

Constraints and learning in the visuo-motor system of *Drosophila*: Inspiration for flight control in micro-air vehicles

1. Introduction

The most challenging aspect for designers of biologically inspired micro-air vehicles (MAVs) is the limitations in payload. In order to achieve a maximum weight of around 10 g including actuators and sensors, we cannot rely only on learning from the kinematics and morphology of insects, but we must also incorporate aspects of their integration of control strategy and kinematic parameters. Most current MAV designs rely on two separate mechanisms for generating thrust (flapping wing-like structures) and yaw torque (usually done by conventional rudder-like structures), whereas insects generate both yaw, pitch and thrust by using the wings. A pre-requisite for a successful future MAV design is therefore the incorporation of the ability to modulate the kinematic parameters of the left and the right wing independently. However, in order to realise such goals we first need to know more about in which ways the fine control of yaw torque, generated mainly by differences in stroke amplitude, is limited by the visual input and motor output in insects. A further interesting aspect of yaw torque control in insects is to what degree the insect has an internal representation of the relationship between its motor output and the resulting yaw, such that it is able to predict how much motor output it needs to generate to turn a certain amount and how this internal representation is affected by previous flight experiences.

To simulate the physical conditions during free flight we developed a physics engine, where we can iteratively solve for the current angular velocity of the visual pattern based on the previous angular velocity, the inertia, the frictional damping coefficient and the current difference in stroke amplitude. This physics engine formed the basis on an analytical model to determine the frictional damping coefficient of the fly under natural conditions. Earlier estimates of the frictional damping coefficient from the literature ignored effects from the wings. In our model where we include the wings we found an approximately 100 times higher damping coefficient. Thus indicating that flight in the small fruit flies might not be inertia driven, as previously thought, but be friction driven. This means that during a saccade - a rapid turning of 90 in 50 ms (Fry et al., 2003) the fly might not need to actively break but can instead rely on damping to stop the turn.

The goal of our study is to investigate aspects of sensitivity and learning in the visuomotor system of insects in order to provide data which can be of use in the development of control systems for biomimetic micro-air vehicles.

3. Results: Visuo-motor constraints

Our numerical modeling, based on body dynamics (mass moments of inertia, body friction) and the properties of the visual system, implies that visually controlled maneuvers in the small fruit fly *Drosophila* require extraordinary fine adjustments in muscle forces and thus wing kinematics within a narrow range of less than 0.25–0.75° stroke amplitude or 1–3% of the animal's total steering capacity. The precision in muscle control required to achieve stable flight thereby predominantly depends on factors that determine the friction on the flapping wings such as wing size, flapping speed or the angle of attack. In *Drosophila*, frictional damping (coefficient = 42 to 84 $\times 10^{-12}$ Nms) is a prominent force during turning that outpaces the fly's inertia approximately 80 to 160-fold. Since wing drag limits maximum turning rate in flight, it acts as a passive brake that helps to stabilize an airborne animal.

Experimental data on tethered *Drosophila* flying in a visual-feedback flight simulator show that the fruit fly can barely stabilize the azimuth motion of a moving target under natural feedback conditions, by adjusting its stroke amplitude-mediated torque for turning (Fig. 3A). Stabilization of the visual environment can be restored, however, when artificially adding passive stability to the animal by increasing simulated body friction above the natural value. During target-orientated flight, fruit flies consistently keep the mean azimuth velocity of the visual environment within the range of the visual system for motion detection ($226 \pm 110^\circ \text{ s}^{-1}$, mean $\pm \text{S.E.}$), suggesting that the motor system adjusts its steering precision to the visual input. Consequently, the break in visually mediated flight control at conditions mimicking free flight, might result from the failure of the muscle system to gradually reduce the stroke amplitudes below a critical value of approximately 0.5° (Fig. 3B).

