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Domino-like propagation of collective U-turns in fish schools

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Abstract

Moving animal groups such as schools of fish or flocks of birds often undergo sudden collective changes of their travelling direction as a consequence of stochastic fluctuations in heading of the individuals. However, the mechanisms by which these behavioural fluctuations arise at the individual level and propagate within a group are still unclear. In the present study, we combine an experimental and theoretical approach to investigate spontaneous collective U-turns in groups of rummy-nose tetra (*Hemigrammus rhodostomus*) swimming in a ring-shaped tank. U-turns imply that fish switch their heading between the clockwise and anticlockwise direction. We reconstruct trajectories of individuals moving alone and in groups of different sizes. We show that the group decreases its swimming speed before a collective U-turn. This is in agreement with previous theoretical predictions showing that speed decrease leads to an amplification of fluctuations in heading in the group, which can trigger U-turns. These collective U-turns are mostly initiated by individuals at the front of the group. Once an individual has initiated a U-turn, the new direction propagates through the group from front to back without amplification or dampening, resembling the dynamics of falling dominoes. The mean time between collective U-turns sharply increases as the size of the group increases. We develop an Ising spin model integrating anisotropic and asymmetrical interactions between fish and their tendency to follow the majority of their neighbours nonlinearly (social conformity). The model quantitatively reproduces key features of the dynamics and the magnitude of collective U-turns observed in experiments.

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1 Introduction

The flexible coordination of fish in schools brings important benefits [1–3]. A striking consequence of this flexibility is the performance of rapid and coherent changes in direction of travel of schools, for instance as a reaction to a predator in the neighbourhood [4, 5]. In many species, it is only a small number of individuals that detects the danger and changes direction and speed, initiating an escape wave that propagates across the entire school. Such waves have been reported, for instance, in anchovies (*Engraulis ringens*) [6], herrings (*Clupea harengus*) [7] and Pacific blue-eyes (*Pseudomugil signifer*) [8]. Besides, sudden collective changes of the state of a school may also happen without external cause as a consequence of stochastic effects [9]. In these cases, local behavioural changes of a single individual can lead to large transitions between collective states of the school, such as between the schooling and milling states. Determining under what conditions fluctuations in individual behaviour, for instance in heading direction, emerge and propagate within a group is a key to understanding transitions between collective states in fish schools and in animal groups in general.

Only few theoretical and experimental studies have addressed these questions [10]. Calovi et al. used a data-driven model incorporating fluctuations of individual behaviour and attraction and alignment interactions among fish to investigate the response of a school to local perturbations (i.e. by an individual whose attraction and alignment behaviour differ from the rest of the group). They found that the responsiveness of a school is maximum near the transition region between the milling and schooling states, where the fluctuations of the polarisation are also maximal [11]. This is entirely consistent with what happens in inert physical systems near a continuous phase transition. For instance, in magnetic systems, it can be proven that the polarisation of the atomic spins of a magnet has diverging fluctuations and response to a perturbation by a magnetic field, as one approaches the transition point (by varying the temperature). The fluctuations of school polarisation are also expected to be strongly amplified at the transition from schooling to swarming observed when the swimming speed of individuals decreases. During such a transition, the behavioural changes of a single individual are more likely to affect the collective dynamics of the school. However, the tendency of fish to conform to the speed and direction of motion of the group can also decrease the fluctuations at the level of the group with increasing group size. Experimentally, it has been shown in mosquito fish (*Gambusia holbrooki*) that individuals reduced the variation of their own speed when swimming in groups rather than alone, suggesting they adjust their to that of others [12]. Social conformity refers to the nonlinear response of individuals to adjust their behaviour to that of the majority [13–16]. When facing two options A and B, an individual's probability to choose one of these options (e.g option A) is less than the frequency of this option in the group (f_A) if this option is not the most common in the group ($f_A < 1/2$) and the probability to choose it is greater than the frequency of this option if it is the majority ($f_A > 1/2$) [15]. Thus, the tendency of an individual to differ in behaviour to the group will decrease as group size increases.

In the present work, we analyse in groups of different size under which conditions individual U-turns occur, propagate through the group, and lead to collective U-turns. We let groups of rummy-nose tetra (*Hemigrammus rhodostomus*) swim freely in a ring-shaped tank. In this set-up, fish schools can only head in two directions, clockwise or anticlockwise, and they regularly switch from one to the other. In a detailed analysis of empirical data, we reconstruct individual trajectories of fish and investigate the effect of group size on both the tendency of individuals to initiate U-turns and the collective dynamics of the U-turns. We develop an Ising-type spin model, a simple model for magnets in the physical context, to investigate the consequences on the dynamics and the propagation of information during U-turns of the local conformity in heading, of the fish anisotropic perception of their environment, and of the asymmetric interactions between fish. We use tools and quantitative indicators from statistical physics to analyse the model. In particular, we introduce the notion of local (respectively, global/total) pseudo energy which, in the context of fish school, becomes a quantitative measure of the "discomfort" of an individual (respectively, of the group) with respect to the swimming direction of the other fish.

