Experimental analysis and modelling of the behavioural interactions underlying the coordination of collective motion and the propagation of information in fish schools

Lecheval, Valentin Jacques Dominique

Chapter 6

General discussion

In this thesis, I have investigated the individual-level interactions and behaviours that underlie the coordination of collective motion and the propagation of information in groups of tropical fish *Hemigrammus rhodostomus*. Here, I summarise and discuss the main results and give an outlook regarding future work.

6.1   Overview of the main results

I discuss the results of this thesis in the light of four topics: 1) the burst-and-coast swimming style, 2) the individual-level interactions and the behavioural rules involved in the coordination of collective swimming, 3) the decision-making processes and the propagation of information within groups and 4) the methodological contributions.

6.1.1   The burst-and-coast swimming behaviour

Burst-and-coast swimming is an intermittent swimming style, adopted by the rummy-nose tetra, *Hemigrammus rhodostomus* (Lopez, 2015). It consists of cyclic bursts of swimming movements followed by a coast phase in which the body of the fish does not move. The quality of the recordings of our experiments (HDTV resolution, 50 Hz) as well as the duration (one to three hours) and the two shapes of our tanks (circular or ring-shaped) have favoured a detailed analysis of this swimming style. Swimming speed of fish in groups of 10 in a ring-shaped tank was on average 7 BL/s, and bursts of speed up to 10 BL/s could be reached in all group sizes. These traits may underlie the efficiency of the burst-and-coast style, as found previously (Weihs, 1974; Videler and Weihs, 1982): fast speeds of 10 BL/s can

be reached and fish can sustain such speeds for more than an hour. We have shown that the control of the speed resulted from a subtle interplay between the respective duration of the burst and coast phase and the adjustment of the acceleration, in response to non-social (i.e. the wall) and social information. We developed a model in which fish make decisions (about their direction, speed and duration of the burst-and-coast cycle) only at the onset of the burst phases and in which the speed of fish during coast phases is a viscous drag accounting for water frictions. The model reproduced qualitatively and quantitatively the empirical spatial distribution of a single fish observed in a circular arena (see Appendix B for a discussion on the asynchronous integration of information by *H. rhodostomus*).

This discrete integration of information has also been suggested in a model for another species that has a burst-and-coast behaviour, the zebrafish (*Danio rerio*, Harpaz et al., 2017). Harpaz et al. have found that the burst phases are best predicted by fish that react to social information and that coast phases are best predicted by a passive mode where only drag forces are applied to fish velocity. These results are similar to ours, although obtained with a different method. These findings suggest a close connection between the swimming style of fish and the mechanisms (e.g. the integration of information) that control the coordination of schools.

6.1.2   Individual-level interactions and behavioural rules involved in the coordination of collective swimming

Following the methodological framework described by Gautrais et al. (2012), we used a bottom-up approach to disentangle and measure the non-social (walls of the experimental tank) and social interactions involved in the behaviour of *H. rhodostomus*. A data-driven model has been developed to assess quantitatively the relevance of the measured interactions.

The interaction of fish with the wall consists of avoidance behaviour, of which the intensity is modulated by the perception of fish. We showed that at each decision of the fish regarding its motion, all non-social information available in a circular tank could be summed up by only one point of the wall. In other words, by making decisions only based on the location of the wall closest to the fish (with respect to the radial distance) suffices to reproduce trajectories of one fish swimming spontaneously in circular tanks of three different radii. Although trajectories of fish are concentrated along the walls, interactions with the wall are repulsive: fish turn away from the wall when they are at less than $2\,\mathrm{BL}$ from it. The avoidance effect is also weaker when fish are parallel to the wall or when the wall is behind them. Thus, the perception of the wall by a fish depends on (i) its distance to

the wall and (ii) its angle to the wall. In particular, how the interaction of avoidance of the wall depends on the angle of the fish to the wall reveals the anisotropic perception of fish, responsible for asymmetric interactions, also found for social stimuli.