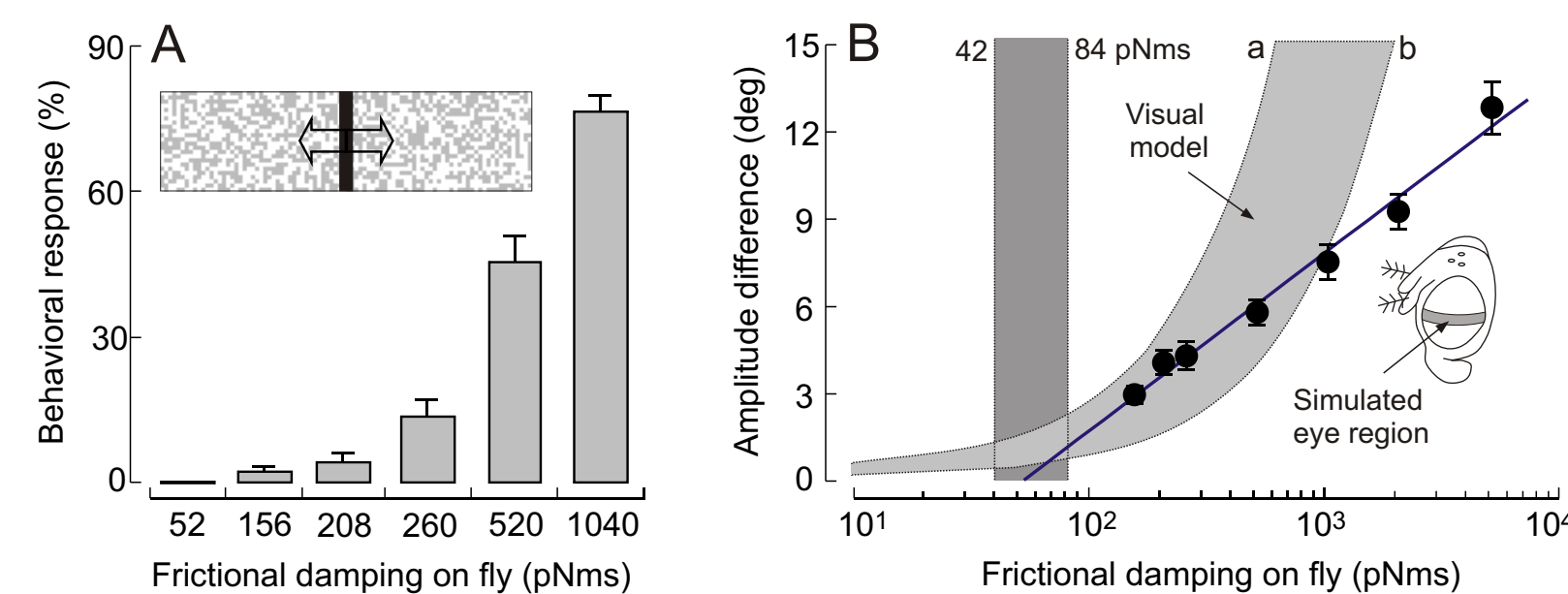


Fig. 3. In a closed-loop flight simulator (5), the tethered fruit fly *Drosophila melanogaster* actively tracks a visual object (12° wide black stripe) on a 360° wide random dot grey background (inset) by changing its torque around the vertical body axis. The velocity of the visual object was modulated by a sinusoidal velocity bias (24° s⁻¹). **(A)** Relative temporal occurrence of object-orientated behavior at which the flies continuously maintained the visual object for at least 1 s in the frontal ±45° region of their compound eyes. **(B)** While stabilizing the visual object, fruit flies adjust their torque according to the simulated body friction by changing the relative difference in stroke amplitude between both wings (black; linear regression fit, $y = 6.1 \log(x) - 10$, $R^2 = 0.98$, $P < 0.0001$, $N = 7$, blue). The light shaded area indicates the upper limit for visual motion detection (±125° s⁻¹), ±390° s⁻¹ [16], 4) which permits the animal to visually control the tracked object (4). Dark shaded area indicates expected body friction during free flight. Simulated mass moment of inertia in *Drosophila* = 0.52×10^{-10} Nms² (3), data sampling period = 16 ms, duration of flight sequences = 45 s; $N = 25$; means ± S.E. Inset in B shows compound eye region used for numerical modeling (4).

4. Results: Visuo-motor learning

Tethered flies in a flight arena readily show stripe fixation in the flight arena during closed-loop (Fig. 3A). However, in open-loop situations flies also attempt to turn towards the stripe. The differences in stroke amplitude between the wings employed by the flies depend on the position of the stripe (Fig. 4; Heisenberg and Wolf, 1984). This indicates that flies have an internal representation of how much torque they need to develop to turn to a certain position. If so this internal representation must be affected by the inertia and the damping of the fly and should be updated if these values change due to increases in weight (egg development by gravid females) or damage to one or both of the wings.

