

## Introduction

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Through evolution, animals have been adapted to enhance their survival and procreation. Because animals of different phyla developed visual systems, the sense of vision appears to be of vital importance. Across different species, visual systems help solving similar problems (such as finding food and mates, and avoiding predators), often leading to similar solutions. In the study of visual systems, one approach is to concentrate on animals with smaller and less complex brains, which are thus easier to investigate. The purpose then is to find some of the basic principles, which can subsequently be applied to the study of more complex visual systems and to the field of robotics. One such group of animals used for this purpose are the blowflies, which are much studied because they are easily available, their eyes and brain are accessible to electrophysiological experiments, and their brains are considerably less complex than that of human brains. The visual system of the blowfly is nevertheless able to solve complex problems with surprising efficiency and agility: these qualities can be admired when trying to catch a fly.

Visual systems are believed to be adapted to the processing of naturally occurring visual input (Atick, 1992; van Hateren, 1992b). An animal must move in its environment, and the movements of its body induce eye movements which determine the natural visual input. Movements of the eyes cause changes in the image projected onto the retina. When the angular velocity of this image exceeds a characteristic velocity, depending on the

spatial acuity and integration time of the photoreceptors, the movements of the eye cause motion blur and consequently image degradation (van Hateren, 1992a). The vector field of local movements of the visual stimulus, due to eye movements or moving objects in the environment, is named the “optic flow” field. The optic flow due to eye movements has a rotational and a translational component, caused by rotations and translations of the eye, respectively (Koenderink, 1986). The translational component of the optic flow can be used for the extraction of the three-dimensional structure of the environment, whereas the rotational component gives no information on this structure (Koenderink and van Doorn, 1987). Although it is possible to disentangle the rotational and translational components of a complex optic flow (Nagle *et al.*, 1997), most animals minimize the rotational optic flow already before the first stage of vision, by performing short and fast saccadic eye movements between periods of fixation, *i.e.*, steady gaze (Land, 1999). During fixation, the rotational component is kept to a minimum (less than the characteristic velocity), and during the saccade, the angular velocity is high only for a short time. Therefore, apart from the easier processing of translational flow, a further advantage of the strategy of saccadic eye movements is that the time of blurred vision is minimized. The saccadic eye movements must cause an important improvement of vision, because they are used by most animals from different phyla, from insects to primates (goldfish: Easter *et al.*, 1974; crab: Paul *et al.*, 1990; blowfly: Land, 1973; Schilstra and van Hateren, 1998b). For a review, see Land (1999).

Figure 1.1A presents a dorsal view of a blowfly. The eyes of the blowfly are fixed to the head, thus the visual input is determined by the head movements. The head is connected to the thorax through a flexible neck. The legs and wings, used in walking and flying, are attached to the thorax. The halteres, also attached to the thorax, are part of a sensory organ sensitive to rotation, and are essential for maintaining stabilization during flying (Nalbach, 1993). Figure 1.1B shows a head of a female *Calliphora vicina*. The visual input is received by the two compound eyes, which have each approximately 6000 ommatidia (Beersma *et al.*, 1977). The ommatidia point into different directions (Figure 1.2A), with the angles between two neighbouring ommatidia approximately 1.3 degrees (Land and Eckert, 1985). Each ommatidium contains a facet lens and eight photoreceptors arranged in a characteristic pattern: two photoreceptors (R7, R8) at the centre, with one on top of the other, and the other six (R1-R6) around them. The lens

