Chapter 4

Active Vision in Blowflies: Strategies and Mechanisms of Spatial Orientation

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Abstract   With its miniature brain blowflies are able to control highly aerobatic flight manoeuvres and, in this regard, outperform any man-made autonomous flying system. To accomplish this extraordinary performance, flies shape actively by the specific succession of characteristic movements the dynamics of the image sequences on their eyes ('optic flow'): They shift their gaze only from time to time by saccadic turns of body and head and keep it fixed between these saccades. Utilising the intervals of stable vision between saccades, an ensemble of motion-sensitive visual interneurons extracts from the optic flow information about different aspects of the self-motion of the animal and the spatial layout of the environment. This is possible in a computationally parsimonious way because the retinal image flow evoked by translational self-motion contains information about the spatial layout of the environment. Detection of environmental objects is even facilitated by adaptation mechanisms in the visual motion pathway. The consistency of our experimentally established hypotheses is tested by modelling the blowfly motion vision system and using this model to control the locomotion of a 'Cyberfly' moving in virtual environments. This CyberFly is currently being integrated in a robotic platform steering in three dimensions with a dynamics similar to that of blowflies.

4.1 Virtuosic Flight Behaviour: Approaches to Unravel the Underlying Mechanisms

Anyone who observes a blowfly landing on the rim of a cup or two flies chasing each other will be fascinated by the breathtaking aerobatics these tiny animals can produce (Fig. 4.1). While the human eye is hardly capable of even following their flight paths, the pursuer fly is quite capable of catching its speeding target. During their virtuosic flight manoeuvres blowflies can make up to 10 sudden, so-called saccadic turns per second, during which they reach angular velocities of up to 4,000°/s [58, 70]. During their flight manoeuvres blowflies rely to a great extent on information from the displacements of the retinal images across the eyes ('optic flow'). This visual motion information is then transformed in a series of processing steps into motor control signals that are used to steer the flight course.

The analysis of neural computations underlying behavioural control often rests on the implicit assumption that sensory systems passively pick up information about their surroundings and process this information to control the appropriate behaviour. This concept, though useful from an analytical point of view, misses one important feature of embodied and situated behaviour: normal behaviour operates under closed-loop conditions and all movements of the animal may shape the sensory input to a large extent. Although we will mainly concentrate in this chapter on the sensory side of the action–perception cycle and, in particular, the processing of visual motion information, our approach is distinguished by envisioning the blowfly as a dynamic system embedded in continuous interactions with its environment.

