

## University of Groningen

### Informative and misinformative interactions in a school of fish

Crosato, Emanuele; Jiang, Li; Lecheval, Valentin; Lizier, Joseph T.; Wang, X. Rosalind; Tichit, Pierre; Theraulaz, Guy; Prokopenko, Mikhail

*Published in:*  
Swarm intelligence

*DOI:*  
[10.1007/s11721-018-0157-x](https://doi.org/10.1007/s11721-018-0157-x)

**IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.**

*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
2018

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Crosato, E., Jiang, L., Lecheval, V., Lizier, J. T., Wang, X. R., Tichit, P., Theraulaz, G., & Prokopenko, M. (2018). Informative and misinformative interactions in a school of fish. *Swarm intelligence*, 12(4), 283-305. <https://doi.org/10.1007/s11721-018-0157-x>

#### Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

#### Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

*Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.*

# Informative and misinformative interactions in a school of fish

Emanuele Crosato<sup>1,5</sup>  · Li Jiang<sup>2,3</sup> · Valentin Lecheval<sup>3,4</sup> · Joseph T. Lizier<sup>1</sup> · X. Rosalind Wang<sup>5</sup> · Pierre Tichit<sup>3</sup> · Guy Theraulaz<sup>3</sup> · Mikhail Prokopenko<sup>1</sup>

Received: 25 November 2017 / Accepted: 1 March 2018 / Published online: 8 March 2018  
© Springer Science+Business Media, LLC, part of Springer Nature 2018

**Abstract** Quantifying distributed information processing is crucial to understanding collective motion in animal groups. Recent studies have begun to apply rigorous methods based on information theory to quantify such distributed computation. Following this perspective, we use transfer entropy to quantify dynamic information flows locally in space and time across a school of fish during directional changes around a circular tank, i.e., U-turns. This analysis reveals peaks in information flows during collective U-turns and identifies two different flows: an informative flow (positive transfer entropy) from fish that have already turned to fish that are turning, and a misinformative flow (negative transfer entropy) from fish that have not turned yet to fish that are turning. We also reveal that the information flows are related to relative position and alignment between fish and identify spatial patterns of information and misinformation cascades. This study offers several methodological contributions and we expect further application of these methodologies to reveal intricacies of self-organisation in other animal groups and active matter in general.

**Keywords** Collective animal behaviour · Collective motion · Fish interactions · Information dynamics

---

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s11721-018-0157-x>) contains supplementary material, which is available to authorized users.

---

✉ Emanuele Crosato  
emanuele.crosato@sydney.edu.au

<sup>1</sup> Complex Systems Research Group and Centre for Complex Systems, Faculty of Engineering & IT, The University of Sydney, Sydney, NSW 2006, Australia

<sup>2</sup> School of Systems Science, Beijing Normal University, Beijing 100875, People's Republic of China

<sup>3</sup> Centre de Recherches sur la Cognition Animale, Centre de Biologie Intégrative (CBI), Centre National de la Recherche Scientifique (CNRS), Université Paul Sabatier (UPS), 31062 Toulouse Cedex 9, France

<sup>4</sup> Groningen Institute for Evolutionary Life Sciences, Centre for Life Sciences, University of Groningen, Nijenborgh 7, 9747AG Groningen, The Netherlands

<sup>5</sup> CSIRO Data61, PO Box 76, Epping, NSW 1710, Australia

## 1 Introduction

Collective motion is one of the most striking examples of aggregated coherent behaviour in animal groups, dynamically self-organising out of local interactions between individuals. It is observed in different animal species, such as schools of fish (Parrish et al. 2002; Sumpter et al. 2008), flocks of birds (Lissaman and Shollenberger 1970; May 1979; Ballerini et al. 2008; Bialek et al. 2012), colonies of insects (Buhl et al. 2006; Fourcassié et al. 2010; Buhl et al. 2010; Attanasi et al. 2014b; Buhl and Rogers 2016) and herds of ungulates (Ginelli et al. 2015). There is an emerging understanding that information plays a *dynamic* role in such a coordination (Sumpter et al. 2008), and that *distributed* information processing is a specific mechanism that endows the group with collective computational capabilities (Bonabeau et al. 1999; Couzin 2009; Albantakis et al. 2014).

Information transfer is of particular relevance for collective behaviour, where it has been observed that small perturbations cascade through an entire group in a wave-like manner (Potts 1984; Procaccini et al. 2011; Herbert-Read et al. 2015; Attanasi et al. 2015), with these cascades conjectured to embody information transfer (Sumpter et al. 2008). This phenomenon is related to underlying causal interactions, and a common goal is to infer physical interaction rules directly from experimental data (Katz et al. 2011; Gautrais et al. 2012; Herbert-Read et al. 2011) and measure correlations within a collective.

Nagy et al. (2010) used a variety of correlation functions to measure directional dependencies between the velocities of pairs of pigeons flying in flocks of up to 10 individuals, extended to 30 in Nagy et al. (2013), reconstructing the leadership network of the flock. As has been shown, this network does not correspond to the dominance hierarchy between birds (Nagy et al. 2013). Information transfer has been extensively studied in flocks of starlings, by observing the propagation of direction changes across the flocks (Cavagna et al. 2013b, a; Attanasi et al. 2014a). More recently, Rosenthal et al. (2015) attempted to determine a communication structure of a school of fish during its collective evasion manoeuvres manifested through cascades of behavioural change. A functional mapping between sensory inputs and motor responses was inferred by tracking fish position and body posture, and calculating visual fields.

The main scientific question we address is how to identify and quantify information processing during decision-making in groups (Giardina 2008; Attanasi et al. 2014a), exacerbated by misinformative and noisy data. In trying to obtain such understanding, it is important to develop predictive models of information propagation among individuals, including behavioural cascades. Specifically, we aim to reveal how information propagates within a group and affects collective decisions (e.g., choosing a common travelling direction). This would provide an objective way to use such information for predictive modelling of behavioural reactions in response to various inputs.

Rather than consider *semantic* or *pragmatic* information, many contemporary studies employ rigorous information-theoretic measures that quantify information as uncertainty reduction, following Shannon (Cover and Thomas 2006), in order to deal with the stochastic, continuous and noisy nature of intrinsic information processing in natural systems (Feldman et al. 2008). Distributed information processing is typically dissected into three primitive functions: the *transmission*, *storage* and *modification of information* (Langton 1990). *Information dynamics* is a recent framework characterising and measuring each of the primitives information-theoretically (Lizier et al. 2014; Lizier 2013). In viewing the state update dynamics of a random process as an information processing event, this framework performs an *information regression* in accounting for where the information to predict that state update

can be found by an observer, first identifying predictive information from the past of the process as *information storage*, then predictive information from other sources as *information transfer* (including both pairwise transfer from single sources, and higher-order transfers due to multivariate effects). The framework has been applied to modelling collective behaviour in several complex systems, such as Cellular Automata (Lizier et al. 2008, 2010, 2012), Ising spin models (Barnett et al. 2013), Genetic Regulatory Networks and other biological networks (Lizier et al. 2011b; Prokopenko et al. 2011; Faes and Porta 2014), and neural information processing (Gómez et al. 2014; Wibrál et al. 2015).

This study proposes a domain-independent, information-theoretic approach to detecting and quantifying individual-level dynamics of information transfer in animal groups using this framework. This approach is based on transfer entropy (Schreiber 2000), an information-theoretic measure that quantifies the directed and time-asymmetric predictive effect of one random process on another. We aim to characterise the dynamics of how information transfer is conducted in space and time within a *biological* school of fish (*Hemigrammus rhodostomus* or rummy-nose tetras, Fig. 1a). Using transfer entropy allows us to consider specifically the information dynamics during collective decision-making, identifying predictive information flows and their spatial patterns, complementing our parallel study which used correlation analysis to identify influential neighbours (Jiang et al. 2017).

We stress that the predictive information transfer should be considered from the observer perspective, that is, it is the observer that gains (or loses) predictability about a fish motion, having observed another fish. In other words, notwithstanding possible influences among the fish that could potentially be reflected in their information dynamics, our quantitative analysis focuses on the information flow within the school which is detectable by an external observer, captured by the transfer entropy. This means that, whenever we quantify a predictive information flow *based on* a source fish *about* a destination fish, we attribute the change of predictability (uncertainty) to a third party, be it another fish in the school, a predator approaching the school or an independent experimentalist. To improve readability, we refer to flow or transfer *from* a source fish *to* a destination fish. Importantly, this predictive information flow may or may not account for the causal information flow affecting the source and the destination (Ay and Polani 2008; Lizier and Prokopenko 2010)—however it does typically indicate presence of causality, either within the considered pair or from some common cause.

We focus on collective direction changes, i.e., collective U-turns, during which the directional changes of individuals progress in a rapid cascade, at the end of which a coherent motion is re-established within the school. Sets of different U-turns are comparable across experiments under the same conditions, permitting a statistically significant analysis involving an entire set of U-turns.

By looking at the *pointwise* or *local* values of transfer entropy over time, rather than at its average values, we are not only able to detect information transfer, but also to observe its dynamics over time and across the school. We demonstrate that information is indeed constantly flowing within the school, and identify the source–destination lag where predictive information flow is maximised (which has an interpretation as an observer-detectable reaction time to other fish). The information flow is observed to peak during collective directional changes, where there is a typical “cascade” of predictive gains and losses to be made by observers of these pairwise information interactions. Specifically, we identify two distinct predictive information flows: (i) an “informative” flow, characterised by positive local values of transfer entropy, from fish that have already changed direction to fish that are turning, and (ii) a “misinformative” flow, characterised by negative local values of transfer entropy, from fish that have not changed direction yet to the fish that are turning. Finally, we identify spatial patterns coupled with the temporal transfer entropy, which we call spatio-informational

motifs. These motifs reveal spatial dependencies between the source of information and its destination, which shape the directed pairwise interactions underlying the informative and misinformative flows. The strong distinction revealed by our quantitative analysis between informative and misinformative flows is expected to have an impact on modelling and understanding the dynamics of collective animal motion.

## 2 Information-theoretic measures for collective motion

The study of Wang et al. (2012) introduced the use of transfer entropy to investigations of collective motion. This work quantitatively verified the hypothesis that information cascades within an (artificial) swarm can be spatiotemporally revealed by *conditional transfer entropy* (Lizier et al. 2008, 2010) and thus correspond to communications, while the collective memory can be captured by *active information storage* (Lizier et al. 2012).