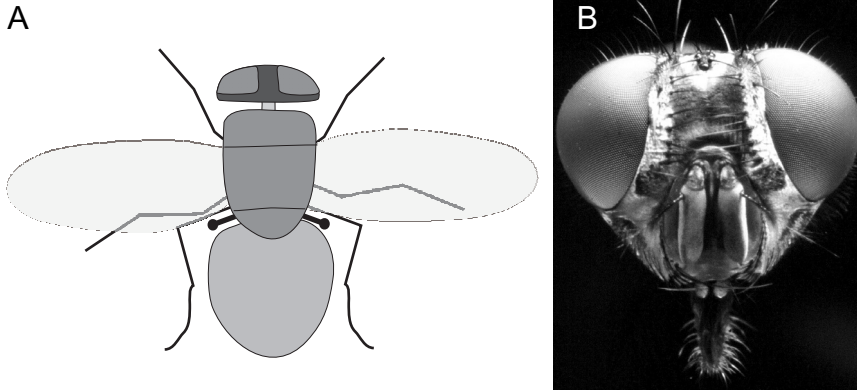


Figure 1.1. (A). Dorsal view of a blowfly. The eyes are part of the head. The head is attached to the thorax through a flexible neck. The six legs, the wings, the halteres and the abdomen are also attached to the thorax. (B). Front view of a female *Calliphora vicina*. Photograph courtesy of H.L. Leertouwer.

concentrates the incoming light on the photoreceptor cells, which detect the incoming light through phototransduction. The photoreceptor cells receive light from slightly different directions, and they are arranged in such a way that six photoreceptors (R1-R6) from six neighbouring ommatidia receive light from the same direction, and send their axons to the same large monopolar cells (LMCs) in the lamina (Hardie, 1985). The visual neurons are arranged retinotopically (*i.e.* in columns with similar structure, corresponding to the ommatidia) in different neuropils (lamina, medulla, lobula and lobula plate) (Figure 1.2B). A description of the organization and connections of the retinotopic neurons can be found, *e.g.*, in Douglass and Strausfeld (2003). An important group of visual interneurons (LPTCs, *i.e.* lobula plate tangential cells) is situated in the posterior part of the lobula plate. On each hemisphere there are approximately 60 LPTCs. Each of them has a specific combination of preferred direction (horizontal or vertical), response mode (graded, spiking or both), projection area (heterolateral or ipsilateral LPTCs) and spatial integration properties (review: Borst and

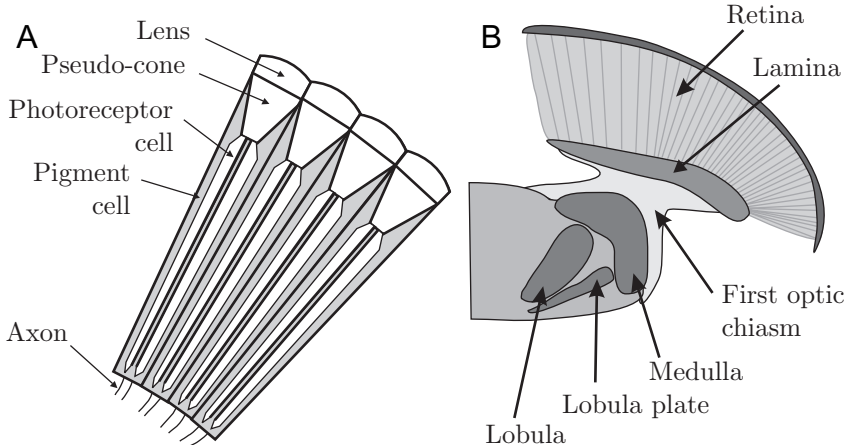


Figure 1.2. (A). Longitudinal section through several ommatidia. (B). Transversal section through the (right) compound eye and the optic lobes.

Haag, 2002). These neurons are believed to have an important role in the visual course control of the fly.