Here we investigate if fruit flies update their internal representation when exposed to different frictional damping coefficient. Our results indicate that flies do change their open-loop response depending on the damping coefficient exposed to in a previous closed-loop situation (Fig. 5A). The flies seem to employ a higher torque (i.e. response amplitude) at higher frictional damping (Fig. 5B).

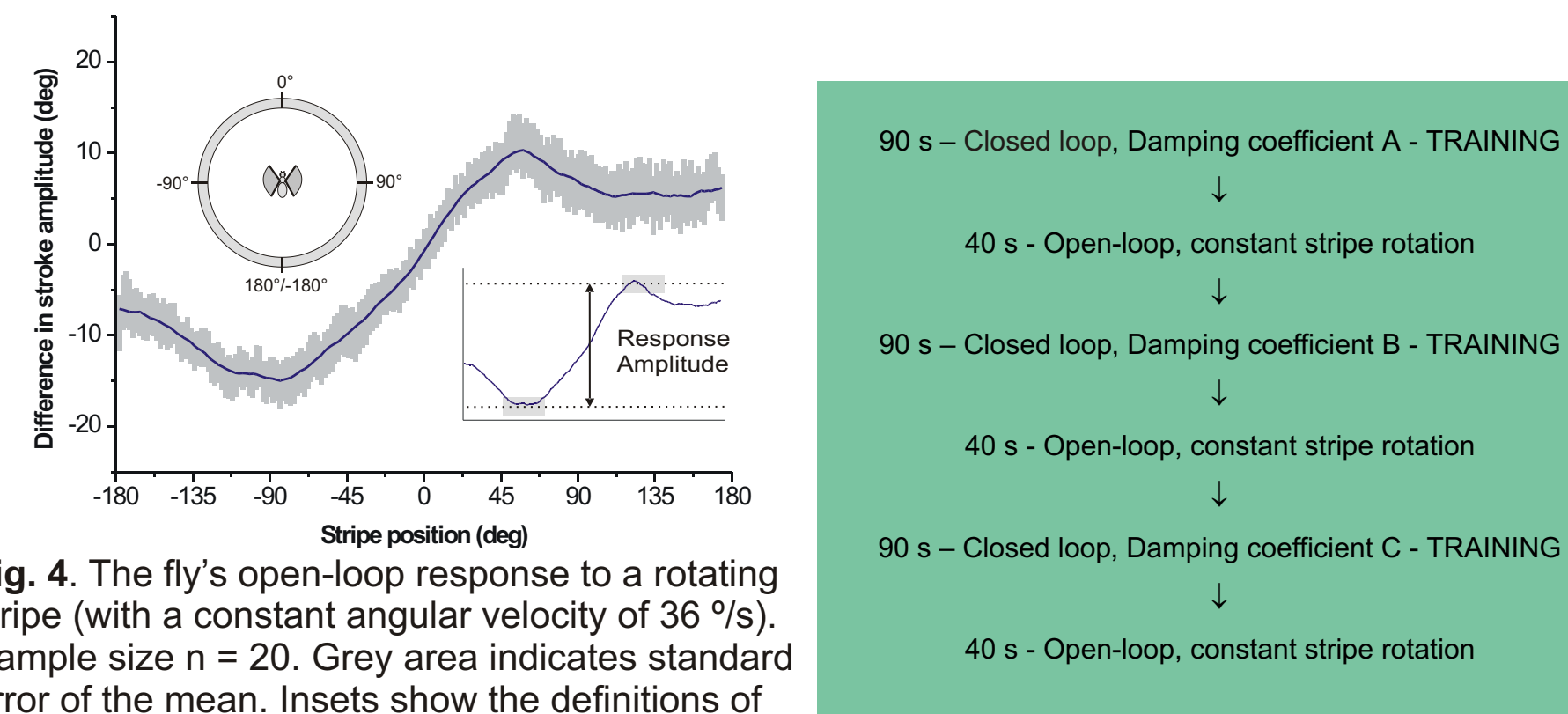


Fig. 4. The fly's open-loop response to a rotating stripe (with a constant angular velocity of 36 °/s). Sample size $n = 20$. Grey area indicates standard error of the mean. Insets show the definitions of stripe position and response amplitude.