Richardson et al. (2013) applied related variants of conditional mutual information, a measure of non-linear dependence between two random variables, to identify dynamical coupling between the trajectories of foraging meerkats. Transfer entropy has also been used to study the response of schools of zebrafish to a robotic replica of the animal (Butail et al. 2014; Ladu et al. 2015), and to infer leadership in pairs of bats (Orange and Abaid 2015) and simulated zebrafish (Butail et al. 2016). Lord et al. (2016) also posed the question of identifying individual animals which are directly interacting with other individuals, in a swarm of insects (*Chironomus riparius*). Their approach used conditional mutual information (called “causation entropy” although it does not directly measure causality (Lizier and Prokopenko 2010)), inferring “information flows” within the swarm over moving windows of time.

Unlike the study of Wang et al. (2012), the above studies quantified average dependencies over time rather than local dependencies at specific time points; for example, leadership relationships in general rather than their (local) dynamics over time. Local versions of transfer entropy and active information storage have been used to measure pairwise correlations in a “swarm” of soldier crabs, finding that decision-making is affected by the group size (Tomaru et al. 2016). Statistical significance was not reported, presumably due to a small sample size. Similar techniques were used to construct interaction networks within teams of simulated RoboCup agents (Cliff et al. 2017).

In this study, we focus on local (or pointwise) transfer entropy (Schreiber 2000; Lizier et al. 2008; Lizier 2014b) for specific samples of time series processes of fish motion, which allows us to reconstruct the dynamics of information flows over time. Local transfer entropy (Lizier et al. 2008), captures information flow from the realisation of a *source* variable  $Y$  to a *destination* variable  $X$  at time  $n$ . As described in Sect. 5, local transfer entropy is defined as the information provided by the source  $\mathbf{y}_{n-v} = \{y_{n-v}, y_{n-v-1}, \dots, y_{n-v-l+1}\}$ , where  $v$  is a time delay and  $l$  is the history length, about the destination  $x_n$  in the context of the past of the destination  $\mathbf{x}_{n-1} = \{x_{n-1}, x_{n-2}, \dots, x_{n-k}\}$ , with a history length  $k$ :

$$t_{y \rightarrow x}(n, v) = \log_2 \frac{p(x_n | \mathbf{x}_{n-1}, \mathbf{y}_{n-v})}{p(x_n | \mathbf{x}_{n-1})}. \quad (1)$$

Importantly, local values of transfer entropy can be negative, while the average transfer entropy is non-negative. Negative values of the local transfer entropies indicate that the source is *misinformative* about the next state of the destination (i.e., it increases uncertainty). Previous studies that used average measures over sliding time windows in order to investigate how information transfer varies over time (Richardson et al. 2013; Lord et al. 2016) cannot detect misinformation because they measure average but not local values.

As an observational measure, transfer entropy does not measure causal effect of the source on the target; this can only be established using interventional measures (Ay and Polani 2008; Lizier and Prokopenko 2010; Chicharro and Ledberg 2012; Smirnov 2013). Rather, transfer entropy measures the predictive information gained from a source variable about the state transition in a target, which may be viewed as *information transfer* when measured on an underlying causal interaction (Lizier and Prokopenko 2010). It should be noted that while some researchers may be initially more interested in causality, the concept of information transfer reveals much about the dynamics that causal effect does not (Lizier and Prokopenko 2010), in particular being associated with emergent local structure in dynamics in complex systems (Lizier et al. 2008; Wang et al. 2012) and with changes in behaviour, state or regime (Boedecker et al. 2012; Barnett et al. 2013), as well as revealing the misinformative interactions described above. As a particular example, local transfer entropy spatiotemporally highlights emergent glider entities in cellular automata (Lizier et al. 2008), which are analogues of cascading turning waves in swarms (also highlighted by transfer entropy (Wang et al. 2012)), while local measures of causality do not differentiate these from the background dynamics (Lizier and Prokopenko 2010).

In general, to understand the processes that govern collective behaviour in animal groups, it is important to disentangle the interactions between fish, how these interactions are combined and how interrelated are the individual behaviours. This can be achieved much more easily by investigating collective behaviour in small groups of individuals. Such methodology (Gautrais et al. 2012; Weitz et al. 2012) has been successfully applied to studies of the individual-level interactions involved in several examples of collective animal behaviour: aggregation in cockroaches (Jeanson et al. 2004, 2005), division of labour, corpse aggregation and nest building in ant colonies (Theraulaz et al. 2002a, b; Khuong et al. 2016), collective motion in groups of pelagic fish (Gautrais et al. 2012; Weitz et al. 2012) and collective motion in human groups (Moussaïd et al. 2009, 2011). Although for schools of minnows (*Phoxinus phoxinus*), two fish schools are qualitatively different from schools containing three or more, the effects seem to level off by the time the school reaches a size of six individuals (Partridge 1980). Collective behaviour, as well as a stereotypical “phase transition”, when an increase in density leads to the onset of directional collective motion, have also been detected in small groups of six glass prawns (*Paratya australiensis*) (Mann et al. 2012). Furthermore, at such intermediate group sizes, it has been observed that multiple fish interactions could often be faithfully factorised into pair interactions in one particular species of fish (Gautrais et al. 2012). The rationale for choosing a limited number of fish is also strengthened by the fact that it allowed us to quantify both the dynamics of collective decisions at the group level and the predictive information flow, while preserving the coordination of swimming in this species that exhibits strong schooling behaviour.

In our study, we investigated information transfer within a school of fish during specific collective direction changes, i.e., U-turns, in which the school collectively reverses its direction. Groups of five fish were placed in a ring-shaped tank (Fig. 1b), a design conceived to constrain fish swimming circularly, with the possibility of undergoing U-turns spontaneously, without any obstacles or external factors. A similar well-controlled environment has been previously successfully used in studies of groups of locusts (Buhl et al. 2006), enabling a large number of replicates which for obvious reasons cannot be done in a natural environment. The choice of a small and cohesive group allows us to focus on pairwise interactions in the context of collective motion, while studies of larger and less cohesive groups could reveal dominance hierarchies and leader-follower relationships, as well as social influence in groups.

In many species of fish, sudden collective changes of the state of a school may happen without external cause as a consequence of stochastic effects (Tunstrøm et al. 2013). 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 (Calovi et al. 2015). Determining how fluctuations in individual behaviour, for instance in heading direction, propagate within a group is a key to understanding transitions between collective states in fish schools and in animal groups in general. In our setup, fish swim in a highly synchronised and polarised manner, and can only head in two directions, clockwise or anticlockwise, regularly switching from one to the other. Our work thus also allows us to analyse in groups how individual U-turns occur, propagate through the group, and ultimately lead to collective U-turns. A total of 455 U-turns have been observed during 10 trials of 1 h duration each.

We computed local transfer entropy between each (directed) pair of fish from time series obtained from fish heading. Specifically, the destination process  $X$  was defined as the directional change of the destination fish, while the source process  $Y$  was defined as the relative heading of the destination fish with respect to the source fish (see Sect. 5). This allowed us to capture the influence of the source-destination fish alignment on the directional changes of the destination. Such influence is usually delayed in time and we estimated the optimal delay [maximising  $\langle t_{y \rightarrow x}(n, v) \rangle_n$  (Wibral et al. 2013), see Sect. 5] at  $v = 6$ , corresponding to 0.12 s. The relative heading is not the only aspect of fish motion and other components can be considered, such as speed and acceleration. Moreover, a heading change in the destination fish could be related to many aspects of the source fish motion other than the heading difference between the two fish. However, in this study, we focus on the relative heading, which we believe is one of the most relevant features to explore in our controlled setup. In order to simplify our terminology, in the remainder of the text, we shall refer to this partial information flow, based on relative heading, as the information flow. It is important to clarify that large direction changes do not imply high values of transfer entropy, even while such measure is based on the heading. Large direction changes (where they are rare events) may have more capacity for information flow; however, there is not necessarily large information flow at these events unless the source fish are predictive of their occurrence.

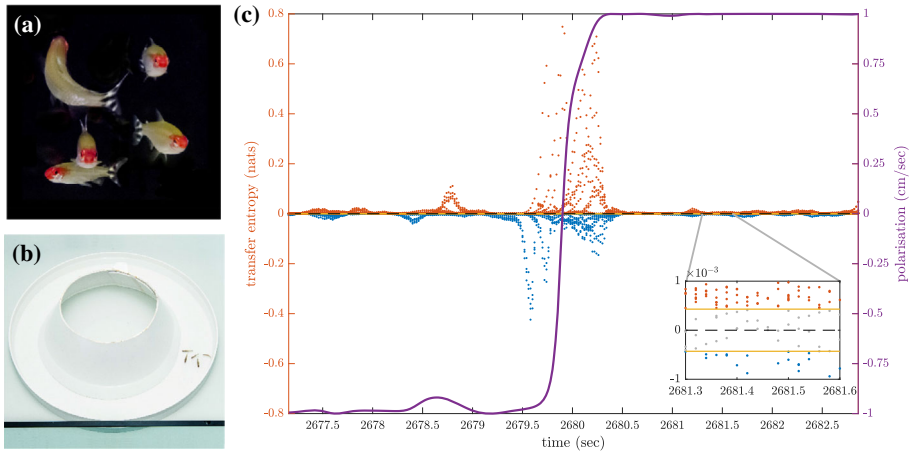
## 3 Results

### 3.1 Information flows during U-turns

In order to represent the school's orientation around the tank, we define its polarisation as its circumferential velocity component, so that it is positive when the school is swimming clockwise and negative when it is swimming anticlockwise (see Sect. 5). The better the school's average heading is aligned with an ideal circular trajectory around the tank, the higher is the intensity of the polarisation. When the school is facing one of the tank's walls, for example in the middle of a U-turn, the polarisation is zero, and the polarisation flips sign during U-turns. Polarisation allows us to map local values of transfer entropy onto the progression of the collective U-turns.

The analyses of transfer entropy over time reveal that the measure clearly diverges from its baseline in the vicinity of U-turns, as shown in the representative U-turn in Fig. 1c (Supplementary Figure S1 shows a longer time interval during which several U-turns can be observed). The figure shows that during regular circular motion, when the school's polarisation is highly pronounced, transfer entropy is low. As the polarisation approaches zero the intensity of transfer entropy grows, peaking near the middle of a U-turn, when polarisation switches its sign.





