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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.