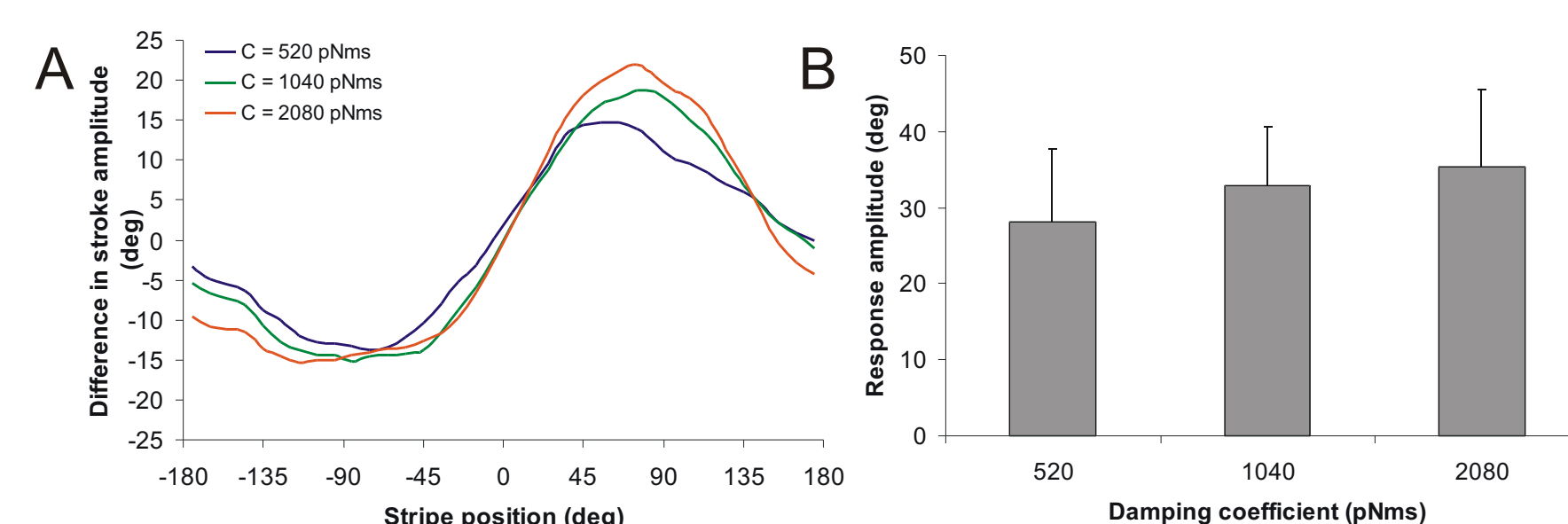


Fig. 5. Visuo-motor learning in *Drosophila melanogaster*. Each fly flies for a total of 390 s and experiences three closed-loop training sequences of 90 s, where it is exposed to a frictional damping coefficient of either 520 pNms, 1040 pNms or 2080 pNms in random order. (A) The fly's open-loop response to a rotating stripe (with a constant angular velocity of 36 °/s). Sample size n = 6. (B). The mean response amplitude at the three frictional damping coefficients. Error bars indicate the standard error of the mean.

5. Results: Learning and experience

To investigate if naive flies, without any prior flight experience, learns better than experienced flies we used naive flies kept in a rearing chamber (Fig. 6). However, our results do not indicate that naive flies are better learners. Small differences in response, however, was found (Fig. 7A) although the difference from before and after training showed no clear trend (Fig. 7B). Interestingly, they seemed to be no difference in the initial internal representation between experienced and naive flies (Fig. 8).

