the corresponding zonal or topological versions (*SI Materials and Methods* has details); values are averaged over all groups of different sizes. CC, correlation coefficient; error bars represent SEM.



Discussion

The main approach that we presented here merges two distinct lines of inquiry of animal behavior: studies of single-animal behavior that have shown “discrete behavioral modes” (39–41) and group behavior models that have focused on qualitatively capturing complex collective behavior emerging in groups of simple interacting individuals described by a single behavioral mode (7, 23, 24, 35, 37). Our results show that individual behavioral modes (*i*) have clear kinematic proxies, (*ii*) suggest distinct information processing/computation modes in individuals, and (*iii*) have a significant impact on group behavior. Beyond giving a better mechanistic model for individual behavior in a group that reflects multiple states of behavior, our approach portrays the group as a collection of diverse individuals that perform computations that seem temporally discrete and context-dependent, with interactions that are dynamic in space and time.

Our approach may also enable a more direct analysis of the relation between the detailed nature of individual computation in a group and the resulting collective behavior. First, traditionally, behavioral modes were described at the level of the group, as in the work by Tunström et al. (9), which reported the existence of three distinct collective states in golden shiners (milling, swarming, and directed motion) and attributed state transitions to changes in speed at the individual level. Our results, however, suggest a functional role of state transitions at the level of the individual, in the emergence of collective states at the

The models that we presented could potentially be improved by further optimization of the spatiotemporal filters used to

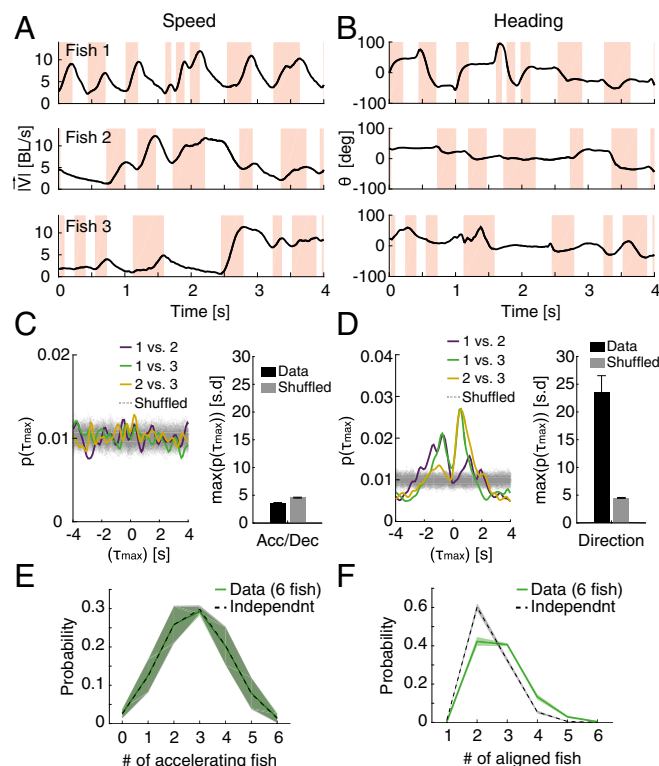


Fig. 6. Asynchronous switching between information processing modes among individual fish in a group and synchronous heading directions of group members. (A) Example of the simultaneous acceleration (pink)/deceleration (white) profiles of three fish in a group. BL, body length. (B) Same as in A but for the heading direction of the fish. (C, Left) Distributions of time difference (τ_{\max}) that gave the maximum correlations between the kinematic states of pairs of fish for 1-s-long windows in a group of three (colored lines) and shuffled controls (light gray) (*SI Materials and Methods*). (C, Right) Peak values of the distribution of time difference (τ_{\max}) shown in C, Left in units of SDs for pairs of fish and for shuffled data averaged over all pairs of fish within all groups of three fish ($n = 6$, $P = 0.99$, t test for matched samples). (D) Same as in C but for the distribution of time difference (τ_{\max}) of the cross-correlation of direction of motion of pairs of fish. Here, directional correlation shows clear structure and peak times ($n = 6$, $P < 0.0005$, t test for matched samples). (E) Average empirical probability distribution $P(a_1, a_2, \dots, a_n)$ of fish kinematic states (acceleration or deceleration), where a_i represents the state of fish i (solid green), and the prediction of a model assuming independence between fish $p(a_1)p(a_2) \dots p(a_n)$ (dashed line); shadings represent SEM. (F) Similar to E for the distribution of heading direction $P(d_1, d_2, \dots, d_n)$, where d_i is the direction of fish i discretized into six evenly sized bins (*SI Materials and Methods*) (solid green), and the distribution obtained under the assumption of independence $p(d_1)p(d_2) \dots p(d_n)$ (dashed line).

describe the visual field of a fish and by adding nonlinear components to the prediction model. A finer dissection of individual behavior into more behavioral modes and modeling the nature of transitions between behavioral states would hopefully give even better characterization of the discrete components of social computation. Moreover, the differences between the RFs inferred under different behavioral contexts reflect a dynamic and possibly learned nature of these computations. Modeling how individual fish use different computations based on personal tendencies, past experience, or current needs would bring us closer to dissecting idiosyncratic behavior and understanding its effect on the group level.

The approach that we presented here can be readily extended to other animal groups, where individual tracking with high spatiotemporal accuracy is possible—such as fish (5–7, 9), birds (12, 14), or mammals (16, 17). It would also be possible to explore the relation between fine motor behavior and group traits and the mapping of sensory and social information into action, possibly in closed loop experimental settings. Combining these models with recordings of neural activity in members of

the group (54, 55) would allow for direct study of social and sensory integration and processing at behavioral and neuronal levels simultaneously.

Materials and Methods

Individual and group behaviors of 147 adult zebrafish, in groups of 2–12, were studied using video tracking in different behavioral contexts in the laboratory using large circular arenas. Individual fish trajectories were extracted using in-house software with fish identities corrected using software from ref. 47. All Experimental procedures were approved by the Institutional Animal Care and Use Committee of the Weizmann Institute of Science. Details of experiments, image processing, analysis, model fitting, and evaluation are described in *SI Materials and Methods*.

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