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Data-driven modelling of social forces and collective behaviour in zebrafish

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ABSTRACT

Zebrafish are rapidly emerging as a powerful model organism in hypothesis-driven studies targeting a number of functional and dysfunctional processes. Mathematical models of zebrafish behaviour can inform the design of experiments, through the unprecedented ability to perform pilot trials on a computer. At the same time, *in-silico* experiments could help refining the analysis of real data, by enabling the systematic investigation of key neurobehavioural factors. Here, we establish a data-driven model of zebrafish social interaction. Specifically, we derive a set of interaction rules to capture the primary response mechanisms which have been observed experimentally. Contrary to previous studies, we include dynamic speed regulation in addition to turning responses, which together provide attractive, repulsive and alignment interactions between individuals. The resulting multi-agent model provides a novel, bottom-up framework to describe both the spontaneous motion and individual-level interaction dynamics of zebrafish, inferred directly from experimental observations.

1. Introduction

Zebrafish are fast emerging as a species of choice in preclinical research (Kalueff and Cachat, 2011; Kalueff et al., 2014; Maximino et al., 2010; Orger and de Polavieja, 2017); the main reasons being its neurogenetic similarities with humans, ease of stocking and maintenance, short intergeneration time, and rich behavioural repertoires in response to environmental and psychoactive compounds (Butail et al., 2013; Kalueff et al., 2013; Lawrence, 2007; Panula et al., 2010). The locomotion of this freshwater species is governed chiefly by forward bursts of acceleration, followed by a period of coasting, or deceleration. Turns are achieved by a conformation of body posture, resulting in a change in heading direction, followed by further forward bursts in the new direction (Danos and Lauder, 2007; Fish et al., 1991; Fuiman and Webb, 1988; Muller et al., 2000).

Data-driven models of zebrafish promise to aid neurobehavioural science, by empowering researchers with computational tools to conduct pilot in-silico experiments, refine experimental observations, and enhance statistical analysis. Much of the existing work has focused on individual response of zebrafish, swimming in isolation (Mwaffo et al., 2014; 2017; Zienkiewicz et al., 2014), to capture key behavioural phenotypes which have been experimentally observed (Kalueff et al., 2013). For example, in Mwaffo et al. (2014), we explained the burst-and-coast swimming style of zebrafish and in Zienkiewicz et al. (2014) we investigated the emergence of thigmotactic response during interactions with tank walls.

A pressing open problem is the derivation of computational models able to capture social interaction between zebrafish swimming in a shoal, and reproduce experimentally observed social behaviour (Calovi et al., 2017; Yoshioka, 2016), Lecheval et al., Filella et al.. An improved understanding of social interactions can help identifying and quantifying the biological advantages of living in groups, and the role of pharmacological manipulations on group behaviour (Shams and Gerlai, 2016)

Formulating an accurate model of zebrafish social behaviour requires the precise quantification of "social forces" between individual fish (Herbert-Read, 2016; Herbert-Read et al., 2011; Katz et al., 2011). Central to this approach is to compute, for each individual at every time-sample, the reaction forces which describe how a focal agent moves, or accelerates, in response to the current "social" configuration of itself and a local neighbour. These config-

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urations are typically described by measurable spatial quantities, for example, the relative position and orientation of a neighbour with respect to the focal individual. Dynamic variables, such as the speed and acceleration of individuals are also taken into account into the description of a pair-wise configuration. The notion of social forces has been successfully applied to study social behaviour of other teleosts, such as golden shiners (Katz et al., 2011) and mosquitofish (Herbert-Read et al., 2011).

In previous work, we presented preliminary models to capture some aspects of the interaction among zebrafish swimming together towards exploring leader-follower relationships. Specifically, in Butail et al. (2016), we examined the interactions between two zebrafish in terms of their turn rate dynamics, without considering speed regulation or wall interaction. In Zienkiewicz et al. (2015), we explored the effects of leaders onto the dynamics of a virtual zebrafish shoal based on a preliminary model of social interaction between conspecifics – developed in more detail in this work.

In this paper, we establish a data-driven model of zebrafish social interaction building on our previous work and on recent analytical methods which have been used to infer interaction behaviours within social animal groups (Eriksson et al., 2010; Herbert-Read et al., 2011; Katz et al., 2011; Lukeman et al., 2010).

In particular, we derive a set of interaction rules to capture the primary response mechanisms which have been observed experimentally (Partridge and Pitcher, 1980; Pitcher, 1986). Inspired by recent models proposed by Gautrais et al. (2012), Calovi et al. (2014) and Collignon et al. (2016), we subsequently incorporate interaction behaviours into our original model framework (Zienkiewicz et al., 2014), in a way which leaves the unique locomotory patterns of individuals intact. Importantly here, we include *dynamic speed regulation* in addition to turning responses, showing that together they better capture experimental observations of attractive, repulsive and alignment interactions between individuals. Variable speed is a fundamental feature of the locomotory patterns of zebrafish and similar species (Fish et al., 1991; Sfakiotakis et al., 1999). Similarly, the ability to modulate forward speed with respect to neighbours has also been proposed as a central mechanism for explaining collective behaviour of similar teleosts (Berdahl et al., 2013; Herbert-Read et al., 2013; 2011; Katz et al., 2011; Strandburg-Peshkin et al., 2013).