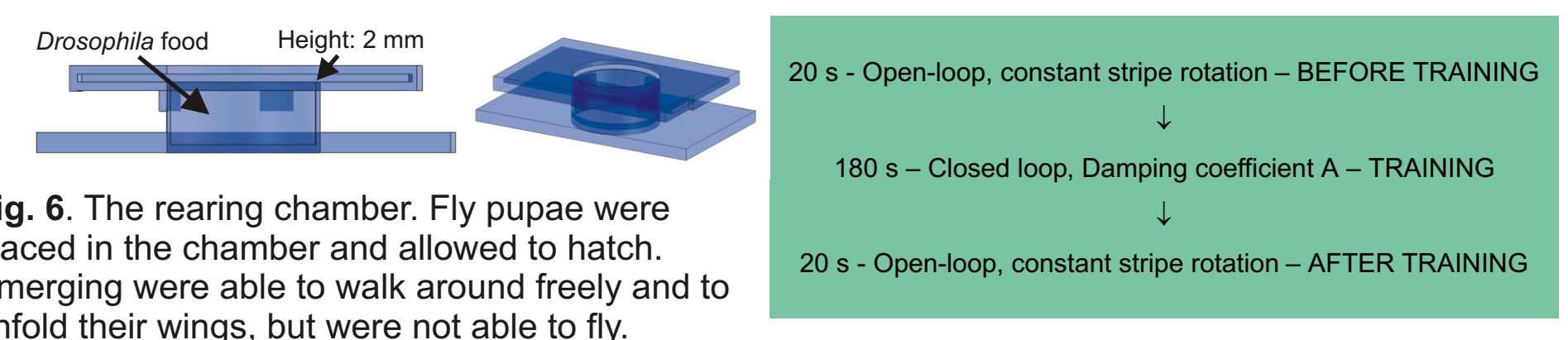


Fig. 6. The rearing chamber. Fly pupae were placed in the chamber and allowed to hatch. Emerging were able to walk around freely and to unfold their wings, but were not able to fly.

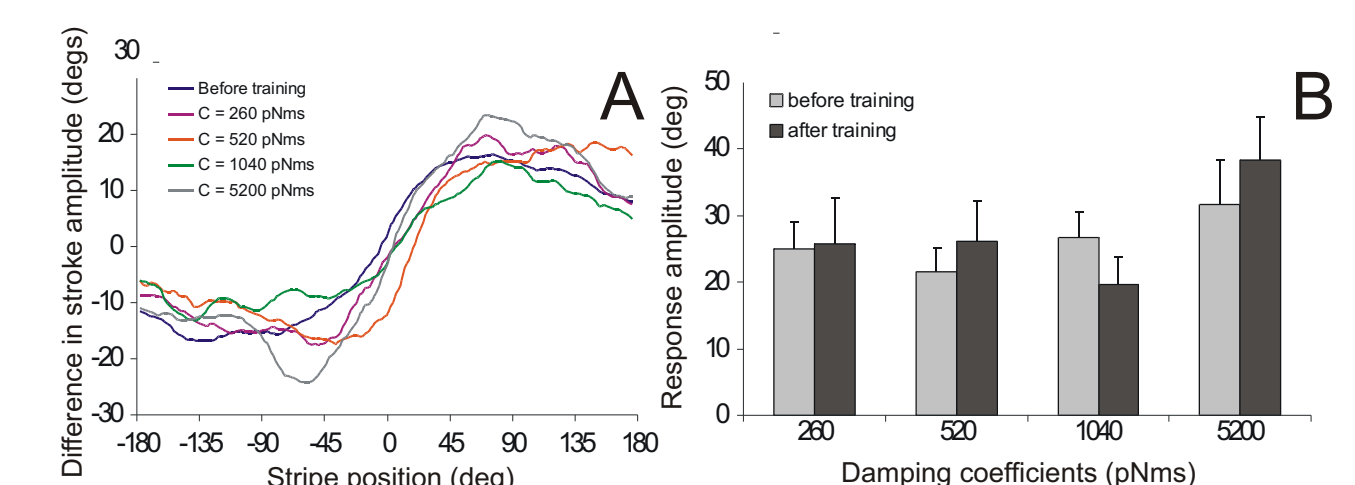


Fig. 7. Visuo-motor learning in naive *Drosophila melanogaster*. Each fly flies for a total of 220 s and is exposed to a frictional damping coefficient of either 260 pNms, 520 pNms, 1040 pNms or 5200 pNms. (A) The fly's open-loop response to a rotating stripe (with a constant angular velocity of 36 °/s). Sample size $n = 5$. (B) The mean response amplitude at the four frictional damping coefficients before and after training. Error bars indicate the standard error of the mean.