**Fig. 1** Transfer entropy within the school during a U-turn. **a** Is a photo of a spontaneous U-turn initiated by a single fish in a group of five *Hemigrammus rhodostomus* fish. **b** Shows the experimental ring-shaped tank. **c** Plots the school's polarisation during a U-turn and the detected transfer entropy over a time interval of approximately 6 s. The purple line represents the school's polarisation, while dots represent local values of transfer entropy between all directed pairs of fish: red dots represent positive transfer entropy and blue dots represent negative transfer entropy. Time is discretised in steps of length 0.02 s and for each time step 20 points of these local measures are plotted, for the 20 directed pairs formed out of 5 fish. The yellow lines in the inset are the thresholds for considering a value of transfer entropy statistically different from zero ( $p < 0.05$  before false discovery rate correction, see Sect. 5). Grey dots between these lines represent values that are not statistically different from zero. Credits to David Villa ScienceImage/CBI/CNRS, Toulouse, 2015, for **a**, **b** (Color figure online)

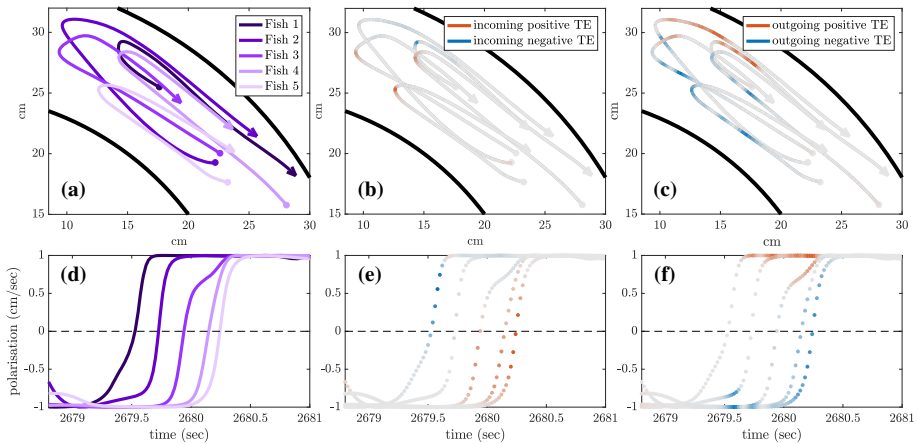
We clarify that the aim here is *not* to establish transfer entropy as an alternative to polarisation for detecting turn; rather, our aim is to use polarisation to describe the overall progression of the collective U-turns and then to use transfer entropy to investigate the underlying information flows in the dynamics of such turns. Indeed, transfer entropy is found to be statistically different from zero at many points outside of the U-turns (see Supplementary Figure S1), although the largest values and most concentrated regions of these are during the U-turns. This indicates that information transfer, based on the heading direction's change, occurs even when fish school together without changing direction; we know that the fish are not executing precisely uniform motion during these in-between periods, and so interpret these small amounts of information transfer as sufficiently underpinning the dynamics of the group maintaining its collective heading. We would like to also point out that information processing during the aligned motion mostly corresponds to the information storage, which can be detected using other information-theoretic measures (Lizier et al. 2012), while only a low information transfer is needed to maintain the alignment.

We also see in Fig. 1c that both positive and negative values of transfer entropy are detected. In order to understand the role of the positive and negative information flows during collective motion, in the next section, we show the dynamics of transfer entropy for individual pairwise interactions.

### 3.2 Informative and misinformative flows

Our analysis revealed a clear relationship between positive and negative values of transfer entropy and the sequence of individual fish turning, which is illustrated in Fig. 2. Figure 2a



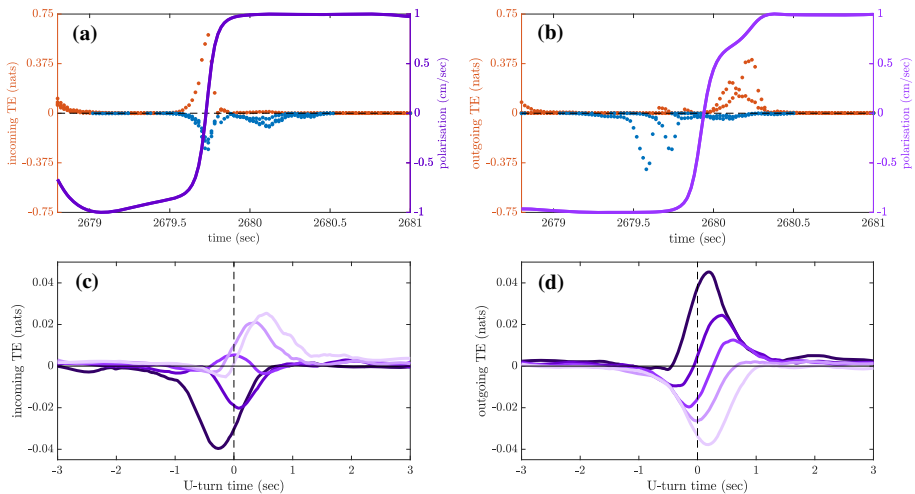


**Fig. 2** Positive and negative information flows during a U-turn. **a** Shows the trajectories of the five fish during the U-turn shown in **c**. The two black lines are the inner and the outer walls of the tank, and each of the five trajectories coloured in different shades of purple correspond to a different fish: from darkest purple for the first fish turning (Fish 1), to the lightest purple for the last (Fish 5). The total time interval is approximately 2 s, during which all fish turn from swimming anticlockwise to clockwise. **d** Depicts the polarisations of the five fish, showing the temporal sequence of fish turns. **b** Shows the fish trajectories again, but this time indicates the value of the *incoming* local transfer entropy to each fish as a destination, averaged over the other four fish as sources. The colour of each trajectory changes as the fish turn: strong red indicates intense positive transfer entropy; strong blue indicates intense negative transfer entropy; intermediate grey indicates that transfer entropy is close to zero. **e** Is obtained analogously to **b**, but the polarisations of the individual fish are shown rather than their trajectories. **c**, **f** mirror **b**, **e**, but where the direction of the transfer entropy has been inverted: the colour of each trajectory or polarisation now indicates the value of the *outgoing* local transfer entropy from each fish as a source, averaged over the other four fish as destinations (Color figure online)

shows the trajectories of individual fish during the same U-turn depicted in Fig. 1c. These trajectories are retraced in Fig. 2d in terms of polarisation of each fish. It is quite clear that there is a well-defined sequence of individual U-turns during the collective U-turn. Moreover, Fig. 2 shows how the transfer entropy maps onto the fish trajectories, both from the fish whose trajectory is traced as a source to the other four fish—i.e., *outgoing* transfer entropy—and, vice versa, from the other four fish to the traced one as a destination—i.e., *incoming* transfer entropy.

The incoming transfer entropy clearly peaks during the destination fish's individual turns and its local values averaged over all sources go from negative, for the first (destination) fish that turns, to positive for the last fish turning (Fig. 2b, e). In the opposite direction, the outgoing transfer entropy (averaged over all destinations) displays negative peaks only before the source fish has turned, and positive peaks only afterwards (Fig. 2c, f). Figure 2 suggests that predictive information transfer intensifies only when a destination fish is turning, with this transfer being informative from source fish that have already turned and misinformative from source fish that have not turned yet.

This phenomenon can be observed very clearly in Fig. 3a, b, which show the transfer entropy in both directions for a single fish (the second fish turning in Figs. 1 and 2). One positive peak of incoming transfer entropy (indicating informative flow) and three negative ones (misinformative flows) are detected when this fish, as a destination, is undergoing the U-turn (Fig. 3a). No other peaks are detected for this fish as a destination. On the other hand, one negative peak of outgoing transfer entropy is detected before the fish, this time as a



**Fig. 3** **a** Shows the polarisation of the *second* fish turning, together with the incoming transfer entropy to that fish as the destination, with the other four fish as the sources: red dots represent positive values and blue dots represent negative values. **b** Mirrors **a**, but with the outgoing transfer entropy from that fish as the source, and the other four fish as destinations. In **c**, each purple line corresponds to a fish, with the shade again reflecting the order in which the fish turn (darkest for first fish to turn, and lightest for the last). Now however (in **c**), rather than corresponding to a single U-turn event, the incoming local transfer entropy (to each fish as a destination, averaged over the other four fish as sources) is averaged over all 455 observed U-turns and is shown as a function of time. The horizontal axis is the relative time of the U-turns, with zero being the time when the average polarisation of the school changes sign. **d** Mirrors **c**, but where the direction of the transfer entropy has been inverted (showing outgoing transfer from each fish in turning order) (Color figure online)

source, has turned, and three positive peaks are detected after the fish has turned (Fig. 3b). These four peaks occur respectively when the first, the third, the fourth and the fifth fish undergo the U-turn, as is evident by comparing Figs. 2d, 3b. A movie of the fish undergoing this specific U-turn is provided in Supplementary Video S1, while a detailed reconstruction of the U-turn, showing the dynamics of transfer entropy over time for each directed pair of fish, is provided in Supplementary Video S2.

In order to demonstrate that the phenomenon described here holds for U-turns in general, and not only for the representative one shown in Fig. 2, we performed an aggregated analysis of all 455 U-turns observed during the experiment. Since the order in which fish turn is not the same in every U-turn, in this analysis, we refer not to single fish as individuals, but rather to fish in the order in which they turn. Thus, when we refer, for instance, to “the first fish that turns”, we may be pointing to a different fish at each U-turn. It is worth noting that, in general, multiple fish can turn at the same time during a U-turn, but averaging over all U-turn events allows us to statistically order turning events, as shown in Fig. 3c, d.

The aggregated results are presented in Fig. 3c, d. Figure 3c shows that incoming transfer entropy peaks for each fish in turning order and gradually grows, from a minimum negative peak corresponding to the first fish turning, to a maximum positive peak corresponding to the last fish turning. Vice versa, Fig. 3d shows that outgoing transfer entropy peaks only positively for the first fish turning, which is an informative source about all other fish turning afterwards. For the last fish that turns the peak is negative, since this fish is misinformative about all other fish that have already turned. The second, third and fourth fish present both a

negative and a positive peak. The intensity of the negative peaks increases from the second fish to the fourth, while the intensity of the positive peak decreases.

In general, the source fish is informative about all destination fish turning after it and misinformative about any destination fish turning before it. This is because the prior turn of a source helps the observer to predict the later turn of the destination, whereas examining a source which has not turned yet itself is actively unhelpful (misinformative) in predicting the occurrence of such a turn. This also explains why, for a source, the negative peaks come before positives.

The sequential cascade-like dynamics of information flow suggests that the strongest sources of predictive information transfer are fish that have already turned. Moreover, our analyses reveal that once a fish has performed a U-turn, its behaviour in general ceases to be predictable based on the behaviour of other fish that swim in opposite direction (in fact such fish would provide misinformative predictions). This suggests an asymmetry of predictive information flows from and to an individual fish during U-turns.