2 Material and Methods

2.1 Experimental procedures and data collection

A group of 70 rummy-nose tetras (*Hemigrammus rhodostomus* were purchased from Amazonie Labège (`http://www.amazonie.com`) in Toulouse, France. This tropical freshwater species swims in a highly synchronised and polarised manner. Fish were kept in 150 L aquariums on a 12:12 hour, dark:light photoperiod, at 27.5° C (±0.8° C) and were fed *ad libitum* with fish flakes. The body length of the fish in the experiments was on average 3.4 cm (± 0.44 cm). The experimental tank (120×120 cm) was made of glass and was set on top of a box to reduce vibrations. It was surrounded by four opaque white curtains and illuminated homogeneously by four LED light panels (Figure S1A). Inside the experimental tank, a ring-shaped corridor was filled with 7 cm of water of controlled quality (50% of water purified by reverse osmosis and 50% of water treated by activated carbon) heated at 27.6° C (±0.9° C) . The corridor was 10 cm wide with a circular outer wall of radius 35 cm. The shape of the circular inner wall was conic and its radius at the bottom was 25 cm. The conic shape was chosen to avoid the occlusion on videos of fish swimming too close to the inner wall. For each trial, n fish were randomly sampled from their breeding tank ($n \in \{1, 2, 4, 5, 8, 10, 20\}$). Fish only participated in a single experiment per day. They were introduced in and acclimatised to the experimental tank during a period of 10 minutes before the trial starts. During each trial of one hour, individuals were swimming

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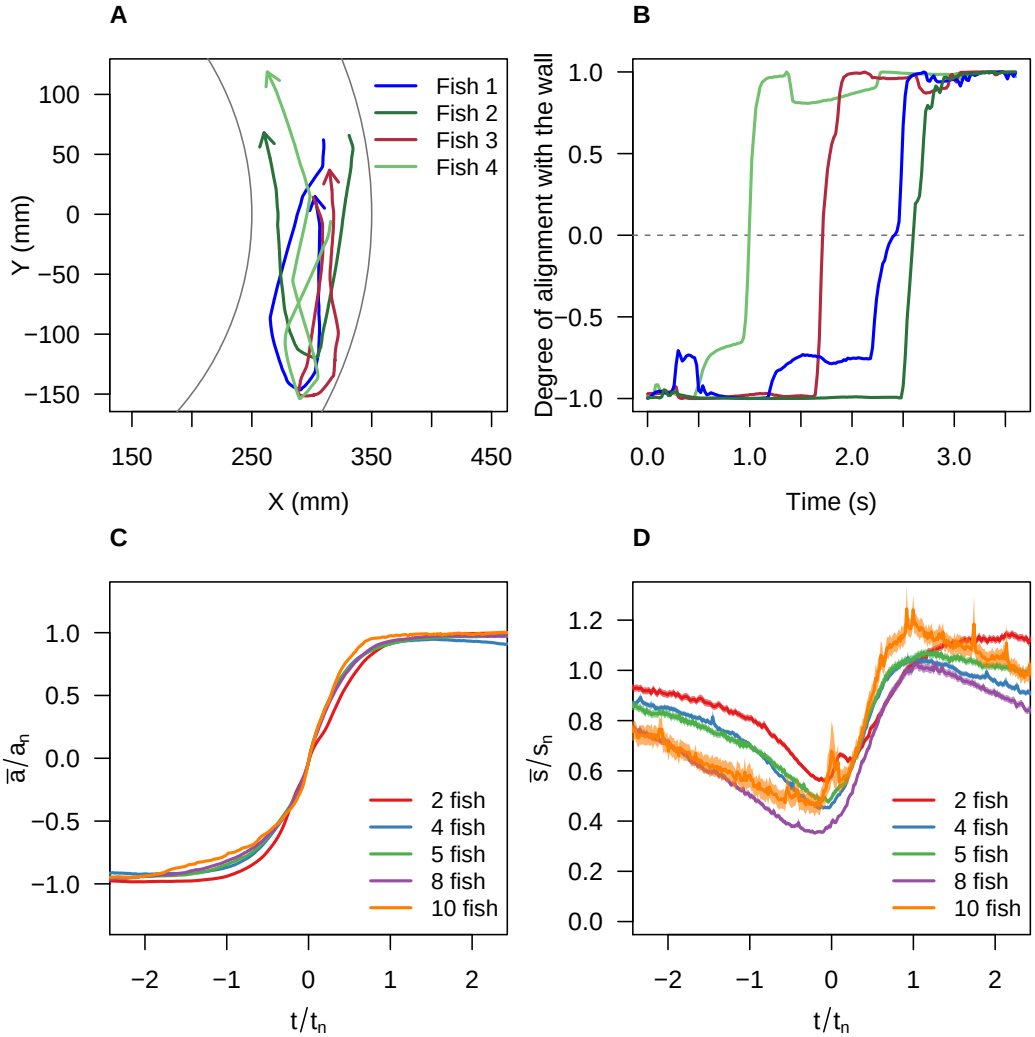

Figure 1. Individual trajectories (A) and degree of alignment $a_i(t)$ of fish with the wall (B) during a U-turn in a group of 4 fish. $a_i = 1$ when the heading of an individual i is parallel to the wall and anticlockwise and $a_i = -1$) when it is clockwise . C) Normalised degree of alignment with the wall averaged over all U-turns against the rescaled time t/t_n for groups of size n, where t_n is a measure of the mean duration of a U-turn. $t = 0$ is set when $\bar{a}/a_n = 0$. D) Average speed of individuals, averaged over collective U-turns ($\bar{s}$) and normalised by the average speed of the group size (s_n) against the rescaled time t/t_n.

freely without external perturbation. For each group size we performed several replications (between 9 and 14, see Table S1). Note that six experiments with a single fish have been discarded because of the inactivity of the individuals. Trajectories of the fish were recorded by a Sony HandyCam HD camera filming from above the set-up at 50Hz (50 frames per second) in HDTV resolution (1920×1080p).

