Head Movements Mediated by Halteres in the Fly, *Musca domestica*

The halteres of flies are the only sense organs of equilibrium that make use of an oscillating mass[1]. It has been known for some time that flies use their halteres to stabilise flight. An angular rotation of the fly around any of the 3 body axes generates a torque at the base of the vibrating haltere; this stimulus is detected by campaniform sensilla, and evokes a compensatory postural change by altering the pitch of the wings during the downstroke[2]. This paper reports a new reflex mediated by the halteres: a compensatory rotation of the head on the neck when the fly experiences a rotation around its longitudinal axis. An analogous reflex is found in locusts, but it is visually mediated[3].

Materials and methods. Houseflies (*Musca domestica*) were rotated about their roll axis and photographed, so that the angle between the sagittal planes of head and body (head deviation) could be measured during the course of the rotation.

Sinusoidal oscillation: in order to show the dependence of head compensation on the halteres, flies were rocked back and forth, 50° on either side of the vertical, by a DC oscillating motor operating at 1.6 Hz. (Hankscraft, Reedsburg, Wisconsin). Such flies were photographed in a brightly lit room with a 16 mm movie camera at 16 frames/sec. This procedure was carried out 3 times for each fly: first, flying with halteres intact, second non-flying with halteres intact, finally flying with both halteres removed.

Constant rotation: in order to show the dependence of head compensation on angular velocity, flying flies were rotated at constant angular velocities of 1.5, 3.0, and 6.0 rotations/sec (rps). During the rotation, the fly was illuminated by a stroboscope flashing 6 times per rotation, and photographed with a motor driven 35 mm still camera. The importance of vision was tested by carrying out the experiment not only in the light (fly illuminated from above by a 40 W light bulb) but also in the dark, with no source of illumination apart from stroboscope flash. The importance of the halteres was tested again by carrying out the experiment before and after removal of the halteres.

Results and discussion. Sinusoidal oscillation: when the fly was flying with halteres intact, the amplitude of head movement was less than the amplitude of body movement by a factor of about two. There was no detectable phase lag between head deviation and body position (Figure 1A); the head of the fly was therefore stabilized. However, when the fly was not flying, or after both halteres had been removed, the head followed the body without compensation (Figures 1B and 1C).

Constant rotation: when the fly was flying with intact halteres, head deviation was proportional to angular velocity up to about 3 rotations/sec. Head deviation at this velocity was about 75° (Figures 2A, filled circles). Removal of the halteres eliminates most of this response (Figure 2A, open triangles). Similar experiments carried out in the dark show that these results are not dependent on visual information (Figure 2B).

There is therefore a reflex movement of the head of a fly which is mediated by the halteres, depends on angular velocity in the roll plane, and tends to stabilize head position (and hence the visual field) during flight. The fact that head deviation is proportional – within limits – to body angular velocity is to be expected, since the effective stimulus to the haltere is torque, itself proportional to angular velocity[1].

The function of the reflex may be seen as part of a visual control system for stabilising flight against deviations about the roll axis. Such a system is already suggested by Faust's[2] work, in which he showed that for roll movements (but not yaw or pitch), a fly without halteres still shows compensatory changes in wing pitch until it is blinded. I assume that the reflex effect of halteres on wing pitch is competent to stabilise flight against small deviations about the roll axis. Under these conditions, the visual field will also be stable and there will be no visual effect on wing pitch. But for large deviations, wing pitch compensation by the halteres may not be sufficient, the head will rotate about the roll axis, and apparent rotation of the visual field will produce a supplementary effect on wing pitch. This interpretation suggests the question: how important is stabilisation of the visual field of a fly? When compensatory head movements were prevented altogether by waxing the head to the body, such flies crashed immediately on release into a lighted room. Control flies flew perfectly well with wax on the thorax only.

