Control of self-motion in dynamic fluids: fish do it differently from bees

Christine Scholtyssek, Marie Dacke, Ronald Kröger and Emily Baird

Vision Group, Department of Biology, Lund University, 22362 Lund, Sweden

To detect and avoid collisions, animals need to perceive and control the distance and the speed with which they are moving relative to obstacles. This is especially challenging for swimming and flying animals that must control movement in a dynamic fluid without reference from physical contact to the ground. Flying animals primarily rely on optic flow to control flight speed and distance to obstacles. Here, we investigate whether swimming animals use similar strategies for self-motion control to flying animals by directly comparing the trajectories of zebrafish (Danio rerio) and bumblebees (Bombus terrestris) moving through the same experimental tunnel. While moving through the tunnel, black and white patterns produced (i) strong horizontal optic flow cues on both walls, (ii) weak horizontal optic flow cues on both walls and (iii) strong optic flow cues on one wall and weak optic flow cues on the other. We find that the mean speed of zebrafish does not depend on the amount of optic flow perceived from the walls. We further show that zebrafish, unlike bumblebees, move closer to the wall that provides the strongest visual feedback. This unexpected preference for strong optic flow cues may reflect an adaptation for self-motion control in water or in environments where visibility is limited.

1. Introduction

To move safely through the environment, animals need to detect potential collisions, perceive and control the distance to nearby obstacles and control the speed with which they are moving relative to these obstacles. This is especially challenging for swimming and flying animals that must control their movement in a dynamic fluid, where measurements of thrust or the speed of air/water movements do not provide reliable information about the speed of self-motion relative to nearby obstacles.

To overcome these challenges, flying animals gain information about self-motion from translational optic flow—the pattern of apparent visual motion that results from moving past objects in the environment. The closer the animal is to a surface and/or the faster it moves, the higher the perceived rate of optic flow. Drosophila, bees and budgerigars use this relationship to control their flight speed by keeping the perceived rate of translational optic flow constant [1–5]. Thus, when flying through cluttered environments, where objects are close and the risk of collision is high, they fly slower than they do in open environments. Furthermore, insects and birds use translational optic flow for collision avoidance; when negotiating a narrow corridor, they fly along its midline, keeping a maximal distance to the nearby surfaces by balancing the rate of optic flow in both eyes [2,4–6].

The use of optic flow to control speed and avoid obstacles thus appears to have evolved as a general mechanism in flying animals as diverse as insects and birds. Do swimming animals, that face similar problems of controlling self-motion in a dynamic fluid, use optic flow in the same way as flying animals? Here, we aim to answer this by testing the hypothesis that zebrafish (Danio rerio) use optic flow to control their self-motion. To investigate whether there are different solutions...
for controlling self-motion in water and air, we also present bumblebees \( \text{Bombus terrestris} \) with exactly the same experimental conditions (in air). This allows us to perform a detailed and direct comparison between swimmers and flyers.

## 2. Material and methods

### (a) Animals

Six 2–3 cm long adult zebrafish (individually identified by their fin patterns) were kept in a 60 l freshwater tank at 26°C under a 12 h light–dark cycle. Bumblebee hives (Koppert UK) were placed in a 17.5 m² flight cage and kept at 25°C under a 12 h light–dark cycle. Trained bees were individually marked with plates glued to their thorax.

### (b) Experimental set-up

The experimental set-up consisted of a 60 cm long, 45 cm high, 16 cm wide tunnel, with circular entrances at each end (figure 1c,d and the electronic supplementary material, figure S1). The tunnel walls were lined with black and white patterns that provided either strong or weak translational optic flow cues (vertical or horizontal stripes, respectively). The spatial frequency was 0.1 cycles degree\(^{-1}\) as seen from the centre of the tunnel. This spatial frequency is above the resolution threshold of zebrafish and bumblebees [7,8]. Three different conditions were tested: (i) vertical stripes on both walls (vert/vert), (ii) horizontal stripes on both walls and (hor/hor) and (iii) vertical stripes on one wall and horizontal stripes on the other (hor/vert, vert/hor; figure 1). The fish were additionally tested with horizontal stripes on one wall and either vertical stripes with 0.05 cycles degree\(^{-1}\) or random chequerboard patterns on the other wall (figure 2). Swim/flight trajectories were filmed at 50 frames s\(^{-1}\) using an overhead camera (Sony HDR-CX730).

For the fish, a holding area was connected to each tunnel end, and the set-up was placed in a 200 dm² glass tank with a water depth of 20 cm. See the electronic supplementary material section for a detailed description of the experimental set-up.

### (c) Procedures

Three pairs of zebrafish (groups 1–3) were trained to swim through the tunnel to receive food rewards. Before testing, they were placed in one of the holding areas. After 3 min of habituation, the entrance to the tunnel was opened and recording started. The fish received food exclusively during testing which was performed every second day. The experimental conditions were tested successively. When each pair of fish completed 40 swims per condition (120 swims per condition in total), the next condition was tested. Flights of bumblebees were recorded over 2 h periods with all three conditions presented daily in a randomized order. In total, 39 bees completed 60 flights per condition.

Swim/flight trajectories were included in the analysis only if the individuals had no visual access to conspecifics, maintained a forward trajectory and did not change height significantly.