We have shown that schools of *H. rhodostomus* were highly cohesive and polarised. We developed a theoretical model to account for the fact that the occurrence of collective U-turns in a ring-shaped tank decreases with increasing group size. The model shows that local social conformity (i.e. the tendency of fish to copy the behaviour of the majority of the neighbours) coupled with anisotropic perception of fish may explain the global properties of the collective U-turns. The social interactions that we measured underlie (at least to some extant) the social conformity implemented in this theoretical model. In particular, we found evidence of repulsion between fish, alignment and attraction. In contrast to previous phenomenological models, these behavioural modes are not set to discrete and arbitrary zones of distances to the neighbouring fish (Aoki, 1982; Huth and Wissel, 1992; Couzin et al., 2002). Instead, there is a continuous combination of attraction and alignment as a function of the distance between fish, as former theoretical studies assumed (Reuter and Breckling, 1994; Kunz and Hemelrijk, 2003). Alignment dominates attraction up to $\sim 2.5\,\mathrm{BL}$ while attraction dominates for larger distances. At very large distances, in the limit of the field of perception, attraction is obviously expected to decrease as well, although we could not measure it in our experimental tanks that were, at most, of a maximum radius of $35\,\mathrm{cm}$. Experimental evidence for alignment interactions is interesting since (i) no alignment is required to produce most of the collective patterns reported in other models of schools (Strömbom, 2011; Strömbom et al., 2015; Huepe et al., 2015) and (ii) alignment was not found in experiments with other species (Katz et al., 2011; Herbert-Read et al., 2011). Whether this is due to differences related to the species or to the methods is still unclear.

We have also investigated how information from multiple sources may be integrated. In our bottom-up approach, this step is crucial to model larger groups from the social and non-social interactions inferred from experiments with 1 or 2 fish. Our hypothesis that a fish only reacts to the strongest stimulus (either social or non-social) is not confirmed by the model, in that it does not reproduce the empirical properties of the polarised schools of *H. rhodostomus*. However, our simulations suggest that such a mechanism may be responsible for swarming species in which individuals are aggregated and loosely polarised.

6.1.3   Propagation of information and decision-making

In Part II (Chapters 4 and 5), we investigated how information propagates in schools of *H. rhodostomus* and leads to collective decisions.

We showed that spontaneous collective U-turns were initiated by individuals that turned around at the front of the school and that this turning was propagated to the back of the school. This is in agreement with the perception anisotropy detected in Part I. The directionality of the propagation of information in the schools during the collective U-turns is confirmed by two independent methods (Appendices A and B).

We find that collective U-turns are preceded by a period during which fish are slowing down. It has been shown in other fish species that speed affects alignment among individuals (Gautrais et al., 2012), leading slow groups to be less polarised than fast groups (Steven V. Viscido et al., 2004; Hemelrijk and Hildenbrandt, 2008; Tunstrøm et al., 2013; Calovi et al., 2014). In general, at slower speed, there is less inertia to turn, resulting in weaker polarisation (Kunz and Hemelrijk, 2003; Hemelrijk et al., 2010) and more fluctuations in the swimming direction of the fish (Marconi et al., 2008; Calovi et al., 2015). As its speed decreases, the fish school is in a state closer to the transition between schooling (strong alignment) and swarming (weak alignment), i.e. where Calovi et al. (2015) have shown that both fluctuations in fish orientation and the sensitivity of the school to a perturbation increase. It is therefore not surprising that U-turns occur after the group has slowed down.

Within the ranges of group sizes we tested (1 to 10 fish), there was no damping nor positive feedback in the temporal propagation of information. Although it could be argued that this result may be different for larger groups, in sheep (*Ovis aries*), an amplification (i.e. the rate of following behaviours increases as the number of individuals committed in the following behaviour increases) has been reported in groups of at least 6 individuals (Pillot et al., 2011). We showed that for the largest group sizes, a heading opposite to that of the majority is hardly propagated, resulting in a strong decrease in the frequency of the collective U-turns with increasing group size. Schools of fish are thus less sensitive to internal local perturbations when the number of individuals increases, thus similar to empirical findings in sheep (Toulet et al., 2015).

Our model shows that consensus about the direction chosen at the group-level is achieved by choosing the direction of the local majority. Assuming that fish interact locally and not with all the group-members, even in the small group sizes we consider, is supported by the work presented in Appendix B that suggests that fish mainly interact with a small number of

influential neighbours (typically 1 or 2). Temporary leadership is explained by the anisotropy in the perception of fish, that favours aligning with frontal individuals. Preliminary results of our conditioning experiments (Chapter 5) show that the composition of the group (i.e. the ratio between informed and non-informed fish) also affects how the group responds to external and aversive perturbations (here, a conditioned stimulus (green light) triggering an escape behaviour). Namely, our results suggest that a critical proportion of conditioned individuals was necessary to reach a consensus and trigger a collective escape. Although it needs to be confirmed by additional replicates, this finding confirm previous results in appetitive conditioning (Miller et al., 2013). We also expect that this critical proportion depends on group size but it is unknown so far how it exactly does so. This would test previous theoretical predictions (Couzin et al., 2005).