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Fig. 4.1 Five snapshots from a high-speed film sequence of a blowfly landing on the rim of a cup. The fly turns by almost 180° within approximately 140 ms
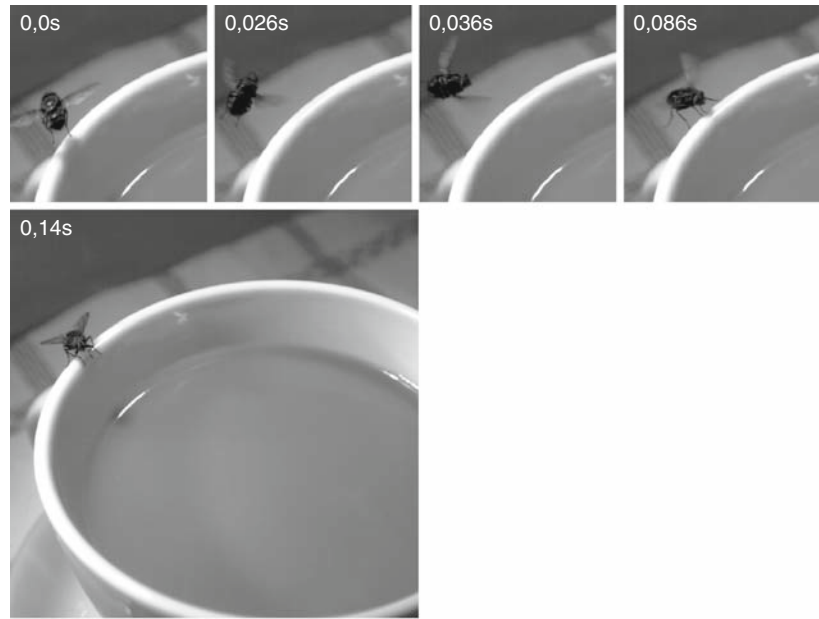
Since it is currently not possible to probe during flight behaviour into the neural circuits processing visual motion information, behavioural and neuronal analyses are done separately. Both types of analyses are interlinked by employing for visual stimulation in experiments at the neural level reconstructions of the image sequences free-flying blowflies have previously seen during their virtuosic flight manoeuvres as well as targeted manipulations of such sequences. Neural analysis can, for methodological reasons, unravel only subsystems at a time, such as in our case a population of motion-sensitive nerve cells in the blowfly visual system. The functional role of the analysed subsystems for the performance of the entire system, i.e. in our case for visually guided behaviour, can therefore hardly be assessed appropriately by experimental analysis alone. Reasons are the non-linearity of most computational mechanisms, the recurrent organisation of many neuronal subsystems and the resulting complex dynamics of neuronal activity, as well as the closed-loop nature of behaviour. These constraints can only be overcome by closely linking and complementing experiments with computational approaches: experimentally established hypotheses are modelled in our CyberFly project, both in software and hardware, and put into the context of the entire system interacting with its environment.

The following aspects of visually guided behaviour of blowflies and the underlying neural computations will be addressed: (1) Flight activity of blowflies will be scrutinised and segregated into sequences of individual prototypical components. The corresponding behaviourally generated visual input, a consequence of the closed action–perception cycle, will then be reconstructed; (2) we will pinpoint what information about self-motion and the outside world is provided by populations of output neurons of the visual motion pathway; and (3) the experimentally established hypotheses on the mechanisms of motion computation, on the coding properties of this population of cells and on how this neural population activity is used to control behaviour are challenged with our CyberFly model under open-loop and closed-loop conditions.

4.2 Active Vision: The Sensory and Motor Side of the Closed Action–Perception Cycle

Optic flow induced on the eyes during locomotion does not only provide information about self-motion of the animal but is also a potent visual cue for spatial

information. Optic flow is the most relevant source of spatial information in flying animals which probably do not have other distance cues at their disposal. Some insects use relative motion very efficiently to detect objects and to infer information about their height [10, 34, 45, 61]. When the animal passes or approaches a nearby object, the object appears to move faster than its background. Motion can thus provide the perceived world with a third dimension. Locusts and mantids, for instance, are known to judge the distance of prey objects based on motion parallax actively generated by peering movements [37]. Moreover, honeybees assess the travelled distance or the distance to the walls of a flight tunnel on the basis of visual movement cues [1, 14, 15, 27, 60, 62, 63, 66]. Hummingbird hawk-moths hovering in front of flowers use motion cues to control their distance to them [16, 33, 53]. Several insect species, such as wasps and honeybees, perform characteristic flight sequences in the vicinity of their nest or of a food source. It has been concluded that the optic flow on the eyes is shaped actively by these characteristic flight manoeuvres to provide spatial information [44, 72–74] (see also Chaps. 1, 7 and 17).

Blowflies employ a characteristic flight and gaze strategy with strong consequences for the optic flow patterns generated on the eyes: Although blowflies are able to fly continuous turns while chasing targets [2, 3], they do not show smooth turning behaviour during cruising flight or in obstacle avoidance tasks. Instead, they keep their gaze almost straight for short flight segments and then execute sharp fast turns, commonly referred to as saccades (Fig. 4.2A,B). These saccades only last for about 50–100 ms. During saccades blowflies may reach rotational velocities of up to 4000°/s and change their body orientation by up to 90° [58]. The head is actively moved so that gaze shifts are even shorter and more precise than those of the body. Active head movements considerably improve stabilisation of the gaze direction between saccades [70]. This behaviour can be interpreted as an active vision strategy stabilising the gaze rotationally as much as possible [31, 57]. The temporal pattern of saccades and intersaccadic intervals as well as the amplitude of saccades may vary systematically depending on the behavioural context. For instance, blowflies, even when flying in a straight tunnel, do not fly in a straight line, but perform a sequence of alternating saccades.

