CONTROL OF HEAD PITCH IN DROSOPHILA DURING REST AND FLIGHT
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Introduction: Drosophila holds its body axis close to horizontal when walking on even ground (body pitch BP = 15°) or when flying fast (v = 1 m/s, BP = 20°). In hoverflight the body axis is held much steeper (v = 0 m/s, BP = 65°; David 1978).

However, under these conditions Drosophila pitches its head downwards (head pitch relative to the thorax: HP = -30.7°± 6.6° SD, N = 16, n = 160, tethered flight). This behaviour stabilizes a distinct orientation of the fly's head in space, and thus the proper alignment of its eyes with the visual surroundings.

Problem: How is this compensatory head pitch during flight elicited and controlled? Head posture was observed from the side by macro-videography under red illumination in different locomotor states of the flies, under various stimulations, and after surgical manipulation.

Results: (1) The downward head pitch is not due to a latching of the neck joint at rest (e.g. Mittelstaedt 1950) and its relaxation during flight, combined with the action of gravity on the head. In Drosophila head pitch is largely the same whether the fly is mounted upside up (HP = -25.3°± 7.3° SD, N = 14) or upside down (HP = -19.9°± 9.6°SD).

(2) Positive or negative stimulation of the fly's graviceptive system (Horn and Lang 1978) can be effected by holding the fly upside up or upside down while its clings to either a paper confetto of 0.5 x body weight or a styrofoam ball of 2.5 x body weight. None of these stimuli elicits a head pitch comparable to that in flight.

(3) Removal of tarsal contact which suspends a strong flight inhibition (Fraenkel 1932) is not sufficient to elicit the full downward head pitch if Drosophila does not actually fly (HP = -6.9°±5.3° SD, N = 16).

(4) Tethering Calliphora by its back elicits via the halteres an upward head pitch which vanishes after haltere amputation (G. Nalbach 1991). In contrast, Drosophila pitches its head, under similar conditions, in the opposite direction (HP = -25.3°± 7.3° SD, N = 14), and the response is largely insensitive to haltere amputation (HP = -19.5°± 9.6°SD).

(5) Flies measure air speed by their antennae (Gewecke 1967), and could control their head pitch accordingly. Surprisingly, however, amputation of both antennae (HP = -31.4°± 5.3°SD, N = 13) does not prevent the head pitch observed in the same flies before amputation (HP = -28.3°±5.0°SD, N = 13).

(6) Head posture could still be influenced by other wind-sensitive organs (e.g. WeisFogh 1949, Pflüger and Tautz 1982) which, however, have not yet been detected in flies. In resting and walking Drosophila laminar wind from ahead does not elicit a downward head pitch at wind speeds up to v = 1 m/s. Likewise, in flying Drosophila the downward head pitch, observed in still air, is not modified by wind up to v = 1 m/s. Apparently, wind has no influence on head posture.

Conclusion: The body axis of Drosophila is elevated more steeply during flight than during resting or walking on even ground. The resulting misalignment of the fly's eyes with the visual surroundings is prevented by a corresponding downward head pitch made during flight. This compensatory head movement is initiated endogeneously, and is overlaid by visual motion compensation described previously (Hengstenberg 1991).

SD = standard deviation, N = number of flies, 10 observations per fly.