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Stabilizing gaze in flying blowflies

When the gaze is moved quickly, vision becomes blurred and the way in which three-dimensional structures are seen can be affected¹. How can these effects be minimized? During flight, blowflies (*Calliphora vicina*) turn both the head and the thorax very quickly, producing gaze shifts which affect vision. Here we show that blowflies reduce the effects of thorax movements on vision by moving the head later, and more quickly, than the thorax. This reduces the time in which gaze is shifting relative to the surroundings, and maximizes the time available for analysing the surroundings.

Gaze shifts present a challenge to vision for at least two reasons. First, it takes time for optic signals to be integrated by the photoreceptors in the eye. If the gaze is shifted, this integration time will result in a blurred image being produced, particularly during fast gaze shifts. Second, the resulting rotational flow of optic signals will interfere with the pattern of optic flow that normally reveals the three-dimensional structure of the surroundings during linear motion¹.

Blowflies can move their two compound eyes by moving the head^{2,3}. The head, which is connected to the thorax by a neck, has appreciable freedom of movement under muscular control^{4,5}. We measured the position and orientation of thorax and head during (almost) free flight by using a modified search coil technique⁶. The thorax usually changes course through a series of short, fast turns⁷, with gradual course

changes occurring less frequently. The head usually turns in synchrony with the thorax but at a higher angular speed (Fig. 1a), with a pattern similar to that of fast eye movements in vertebrates⁸.

The average angles of yaws and rolls (Fig. 1b) during head–thorax turns of 10–20 degrees to the left (the most common yaw angle; turns of other angles follow similar time courses) are shown in Fig. 1c,d. A turn starts with a rotation of the thorax. The thorax yaw (Fig. 1c) is not immediately accompanied by a head yaw relative to the surroundings, as it is first compensated by a rotation of the head in the opposite direction relative to the thorax. After about 10 milliseconds, the head starts to rotate in the same direction as the thorax. It reaches its highest yaw velocity relative to the thorax at about the same time as the thorax reaches its highest yaw velocity relative to the surroundings. When the head approaches its final orientation relative to the surroundings, it decelerates, and finally rotates in the opposite direction to the thorax. The result is a stabilized yaw of the head roughly 10 milliseconds before the thorax rotation is finished. As a result of the shortening of the head turn compared with the thorax turn, the period of blurred vision during course changes is reduced by roughly one-third.

Like aeroplanes, flies usually make banked turns⁷, in which large changes in yaw are accompanied by large rolls of the thorax. The head can partly correct the visual consequences of this by performing a counter roll⁹ (Fig. 1d). The residual roll movement of the head relative to the surroundings is small (typically less than 5 degrees). Rotations in the pitch direction (not shown) are also usually small.

We can deduce the visual consequences of coupled thorax and head turns from Fig. 2. We divided the total flight time into episodes during turns and episodes between turns. During turns, the yaw velocity of the head is higher than that of the thorax (Fig. 2a). As the photoreceptor integration time for the light level during the measurements was roughly 10 milliseconds,

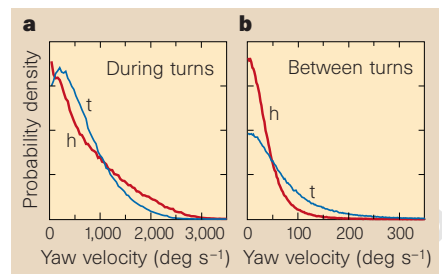


Figure 2 Gaze stabilization between turns. **a**, Probability densities of yaw velocities during turns, showing that yaw velocities of the head (h) reach higher values than those of the thorax (t). Total flight time was 703 seconds by four flies, during which time 6,697 turns were made. **b**, Between turns, yaw velocities of the head are significantly lower than those of the thorax, and both are much lower than during turns. More detailed figure legends are available as Supplementary information.

and the angular resolution of the photoreceptors is 1–2 degrees, angular velocities higher than 100–200 degrees per second will cause significant blur in the fly’s visual system. The high angular velocity of the head during turns therefore makes it impossible to see details. Between turns, however, the head is more stable than the thorax (Fig. 2b), mostly within a velocity range that gives little blur attributable to rotation.

The triphasic movement of the head in the yaw direction (Fig. 1c) probably acts to maximize the periods of stable gaze by minimizing the duration of the gaze shift. The extra angular velocity produced by the neck muscles is effective because it peaks at about the same time as the peak of the thorax angular velocity. The effective duration of the most common gaze shifts is not much longer than the integration time of the photoreceptor. Because at least one integration period is lost by making a gaze shift anyway, the roughly 1.5 integration periods lost during a typical blowfly turn seem to be a reasonable compromise between minimal visual impediment and very fast movement.

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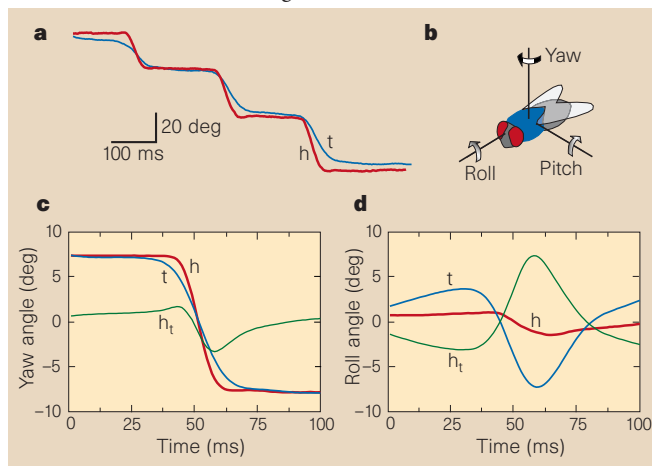


Figure 1 Turns in blowflies. **a**, Turns in the yaw direction of the thorax (t) are joined by faster turns of the head (h); angles relative to surroundings. **b**, Rotations have an ordered sequence of yaw, pitch and roll (Fick coordinate system¹⁰); signs comply with aeronautical conventions. **c**, **d**, Yaw or roll of thorax and head in turns of 10–20 degrees (average of 713 turns of 4 flies); h_t shows yaw or roll of head relative to thorax.

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