The frequency and amplitude of these vary with the width of the flight tunnel (Kern et al. in prep.).

As a consequence of the saccadic strategy of flight and gaze control the rotational and translational components of the optic flow are largely segregated at the behavioural level. In blowflies, this strategy is not obviously reflected as sharp bends in the path of the body's centre of mass. Changes in orientation do not immediately result in changes in flight direction due to sideward drift after a body saccade, presumably caused by the inertia of the blowfly [58]. In this regard blowflies appear to differ from the much smaller fruitflies ([65]; Chap. 17).

So far, we mainly decomposed behaviour into just two prototypical components, saccades and straight flight segments during the intersaccadic intervals. This segmentation was mainly based on the horizontal components of movement. Does the segmentation of behaviour into distinct prototypical movements generalise if we consider all six degrees of freedom of locomotion? To answer this question we decomposed behavioural free-flight sequences into their constituent prototypical movements by clustering algorithms. Clustering approaches have been successfully applied, for instance, to classify basic skills and behaviours within observation data of humans and also in computer science and robotics when controlling the movements of artificial agents [56, 67, 68]. In contrast to classical behavioural analysis, clustering methods (such as k-means; [28]) allow us to analyse vast amounts of data in a relatively short time. The large database enables us to assess the relative frequency and the characteristic sequences of prototypical movements occurring in different behavioural contexts. We applied k-means clustering to the six-dimensional set of translational and rotational velocities obtained from cruising flight sequences in an indoor flight arena.

We could identify nine stable prototypical movements as behavioural building blocks during cruising behaviour of blowflies. Even if all six degrees of freedom of self-movement are taken into account (Fig. 4.2B,C), the prototypical movements can be classified into two distinct main classes, i.e. rotational movements, on the one hand, and translational movements, on the other hand (Fig. 4.2D). Within the translation class of prototypes, for instance, prototypes reflecting almost pure forward translation and