2.2 Data extraction and pre-processing

Except for the group size of 20 fish, the position of each individual per frame was tracked with idTracker 2.1 [17]. Sometimes, fish were misidentified by the tracking software, for instance when two fish were swimming too close to each other. All sequences that were missing a maximum of 50 consecutive positions were interpolated. For groups of 20 fish, only the number of collective U-turns and the time interval between two consecutive U-turns have been recorded.

Time series of positions were converted from pixels to meters and the origin of the coordinate system was set to the centre of the ring-shaped tank. Body lengths and headings of fish were measured on each frame using the first axis of a principal component analysis of the fish shape issued by idTracker. Table S1 summarises the data collected in our study.

2.3 Detection and quantification of individual and collective U-turns

Since fish swim in a ring-shaped tank, their heading can be converted into a binary value: clockwise or anticlockwise. Before a collective U-turn, the fish are all moving in the same direction, clockwise or anticlockwise. When one fish changes its heading to the opposite direction, this turn may propagate to other fish. For an example of collective U-turns,

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see Video S1.

From the heading φ_i and angular position θ_i (defined with respect to positive x-axis) of an individual i at time t (Figure S2), the angle of the fish relative to the wall is computed as:

$$\theta_{wi}(t) = \varphi_i(t) - \theta_i(t) \quad (1)$$

and thus the degree of alignment to the circular wall is:

$$a_i(t) = \sin(\theta_{wi}(t)) \quad (2)$$

The degree of alignment a_i between a fish i and the outer wall is 1 when it is moving anticlockwise, -1 when moving clockwise and 0 when it is perpendicular to the wall. When a group of fish makes a collective U-turn, the degree of alignment to the wall averaged over all individuals of the group $\bar{a}$ changes sign (from negative to positive or vice versa). We used this as the criterion for detecting collective U-turns automatically from the smoothed time-series of $\bar{a}$ using a centred moving average over 9 consecutive frames. Figure 1A shows individual trajectories during a typical collective U-turn in a group of 4 fish and Figure 1B reports the corresponding change of direction of motion performed by each individual i (this is detected by the change of sign of the degree of alignment with the wall a_i). A collective U-turn in a group of n fish starts when the degree of alignment to the wall a_i of the fish i that initiates the U-turn is 0 and it ends when the degree of alignment to the wall a_j of the last fish j that turns is 0. For each collective U-turn, we ranked the order with which each individual turned r_i (where $r_i = 1$ refers to the individual i initiating it) and the spatial positions of each individual at the initiation of the U-turn. In order to compare the spatial positions of individuals swimming in groups of various shapes, we compute at the beginning of the U-turns $\Phi_i = -(\theta_i - \theta_f)/(\theta_f - \theta_l)$, where the angle $\theta_i - \theta_f$ between each individual and the fish in front of the group, normalised by the angle $\theta_f - \theta_l$ between the first and last fish. We discretised $\Phi \in [0, 1]$ in n cells with increasing indices and the spatial position π_i is given by the index of the cell that contains Φ_i. π_i is 1 if an individual is very close to the front of the group when the first individual turns and n if it is close to the back of the group at this time.

To compute the ranks of turning and the spatial positions of individuals at the initiation of the U-turns, we needed to make sure that fish were responding to the initiation of a specific U-turn (and not to a previous U-turn very close in time). Therefore, we only considered situations where fish were swimming for at least 2 seconds in the same direction before and after the U-turns. For the total number of replicates and collective U-turns for each group size, see Table S1.

3 Results

3.1 Spatiotemporal dynamics of collective U-turn

Hemigrammus rhodostomus forms highly cohesive schools during our experiments (Figure S4A). There is a high tendency for fish to adjust their speed and heading to that of their group-members. In a former study [18], we have shown that this is achieved through attraction and alignment interactions that have been precisely measured. Larger groups show a lower number of collective U-turns. Figure 2 indicates that the average time interval between two collective U-turns in groups of 10 fish (one U-turn every 20 min) is two orders of magnitude times that in groups of 2 fish (one U-turn every 0.2 min). In experiments in which no collective U-turn was observed (grey triangles on Figure 2), we took the total period of observation as the interval till the next U-turn; the average time between U-turns λ_n found in groups of 4, 8, 10 and 20 fish are therefore underestimating the actual averages. Note that the variance of the average time interval between U-turns ρ_n^l per experiment l is large, especially in groups of 5 and 8 fish.