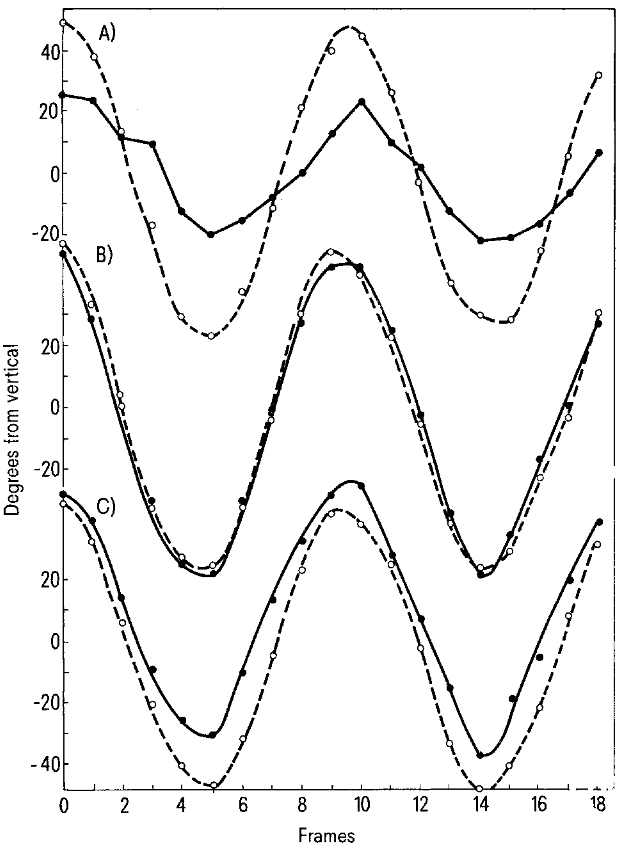

Fig. 1. Head and body angles during sinusoidal oscillation. A fly is rocked back and forth about its roll axis, 50° on either side of the vertical at a frequency of 1.6 Hz. Body angle (○) and head angle (●) are plotted against frame number in the filmed record. A) Flying with halteres intact; head movement has about half the amplitude of body movement. B) Fly prevented from flying by a paper ball between the tarsi; the head moves with the body. C) Flying with both halteres removed; the head moves with the body.

1 J. W. S. PRINGLE, Phil. Trans. R. Soc. B *233*, 347 (1948).
2 R. FAUST, Zool. Jb., Physiol., *63*, 325 (1952).
3 J. THORSON, Science *145*, 69 (1964).

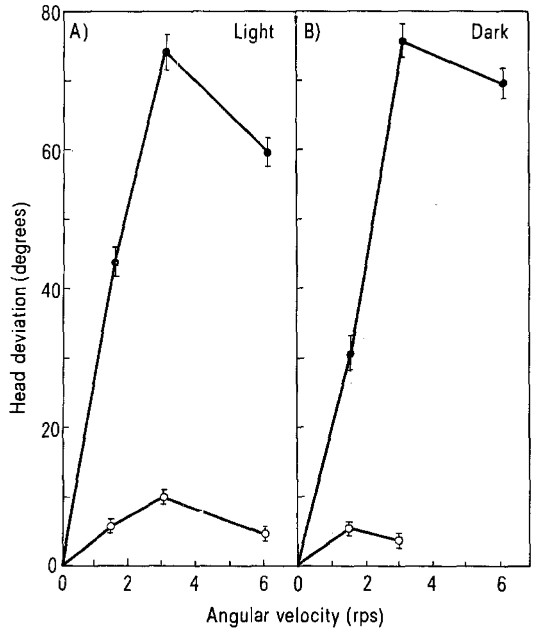

Fig. 2. Head deviation at different angular velocities. A fly is rotated at constant velocity about the roll axis. Mean head deviation (± SEM) is plotted against the flys angular velocity when the halteres are intact (●) and after they have been destroyed (○). Stroboscopic illumination. A) Additional constant illumination is provided by a 40-W light bulb 25 cm above the fly. B) No lighting other than stroboscope flashes.

There are some interesting analogies between this postural control system and that found in vertebrates. The halteres of flies and the semi-circular canals of vertebrates are analogous in detecting rotational movement. Indeed the response of both organs is proportional to angular velocity, although for quite different reasons[4]. In vertebrates, semi-circular canals have efferent control not only over postural muscles, but also over muscles stabilizing the visual field. A similar rôle has now been demonstrated for the halteres of flies[5].