Fig. 4.2 Flight sequence of a free-flying blowfly and its decomposition into prototypical movements. (**A**) Section of the flight sequence. The position of the head and its orientation as seen from above are indicated every 10 ms by a *dot* and a *line*, respectively (behavioural data: courtesy J.H. van Hateren, University of Groningen, NL). (**B**) Rotational velocities (yaw, pitch, roll) of the head for the flight sequence shown in (**A**). Note the saccadic structure of rotational movements. (**C**) Translational velocities (forward, sideward, lift) for the same flight sequence as shown in (**A**). The translational velocities predominantly change on a slower timescale than the rotational velocities and do not show an obvious saccadic structure. (**D**) Prototypical movements into which the flight sequence shown in (**A**) can be decomposed. Four saccadic (two rightward and two leftward saccadic prototypes) and five translational prototypes were identified. Each prototype is characterised by a distinct combination of rotational and translational movements
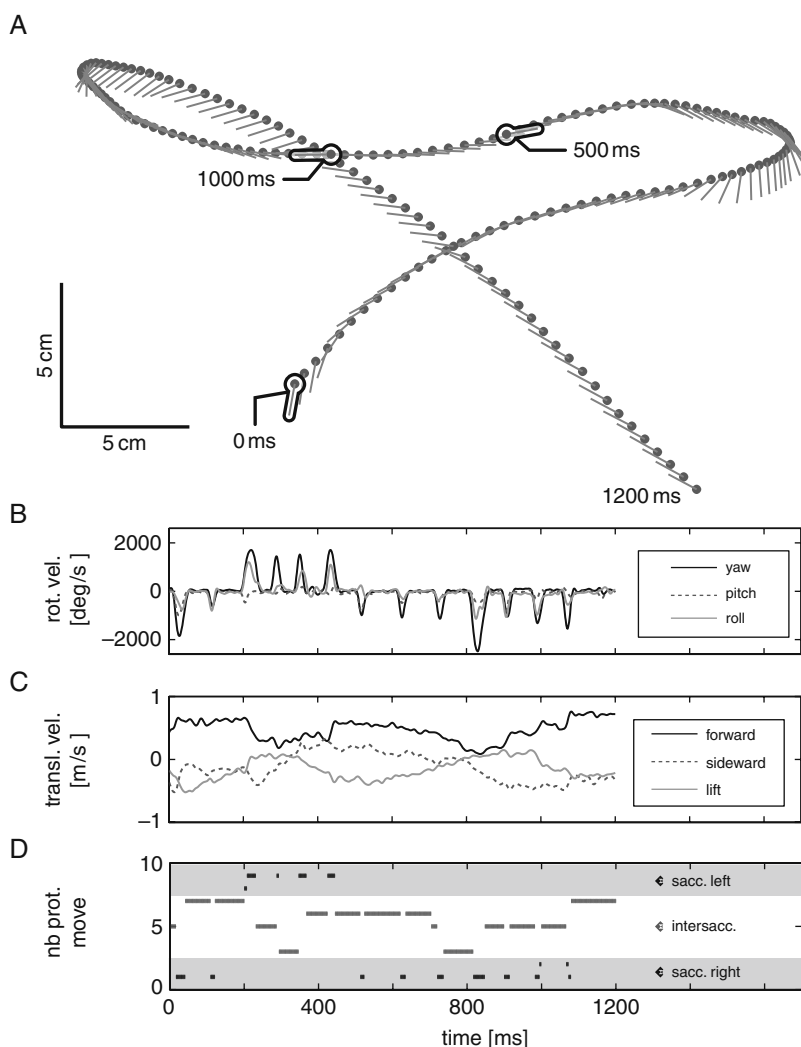
prototypes characterised by a strong sideward component can be distinguished.

Organising behaviour as a sequence of prototypical movements leads to a tremendous complexity reduction which is likely to be favourable for both motor control and sensory information processing. The prototypical movements are thought to be selected from a limited pool of possible movement prototypes according to a strategy that depends on the respective behavioural context. This strategy may simplify motor control tremendously. Because of the closed-loop nature of behaviour, the different types of prototypical movements go along with retinal image displacements which are characterised by distinct spatiotemporal features. We could show that the sensory input is shaped by the very nature of the prototypical movements in a way that greatly facilitates the neuronal analysis of complex sensory information. The corresponding optic flow is either mainly rotational (i.e. during saccades) or translational (i.e. during the intersaccadic intervals).

The behavioural segregation of rotational and translational self-movements enables flies to gather spatial information about the three-dimensional layout of their environment during intersaccadic flight sections by relatively simple computational means. The optic flow component resulting from translational self-motion depends on distance of environmental objects from the observer, whereas the rotational optic flow component is independent of the distance [35]. Thus,

only the translational optic flow component contains spatial information. It should be noted that, although translational optic flow contains information about the three-dimensional layout of the environment, it does not directly provide information about metric distances. Rather, spatial information derived from optic flow is only relative, because it depends on (i) the velocity of the observer, (ii) his/her distance to objects in the surroundings and (iii) the location of the objects in the visual field relative to the direction of translation. Although it is mathematically possible to decompose optic flow fields into their rotational and translational components [8, 50, 54], blowflies and other insects appear to avoid the heavy computational effort by a smart behavioural strategy that keeps largely apart rotational and translational flow components from the bottom up.

It is not yet clear how this behavioural strategy is accomplished. In particular, the underlying head–body coordination is demanding, because it leads to almost perfect gaze stabilisation between saccades within only few milliseconds, while the body still shows residual slow rotational movements [70]. We can only surmise that feed-forward control and/or mechanosensory information may play a major role, whereas visual feedback might be too slow on the relevant short timescale.