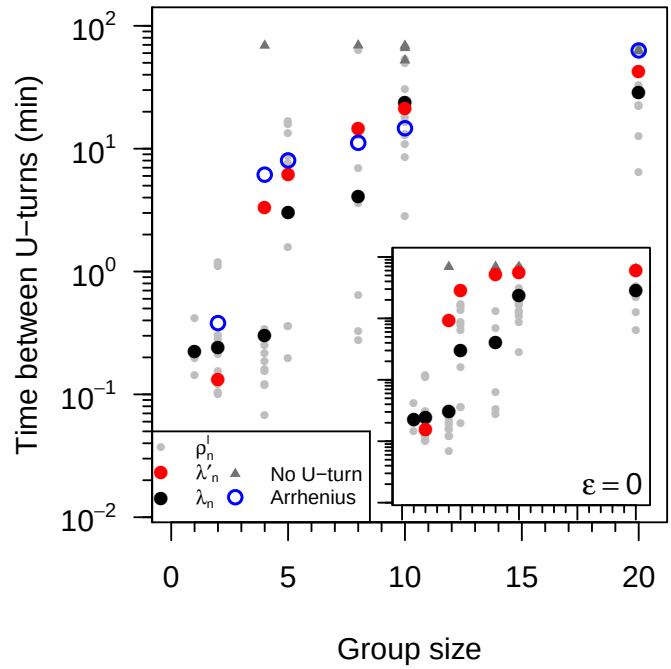

Figure 2. Average time between two consecutive collective U-turns as a function of group size. Average time between collective U-turns of each experiment l with n fish defined as the duration of an experiment divided by the number of collective U-turns performed during this experiment: $\rho_n^l = T_n^l/u_n^l = 1/\tau_n^l$ (grey dots). Experiments without collective U-turn are indicated by a grey triangle, with $\rho_n^l = T_n^l/1$. Average of the log of the average time between collective U-turns over all experiments $\lambda_n = \exp(\langle\log(\rho_n^l)\rangle)$ (black dots) and over 1000 simulations $\lambda'_n = \exp(\langle\log(\rho_n'^l)\rangle)$ ($J = 1.23$ and $\epsilon = 0.31$; red dots). Prediction of the Arrhenius law (open blue circles). Inset: same results of the model without asymmetric influence ($J = 1.23$ and $\epsilon = 0$).

Thus, as group size increases, the number of collective U-turns decreases, possibly because the propensity of a fish to initiate or propagate a U-turn may decrease. Like in many other species, individual fish tend to adopt the behaviour of the majority of the group members and thus inhibit the initiation of U-turns [12].

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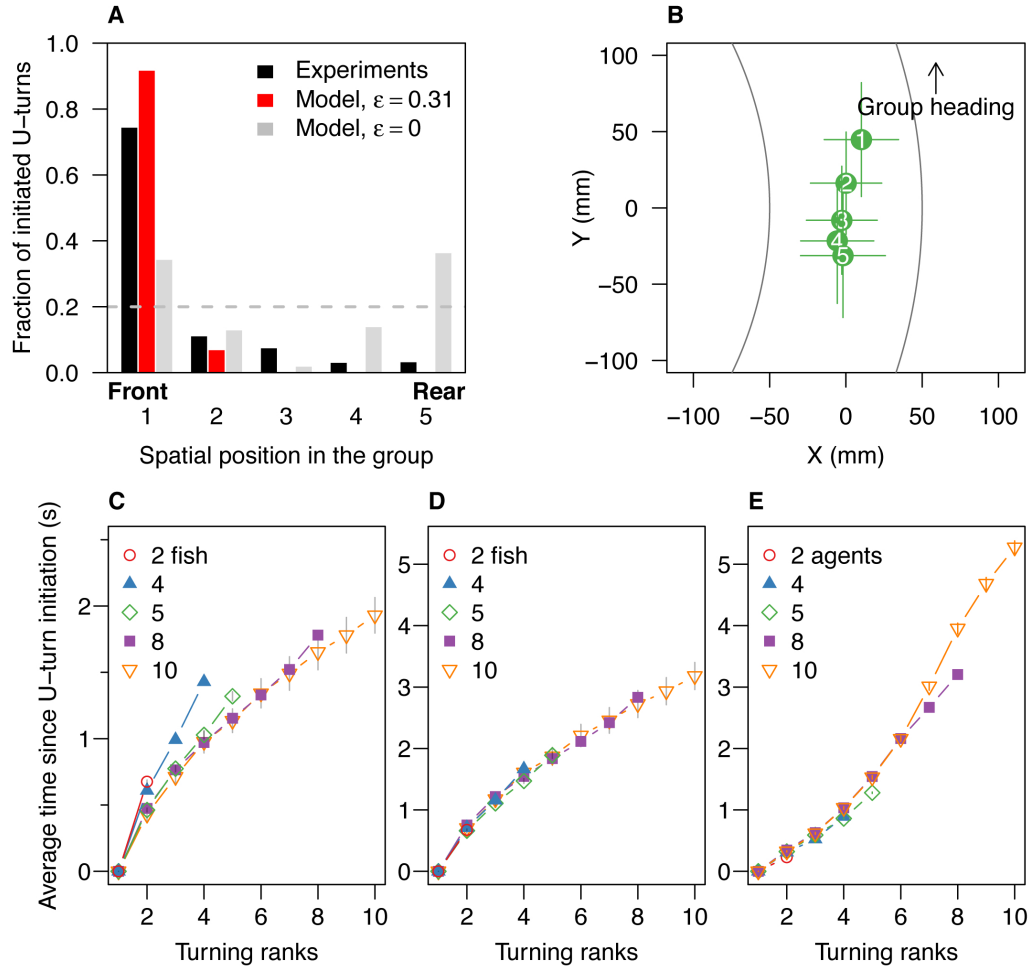

Figure 3. Spatiotemporal propagation of collective U-turns. A) Spatial position distribution of the initiator in groups of 5 fish in experiments (black) and in simulations with asymmetric influence ($J = 1.23$ and $\epsilon = 0.31$) (red) and without asymmetric influence ($J = 1.23$ and $\epsilon = 0$) (grey). Spatial positions go from 1 (position at the front) to 5 (position at rear; see text). Dashed line shows the uniform distribution $1/5 = 0.2$, when spatial position has no effect on the initiation of collective U-turns. B) Average relative positions (± sd) of all individuals at initiation of collective U-turns, ranked by order of turning (i.e. rank 1 is initiator) in groups of 5. Positions have been corrected so that all groups move in the same direction, with the outer wall at their right hand-side. The origin of the coordinate system is set to the centroid of the average positions of individuals. Average time interval since the beginning of a collective U-turn for each rank of turning by an individual and group size in experiments (C and D) and in simulations (E). In D, the time is scaled by the factor $r_n = s_n/s_2$, where s_n is the average speed of groups of size n, revealing a behaviour almost independent of n.