### 3.3 Spatial motifs of information transfer

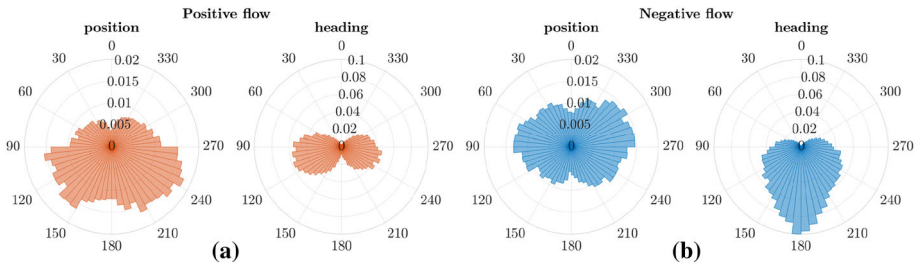
It is reasonable to assume that predictive information transfer in a school of fish results from spatial interactions among individuals. We investigated the role of pairwise spatial interactions in carrying the positive and negative information flows that we detected in the previous section, looking for spatial patterns of information and misinformation transfer.

In particular, we established the statistics of the relative position and heading of the destination fish relative to the source fish, at times when the transfer entropy from the source to the destination is more intense. For this purpose, we used radial diagrams (see Fig. 4) representing the relative data in terms of transfer entropy, focusing separately on their positive (informative) and negative (misinformative) values. In each diagram, we aggregate data from all 455 U-turns and all pairs. The diagrams show clear spatial patterns coupled with the transfer entropy, which we call spatio-informational motifs.

We see that positive information transfer is on average more intense from source fish to: (a) other fish positioned behind them (Fig. 4a, left), and (b) to fish with headings closer to perpendicular rather than parallel to them (Fig. 4a, right). We know from Figs. 2 and 3 that positive transfer entropy is detected from source fish that have already turned to destination fish that are turning. Thus, Fig. 4a suggests that a source is more informative about destination fish that are left behind it after a turn, most intensely when the destination fish are executing their own turning manoeuvre to follow the source. Directional relationships from individuals in front towards others that follow were observed in previous works on birds (Nagy et al. 2010), bats (Orange and Abaid 2015) and fish (Katz et al. 2011; Herbert-Read et al. 2011; Rosenthal et al. 2015).

For negative information transfer (Fig. 4b), we see a different spatio-informational motif. Negative information transfer is on average more intense to fish generally positioned at the side and with opposite heading. This aligns with Figs. 2 and 3 in that negative transfer entropy typically flows from fish that have not turned yet to those which are turning.

In summary, transfer entropy has a clear spatial signature, showing that the spatio-informational dependencies in the studied school of fish are not random but reflect specific interactions.



**Fig. 4** Spatio-informational motifs. Each diagram is a circle centred on a source fish with zero heading, providing a reference. In each diagram, space is divided into 60 angular sectors measuring  $6^\circ$ . Within each circle, we group all pairwise samples from all 455 U-turns such that the source fish is placed in the centre and the destination fish is placed within the circle in one of the sectors. The left circles in **a**, **b** aggregate the relative positions of destination fish, while the right circles aggregate the relative headings of destination fish. The value of each radial sector (for both position and heading) represents the average of the corresponding values of either positive (**a**) or negative (**b**) transfer entropy. For example, the value in each sector of the left diagram of **a** represents the average positive transfer entropy for a destination fish, given it has relative position in that sector with respect to the source fish: all positive values of transfer entropy corresponding to each sector are summed and divided by the total number of values corresponding to that sector. The value in each sector of the right diagram of **a** represents the average positive transfer entropy for a destination fish, given that its heading diverges from the one of the source by an angle in that sector. **b** Mirrors **a** this negative transfer entropy. The source fish data are taken from the time points corresponding to the time delay  $\nu$  with respect to the source

## 4 Discussion

Information transfer within animal groups during collective motion is hard to quantify because of implicit and distributed communication channels with delayed and long-ranged effects, selective attention (Riley and Leith 1976) and other species-specific cognitive processes. Here, we presented a rigorous framework for detecting and measuring predictive information flows during collective motion, by attending to the dynamic statistical dependence of directional changes in destination fish on relative heading of sources. This predictive information flow should be interpreted as a change (gain or loss) in predictability obtained by an observer. Importantly, the information-theoretic nature of the measure means that it is applicable to other stochastic interactions; more stochastic dynamics would require more data and suitable video capture resolution to identify the salient flows. Furthermore, one may consider methods of statistical mechanics and information thermodynamics in studies of collective motion distributed over large systems (Bialek et al. 2012; Crosato et al. 2018).

We studied *Hemigrammus rhodostomus* fish placed in a ring-shaped tank which effectively only allowed the fish to move straight ahead or turn back to perform a U-turn. The individual trajectories of the fish were recorded for hundreds of collective U-turns, enabling us to perform a statistically significant information-theoretical analysis for multiple pairs of source and destination fish. The experimental setup used in this study has been chosen to focus on collective U-turns, but the information flow analysis has been applied in other situations with more complex collective behaviour, e.g., general swarming behaviour with different constraints (Wang et al. 2012; Miller et al. 2014; Tomaru et al. 2016), and swarming behaviour with leaders (Sun et al. 2014; Orange and Abaid 2015).

Transfer entropy was used in detecting pairwise time delayed dependencies within the school. By observing the local dynamics of this measure, we demonstrated that predictive information flows intensify during collective direction changes—i.e., the U-turns—a hypothesis that until now was not verified in a real biological system. Furthermore, we identified

two distinct predictive information flows within the school: an informative flow from fish that have already preformed the U-turn to fish that are turning, and a misinformative flow from fish that have not preformed the U-turn yet to the fish that are turning.

We also explored the role of spatial dynamics in generating the influential interactions that carry the information flows, another well-known problem. In doing so, we mapped the detected values of transfer entropy against each fish's relative position and heading, identifying clear spatio-informational motifs. Importantly, the positive and negative predictive information flows were shown to be associated with specific spatial signatures of source and destination fish. For example, positive information flow is detected when the source fish is in front of the destination, similarly to what was already observed in previous works on animals (Nagy et al. 2010; Katz et al. 2011; Herbert-Read et al. 2011; Rosenthal et al. 2015; Orange and Abaid 2015). The identified sequential cascade-like dynamics of information flow is well-pronounced, suggesting that this pattern will be retained in larger schools—this however remains a subject of future research.

In a previous work, the analysis of short-term directional correlations between fish on the same experimental data has shown that, when the group changes direction, individual fish respond to a limited number of influential neighbours, typically one or two which are not necessarily the closest ones (Jiang et al. 2017). Moreover, fish continuously change who they are interacting with. In this study, using a complementary approach, we show that a fish that has just made a U-turn may also decide to ignore the input of other fish moving in opposite direction (which is shown by the misinformation flow). A fish can thus choose to move in the opposite direction of the majority. This suggests that the behavioural tendency of a fish to align in the direction of the majority of its neighbours, which is a manifestation of social conformity and implemented in most models of collective motion, can be “shut down” for some time. When these events occur, a fish can temporarily take the lead of a group thanks to the behavioural contagion. Our analysis provides a way to create a quantitative model for predictive information flow between fish and thus brings a better understanding of the processes underlying collective decisions in fish groups and animal groups in general.

Local transfer entropy as it was applied in this study reveals the dynamics of *pairwise* information transfer. It is well known that multivariate extensions to the transfer entropy, e.g., conditioning on other information sources, can be useful in terms of eliminating redundant pairwise relationships while also capturing higher-order relationships beyond pairwise (i.e. synergies) (Lizier et al. 2008, 2010; Lizier and Prokopenko 2010; Vakorin et al. 2009; Williams and Beer 2011; James et al. 2016), and as such the identification of *effective* neighbourhoods cannot be accurately inferred using pairwise relationships alone. Transfer entropy comprises both (i) a unique component from the source, and (ii) a synergistic component from the source in the context of the target, as has been clarified by Williams and Beer (2011), among others. While we can learn more by measuring these components separately (for which well accepted measures have not yet been developed), both capture important aspects of the concept of information transfer. Thus, we argue that focussing on the unique component alone would not align with the popularly understood concept of information transfer. Improvements are possible by adapting algorithms for deciding when to include higher-order multivariate transfer entropies (and which variables to condition on), developed to study effective networks in brain imaging data sets (Lizier and Rubinov 2012; Faes et al. 2011; Marinazzo et al. 2012; Stramaglia et al. 2012), to collective animal behaviour, as such methods can eliminate redundant connections and detect synergistic effects. Whether or not such algorithms will prove useful for swarm dynamics is an open research question, with conflicting findings that first suggest that multiple fish interactions could be faithfully fac-

torised into simply pair interactions in one species (Gautrais et al. 2012) but conversely that this may not necessarily generalise (Katz et al. 2011).

In any case, such adaptations to capture multivariate effects will be non-trivial, as it must handle the short-term and dynamic structure of interactions across the collective. Early attempts have been made using (a similar measure to) conditional TE—on average over time windows—in collectives under such algorithms (Lord et al. 2016); however, it remains to be seen what such measures reveal about the collective dynamics on a local scale.

In summary, we have proposed a novel information-theoretic framework for studying the dynamics of information transfer in collective motion and applied it to a school of fish, without making any specific assumptions on fish behavioural traits and/or rules of interaction. This framework can be applied to studies of other biological collective phenomena, such as swarming and flocking, artificial multi-agent systems and active matter in general.

## 5 Methods

A general scheme of the methodology from the animal experimentation to the analysis of the information flows is provided in Fig. 5.

### 5.1 Experimental procedures

A group of 70 *Hemigrammus rhodostomus* (rummy-nose tetras) were purchased from Amazonie Labège (<http://www.amazonie.com>) in Toulouse, France. Fish were kept in 150 L aquariums on a 12:12 h, dark/light photoperiod, at 27.7 °C ( $\pm 0.5$  °C) and were fed *ad libitum* with fish flakes. Body lengths of the fish used in these experiments were on average 31 mm ( $\pm 2.5$  mm). This species was chosen because it exhibits a strong schooling behaviour and it is very easy to handle in controlled conditions (Jiang et al. 2017; Lecheval et al. 2017). Moreover, individuals perform a *burst-and-coast* type of swimming that involves sharp directional changes, which implies a series of separate behavioural decisions in time and space. It is likely that an information-theoretic analysis would be able to better temporally resolve information flows associated with these transitions, as compared to more continuous dynamics [such as exhibited by *Khulia mugil* (Gautrais et al. 2012)].<sup>1</sup> Further, when swimming in a ring-shaped tank, schools of rummy-nose tetra hardly ever split despite collective U-turns, because of their social interactions relying on attraction and alignment (Calovi et al. 2018).