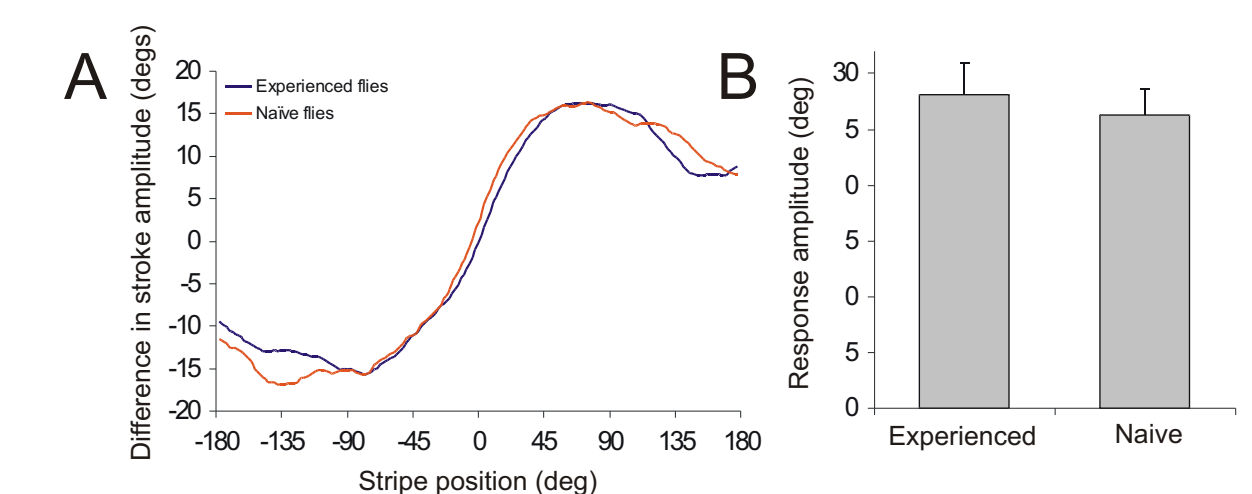


Fig. 8. The internal representation of the visuo-motor system in naive and experienced flies. (A) The fly's open-loop response to a rotating stripe (with a constant angular velocity of 36°/s). Sample size is $n = 19$ for the experienced flies and $n = 20$ for the naive flies. (B) The mean response amplitude for naive and experienced flies. Error bars indicate the standard error of the mean.

6. Discussion

We found that fruit flies kinematic appears to be friction driven and our results indicate that the visuo-motor system limits the fine control of the wing stroke amplitude to around $\pm 1.5^\circ$ and that visual stabilisation of a stripe panorama is not possible at a natural damping coefficient. The inability of fruit flies to visually control their flight at a natural damping coefficient is likely to be due to constraints of the visuo-motor system. In free flight the haltere feedback probably improves the fine control by allowing either a higher spatial resolution of wing stroke amplitudes or a higher temporal resolution by decreasing the time lag in response time. This, however, raises the question of how non-dipteran flies manage to control their flight without the benefit of halteres. One explanation could be that all or most insects possess mechanosensory devices that work similar to the halteres of flies. A recent study found that the antennae of hawk moths vibrate and experience Coriolis forces during aerial manoeuvres and thus work as mechanosensors (Sane et al., 2007).

We found, furthermore, that flies have a pre-set internal representation between its motor output and its resultant yaw movement, but that there exists some plasticity in the system allowing the flies to modify their internal representation in response to changes in physical parameters. The internal representation, though, was the same for experienced and naive flies, indicating that the initial value of the internal representation is either genetically determined or based on an assessment of the fly's morphological parameters such as weight, length and wing size.

In relation to the design of MAVs, then depending on the size criteria the MAV should be designed in such a way to make use of friction driven flight aerodynamics. This can reduce the need for breaking during turning and thus minimise the need for active control. The first part also offers a warning to the designers of MAVs. If flapping wings should be used in future MAVs both as a thrust and a yaw torque generators, then it is necessary to include very fine control mechanisms. Even small changes between the two wings in the difference of stroke amplitude and in other force generating parameters (angle of attack, flip start and flip duration) can result in large yaw forces. However, our study show that vision can be an adequate control strategy giving that good enough fine control of the actuators can be implemented. The learning experiments suggest that it would be advantageous to equip the robot with a pre-programmed knowledge of how its owns actuator output is related to actual steering movement, and that some kind of plasticity should be incorporated, where the robot can update its knowledge in different flight conditions or if it gets damaged. However, more detailed studies are needed on the control strategies found in flying insects in addition to numerical modelling of these strategies before an optimal control strategy for MAVs can be developed.

The study reminds us that when getting inspiration from nature, we cannot only focus on one aspect such as morphology or control, instead we need to integrate the control

References

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