As shown in Figure 1C, the dynamics of collective U-turns, and in particular the evolution of the mean alignment $\bar{a}$, is similar for all group sizes, once time is rescaled by the mean U-turn duration (see SI for the method used to compute the scaling parameter t_n, which is an effective measure of the U-turn duration). Figure S5 shows that t_n, and hence the duration of a collective U-turn, increases approximately linearly with group size. In groups of all sizes, fish decrease their velocity before turning collectively (Figure 1D). The duration of this deceleration (and then acceleration) phase is much longer than the time for the group to complete a U-turn (compare Figure 1C and Figure 1D). Moreover, the speed minimum of the group in Figure 1D is reached near the midpoint of the U-turn, when $t = 0$ and the mean alignment is $\bar{a} = 0$ in Figure 1C.

Our results show that the propagation of information is on average sequential, both in space and time. This resembles a chain of falling dominoes, for which the time interval between successive falls is constant, without any positive feedback.

Collective U-turns are usually initiated at the front of the school and the change of swimming direction propagates towards the rear (Figures 3A and B and S7). Note that Figure 3B does not show the actual shape of groups but only the average and relative positions of fish. In particular, the x-coordinates are not perfectly centred on 0 (the centroid of the average positions) for all turning ranks because the foremost fish tends to swim significantly closer to the outer wall than the fish swimming at the rear, in line with previous results in groups of two fish in the same species [18].

Although the time interval between the turning of the first and the second fish is a bit longer than it is for others,

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the time interval between the successive turns of individuals is almost constant in a given group size (Figure 3C). This can be derived from the fact that the time since the initiation of the collective U-turn increases linearly with the turning rank. The linear propagation of information in all group sizes suggests that, for a given group size there is no amplification of the individual tendency to perform a U-turn: the time between two successive individuals performing U-turns does not decrease with the number of fish that already performed a U-turn. This suggests that individuals only pay attention to a small number of neighbours at a given time as it has been shown by Jiang et al. [19].

The time interval between subsequent individuals making a U-turn decreases with group size (see Figure 3C, the slopes decrease with n, or Figure S9). However, when this time interval is multiplied by a factor r_n proportional to the average speed s_n per group size n ($r_n = s_n/s_2$), these time intervals for different group sizes n collapse on the same curve (Figure 3D). This suggests that the shorter reaction time of fish in larger groups is mostly due to the faster swimming speed of these groups. Larger groups swim faster (Figure S4B), presumably because fish are interacting with a greater number of neighbours, because they are closer to each other (Figure S4C). This makes sense in the context of collective swimming. Indeed, fish have to avoid collisions with obstacles and other fish and the faster they swim, the shorter their reaction time, a well-known psycho-physiological principle [20].

In summary, our results show that U-turns are mostly initiated by fish located at the front of the school. U-turns are preceded by a decrease in the speed of the group. Once the U-turn has been initiated, the wave of turning propagates in a sequential way, suggesting that fish mainly copy the behaviour of a small number of individuals.

3.2 Modelling collective U-turn dynamics in groups of fish

To better understand the propagation of information by individuals in a group, we use an Ising-type spin model [21]. Here, we study the influence of group size on the individual and collective propensity to change swimming direction. Ising-type spin models are of particular interest to study the time interval between directional changes for systems of various sizes [22]. Each agent i has a direction of motion $d_i \in \{-1, 1\}$ with $d_i = -1$ representing swimming clockwise and $d_i = 1$ swimming anticlockwise. A U-turn performed by an agent i corresponds to a transition from d_i to $-d_i$. In the model, the relative positions of individuals and the interaction network (i.e. the influential neighbours η_i of an agent i) are kept fixed in time (Figure S3). Agents are positioned in staggered rows (see Figure S4D for experimental data supporting an oblong shape that becomes longer when the group size increases, as previously found by others, e.g. [23]) and only interact with their direct neighbours. The strength of interactions between an agent i and its neighbour j is weighted by a parameter $\alpha_{ij} \in [0, 2]$ that depends on the spatial position of j relatively to i. α_{ij} controls the asymmetry of the interactions between individuals, assuming that fish react stronger to frontal stimuli, in agreement with previous experimental results on this species (*H. rhodostomus*) [18]. Namely, $\alpha_{ij} = 1 + \epsilon$ when agent j is in front of agent i, $\alpha_{ij} = 1$ if j is at the side of i, and $\alpha_{ij} = 1 - \epsilon$ if j is behind i. We assume that the strength of interactions does not change with the number of individuals involved so that the asymmetry coefficient $\epsilon \in [0, 1]$ is kept constant for all group sizes.

The propensity of an individual i to make a U-turn depends on the state of its neighbours η_i and on the interaction matrix α_{ij}. The "discomfort" of an agent i in a state d_i is given by:

$$E_i = -d_i \sum_{j \in \eta_i} J_{ij} d_j, \quad J_{ij} = \alpha_{ij} J, \tag{3}$$

with J_{ij} the coupling constant between two neighbours i and j, set by the two positive parameters of the model, ϵ and J. When the anisotropy and asymmetry of perception is ignored ($\epsilon = 0$), $\alpha_{ij} = 1$ for all neighbouring pairs (i, j). E_i is minimal (and negative) when the focal fish i and its neighbours point in the same direction, and maximal (and positive) if the focal fish i points in the opposite direction of its aligned neighbours. A small value of $|E_i|$ corresponds to its neighbours pointing in (possibly random) directions nearly averaging to zero.