In conclusion, the active flight and gaze strategy of blowflies as well as those of many insect species may have been shaped during evolution by requirements of image motion processing. This behavioural strategy can help to reduce the complexity of the sensory input by structuring the movements in an adaptive way. Active vision strategies may thus facilitate the extraction of spatial cues by smart, i.e. relatively simple, mechanisms. Such mechanisms may also be relevant when engineering lightweight autonomous air vehicles.

4.3 Extracting Spatial Information from Actively Generated Optic Flow

The blowfly visual motion pathway is well adapted to make use of the structured visual input resulting from the saccadic flight and gaze strategy when extracting spatial information from optic flow. As the blowfly visual system is optimised for reliable performance in

virtuosic flight behaviour and is amenable to a broad spectrum of neuronal and behavioural methods it has proved to be a good model system for tracing the computations which serve to process image motion proceeding from the eyes [7, 10, 13, 20]. Retinal image displacements are not perceived directly by the eye. Rather, the photoreceptors in the retina register just a spatial array of brightness values continuously changing in time. From this, the nervous system has to go through a series of steps to evaluate information on the image movements.

In the blowfly visual system motion is initially processed in the first and second visual areas of the brain by successive layers of retinotopically arranged columnar neurons. One major function of the first visual area is to remove spatial and temporal redundancies from the incoming retinal signals and to maximise the transfer of information about the time-dependent retinal images by adaptive neural filtering [29, 43, 69]. There is evidence that direction selectivity is first computed by retinotopically arranged local movement detectors in the most proximal layers of the second visual area (review in [9, 64]). The performance of such local movement detection circuits can be accounted for by a computational model, the correlation-type motion detector, often referred to as elementary motion detector (EMD) ([6, 11, 12, 36, 64]; for hardware implementations of local movement detectors, see Chap. 8). This model explains neuronal responses to a wide range of motion stimuli including those that are experienced during highly aerobatic flight manoeuvres [48]. EMDs correlate the brightness data of adjacent light-sensitive cells receiving appropriately filtered brightness signals from neighbouring points in visual space and subtract the outputs of two such correlation units with opposite preferred directions. Movement is signalled when the input elements report the same brightness value in immediate succession. During this process, each motion detector reacts with a large excitatory signal to movement in a given direction and with a negative, i.e. inhibitory, signal to motion in the opposite direction. The responses of EMDs depend not only on image velocity but also on the contrast, the spatial frequency content and orientation of the pattern elements [5, 12]. As a result of these coding properties the representations of local motion information in biological systems, such as the blowfly, are likely to differ considerably from the veridical retinal velocities forming the optic flow (review in [10, 12]).

Since behaviourally relevant information is contained in the global features of optic flow rather than in the local velocities, EMD signals from large areas of the visual field need to be combined. Accordingly, in a variety of animal groups ranging from insects to primates, neurons sensitive to optic flow were found to have large receptive fields (reviews in [5, 42]; see also