Usually, the visual system of the blowfly is studied without using a natural environment and without actual eye movements, because it is technically difficult to record the three-dimensional movements of the eyes with sufficient accuracy by using video systems. There is a different approach, allowing recording of movements with high accuracy, which has been used in the study of flying *Calliphora* (Schilstra and van Hateren, 1998a). Blowflies spend an important proportion of their time walking (Dethier, 1976), making it interesting to study the normal movements of the walking fly and its consequences for vision. Before the present study the movements of the eyes of walking flies have not been measured, and thus it was not known whether the eyes perform saccades during walking. We therefore extended the measurements on flying *Calliphora* to walking *Calliphora*, and to flying and walking *Lucilia*. As an example of a short walk, the arrows in Figure 1.3 show the position and orientation of the head of a fly with a 20 ms interval. It is interesting to note that the fly can walk sideways, that it keeps its

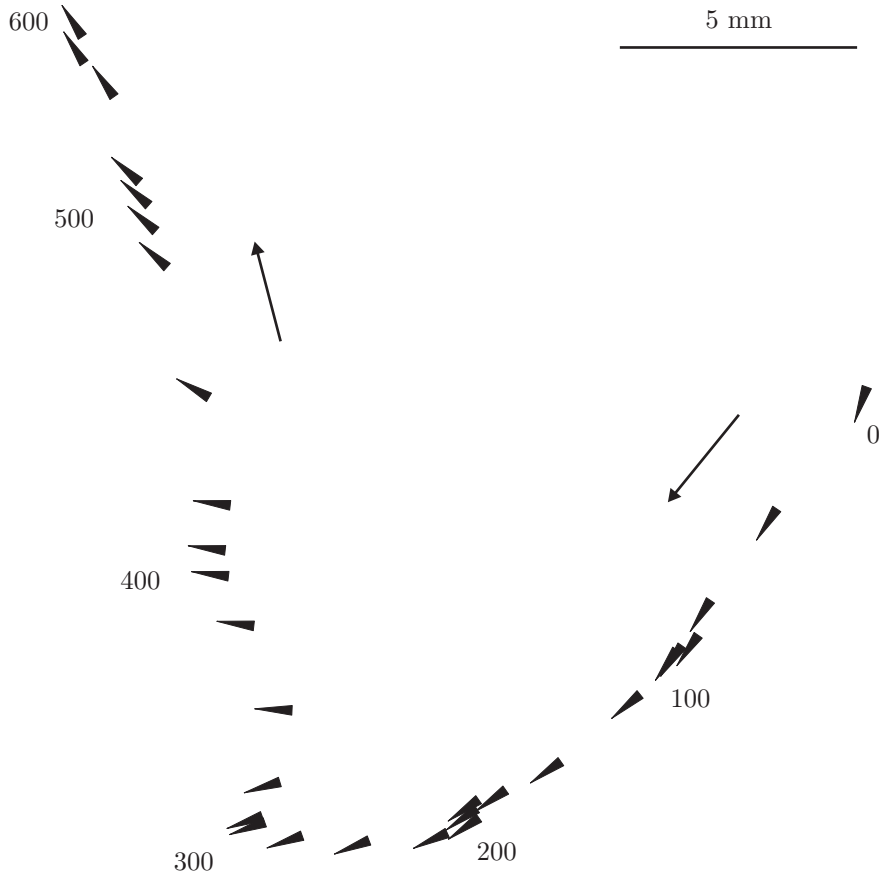


Figure 1.3. Example of walking. Each arrow head indicates the position and orientation of the head of the blowfly with an interval of 20 ms. The fly is walking into the direction of the long arrows. The numbers indicate the time elapsed from the first position, in milliseconds. The walking trace is complex, inviting a deeper study.

walking velocity approximately constant, and that the orientation of the head is constant for short intervals (about 100 ms), thus groups of nearby arrows have the same orientation. For a short time, right after 300 ms from start, the fly even walks backwards. The walking behaviour is thus by no means simple, and it will be further investigated in this thesis.

## Outline of the thesis

Chapter 2 describes in detail the method that was used for measuring, with high accuracy, the orientation and position of the head and thorax of walking and flying insects. Several improvements of the existing experimental procedure are presented.