If an individual flips ($d'_i = -d_i$), the new discomfort is $E'_i = d_i \sum_{j=\{\eta_i\}} J_{ij} d_j$, and we have

$$\Delta E_i = E'_i - E_i, \tag{4}$$

$$= 2J d_i \sum_{j \in \eta_i} \alpha_{ij} d_j. \tag{5}$$

$\Delta E_i < 0$ when an agent flips to the most common state of its neighbours η_i whereas $\Delta E_i > 0$ when it flips to the state opposite to this most common state. In physics, such a model favouring alignment between close spins is known as the Ising model, which crudely describes ferromagnetic materials, i.e. magnets. In this $\epsilon = 0$ case,

$$\mathrm{E} = \frac{1}{2} \sum_{i=1}^{n} E_i \tag{6}$$

corresponds to the total actual *energy* of the magnetic system. In this context, the fully polarised state where all fish are aligned corresponds to so called ground-state energy, the lowest possible energy of the system. For $\epsilon \neq 0$, the asymmetry between the perception of i by j and that of j by i breaks this interpretation in terms of energy [18]. Yet, for $\epsilon > 0$, it is still useful to define E as a pseudo energy, as will be discussed later, since it remains a good indicator of the collective discomfort of the group, i.e. the lack of heading alignment within the group.

The dynamics of the model is investigated using Monte Carlo numerical simulations inspired of the Glauber dynamics [24]. Within this algorithm, at each time step $t_{k+1} = t_k + 1/n$ (n is the number of agents), an agent is drawn randomly and turns (update d_i to $d'_i = -d_i$) with

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the acceptance probability

$$P = \frac{1}{2} - \frac{1}{2}\tanh(\frac{\Delta E_i}{2}), \tag{7}$$

which is a sigmoid, going from $P \to 1$ for $\Delta E_i \to -\infty$ (maximal acceptance if the discomfort decreases sharply), to $P \to 0$ for $\Delta E_i \to +\infty$ (no direction switch if the discomfort would increase dramatically). The acceptance probability P represents the social conformity in our model and its strength (i.e. the nonlinearity of P) is mainly controlled by the parameter J (Figure S6B). For large $J > 0$, this dynamics will favour the emergence of strongly polarised states, while for $J = 0$, all fish directions will appear with the same probability during the dynamics. Hence, J controls the directional stiffness of the fish group, while ϵ describes the fish anisotropic perception of their environment, and the asymmetric interactions between fish.

For given J and ϵ, we compute numerically the prediction for the number of collective U-turns u'_n for a group of size n made during T' Monte-Carlo time steps. We define the error function

$$\Delta = \sum_n (\frac{\tau'_n}{\tau_n} - 1)^2 \tag{8}$$

with $\tau_n = \frac{u_n}{T_n}$ the experimental rate of collective U-turns (with T_n the total duration of all the experiments of the group size n, in minutes), $\tau'_n = \frac{u'_n}{T' t_0}$ the rate of collective U-turns in simulations. t_0 has the dimension of a time and translates Monte-Carlo time into actual experimental minutes, and is determined by minimising the error Δ, i.e. by solving the equation $\frac{\partial \Delta}{\partial t_0} = 0$.

After inspecting the (J, ϵ) parameter space, we find that the parameter values $J = 1.23$ and $\epsilon = 0.31$ lead to a fair agreement between the model and experimental data, as will be shown in the next section.

3.3 Simulation results versus experimental data

Our model quantitatively reproduces the effect of group size on the dynamics of collective U-turns (Figure 2). This suggests that the tendency of individuals to initiate U-turns and move in the opposite direction of the whole decreases with group size. However, note the poor agreement between simulations and experimental data in groups of 4. This result, along with the U-turn duration being longer than expected in this group size (Figure 1), suggests that in groups of 4 fish the information propagates differently in time than in the other group sizes. One explanation for this may be related to the age and body size of the fish, since body size influence the strength of interactions between fish [25]. In experiments with 4 and 8 fish (and in 5 experiments with 10 fish), individuals were one year older than in the other experiments, and their body size was significantly greater (Table S1, body length on average of 32 mm±0.22 in 2014 vs 36 mm±0.34 in 2015, Welch's t-test, $t = -10.875$, $p < 0.01$).

Even though there is no strict notion of energy in our model (because of the asymmetry parameter $\epsilon > 0$ used to represent fish anisotropic and asymmetric interactions that breaks the notion of energy), we can still compute the mean pseudo energy barrier $\Delta \mathrm{E}_n$ as a function of group size n. With the interpretation of E (respectively, E_i) as a quantitative indicator of the discomfort of the group (respectively, of the fish i), the (pseudo) energy barrier $\Delta \mathrm{E}_n$ is hence a measure of the collective effort of the group to switch direction. It corresponds to the mean difference between the maximum value of the pseudo energy E during the U-turn period and the reference energy computed when all the agents have the same direction (i.e. before and after the U-turn). We find that the energy barrier $\Delta \mathrm{E}_n$ increases sublinearly with group size n (Figure S11). We then expect that the higher/larger is the (pseudo) energy barrier $\Delta \mathrm{E}_n$, the more difficult it will be for the group to switch direction, as it must necessarily pass through an intermediate state of greater discomfort as the group size n increases. As a consequence, the average time between U-turns is also expected to increase as n and the (pseudo) energy barrier $\Delta \mathrm{E}_n$ increase. In fact for $\epsilon = 0$, for which E represents a true energy, this mean time interval between direction changes is exactly given by the Arrhenius law, which can be analytically proven for our spin model evolving according to the Glauber Monte Carlo dynamics. In physical chemistry, the Arrhenius law describes for instance the switching time between two states A and B of a molecule, separated by an energy barrier associated to an intermediate state through which the molecules must necessarily pass to go from state A to state B. The Arrhenius law stipulates that the mean transition time τ between two states separated by an energy barrier $\Delta \mathrm{E}_n$ grows like