Zusammenfassung. Ein bisher unbekannter, durch die Halteren ausgelöster Reflex wird für *Musca domestica* beschrieben: kompensatorische Kopfdrehung bei Rotation um die Längsachse während des Fluges.

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[4] G. Melvill Jones, Prog. Brain Res. *37*, 139 (1972).

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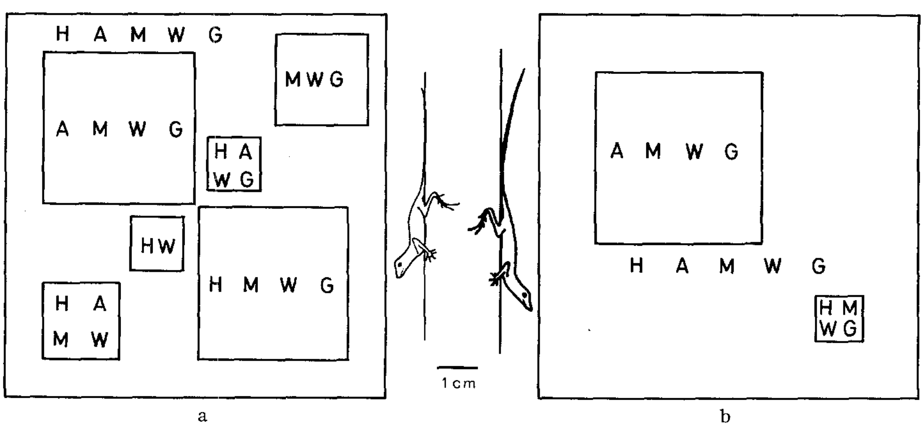
Die innerartliche Variabilität der Beutewahl beuteerfahrungsloser *Anolis*

Individuen einer polyphagen Tierpopulation können sich auf verschiedene Nahrung spezialisieren, und zwar auf zwei Weisen[1]. Modell a): «Spezialisten» nutzen im Grenzfall jeweils verschiedene, sich nur teilweise überschneidende Bereiche des Beutespektrums der ganzen Population. Modell b): Alle Individuen («Generalisten») der Population haben einen bestimmten Bereich des Beutespektrums gemeinsam, den sie jeweils verschieden weit überschreiten. Darüberhinaus sind vielfältige Kombinationen beider Modelle denkbar.

Die ausgeprägte individuelle Variabilität der Beutewahl auf Jamaika lebender *Anolis lineatopus* (Rept., Iguanidae)[2] wurde an Jungtieren auf Art und Zustandekommen untersucht. Frischgeschlüpfte fressen frühestens mit 3 Tagen, mit 5 Tagen tun es alle. Wir boten 75 vom Schlüpfen an gegeneinander sichtisolierten und beuteerfahrungslosen *Anolis* vom 5. Tag an 5 Beutetiertypen, nämlich Heimchenlarven (*Acheta domesticus*), Rollasseln (*Armadillidium spec.*), Mehlwürmer (*Tenebrio molitor*), Larven des Getreideschimmelkäfers (*Alphitobius diaperinus*) sowie Raupen der Grossen und Kleinen Wachsmotte (*Galleria melonella, Achroea grisella*) je 5 min lang, und

[1] P. H. Klopfer, *Ökologie und Verhalten* (Fischer, Stuttgart 1968).
[2] E. Curio, Z. Tierpsychol. *27*, 899 (1970).



Individuelle Variabilität der Annahme 5 verschiedener Beutearten bei jeweils beuteerfahrungslosen *Anolis lineatopus* (a) und ihre Veränderung nach 5 Wochen Fressen (b). Fläche der Quadrate proportional dem relativen Anteil des jeweiligen Verhaltenstyps; daneben *Anolis* zu den Versuchszeitpunkten. Annahme: H, Heimchen; A, Assel; M, Mehlwurm; W, Wachsraupe; G, Getreideschimmelkäferlarve.