The experimental tank measured 120 × 120 cm was made of glass and set on top of a box to isolate fish from vibrations. The setup, placed in a chamber made by four opaque white curtains, was surrounded by four LED light panels giving an isotropic lighting. A ring-shaped tank made from two tanks (an outer wall of radius 35 cm and an inner wall, a cone of radius 25 cm at the bottom; both shaping a corridor of 10 cm) was set inside the experimental tank 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 28.1 °C ( $\pm 0.7$  °C). The conic shape of the inner wall has been chosen to avoid the occlusion on videos of fish swimming too close to the inner wall that would occur with straight walls.

Five fish were randomly sampled from their breeding tank for each trial. Fish were ensured to be used only in one experiment per day at most. Fish were left for 10 min to habituate

<sup>1</sup> With that said, we have also shown that techniques employed in this study are also successful in identifying information flows in groups with smoother motion dynamics (Wang et al. 2012; Miller et al. 2014).



before the start of the trial. A trial consisted of 1 h of fish swimming freely (i.e. without any external perturbation).

## 5.2 Data extraction and pre-processing

Fish trajectories were recorded by a Sony HandyCam HD camera filming from above the setup at 50Hz (50 frames per second) in HDTV resolution (1920 × 1080p). Videos were converted from MTS to AVI files with the command-line tool FFmpeg 2.4.3. Positions of fish on each frame were tracked with the tracking software idTracker 2.1 (Pérez-Escudero et al. 2014).

When possible, missing positions of fish have been manually corrected, only during the collective U-turn events detected by the sign changes of polarisation of the fish groups. The corrections have involved manual tracking of fish misidentified by idTracker as well as interpolation or merging of positions in the cases where only one fish was detected instead of several because they were swimming too close from each other for a long time. All sequences less or equal than 50 consecutive missing positions were interpolated. Larger sequence of missing values have been checked by eye to check whether interpolating was reasonable or not—if not, merging positions with closest neighbours was considered. All tracked positions have been monitored by eye during all U-turn events to make sure that any manual corrections improved the quality of the data set of positions. The entire process of manual changes and eye checking required three weeks. No U-turns were omitted from the analysis.

Time series of positions has been converted from pixels to metres, and the origin of the coordinate system  $\mathcal{O}(0, 0)$  has been set to the centre of the ring-shaped tank. The resulting data set contains 9273720 data points (1854744 for each fish) from all the ten trials. Velocity was numerically derived from position using the symmetric difference quotient two-point estimation (Larson 1983). Heading was then computed as the four-quadrant inverse tangent of velocity and used to compute transfer entropy.

## 5.3 Polarisation

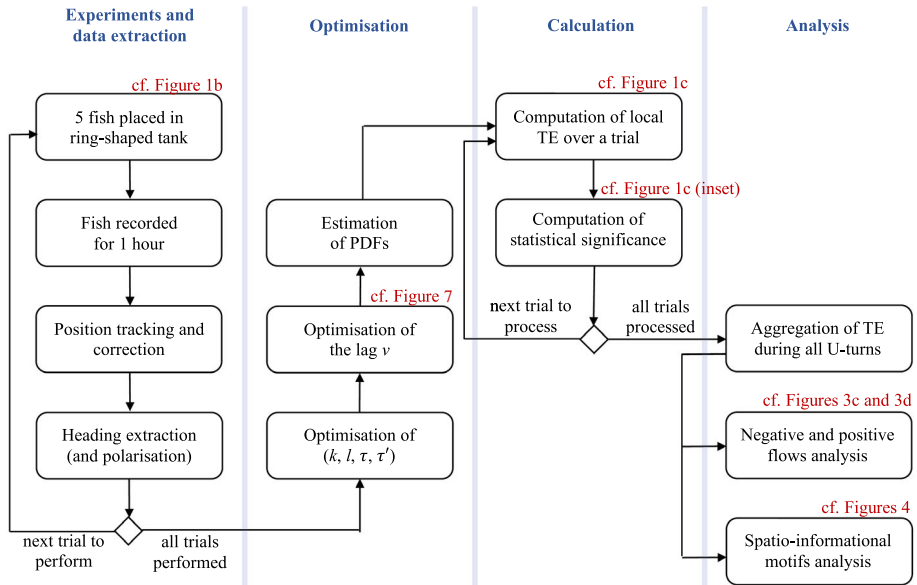
The polarisation is used to represent the orientation of a fish or of the whole school around the tank, which can be clockwise or anticlockwise, and is defined as the circumferential velocity component of the velocity a fish or of the whole school. Let  $Z$  and  $\dot{Z}$  be the two-dimensional position and normalised velocity of a fish, defined as Cartesian vectors with the centre of the tank being the origin—in case of the whole school,  $Z$  and  $\dot{Z}$  are averaged over all fish. The fish direction along an ideal circular clockwise rotation is described by a unit vector  $z = \frac{\omega \times Z}{|\omega \times Z|}$ , where  $\omega$  is a vector orthogonal to plane of the rotation, chosen using the left-hand rule. In other words,  $z$  is the azimuthal unit vector of the fish heading  $\theta$ .

The polarisation is defined as  $\dot{Z} \cdot z$ , so that it is positive when the fish is swimming clockwise and negative when it is swimming anticlockwise. Also, the better  $\dot{Z}$  is aligned with  $z$  or  $-z$ , the higher is the intensity of the polarisation. On the contrary, as  $\dot{Z}$  deviates from  $z$  or  $-z$ , the polarisation decreases and eventually reaches zero when  $\dot{Z}$  and  $z$  are orthogonal. As a consequence, during a U-turn, the intensity of the polarisation decreases and becomes zero at least once, before it increases again with the opposite sign.

## 5.4 Local transfer entropy

Transfer entropy (Schreiber 2000) is defined in terms of Shannon entropy, a fundamental measure in information theory (Cover and Thomas 2006) that quantifies the uncertainty of random





**Fig. 5** General scheme of the methodology. For each of the 10 trials of the experiment, 5 fish were randomly chosen and placed in the ring-shaped tank, where they were let swimming free for 1 h while being recorded. The position of the fish over time was tracked from the produced videos, and the heading extracted from the position. Once all time series of fish heading were created, for each fish and during all trials, they were used in order to optimise the embedding parameters and the lag between source and destination fish. The conditional probability distributions involved in the computation of transfer entropy were then estimated using the heading time series of all trials. Subsequently, the local values of transfer entropy at each time step were calculated for each trial, as well as their statistical significance. Finally, local values of transfer entropy around every U-turns were aggregated in order to perform the analyses presented in Sects. 3.2 and 3.3

variables. Shannon entropy of a random variable  $X$  is  $H(X) = -\sum_{x \in X} p(x) \log_2 p(x)$ , where  $p(x)$  is the probability of a specific instance  $x$  of  $X$ .  $H(X)$  can be interpreted as the minimal expected number of bits required to encode a value of  $X$  without losing information. The joint Shannon entropy between two random variables  $X$  and  $Y$  is  $H(X, Y) = -\sum_{x \in X} \sum_{y \in Y} p(x, y) \log_2 p(x, y)$ , where  $p(x, y)$  is the joint probability of instances  $x$  of  $X$  and  $y$  of  $Y$ . This quantity allows the definition of conditional Shannon entropy as  $H(X|Y) = H(X, Y) - H(X)$ , which represents the uncertainty of  $X$  knowing  $Y$ .

In this study, we are interested in local (or pointwise) transfer entropy (Fano 1961; Lizier 2014b) for specific instances of time series processes of fish motion, which allows us to reconstruct the dynamics of information flows over time. Shannon information content of an instance  $x_n$  of process  $X$  at time  $n$  is defined as  $h(x_n) = -\log_2 p(x_n)$ . The quantity  $h(x_n)$  is the information content attributed to the specific instance  $x_n$ , or the information required to encode or predict that specific value. Conditional Shannon information content of an instance  $x_n$  of process  $X$  given an instance  $y_n$  of process  $Y$  is defined as  $h(x_n|y_n) = h(x_n, y_n) - h(x_n)$ .

Local transfer entropy is defined as the information provided by the source  $\mathbf{y}_{n-v} = \{y_{n-v}, y_{n-v-1}, \dots, y_{n-v-l+1}\}$ , where  $v$  is a time delay and  $l$  is the history length, about the destination  $x_n$  in the context of the past of the destination  $\mathbf{x}_{n-1} = \{x_{n-1}, x_{n-2}, \dots, x_{n-k}\}$ , with a history length  $k$ :

$$\begin{aligned}
 t_{y \rightarrow x}(n, v) &= h(x_n | \mathbf{x}_{n-1}) - h(x_n | \mathbf{x}_{n-1}, \mathbf{y}_{n-v}) \\
 &= \log_2 \frac{p(x_n | \mathbf{x}_{n-1}, \mathbf{y}_{n-v})}{p(x_n | \mathbf{x}_{n-1})}.
 \end{aligned}
 \tag{2}$$

Transfer entropy  $T_{Y \rightarrow X}(v)$  is the average of the local transfer entropies  $t_{y \rightarrow x}(n, v)$  over samples (or over  $n$  under a stationary assumption). The transfer entropy is asymmetric in  $Y$  and  $X$  and is also a dynamic measure (rather than a static measure of correlations) since it measures information in state transitions of the destination.

In order to compute transfer entropy here, the source variable  $Y$  and destination variable  $X$  are defined in terms of the fish heading. Specifically,  $X$  is the first-order divided difference (Newton’s difference quotient) of the destination fish heading, while  $Y$  is the difference between the two fish headings at the same time. Let  $\theta_S$  and  $\theta_D$  be, respectively, the heading time series of the source and the destination fish. We then construct variables  $X$  and  $Y$  as follows, for all time points  $n$  (cf. Fig. 6 for an illustration of the headings involved):

$$x_n = \theta_n^D - \theta_{n-1}^D, \tag{3}$$

$$y_n = \theta_n^D - \theta_n^S. \tag{4}$$

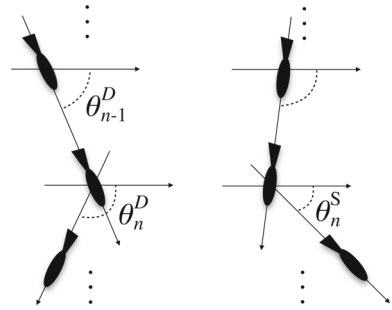
Thus,  $y_n$  represents the relative heading of the destination fish with respect to the source fish, while  $x_n$  represents the directional change of the destination fish. The variables were so defined in order to capture directional changes of the destination fish in relation to its alignment with the source fish, which is considered an important component of movement updates in swarm models (Reynolds 1987).