6.1.4 Methodological contributions

In the introduction of this thesis, I have discussed the challenges of the study of complex biological phenomena like collective motion in fish schools. To cope with the complexity, we used a diversity of methods tightly combining experiments, data analyses and computational modelling. These methods may be of interest to others in the field of Collective Behaviour and in related fields such as, for instance, Ecotoxicology, where accurate quantification of the (collective) behaviour of fish is critical to state the effects of toxic chemicals.

In Chapter 2, we used a bottom-up experimental approach to measure the interactions involved in the coordination of schools, as was previously done with another species (Gautrais et al., 2009, 2012). The large amount of experimental data that we have collected has motivated the use of a new method to measure social and non-social interactions. This method limits the number of parameters that we need to fit and provides an explicit model, in contrast to the force-map method used by others (Katz et al., 2011). In our case, to disentangle the social interactions and given the aimed resolution, a three-dimensional map of the angle turned as a function of the distance to the neighbour, the angular position of the neighbour and the relative orientation between the focal fish and its neighbour would have required fitting 36,000 parameters (and thus more empirical data points than the 173,817 burst-and-coast cycles we obtained from 1117 min of videos at 50 Hz), while our method required only fitting of 200 parameters and provided an explicit model.

In the former work with the bottom-up approach (Gautrais et al., 2009, 2012), the interactions of a fish with the walls of the tank and with other

fish were phenomenological – the mathematical functions in the model were motivated by the fit to data. Here, we favoured a normative model (Laan et al., 2017), in which the equations in our model are derived from a logical framework based on physical analogies and symmetry considerations. Thus, the equations used in our model to depict non-social and social interactions may have greater generality when applied to new species.

In Chapter 3, we specifically address how fish integrate information from multiple (social and non-social) sources. We developed a new method based on behavioural action maps derived from experimental data. We tested hypotheses regarding the integration of information. Despite the negative outcome regarding the hypothesis tested (namely, that fish would only react to the strongest stimulus when making a decision), the method will still be used to test alternative hypotheses. Because the method does not require any assumption regarding the interaction mechanisms, it is likely that it can be applied to a variety of fish species, even if their swimming behaviour strongly differs from *H. rhodostomus*. However, the method has drawbacks: it assumes that the individual interactions found in groups of 1 and 2 fish are identical to those in larger groups and that the turning angle is a proxy of the importance of a stimulus. Moreover, hypotheses different from ours and involving averaging over several stimuli may sum the error in the measurements (tracking and data treatment) over all stimuli. We emphasise that our results suggest the importance of investigating the mechanism of integration of information, which is rarely studied in the context of collective motion.

In Chapter 4, we used the formalism of the Ising model, developed in Statistical Physics, to investigate the propagation of collective U-turns. We derive a formal definition of local social conformity from the framework of Ising models. This definition is combined with anisotropic perception. Ising models have been widely used to account for collective decisions in humans (Castellano et al., 2009). We think that this formalism, coupled with the interaction mechanisms, may be of interest in animal collective behaviour, to explain patterns where there is consensus at the global level (Ward et al., 2008; Sumpter and Pratt, 2009; Ward et al., 2012).

In Chapter 5, we investigate the relevance of conditioning experiments in studies of collective behaviour of fish. Conditioning experiments may be interesting in the field for the manipulation of behaviour in a controlled way (Pillot et al., 2010, 2011; Miller et al., 2013; Toulet et al., 2015). In the experiment, we aimed to control (i) which individual would react to a green light (i.e. the conditioned individuals), and (ii) how they would react to it (by escaping away from it). In the present case, we did not entirely succeed

to control the identity of the first responder because green light also has an effect on naïve fish. This needs be improved in future experiments, by either changing the conditioning stimulus (or by reducing its intensity) or by familiarising the naive fish to the green light. We did, however, manage to train fish to escape a green light, thus controlling (to some extent) that the green light is perceived as a threat. These results motivate future use of this method to investigate how the proportion of informed individuals among group members affects the propagation of information in the whole group, in particular in the context of escapes.