$$\tau = \tau_0 \exp\left(\frac{\Delta \mathrm{E}_n}{T}\right), \tag{9}$$

where τ_0 is a time scale independent of n and T plays the role of the temperature [26]. We find that the (pseudo) Arrhenius law reproduces fairly well the experimental mean interval between U-turns as a function of group size n, presented in Figure 2, with $\tau_0 \approx 0.09$ min and $T \approx 1.9$.

The sequential propagation of information is also reproduced well by the simulations of the model, both in space (Figure 3A, S7 and S8) and time (Figures 3C and S10). When the perception of agents is isotropic (i.e. $\epsilon = 0$), the location of the U-turn initiation is no longer mainly at the front of the group but depends on the number of influencing neighbours (Figures 3A and S3). The lower the number of influential neighbours, the higher the number of collective U-turns. With the group shape chosen in our simulations of groups of 5, the agents triggering most of the U-turns (70%) are the first and last agents because they only have two influencing neighbours (against 3 for the second and the last but one and 4 for the third that initiates less than 3% of the U-turns). Regarding the propagation in time, simulations reproduce the linear propagation of information at the individual scale, except for the largest group size. Figure 4A and B show that once rescaled by the U-turn duration, the average direction profile is nearly independent of the group size, and that the model prediction is in good agreement with experimental data. It takes about the same

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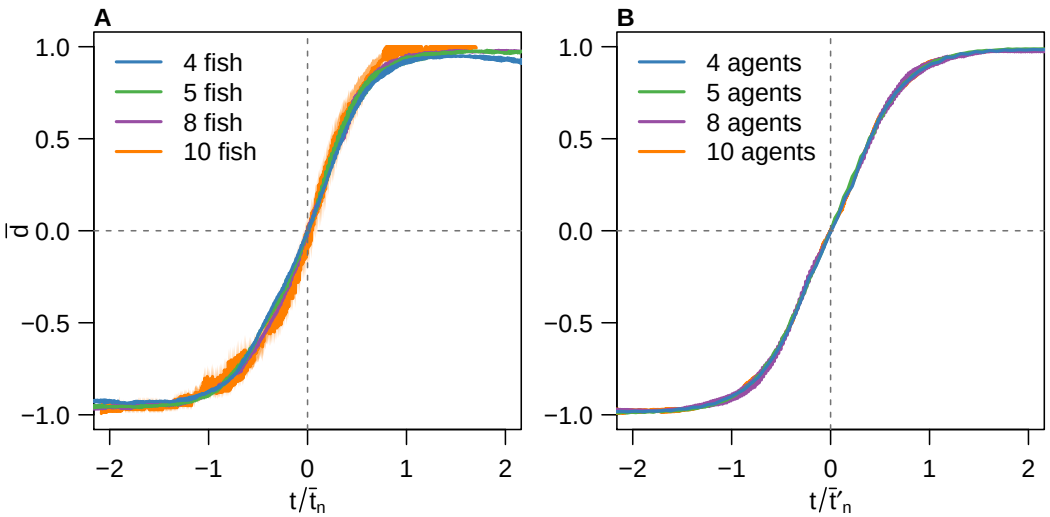

Figure 4. Direction of swimming $\bar{d} \leftarrow -\bar{d} \times d_0$ averaged over all collective U-turns as a function of scaled time $t/\bar{t}_n$ and $t/\bar{t}'_n$ for all group sizes in (A) experiments and (B) model. d_0 is the sign of the direction of swimming when the collective U-turn starts. t_n and $\bar{t}'_n$ are obtained by data scaling (see supplementary methods). The shadows stand for the standard error. In contrast to Figure 1, $t = 0$ is set to the time $(t_E - t_S)/2$ (experiments) or $(t'_E - t'_S)/2$ (model), where t_S stands for the start of the collective U-turn (first frame where at least one direction $-d_i \times d_0$ is positive) and t_E for the end of the collective U-turn (first frame where all directions $-d_i \times d_0$ are positive). Experimental curves on A have also been rescaled so that $\bar{d}(t = 0) = 0$.

amount of time to turn the first and second half of the fish, both in experiments and in the model, although the first half of the fish is slightly slower to turn than the second half in experiments. This is consistent with the results reported on Figure 3C, where the interval between the turning of the first and the second fish was longer than between the turns of the following fish. The durations of collective U-turns are Log-normally distributed, both in experiments and in the model (Figure S12).

Despite its simplicity and having only two free parameters (J and ϵ), our model reproduces quantitatively the experimental findings, both at the collective scale (the frequency of collective U-turns, average direction profile, duration of U-turns...) and at the individual scale (the spatiotemporal features of the propagation of information). Note that a linear response of the agents to their neighbours cannot reproduce the order of magnitude of the U-turn durations measured in the experiments (Figure S6). Social conformity is thus a good candidate as an individual mechanism underlying the observed patterns including the time interval between successive collective U-turns for different group sizes, the distribution of the U-turn duration and the spatial propagation.