Given the definition of the variables (3) and (4), we computed local transfer entropy  $t_{y \rightarrow x}(n, v)$  using Eq. (2), where  $v$  was determined as described in Sect. 5.5 that follows. The past state  $\mathbf{x}_{n-1}$  of the destination in transfer entropy was defined as a vector of an embedding space of dimensionality  $k$  and delay  $\tau$ , with  $\mathbf{x}_{n-1} = \{x_{n-1-j\tau}\}$ , for  $j = \{0, 1, \dots, k - 1\}$ . Finding optimal values for  $k$  and  $\tau$  is also described in Sect. 5.5. The state of the source process  $\mathbf{y}_{n-v}$  was also defined as a vector of an embedding space whose dimensionality  $l$  and delay  $\tau'$  were similarly optimised. The local transfer entropy  $t_{y \rightarrow x}(n, v)$  computed on these variables therefore tells us how much information ( $l$  time steps of) the heading of the destination relative to the source adds to our knowledge of the directional change in the destination (some  $v$  time steps later), in the context of  $k$  past directional changes of the destination. We note that while turning dynamics of the destination may contain more entropy (as rare events), there will only be higher transfer entropy at these events if the source fish is able to add to the prediction of such dynamics.

Computing transfer entropy requires knowledge of the probabilities of  $x_n$  and  $y_n$  defined in (3) and (4). These are not known a priori, but the measures can be estimated from the data samples using existing techniques. In this study, this was accomplished by modelling the probability distribution function as a multivariate Gaussian distribution (making the transfer entropy proportional to the Granger causality (Barnett et al. 2009)). This technique is the simplest first-order estimation available and well applied for transfer entropy (Marinazzo et al. 2012). We used the JIDT software implementation (Lizier 2014a).

Also, we assume stationarity of behaviour and homogeneity across the fish, such that we can pool together all pairwise samples from all time steps, for all trials, maximising the number of samples available for the calculation of each measure. For performance efficiency, we make calculations of the local measures using 10 separate sub-sampled sets (sub-sampled evenly across the trials), then recombine into a single resultant information-theoretic data set.

**Fig. 6** Illustration of the headings from which the source and destination variables are constructed



## 5.5 Parameter optimisation

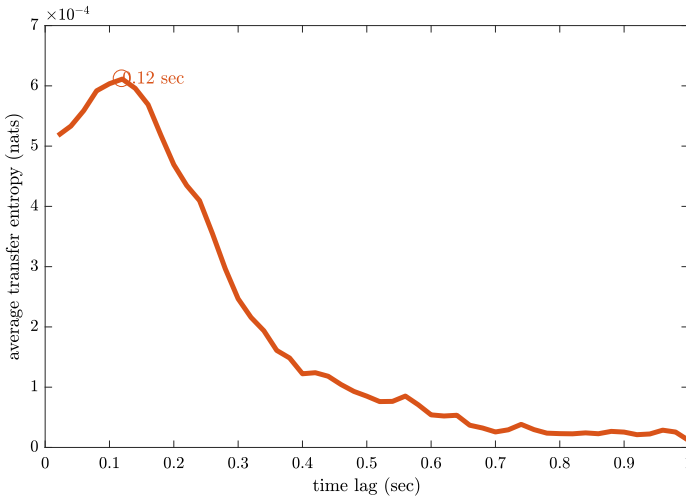
The embedding dimensionality and delay for the source and the past state of the destination need to be appropriately chosen in order to optimise the quality of transfer entropy. The combination  $(k, \tau)$  for the past state of the destination, as well as the combination  $(l, \tau')$  for the source, have been optimised separately by minimising the global self-prediction error, as described in Ragwitz and Kantz (2002) and Wibral et al. (2014). In the case of Markov processes, the optimal dimensionality of the embedding is the order of the process. Lower dimensions do not provide the same amount of predictive information, while higher dimensions add redundancy that weaken the prediction. For non-Markov processes, the algorithm selects the highest dimensionality found to contribute to self-prediction of the destination while still being supported by the finite amount of data that we have. Values of the dimensionality between 1 and 10 have been explored in combination with values of the delay between 1 and 5. The optimal combinations were found to be the same for both the source and the past of the destination:  $k = l = 3$ ,  $\tau = \tau' = 1$ .

The lag  $v$  was also optimised. This was done by maximising the average transfer entropy (after the optimisation of  $k$ ,  $\tau$ ,  $l$  and  $\tau'$ ) as per the technique of Wibral et al. (2013), Faes et al. (2014) used in, e.g., Razak and Jensen (2014), Materassi et al. (2014), Dimitriadis et al. (2016) and Khadem et al. (2016), over lags between 0.02 and 1 s, at time steps of 0.02 s. The average transfer entropy was observed to grow and reach a local maximum at  $v = 6$  (0.12 s), and then decrease for higher values (see Fig. 7). This result might have a biological interpretation: it is plausible that the response to behaviour of the other fish is delayed by both a communication and a reaction times, which would both be included in this lag.

## 5.6 Statistical significance of estimates of local transfer entropy

Theoretically, transfer entropy between two independent variables is zero. However, a non-zero bias (and a variance of estimates around that bias) is likely to be observed when, as in this study, transfer entropy is numerically estimated from a finite number of samples. This leads to the problem of determining whether a non-zero estimated value represents a real relationship between two variables, or is otherwise not statistically significant (Wibral et al. 2014).

There are known statistical significance tests for the average transfer entropy (Vicente et al. 2011; Lizier et al. 2011a; Lizier 2014a), involving comparing the measured value to a null hypothesis that there was no (directed) relationship between the variables. For an average transfer entropy estimated from  $N$  samples, one surrogate measurement is constructed by resampling the corresponding  $\mathbf{y}_{n-v}$  for each of the  $N$  samples of  $\{x_n, \mathbf{x}_{n-1}\}$  and then computing the average transfer entropy over these new surrogate samples. This process



**Fig. 7** Time lag optimisation. The red line represents the average transfer entropy (with  $k = l = 3$ ,  $\tau = \tau' = 1$ ) over all samples, as a function of the time delay between the source variable and the destination variable, for time delays between 0.02 and 1 s (1–50 time cycles) (Color figure online)

retains  $p(x_n | \mathbf{x}_{n-1})$  and  $p(\mathbf{y}_{n-v})$ , but not  $p(x_n | \mathbf{y}_{n-v}, \mathbf{x}_{n-1})$ . Many surrogate measurements are repeated so as to construct a surrogate distribution under this null hypothesis of no directed relationship, and the transfer entropy estimate can then be compared in a statistical test against this distribution. For the average transfer entropy measured via the linear-Gaussian estimator, it is known that analytically the surrogates (in nats, and multiplied by  $2 \times N$ ) asymptotically follow a  $\chi^2$  distribution with  $l$  degrees of freedom (Geweke 1982; Barnett and Bossomaier 2012). We use this distribution to confirm that the transfer entropy at the selected lag of 0.12 s (and indeed all lags tested) is statistically significant compared to the null distribution (at  $p < 0.05$  plus a Bonferroni correction for the multiple comparisons across the 50 candidate lags).

Next, we introduce an extension of these methods in order to assess the statistical significance of the *local* values. This simply involves constructing surrogate transfer entropy measurements as before, however this time retaining the local values within those surrogate measurements and building a distribution of those surrogates. Measured local values are then statistically tested against this null distribution of local surrogates to assess their statistical significance.

We generated ten times as many surrogate local values as the number of actual local estimates, with a total of approximately 371 million local surrogates. This large set of surrogate local values was used to estimate  $p$  values of actual local values of the transfer entropy. If  $p$  value is sufficiently small, then the test fails and the value of the transfer entropy is considered significant (the value represents an actual relationship). The Benjamini and Hochberg (1995) procedure was used to select the  $p$  value cutoff while controlling for the false discovery rate under ( $N$ ) multiple comparisons.

## Data accessibility

The datasets generated and analysed during the current study are available from the corresponding author on request.

**Author contributions** GT designed research; VL, PT and GT performed research; VL, LJ, PT, RW and GT analysed data. EC, JL, RW and MP developed information dynamics methods, performed information-theoretic analysis, and identified information flows and motifs. EC designed, developed and run software for the information-theoretic analysis. GT, JL, EC and MP conceived and analysed information cascade. EC, JL and MP wrote the paper. GT and VL edited the manuscript and contributed to the writing.

**Funding** E.C. was supported by the University of Sydney’s “Postgraduate Scholarship in the field of Complex Systems” from Faculty of Engineering & IT and by a CSIRO top-up scholarship. L.J. was supported by a grant from the China Scholarship Council (CSC NO.201506040167). V.L. was supported by a doctoral fellowship from the scientific council of the University Paul Sabatier. This study was supported by grants from the Centre National de la Recherche Scientifique and University Paul Sabatier (project Dynabanc). J.L. was supported through the Australian Research Council DECRA grant DE160100630. M.P. was supported by The University of Sydney’s DVC Research Strategic Research Excellence Initiative (SREI-2020) project, “CRISIS: Crisis Response in Interdependent Social-Infrastructure Systems” (IRMA 194163). Sydney Informatics Hub at the University of Sydney provided access to HPC computational resources that have contributed to the research results reported within the paper.

### Compliance with ethical standards

**Conflict of interest** The authors declare no conflict of interest.

**Ethical standard** All experiments have been approved by the Ethics Committee for Animal Experimentation of the Toulouse Research Federation in Biology N1 and comply with the European legislation for animal welfare.