Our multi-agent model provides a novel, bottom-up framework to describe both the spontaneous motion and individual-level interaction dynamics of zebrafish — inferred directly from experimental observations. In contrast to the conclusions of a similar study (Katz et al., 2011), we also report evidence of an explicit alignment mechanism between co-swimming zebrafish. Specifically, we use force-mapping analysis to decompose the observed turning responses into distinct attractive and alignment components. These behaviours are subsequently included in the model construction, by determining the relative contributions of each response, as a function of the spatial configuration of zebrafish pairs.

2. Social-force mapping of zebrafish interactions

The first step towards a comprehensive mathematical model is the identification of the social forces acting on an individual zebrafish as a result of the presence of its conspecifics. These forces are measured from the acceleration of a focal fish at any instant in time — ignoring strictly physical quantities such as mass and momentum. The assumption is that by analysing experimental trajectory data from periods in which fish are swimming in close proximity, we can isolate the accelerations due to their specific interaction responses. Provided sufficient data is collected, accelerations due to interactions are manifested against the residual (random) background from the spontaneous motion of individuals. In this study, we therefore consider composites of multiple observations of zebrafish pairs, swimming together for extended periods of time.

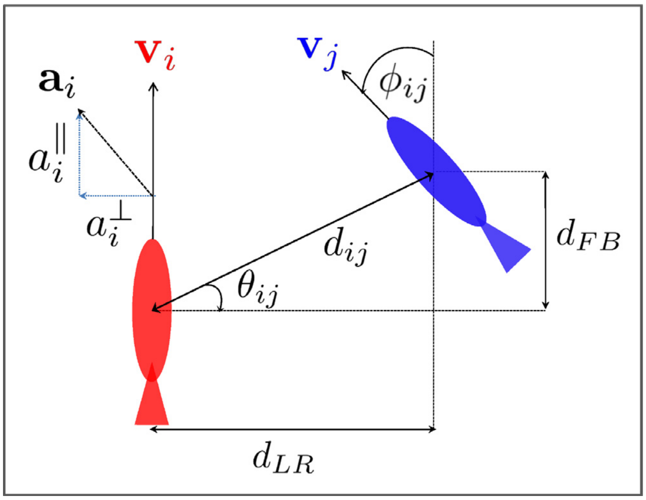

Fig. 1. Fish interaction coordinate system and separation metrics. Cartesian coordinate system in frame of focal fish i, separated from its neighbour j by d_{ij} with front-back distance $d_{FB} = d_{ij} \sin\theta_{ij}$ and left-right distance $d_{LR} = d_{ij}\cos\theta_{ij}$ with respect to its velocity $\mathbf{v}_i$ (orientation). Angle θ_{ij} is formed between the heading direction of fish i and the relative position of fish j; with ϕ_{ij} giving the relative orientation (heading angle) of fish j with respect to fish i. The tank frame acceleration vector $\mathbf{a}_i$ is decomposed into a tangential acceleration $a_i^{\|}$ and a radial acceleration $a_i^{\perp}$ in the focal fish frame as shown.

2.1. Data collection

The experiments described in this study, similar to those in Zienkiewicz et al. (2014), are designed to extract sufficient information from live zebrafish in order to reconstruct swimming trajectories — specifically in terms of position, speed, angular velocity (turn-rate) and associated accelerations as a function of time.

We use 18×20 min observations of swimming zebrafish *pairs* from experiments carried out at the Dynamical Systems Laboratory of New York University. Each pair was video recorded from above a shallow (10 cm depth), circular tank after which trajectory data was extracted to obtain unique time-series of centroid positions $\mathbf{x}_i(t)$ for each fish i at time t (see online supporting information (SI): video V1).

The depth of water in the experimental tank is designed to reflect the natural habitat of zebrafish which occupy shallow, slow-flowing waters (Spence et al., 2008). The primary component of their collective motion is therefore in the plane, justifying our analysis based on two-dimensional data captured from a single overhead perspective. Ultimately from this data we are able to compute linear components of the fish's acceleration: $a_i^{\|}$ in the direction of motion, and $a_i^{\perp}$ in the radial direction, perpendicular to the fish's heading direction (Fig. 1). Turning behaviour is further characterised by computing angular turn-rates $\omega_i(t)$ and the angular accelerations $\dot{\omega}_i(t)$. The same dataset is utilized in Butail et al. (2016) and Zienkiewicz et al. (2015).

In what follows, we show how this information is obtained and subsequently analysed to infer average interaction responses of a fish with respect to its neighbours. Specifically, we present and discuss the results of force mapping analysis for experimental observations of co-swimming zebrafish pairs. For each mapping described, data is averaged over all 18 pair observations, taking each fish in turn as the focal fish. Using a coordinate system in the frame of the focal fish (Fig. 1), we compute population density and force maps such that the focal fish's orientation is aligned with the y-axis of each plot.