4 Discussion

How information propagates among individuals and determines behavioural cascades is crucial to understand the emergence of collective decisions and transitions between collective states in animal groups [27–30]. Here we addressed these questions by analysing the spontaneous collective U-turns in groups of fish.

We find that collective U-turns are preceded by a slowing down to a speed slower than the average. It has been shown in other fish species that speed controls alignment between individuals [31], leading slow groups to be less polarised than fast groups [9,32–34]. In general, at slower speed there is less inertia to turn, resulting in weaker polarisation [23,35] and thus an increase of the fluctuations in the swimming direction of the fish [36]. Moreover, as the fish speed decreases, the fish school is in a state closer to the transition between the schooling (strong alignment) and swarming (weak alignment) states, where [34] have shown that both fluctuations in fish orientation and the sensitivity of the school to a perturbation increase. It is therefore not surprising that U-turns occur after the group has slowed down.

U-turns are mostly initiated by the fish located at the front of the group. At the front, individuals experience the influence from the other fish least. This is due to the perception anisotropy which leads individuals interacting more strongly with a neighbour ahead than behind. Therefore, frontal individuals are more subjects to heading fluctuations and less inhibited to initiate U-turns. Similarly, in starling flocks, the birds that initiate changes in collective travelling direction are found at the edges of the flock [37].

We found no evidence for dampening or amplification of information as fish adopt a new direction of motion. Although not measured at the individual level, a similar absence of dampening has been reported in anchovies during the formation and propagation of escape waves in reaction to sea lions attacks [6]. Moreover, on average, turning information propagates faster in larger groups: 0.19 s per individual in groups of 10 fish, and 0.26 s per individual in groups of 5 fish (Figure S9). This appears to be the consequence of the increase of the swimming speed with group size, which requires that individuals react faster. Indeed, our results

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show that the interval between successive turns of individuals during a collective U-turn decreases with swimming speed, although distance between individuals may also play a role [19]. However, the mean time interval between successive individual U-turns is almost constant and independent of the group size, once time has been rescaled by the group velocity. This points to a domino-like propagation of the new direction of motion across the group. This sequential spatiotemporal propagation of information also suggests that each fish interacts with a small number of neighbours.

We found that the level of homogeneity in the direction of motion of the schools increases with group size resulting in a lower number of collective U-turns. This phenomenon has been previously described in other fish species [12, 38] as well as in locusts in a similar set-up [39].

In order to better understand the impact of social conformity, anisotropy and asymmetry of interactions, and group size on the propagation of information during U-turns, we developed an Ising-type spin model in which fish adopt probabilistically the direction of the majority of their neighbours, in a nonlinear way (social conformity) influenced by the anisotropic and asymmetrical interactions between fish. Since the probability that a fish chooses a direction is a nonlinear function of the number of other fish having already chosen this direction, as previously shown [40–42], it is thus more difficult for a fish to initiate or propagate a U-turn the larger the number of fish swimming in the opposite direction [15]. The model also introduces quantitative indicators of the individual and collective discomfort (lack of alignment of heading among group members), the latter being represented by a measure of global pseudo energy of the group. Larger groups have to overcome a larger pseudo energy barrier to switch between the clockwise and anticlockwise fully polarised states. In physics and chemistry, the exponential increase of the switching time between two states as a function of this energy barrier is described by the Arrhenius law, which can be actually proven using the tools of statistical physics. We find that direct numerical simulations of the model and an effective Arrhenius law both quantitatively reproduce the sharp increase of the mean time between U-turns as the group size increases. The model also shows that asymmetric interactions and the anisotropic perception of fish are not essential to explain the decrease of collective fluctuations and hence the U-turns frequency as the group size increases. Social conformity [13, 16] (controlled by the magnitude of our parameter J) suffices to cause fewer fluctuations with increasing group size, leading to an increased robustness of the polarised state ("protected" by increasing pseudo energy barriers).

Moreover, our model reveals that the front to back propagation of information results from the perception anisotropy and asymmetry of the fish (our ϵ parameter). Without perception anisotropy and asymmetry, U-turns are initiated by the fish that have fewer influential neighbours (in our simulations, those are the fish at the boundary of the group – all individuals would have the same probability to initiate a U-turn with periodic boundary conditions) and propagated to their neighbours without favouring any direction. Finally, the duration of a U-turn as a function of group size is quantitatively reproduced by the model, while the simulated mean direction temporal profiles during U-turns are very similar to the experimental ones, and are independent of the group size, once time is properly rescaled by the mean U-turn duration for the corresponding group size.

In summary, our work supports that social conformity, asymmetric interactions, and the anisotropic perception of fish are key to the sequential propagation of information without dampening in fish schools. Future work will be needed to disentangle the respective roles of the network topology and the actual functional forms of social interactions between fish on the propagation of information.

Ethics statement

Experiments have been approved by the Ethics Committee for Animal Experimentation of the Toulouse Research Federation in Biology N°1 and comply with the European legislation for animal welfare.

Contribution of authors

C.K.H. and G.T. conceived and designed the study; V.L. and P.T. performed research; V.L. and C.S. developed the model; V.L., L.J., C.S., and P.T. analysed data; V.L., C.H.K., C.S., and G.T. wrote the paper.

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