## References

- Albantakis, L., Hintze, A., Koch, C., Adami, C., & Tononi, G. (2014). Evolution of integrated causal structures in animats exposed to environments of increasing complexity. *PLOS Computational Biology*, *10*(12), 1–19.
- Attanasi, A., Cavagna, A., Del Castello, L., Giardina, I., Grigera, T. S., Jelić, A., et al. (2014a). Information transfer and behavioural inertia in starling flocks. *Nature Physics*, *10*(9), 691–696.
- Attanasi, A., Cavagna, A., Del Castello, L., Giardina, I., Jelic, A., Melillo, S., et al. (2015). Emergence of collective changes in travel direction of starling flocks from individual birds’ fluctuations. *Journal of The Royal Society Interface*, *12*(108), 20150319.
- Attanasi, A., Cavagna, A., Del Castello, L., Giardina, I., Melillo, S., Parisi, L., et al. (2014b). Collective behaviour without collective order in wild swarms of midges. *PLOS Computational Biology*, *10*(7), 1–10.
- Ay, N., & Polani, D. (2008). Information flows in causal networks. *Advances in Complex Systems*, *11*(01), 17–41.
- Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., et al. (2008). Interaction ruling animal collective behavior depends on topological rather than metric distance: evidence from a field study. *Proceedings of the National Academy of Sciences*, *105*(4), 1232–1237.
- Barnett, L., Barrett, A. B., & Seth, A. K. (2009). Granger causality and transfer entropy are equivalent for gaussian variables. *Physical Review Letters*, *103*, 238701.
- Barnett, L., & Bossomaier, T. (2012). Transfer entropy as a Log-Likelihood ratio. *Physical Review Letters*, *109*, 138105.
- Barnett, L., Lizier, J. T., Harré, M., Seth, A. K., & Bossomaier, T. (2013). Information flow in a kinetic ising model peaks in the disordered phase. *Physical Review Letters*, *111*(17), 177203.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B (Methodological)*, *57*(1), 289–300.
- Bialek, W., Cavagna, A., Giardina, I., Mora, T., Silvestri, E., Viale, M., et al. (2012). Statistical mechanics for natural flocks of birds. *Proceedings of the National Academy of Sciences*, *109*(13), 4786–4791.
- Boedecker, J., Obst, O., Lizier, J. T., Mayer, N. M., & Asada, M. (2012). Information processing in echo state networks at the edge of chaos. *Theory in Biosciences*, *131*(3), 205–213.
- Bonabeau, E., Dorigo, M., & Theraulaz, G. (1999). *Swarm intelligence: From natural to artificial systems*. Oxford: Oxford University Press.

- Buhl, J., & Rogers, S. (2016). Mechanisms underpinning aggregation and collective movement by insect groups. *Current Opinion in Insect Science*, 15, 125–130.
- Buhl, J., Sumpter, D. J. T., Couzin, I. D., Hale, J. J., Despland, E., Miller, E. R., et al. (2006). From disorder to order in marching locusts. *Science*, 312(5778), 1402–1406.
- Buhl, J., Sword, G. A., Clissold, F. J., & Simpson, S. J. (2010). Group structure in locust migratory bands. *Behavioral Ecology and Sociobiology*, 65(2), 265–273.
- Butail, S., Ladu, F., Spinello, D., & Porfiri, M. (2014). Information flow in animal-robot interactions. *Entropy*, 16(3), 1315–1330.
- Butail, S., Mwaffo, V., & Porfiri, M. (2016). Model-free information-theoretic approach to infer leadership in pairs of zebrafish. *Physical Review E*, 93(4), 042411.
- Calovi, D. S., Litchinko, A., Lecheval, V., Lopez, U., Pérez Escudero, A., Chaté, H., et al. (2018). Disentangling and modeling interactions in fish with burst-and-coast swimming reveal distinct alignment and attraction behaviors. *PLOS Computational Biology*, 14(1), 1–28.
- Calovi, D. S., Lopez, U., Schuhmacher, P., Chaté, H., Sire, C., & Theraulaz, G. (2015). Collective response to perturbations in a data-driven fish school model. *Journal of The Royal Society Interface*, 12(104), 20141362.
- Cavagna, A., Giardina, I., & Ginelli, F. (2013a). Boundary information inflow enhances correlation in flocking. *Physical Review Letters*, 110(16), 168107.
- Cavagna, A., Queirós, S. M. D., Giardina, I., Stefanini, F., & Viale, M. (2013b). Diffusion of individual birds in starling flocks. *Proceedings of the Royal Society of London B: Biological Sciences*, 280(1756), 20122484.
- Chicharro, D., & Ledberg, A. (2012). When two become one: The limits of causality analysis of brain dynamics. *PLOS ONE*, 7(3), 1–16.
- Cliff, O. M., Lizier, J. T., Wang, X. R., Wang, P., Obst, O., & Prokopenko, M. (2017). Quantifying long-range interactions and coherent structure in multi-agent dynamics. *Artificial Life*, 23(1), 34–57.
- Couzin, I. D. (2009). Collective cognition in animal groups. *Trends in Cognitive Sciences*, 13(1), 36–43.
- Cover, T. M., & Thomas, J. A. (2006). *Elements of Information Theory*. New York: Wiley-Interscience.
- Crosato, E., Spinney, R. E., Nigmatullin, R., Lizier, J. T., & Prokopenko, M. (2018). Thermodynamics and computation during collective motion near criticality. *Physical Review E*, 97, 012120.
- Dimitriadis, S., Sun, Y., Laskaris, N., Thakor, N., & Bezerianos, A. (2016). Revealing cross-frequency causal interactions during a mental arithmetic task through symbolic transfer entropy: A novel vector-quantization approach. *IEEE Transactions on Neural Systems and Rehabilitation Engineering*, 24(10), 1017–1028.
- Faes, L., Marinazzo, D., Montalto, A., & Nollo, G. (2014). Lag-specific transfer entropy as a tool to assess cardiovascular and cardiorespiratory information transfer. *IEEE Transactions on Biomedical Engineering*, 61(10), 2556–2568.
- Faes, L., Nollo, G., & Porta, A. (2011). Information-based detection of nonlinear granger causality in multivariate processes via a nonuniform embedding technique. *Physical Review E*, 83(5), 051112.
- Faes, L., & Porta, A. (2014). Conditional Entropy-Based evaluation of information dynamics in physiological systems. In M. Wibral, R. Vicente, & J. T. Lizier (Eds.), *Directed information measures in neuroscience, understanding complex systems* (pp. 61–86). Berlin: Springer.
- Fano, R. M. (1961). *Transmission of information: A statistical theory of communications*. Cambridge, MA: M.I.T Press.
- Feldman, D. P., McTague, C. S., & Crutchfield, J. P. (2008). The organization of intrinsic computation: Complexity-entropy diagrams and the diversity of natural information processing. *Chaos*, 18(4), 043106.
- Fourcassié, V., Dussutour, A., & Deneubourg, J. L. (2010). Ant traffic rules. *The Journal of Experimental Biology*, 213(14), 2357–2363.
- Gautrais, J., Ginelli, F., Fournier, R., Blanco, S., Soria, M., Chaté, H., et al. (2012). Deciphering interactions in moving animal groups. *PLOS Computational Biology*, 8(9), 1–11.
- Geweke, J. (1982). Measurement of linear dependence and feedback between multiple time series. *Journal of the American Statistical Association*, 77(378), 304–313.
- Giardina, I. (2008). Collective behavior in animal groups: Theoretical models and empirical studies. *Human Frontier Science Program Journal*, 2(4), 205–219.
- Ginelli, F., Peruani, F., Pillot, M. H., Chaté, H., Theraulaz, G., & Bon, R. (2015). Intermittent collective dynamics emerge from conflicting imperatives in sheep herds. *Proceedings of the National Academy of Sciences*, 112(41), 12729–12734.
- Gómez, C., Lizier, J. T., Schaum, M., Wollstadt, P., Grützner, C., Uhlhaas, P., et al. (2014). Reduced predictable information in brain signals in autism spectrum disorder. *Frontiers in Neuroinformatics*, 8, 9.
- Herbert-Read, J. E., Buhl, J., Hu, F., Ward, A. J., & Sumpter, D. J. (2015). Initiation and spread of escape waves within animal groups. *Royal Society open science*, 2(4), 140355.

- Herbert-Read, J. E., Perna, A., Mann, R. P., Schaerf, T. M., Sumpter, D. J. T., & Ward, A. J. W. (2011). Inferring the rules of interaction of shoaling fish. *Proceedings of the National Academy of Sciences*, 108(46), 18726–18731.
- James, R. G., Barnett, N., & Crutchfield, J. P. (2016). Information flows? A critique of transfer entropies. *Physical Review Letters*, 116(23), 238701.
- Jeanson, R., Deneubourg, J. L., & Theraulaz, G. (2004). Discrete dragline attachment induces aggregation in spiderlings of a solitary species. *Animal Behaviour*, 67(3), 531–537.
- Jeanson, R., Rivault, C., Deneubourg, J. L., Blanco, S., Fournier, R., Jost, C., et al. (2005). Self-organized aggregation in cockroaches. *Animal Behaviour*, 69(1), 169–180.
- Jiang, L., Giuggioli, L., Perna, A., Escobedo, R., Lecheval, V., Sire, C., et al. (2017). Identifying influential neighbors in animal flocking. *PLOS Computational Biology*, 13(11), 1–32.
- Katz, Y., Tunström, K., Ioannou, C. C., Huepe, C., & Couzin, I. D. (2011). Inferring the structure and dynamics of interactions in schooling fish. *Proceedings of the National Academy of Sciences*, 108(46), 18720–18725.
- Khadem, A., Hossein-Zadeh, G. A., & Khorrani, A. (2016). Long-range reduced predictive information transfers of autistic youths in EEG sensor-space during face processing. *Brain topography*, 29(2), 283–295.
- Khuong, A., Gautrais, J., Perna, A., Sbaï, C., Combe, M., Kuntz, P., et al. (2016). Stigmergic construction and topochemical information shape ant nest architecture. *Proceedings of the National Academy of Sciences*, 113(5), 1303–1308.
- Ladu, F., Mwaffo, V., Li, J., Macrì, S., & Porfiri, M. (2015). Acute caffeine administration affects zebrafish response to a robotic stimulus. *Behavioural Brain Research*, 289, 48–54.
- Langton, C. G. (1990). Computation at the edge of chaos: Phase transitions and emergent computation. *Physica D*, 42(1–3), 12–37.
- Larson, L. (1983). The symmetric derivative. *Transactions of the American Mathematical Society*, 277(2), 589–599.
- Lecheval, V., Jiang, L., Tichit, P., Sire, C., Hemelrijk, C. K., & Theraulaz, G. (2017). Domino-like propagation of collective u-turns in fish schools. submitted to bioRxiv.
- Lissaman, P. B. S., & Shollenberger, C. A. (1970). Formation flight of birds. *Science*, 168(3934), 1003–1005.
- Lizier, J. T. (2013). *The local information dynamics of distributed computation in complex systems*, Springer Theses. Berlin: Springer.
- Lizier, J. T. (2014a). JIDT: An information-theoretic toolkit for studying the dynamics of complex systems. *Frontiers in Robotics and AI*, 1, 11.
- Lizier, J. T. (2014b). Measuring the dynamics of information processing on a local scale in time and space. In M. Wibral, R. Vicente, & J. T. Lizier (Eds.), *Directed information measures in neuroscience, understanding complex systems* (pp. 161–193). Berlin: Springer.
- Lizier, J. T., Heinze, J., Horstmann, A., Haynes, J. D., & Prokopenko, M. (2011a). Multivariate information-theoretic measures reveal directed information structure and task relevant changes in fMRI connectivity. *Journal of Computational Neuroscience*, 30(1), 85–107.
- Lizier, J. T., Pritam, S., & Prokopenko, M. (2011b). Information dynamics in small-world boolean networks. *Artificial Life*, 17(4), 293–314.
- Lizier, J. T., & Prokopenko, M. (2010). Differentiating information transfer and causal effect. *The European Physical Journal B*, 73(4), 605–615.
- Lizier, J. T., Prokopenko, M., & Zomaya, A. Y. (2008). Local information transfer as a spatiotemporal filter for complex systems. *Physical Review E*, 77(2), 026110.
- Lizier, J. T., Prokopenko, M., & Zomaya, A. Y. (2010). Information modification and particle collisions in distributed computation. *Chaos*, 20(3), 037109.
- Lizier, J. T., Prokopenko, M., & Zomaya, A. Y. (2012). Local measures of information storage in complex distributed computation. *Information Sciences*, 208, 39–54.
- Lizier, J. T., Prokopenko, M., & Zomaya, A. Y. (2014). A framework for the local information dynamics of distributed computation in complex systems. In M. Prokopenko (Ed.), *Guided self-organization: Inception, emergence, complexity and computation* (Vol. 9, pp. 115–158). Berlin: Springer.
- Lizier, J. T., & Rubinov, M. (2012). Multivariate construction of effective computational networks from observational data. Technical Report Preprint 25/2012, Max Planck Institute for Mathematics in the Sciences.
- Lord, W. M., Sun, J., Ouellette, N. T., & Bollt, E. M. (2016). Inference of causal information flow in collective animal behavior. *IEEE Transactions on Molecular, Biological and Multi-Scale Communications*, 2(1), 107–116.