6.2   Outlook and future work

By focusing on a single species of fish and combining various methods, we have improved our understanding of the behavioural and cognitive mechanisms that govern the schooling behaviour in *H. rhodostomus*. Still, for establishing causal links from the neural scale to the collective scale and providing arguments regarding the fitness of the collective patterns, future work is required. This will be briefly looked at below.

6.2.1   Neural and cognitive scales

We described the burst-and-coast style of fish swimming spontaneously. Future research regarding the motor actions involved in the reactions of fish is required for deriving causal links from the neural scale to the behavioural scale. An interesting method using a virtual reality system has recently been suggested with larvae of zebrafish (Jouary et al., 2016). The authors have made a classification of the possible movements of the tail of the larvae and then monitored the reactions of the larvae in a controlled virtual environment. The changes in the visually induced environment are made thanks to the connection between the motor reaction and the behavioural action. The aim is, eventually, to link the neural activity to the motor reaction inducing a behavioural action, in response to a specific set of stimuli.

In *H. rhodostomus*, we monitored the angle made by the body of the fish and its tail, in particular during the burst phases. We find, for instance, that there is a clear positive correlation between the maximum angle made by the fish during the burst phase and the magnitude of the angle turned (i.e. the stronger the fish bends, the more it turns) (Figure 6.1). Classifying the motor repertoire of the fish (especially regarding the body angle) and mapping it to the behavioural reactions inferred in Chapters 2 and 3 (regarding control of speed and direction) may be a first step to connect the
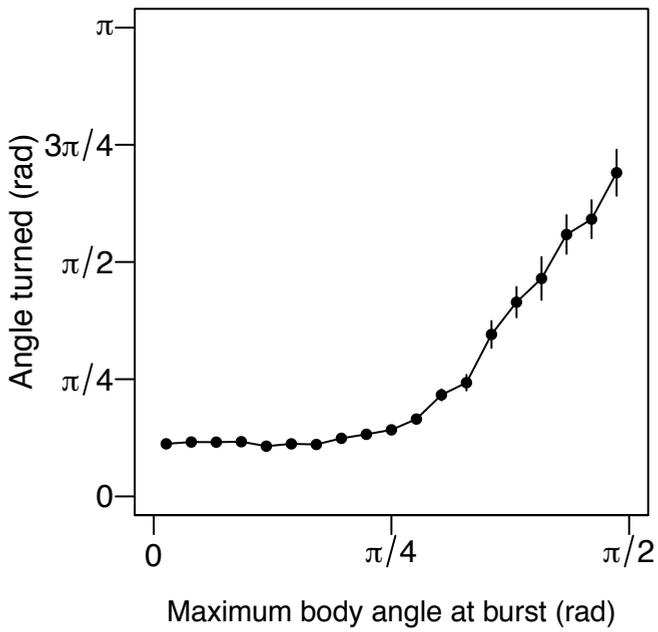
Figure 6.1: Average angle turned versus the maximum body angle of the fish during burst phases. Vertical lines stand for the standard error.

motor reactions of fish to their behavioural responses and thus derive the causal link between the neural activity and the behaviour of the individuals.

6.2.2 Evolutionary perspective

Unfortunately, the animals used in this thesis have all been bred in captivity and were not captured in nature. The ecology of *H. rhodostomus* is not known and we also do not know how our captive animals differ from wild individuals. This prevents any inference about the functions of the schooling behaviour detailed in this manuscript. The general relevance of this study is thus still to be addressed. It is likely that the swimming style of a species constrains the (collective) behavioural repertoire. Characterising in detail the burst-and-coast behaviour of other species (such as the zebrafish, as recently has been done) may provide relevant benchmarks to compare the species and their collective behaviour (Harpaz et al., 2017; Laan et al., 2017). We note that the methods developed in these experimental studies have already been used to examine the impact of predation on schooling behaviour, thanks to measurements based on the burst-and-coast behaviour (Herbert-Read et al., 2017). Such studies, conducted with wild animals and using the quantitative methods developed with controlled experiments to investigate behaviours in detail, are of great interest to learn about the ecological functions of schooling.