Trajectories were analysed over the mid 40 cm of the tunnel. Velocity was calculated as the average of the ratio of the distance travelled between successive frames and the time step between the frames. Position was calculated by finding the average lateral distance from the midline of the tunnel.

We used R [9] and lme4 to perform linear-mixed-effects analysis of the relationship between the optic flow condition and the lateral position in the tunnel or the movement velocity. We added condition as a fixed effect and individual (bees) or group (fish) as random effects. We had intercepts for individuals (bees) or groups (fish) as well as by individual or by group random slopes. \( p \)-Values were obtained by likelihood-ratio tests of the full model against a model without condition as an effect.

## 3. Results and discussion

### (a) Speed

Figure 1a,b compares the distribution and the means of the velocities of zebrafish and bumblebees under the three different experimental conditions. The swimming velocity of zebrafish was not affected by the amount of visual feedback they obtained from the tunnel walls (\( \chi^2 = 2.5173, p = 0.28 \)). By contrast, the flight velocities of bumblebees were lowest when the amount of visual feedback in the horizontal plane was highest (vert/vert), increased when the visual feedback on one wall was reduced (vert/hor, hor/vert; effect size = 12.5 cm s\(^{-1}\), \( \chi^2 = 25.223, p < 0.0001 \)) and increased even further when the amount of visual feedback was reduced on both tunnel walls (hor/hor; effect size = 8.22 cm s\(^{-1}\), \( \chi^2 = 19.961, p < 0.0001 \)). The overall lack of a correlation between swimming velocity and amount of visual feedback in the zebrafish suggests that fish—unlike insects [1,3,4]—do not control speed by keeping the angular velocity of the translational optic flow in the lateral visual field constant, at least not under the given experimental conditions. How then could fish control their swimming speed?

In still water, fish could use hydrodynamic information obtained via their superficial neuromasts to determine their velocity [10]. The findings that the swimming behaviour in steady flows and still water is not altered when the lateral line is blocked and when high contrast visual stimuli are present [11,12] do, however, argue for a visual control mechanism of swim speed in sighted fish. Furthermore, hydrodynamic perception of speed is inhibited by the presence of currents [13,14], leaving vision as the only sense available for estimating ground speed. The missing correlation between the amount of visual feedback and the swimming velocities in zebrafish does not necessarily exclude the use of optic flow for speed control. It is possible, for example, that zebrafish measure the angular velocity of optic flow to monitor their momentary speed, rather than to adjust swimming speed to match a fixed angular velocity of optic flow.

### (b) Centring

Figure 1c–f compares the position of zebrafish and bumblebees relative to the midline of the tunnel. When optic flow cues on both walls of the tunnel were strong (vert/vert), the zebrafish tended to swim closer to one of the two walls, which is reflected in the broad distribution of the mean positions (figure 1c). In the same condition, the bees instead flew along the midline of the tunnel (balancing the rate of optic flow in both eyes [2]; figure 1f). When we reduced the amount of visual feedback on both walls (hor/hor), the zebrafish tended to swim closer to the midline, unlike the bees, which failed to centre accurately in this condition. When we created an imbalance in the optic flow (hor/vert, vert/hor), zebrafish had a strong tendency to swim closer to the wall that provided stronger visual feedback (effect size = 3.51 cm, \( \chi^2 = 14.20, p < 0.001 \), figure 1c,e), whereas the bumblebees (in an attempt to balance the rate of optic
flow in both eyes [6]) flew further away from this wall (effect size = 6.32 cm, $\chi^2 = 78.36$, $p < 0.0001$, figure 1d,f). When we substituted the vertical stripes with random chequerboard patterns or when we doubled the width of the vertical stripes (thereby changing the spatio-temporal properties of the patterns but not the apparent rate of optic flow they generated), the fish continued to swim closer to the wall that provided them with the stronger visual feedback (checks: effect size = 2.29, $\chi^2 = 6.1$, $p < 0.05$; vertical stripes: effect size = 2.64, $\chi^2 = 11.764$, $p < 0.001$, figure 2). This result suggests that zebrafish reacted to manipulations of the apparent rate of optic flow (rather than the spatio-temporal frequency of the patterns), but in the opposite way to flying insects.

What may be the advantage of a preference for strong optic flow cues when controlling self-motion? Underwater, visibility is much more restricted than in air owing to floating particles that absorb and scatter light. Zebrafish live in waters
behaviours when deprived of visual feedback [16]. Because fish are buoyant and can stop abruptly without facing the danger of gravitational acceleration, the strategy of staying close to surfaces that provide strong visual feedback is less dangerous than it would be for bees. The preference for strong optic flow cues in zebrafish may thus reflect an adaptation to control self-motion underwater where visibility is limited, and the consequences of collisions are less severe than for flying animals. This will be tested by investigating whether fish that inhabit clear waters react differently to manipulations in the visual feedback than zebrafish.

4. Summary

Swimmers and fliers share the problem of controlling movement in a dynamic fluid, but when cruising through the same experimental set-up (in water and air), they do not apply the same strategy for visual self-motion control. We found that zebrafish, unlike bumblebees, do not control their velocity by keeping the rate of optic flow constant and that they do not balance the rate of optic flow perceived in both eyes. Instead, they swim closer to features that provide them with strong visual cues. This unexpected preference for strong optic flow cues may reflect an adaptation for self-motion control in water or in environments where visibility is limited.

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References