Chapter 3 presents measurements of the thorax of walking blowflies. The orientation of the thorax is often very different from the direction of walking. The orientation and position changes of the thorax are saccadic, and the orientation saccade leads on average the position saccade. For turning, the blowflies use several different, characteristic manoeuvres.

In Chapter 4, the movements of head and thorax of walking and flying blowflies were measured. The head partly compensates the thorax rotations. Both head and thorax are shown to perform saccades during walking, and the saccades of the head are faster than the saccades of the thorax. The walking and flying behaviours of *Calliphora* and *Lucilia* are compared.

## References

- Atick, J.J. (1992). Could information theory provide an ecological theory of sensory processing? *Network* 3, 213-251.
- Beersma, D.G.M., Stavenga, D.G., and Kuiper, J.W. (1977). Retinal lattice, visual field, and binocularities in flies. *J. Comp. Physiol.* 119, 207-220.
- Borst, A., and Haag, J. (2002). Neural networks in the cockpit of the fly. *J. Comp. Physiol. A* 188, 419-437.

- Dethier, V.G. (1976). The hungry fly. A physiological study of the behaviour associated with feeding. Cambridge, MA: Harvard University Press.
- Douglass, J.K., and Strausfeld, N.J. (2003). Anatomical organization of retinotopic motion-sensitive pathways in the optic lobes of flies. *Microsc. Res. Tech.* 62, 132-150.
- Easter, S.S., Johns, P.R., and Heckenlively, D. (1974). Horizontal compensatory eye movements in goldfish (*Carrassius auratus*). I. The normal animal. *J. Comp. Physiol.* 92, 23-35.
- Hardie, R.C. (1985). Functional organization of the fly retina. In: Progress in sensory physiology (ed. D. Ottoson), vol. 5, pp. 1-79. Berlin: Springer.
- Koenderink, J.J. (1986). Optic flow. *Vision Res.* 26, 161-180.
- Koenderink, J.J., and van Doorn, A.J. (1987). Facts on optic flow. *Biol. Cybern.* 56, 247-254.
- Land, M.F. (1973). Head movements of flies during visually guided flights. *Nature* 243, 299-300.
- Land, M.F., and Eckert, H. (1985). Maps of the acute zones of fly eyes. *J. Comp. Physiol. A* 156, 525-538.
- Land, M.F. (1999). Motion and vision: why animals move their eyes. *J. Comp. Physiol. A* 185, 341-352.
- Nagle, M.G., Srinivasan, M.V., and Wilson, D.L. (1997). Image interpolation technique for measurement of egomotion in 6 degrees of freedom. *J. Opt. Soc. Am.* 14, 3233-3241.
- Nalbach, G. (1993). The halteres of the blowfly *Calliphora*. I. Kinematics and dynamics. *J. Comp. Physiol. A* 173, 293-300.
- Paul, H., Nalbach, H.-O., and Varjú, D. (1990). Eye movements in the rock crab *Pachygrapsus marmoratus* walking along straight and curved paths. *J. Exp. Biol.* 154, 81-97.
- Schilstra, C., and van Hateren, J.H. (1998a). Using miniature sensor coils for simultaneous measurement of orientation and position of small, fast-moving animals. *J. Neurosci. Meth.* 83, 125-131.

Schilstra, C. and van Hateren, J. H. (1998b). Stabilizing gaze in flying blowflies. *Nature* 395, 654.

Strausfeld, N.J., Seyan, H.S. and Milde, J.J. (1987). The neck motor system of the fly *Calliphora erythrocephala*. I. Muscles and motor neurons. *J. Comp. Physiol. A* 160, 205-224.

van Hateren, J.H. (1992a). Theoretical predictions of spatiotemporal receptive fields of fly LMCs, and experimental validation. *J. Comp. Physiol. A* 171, 157-170.

van Hateren, J.H. (1992b). Real and optimal neural images in early vision. *Nature* 360, 68-69.