- Mann, R. P., Perna, A., Strömbom, D., Garnett, R., Herbert-Read, J. E., Sumpter, D. J. T., et al. (2012). Multi-scale inference of interaction rules in animal groups using bayesian model selection. *PLoS Computational Biology*, 8(1), 1–12.
- Marinazzo, D., Pellicoro, M., & Stramaglia, S. (2012). Causal information approach to partial conditioning in multivariate data sets. *Computational and Mathematical Methods in Medicine*, 2012, 303601. [https://doi.org:1155/2012/303601](https://doi.org/1155/2012/303601).
- Materassi, M., Consolini, G., Smith, N., & De Marco, R. (2014). Information theory analysis of cascading process in a synthetic model of fluid turbulence. *Entropy*, 16(3), 1272–1286.
- May, R. M. (1979). Flight formations in geese and other birds. *Nature*, 282, 778–780.
- Miller, J. M., Wang, X. R., Lizier, J. T., Prokopenko, M., & Rossi, L. F. (2014). Measuring information dynamics in swarms. In M. Prokopenko (Ed.), *Guided self-organization: Inception, emergence, complexity and computation* (Vol. 9, pp. 343–364). Berlin: Springer.
- Moussaïd, M., Helbing, D., Garnier, S., Johansson, A., Combe, M., & Theraulaz, G. (2009). Experimental study of the behavioural mechanisms underlying self-organization in human crowds. *Proceedings of the Royal Society of London B: Biological Sciences*, 276(1668), 2755–2762.
- Moussaïd, M., Helbing, D., & Theraulaz, G. (2011). How simple rules determine pedestrian behavior and crowd disasters. *Proceedings of the National Academy of Sciences*, 108(17), 6884–6888.
- Nagy, M., Ákos, Z., Biro, D., & Vicsek, T. (2010). Hierarchical group dynamics in pigeon flocks. *Nature*, 464(7290), 890–893.
- Nagy, M., Vásárhelyi, G., Pettit, B., Roberts-Mariani, I., Vicsek, T., & Biro, D. (2013). Context-dependent hierarchies in pigeons. *Proceedings of the National Academy of Sciences*, 110(32), 13049–13054.
- Orange, N., & Abaid, N. (2015). A transfer entropy analysis of leader-follower interactions in flying bats. *The European Physical Journal Special Topics*, 224(17), 3279–3293.
- Parrish, J. K., Viscido, S. V., & Grünbaum, D. (2002). Self-organized fish schools: an examination of emergent properties. *Biological Bulletin*, 202(3), 296–305.
- Partridge, B. (1980). The effect of school size on the structure and dynamics of minnow schools. *Animal Behaviour*, 28(1), 68–IN3.
- Pérez-Escudero, A., Vicente-Paje, J., Hinz, R. C., Arganda, S., & de Polavieja, G. G. (2014). idTracker: Tracking individuals in a group by automatic identification of unmarked animals. *Nature Methods*, 11(7), 743–748.
- Potts, W. K. (1984). The chorus-line hypothesis of manoeuvre coordination in avian flocks. *Nature*, 309(5966), 344–345.
- Procaccini, A., Orlandi, A., Cavagna, A., Giardina, I., Zoratto, F., Santucci, D., et al. (2011). Propagating waves in starling, *sturnus vulgaris*, flocks under predation. *Animal Behaviour*, 82(4), 759–765.
- Prokopenko, M., Lizier, J. T., Obst, O., & Wang, X. R. (2011). Relating Fisher information to order parameters. *Physical Review E*, 84(4), 041116.
- Ragwitz, M., & Kantz, H. (2002). Markov models from data by simple nonlinear time series predictors in delay embedding spaces. *Physical Review E*, 65, 056201.
- Razak, F. A., & Jensen, H. J. (2014). Quantifying ‘causality’ in complex systems: Understanding transfer entropy. *PLOS ONE*, 9(6), e99462.
- Reynolds, C. W. (1987). Flocks, herds and schools: A distributed behavioral model. In *SIGGRAPH '87 Proceedings of the 14th annual conference on computer graphics and interactive techniques*. ACM, New York, NY, USA (Vol. 21, pp. 25–34).
- Richardson, T. O., Perony, N., Tessone, C. J., Bousquet, C. A., Manser, M. B., & Schweitzer, F. (2013). Dynamical coupling during collective animal motion. [arXiv:1311.1417](https://arxiv.org/abs/1311.1417).
- Riley, D. A., & Leith, C. R. (1976). Multidimensional psychophysics and selective attention in animals. *Psychological Bulletin*, 83(1), 138.
- Rosenthal, S. B., Twomey, C. R., Hartnett, A. T., Wu, H. S., & Couzin, I. D. (2015). Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion. *Proceedings of the National Academy of Sciences*, 112(15), 4690–4695.
- Schreiber, T. (2000). Measuring information transfer. *Physical Review Letters*, 85(2), 461–464.
- Smirnov, D. A. (2013). Spurious causalities with transfer entropy. *Physical Review E*, 87, 042917.
- Stramaglia, S., Wu, G. R., Pellicoro, M., & Marinazzo, D. (2012). Expanding the transfer entropy to identify information circuits in complex systems. *Physical Review E*, 86, 066211.
- Sumpter, D., Buhl, J., Biro, D., & Couzin, I. (2008). Information transfer in moving animal groups. *Theory in Biosciences*, 127(2), 177–186.
- Sun, Y., Rossi, L. F., Shen, C. C., Miller, J., Wang, X. R., Lizier, J. T., et al. (2014). Information transfer in swarms with leaders. [arXiv:1407.0007](https://arxiv.org/abs/1407.0007).
- Theraulaz, G., Bonabeau, E., Nicolis, S. C., Solé, R. V., Fourcassié, V., Blanco, S., et al. (2002a). Spatial patterns in ant colonies. *Proceedings of the National Academy of Sciences*, 99(15), 9645–9649.

- Theraulaz, G., Bonabeau, E., Sole, R. V., Schatz, B., & Deneubourg, J. L. (2002b). Task partitioning in a ponerine ant. *Journal of Theoretical Biology*, 215(4), 481–489.
- Tomaru, T., Murakami, H., Niizato, T., Nishiyama, Y., Sonoda, K., Moriyama, T., et al. (2016). Information transfer in a swarm of soldier crabs. *Artificial Life and Robotics*, 21 (2), 177–180.
- Tunström, K., Katz, Y., Ioannou, C. C., Huepe, C., Lutz, M. J., & Couzin, I. D. (2013). Collective states, multistability and transitional behavior in schooling fish. *PLOS Computational Biology*, 9(2), 1–11.
- Vakorin, V. A., Krakovska, O. A., & McIntosh, A. R. (2009). Confounding effects of indirect connections on causality estimation. *Journal of Neuroscience Methods*, 184(1), 152–160.
- Vicente, R., Wibral, M., Lindner, M., & Pipa, G. (2011). Transfer entropy—A model-free measure of effective connectivity for the neurosciences. *Journal of Computational Neuroscience*, 30(1), 45–67.
- Wang, X. R., Miller, J. M., Lizier, J. T., Prokopenko, M., & Rossi, L. F. (2012). Quantifying and tracing information cascades in swarms. *PLOS ONE*, 7(7), 1–7.
- Weitz, S., Blanco, S., Fournier, R., Gautrais, J., Jost, C., & Theraulaz, G. (2012). Modeling collective animal behavior with a cognitive perspective: A methodological framework. *PLOS ONE*, 7(6), 1–16.
- Wibral, M., Lizier, J. T., & Priesemann, V. (2015). Bits from brains for biologically-inspired computing. *Frontiers in Robotics and AI*, 2, 5.
- Wibral, M., Pampu, N., Priesemann, V., Siebenhühner, F., Seiwert, H., Lindner, M., et al. (2013). Measuring information-transfer delays. *PLOS ONE*, 8(2), 1–19.
- Wibral, M., Vicente, R., & Lindner, M. (2014). Transfer entropy in neuroscience. In M. Wibral, R. Vicente, & J. T. Lizier (Eds.), *Directed information measures in neuroscience, understanding complex systems* (pp. 3–36). Berlin: Springer.
- Williams, P. L., & Beer, R. D. (2011). Generalized measures of information transfer. [arXiv:1102.1507](https://arxiv.org/abs/1102.1507).