Analysis of Pressure Forces During Spontaneous Turns in Zebrafish

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1 Introduction

Energetic efficiency has long been considered an important feature of routine animal behaviors, such as steady-speed locomotion. In the fluid environment fishes use body undulations to navigate and propel themselves forward and it has been shown that undulatory swimmers are remarkably energy efficient [1]. In this context most studies have focused on aspects of energy efficiency in steady swimming, however, fishes rely heavily on unsteady behaviors (turns, accelerations) during crucial tasks like navigation, feeding, and predator avoidance. Some of these unsteady behaviors, such as routine turning (e.g. 10 times per minute in *D. rerio* [2]) are occurring frequently enough that we expect these behaviors to also have high energetic efficiency. Despite these expectations, few studies have focused on the dynamics and resulting energetics of routine turning, in part due to methodological limitations.

Here, we focus on turning behaviors by means of body undulations and ask to what extent these maneuvers are performed in an energy efficient manner. For this purpose, we systematically recorded and investigated frequently observed voluntary turns in freely swimming adult zebrafish (*Danio rerio*). Previous work on the hydrodynamics of turning zebrafish has shown lower vortex circulation in larvae compared to adults due to viscous effects [3]. In addition, Mwaffo et al. [4] have recently investigated vortex shedding patterns of burst-and-coast behavior in zebrafish swimming against water currents and compared pressure patterns to steady swimming. We analyzed efficiency during turns by extracting full body kinematics and computing distributed pressure forces along the swimming body from high-speed video recordings and particle image velocimetry analysis. Our preliminary results in still water suggest that zebrafish could recover parts of their effort during turns by exploiting the forces exerted by the accelerated surrounding fluid.

2 Methods

We swam two individual zebrafish *Danio rerio*, one at a time, in still water inside a tank of dimensions 13 cm x 8.5 cm at a water depth of 3 cm. Fish were recorded from two synchronized views (bottom and side) with high-speed cameras at 1 kHz and a resolution of 1024 x 1024 pixels. As in [5], we seeded the water with nearly neutrally buoy-ant algae particles ($10\mu m$) and used brightfield illumination from room and additional infrared lights to increase contrast between the fish and the background. Utilizing a narrow depth-of-field allowed us to record in-focus particles in a thin plane of fluid, thereby providing conditions for particle image velocimetry analysis without an external laser sheet. Only zebrafish turning maneuvers that were identified (using the side view) to take place in the plane of focus were considered for the analysis.

High-speed videos were processed in DaVis 8.3 (LaVision), where fish were first automatically masked and fluid velocity fields (64 x 64 velocity vectors) were subsequently obtained using cross-correlation. We further used the algorithm provided by the Queen 2.0 software [6] running in MATLAB to compute the pressure fields.

In addition, midlines were manually tracked in every 10-th frame and interpolated in between. Finally, amplitudes of pressure forces were computed along 500 equally spaced points along the body outline based on the nearest computed pressure values [7] (corresponding directions were defined to be normal to the body outline assuming predominately pressure forces opposed to shear stresses). The body was further divided into 10 equal-length segments and for each segment the forces along the body outline were integrated to obtain a resulting force for each segment.

3 Preliminary results

We present our preliminary results here on the basis of the representative example shown in Figure 1. The Reynolds number in this particular example was $Re = 1351$ (body length: 19.1 mm, head speed: 70.1 mm/s). Zebrafish swam in a burst-and-coast manner characterized by straight body postures at the beginning and end of a turn. We determined turning angle by measuring the angle between start and end position. In our initial experiments we observed a large range of angles from small turns of around $30°$ up to turns of $180°$. For convenience we define the *turn-side* as the side of the body in the direction of the turn and the *opposing-side* as the side of the body away from the turning direction. In many of our initial experiments we made the following observations: In the first phase of the turn (Fig.1F) the mid-section of the body is bent. As a consequence water flows towards the body at the turn-side, which is also indicated by a corresponding negative pressure region. In the second
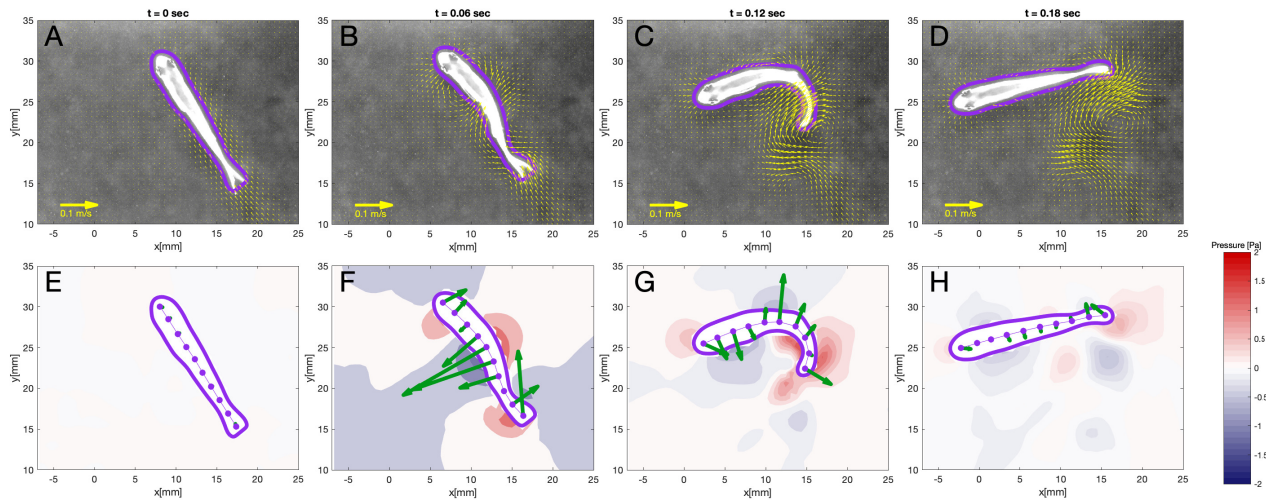
Figure 1: Consecutive velocity fields (**A-D**) of a representative example zebrafish turning maneuver. The yellow vectors show the fluid velocity at different grid points, whereas the purple line indicates the body outline. (**E-H**) show the corresponding computed pressure fields. The interconnected purple dots indicate the body midline and the green arrows represent the resulting external forces exerted by the fluid on the body.

phase of the turn (Fig.1G) the head section is aligned with the final body direction, whereas mid and tail sections are moving towards a straight body position. Interestingly, we find that at this point a positive pressure region at the turn-side has built up, indicating that the fluid is exerting positive work on the body (green arrows in Fig.1G corresponding with movement direction).

4 Discussion and future steps

Given the positive work exerted on the body by the fluid, there are two main possible implications for the internal dynamics of the body. One possibility is that the body is passively moved in the second phase of the turn, requiring little or no actuation from the musculature. A second possibility is that the body is actively resisting in this second phase, e.g. to prevent the caudal part of the body from overshooting the turn. Both cases could lead to a reduced muscle effort.
Furthermore, benefiting from the accelerated fluid pushing against the body in the second phase is predominantly determined by the first phase of the turn. A faster initial bending will lead to larger flows, however this also requires larger initial energy input. Therefore, we predict there is an optimal bending speed, duration and magnitude to execute an efficient turn, however computational models (e.g. [8]) will be required to address this prediction. This work directly improves understanding of efficient turning and could possibly be applied to undulatory swimming robots where exploiting negative work is useful for energy recovery.

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