Vision is a fundamental sense of most animals. The sensory organs of vision are the eyes, and their movements determine the visual input. Visual systems have certain spatio-temporal characteristics and limitations, which make their efficiency dependent on the strategy of eye movements. It is thus important to study the strategy of normal eye movements and apply this knowledge to the further study of visual systems.

In this thesis eye movements of walking and flying blowflies are studied in detail. Eye movements of small insects are difficult to measure with a spatio-temporal accuracy comparable with that of the eyes, and current video techniques do not allow an accurate reconstruction of the visual input. In this thesis an existing technique is used, based on search-coils in magnetic fields, which can measure eye movements with a spatio-temporal accuracy comparable to that of the eyes. The principle of the technique is described in detail in Chapter 2, together with several improvements. By using a glass plate with grooves, which allows a fast and precise placement of the coil used for calibrating the magnetic field, the calibration procedure was significantly improved. For recording from small flies, new coil triplets of 1 mm diameter were developed and manufactured.

The most important result of the experiments is that the head and thorax movements of both walking and flying blowflies are saccadic (operating with fast, abrupt turns, Chapter 4). The saccades occur at a rate of 5 to 10 sac-
cades/s. Regardless of the saccade size, head saccades last approximately 25 ms, and thorax saccades last longer. Between saccades, the head and thorax are held almost stable, with the head more stable than the thorax. For the three species we investigated (*Calliphora vicina*, *Lucilia cuprina* and *Lucilia caesar*), the saccades are similar, in accordance with the fact that these species are closely related. The saccades of walking and flying flies only differ in detail. One consequence of the saccades is that the proportion of time with low angular velocities is substantially increased, which benefits vision.

Head and thorax saccades occur almost simultaneously, probably as a consequence of the fact that the head can only rotate in the yaw direction (rotation about a vertical axis) by about 20 degrees, thus large saccades require that the head and thorax saccades are synchronized. For a typical flying saccade, the peak angular velocities of the head and thorax occur simultaneously. The head saccade is faster than that of the thorax, leaving two short periods at the beginning and end of the saccade, where the thorax is performing its saccade, while the head is held stable with respect to the surroundings. This is accomplished by a counter-rotation of the head relative to the thorax. For a typical walking saccade, the head and thorax saccades start simultaneously. The head reaches its peak angular velocity earlier than the thorax, and finishes its saccade sooner than the thorax. Between the end of the head saccade and the end of its corresponding thorax saccade, the head is held stable relative to the surroundings by a counter-rotation. Walking saccades thus start simultaneously, while in flying saccades, peak angular velocities coincide. A possible explanation for this difference is that in flight, stabilisation may be easier to maintain by first allowing the thorax to pick up velocity before starting the head saccade. In walking, stability is less of an issue, because the flies always keep at least three legs in contact with the ground, allowing the flies to start the head saccade immediately.

At the beginning and end of saccades there are short periods when the head is held steady while the thorax performs its saccade. Probably this stabilization of the head at high angular velocities during saccades is performed under the control of the halteres, while the stabilization of the head between saccades may be mainly under visual control. Flies would arguably have had a simpler design if their head would have been fixed to the thorax, because then they would not have needed the complex mechano-sensory system used
for head movements. However, the mobile head is helpful, because it allows a better stabilization of the eyes during walking and flying manoeuvres. Moreover, the peak angular velocity of the head during saccades is significantly higher than that of the thorax. The energy required for rotating only the head with this higher angular velocity is less than the energy required for rotating its entire body with this velocity.

Compared with a hypothetical fly performing smooth, non-saccadic rotations, a fly performing (thorax) saccades increases the proportion of time with low angular velocity (Chapter 4). The superimposed head saccades further increase this proportion. The combined effect of thorax and head saccades is that the probability of angular velocities lower than 20 degrees/s is substantially increased. The strategy of using saccadic eye movements, which result in low angular velocities for a larger proportion of time, improves vision in at least two ways. First, the blurring due to the integration time of the photoreceptors is reduced. Second, at low angular velocities, the translational component of the optic flow dominates. The three-dimensional structure of the environment can be extracted from this component of the optic flow. If the eyes are also rotating, the optic flow receives an additional rotational component, which complicates the extraction of the three-dimensional structure. This is probably the main reason for the existence of saccades in blowflies, because the increase of probability is in the range of 0 - 20 degrees/s, well below the velocity where blurring becomes significant (approximately 150 degrees/s). It is likely that the (saccadic) turning behaviour is determined by the constraints of 1) minimizing the energy consumed for turning and visual processing, while 2) maximizing the probability of low angular velocities and 3) minimizing the proportion of time with angular velocities larger than the velocity where blurring starts to become important. These constraints are important for most animals with good vision and may have guided, at least partly, the evolution of saccadic eye movements in animals in different phyla.

Blowflies walk in a saccadic-like manner, accelerating and slowing down with a frequency of 5-10 Hz (Chapter 3). The walking velocity and turning angular velocity are correlated: peaks in walking and turning velocity occur at approximately the same time, with the angular velocity peak occurring on average slightly before the walking velocity peak. Moreover, higher walking velocity corresponds with higher angular velocity, thus on average they
speed up when turning faster. This is probably due to the fact that the fly keeps at least 3 legs on the ground at any moment, which limits the turning velocity by the stepping frequency. Flies often walk sideways, and angles of 45 degrees between the orientation of the thorax and the tangent to the walking path are frequent. Between saccades, the head is typically aligned with the thorax, resulting in an eccentric translational optic flow. It is possible that flies use this eccentricity to gauge the distance to objects situated in the front of the animal. While walking, the flies perform complex manoeuvres in order to turn, from walking on curved paths (for slower turns) to 2-phase or 3-phase turns (with increasing turning velocity). Regardless of the turning manoeuvre involved, the orientation of the fly changes always in a series of saccades.

The recordings of walking and flying blowflies obtained in this thesis have a high spatial and temporal resolution, sufficient for reconstructing the natural visual input with a resolution as sensed by the eyes of the fly. These recordings can constitute the starting point in the further study of the natural visual input and its processing by the (blow)fly visual system. The next logical steps are to reconstruct the visual input, use it in further studies of the characteristics of the natural optic flow, and use it as a stimulus in electrophysiological experiments studying different neurons in the visual system.