Chap. 5). In blowflies, spatial pooling is accomplished by an ensemble of individually identifiable motion-sensitive neurons, the so-called tangential cells (TCs) [7, 10, 13, 24, 38]. TCs are thought to spatially pool on their large dendrites the output signals of many local motion detectors received via excitatory and inhibitory synapses. The local motion detectors are activated
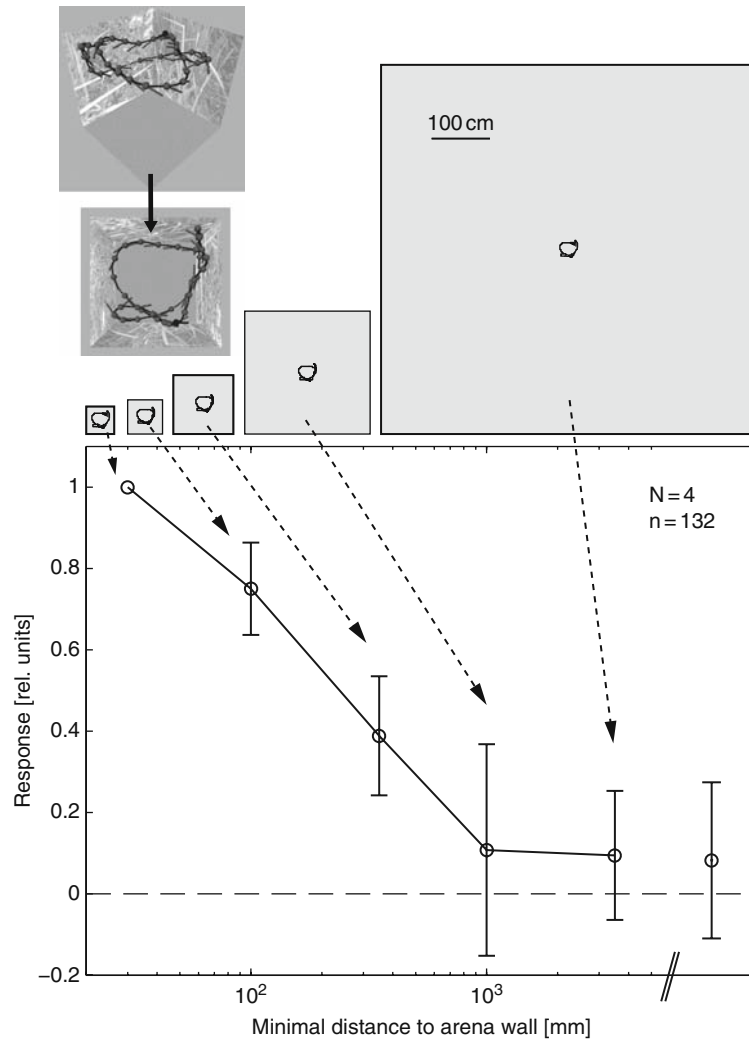

Fig. 4.3 Significance of three-dimensional layout of the environment for responses of HS cells during intersaccadic intervals is shown by manipulating the distance of the fly to the walls of the flight arena. This was accomplished by increasing the size of the virtual arena while keeping the flight trajectory the same as in the original arena (see sketches of top views of the arenas above the data plot). HS cells were stimulated with the image sequences as would have seen by free-flying blowflies in the original flight arena and different virtual flight arenas. The data are based on six different trajectories (one of them shown from different perspectives in *inset*). In addition, the translational movements were completely omitted and the fly only rotated with its natural rotation velocity in the centre of the arena (right data point). The mean response amplitudes between saccades decrease substantially when the distance of the animal to the arena wall gets smaller. For a minimal distance of approx. 1 m, virtually the same intersaccadic responses are obtained as without any translational movement at all. Data are averages based on 4 HSN cells and a total of 132 stimulus repetitions

either by downward, upward, front-to-back or back-to-front motion. However, the actual preferred directions change somewhat across the visual field according to the geometrical lattice axes of the compound eye [41, 52]. Two classes of TCs, the 3 HS cells [22, 23, 40] and the 10 VS cells [25, 26, 39], have been analysed in particular detail with respect to encoding the optic flow generated by self-motion of the fly. Whereas the dominant preferred direction of motion of HS cells is ipsilateral front-to-back motion in different overlapping areas of the visual field [23, 40], the dominant preferred direction of motion of VS cells is downward motion in overlapping neighbouring vertically oriented stripes of the visual field [17, 39]. HS and VS cells are output elements of the visual motion pathway and thought to be involved in controlling visually guided orientation behaviour.

We could recently show that the populations of HS and VS cells make efficient use of the saccadic flight and gaze strategy of blowflies to represent spatial information. The head trajectories of flying blowflies and thus – because of their immobile eyes in the head capsule – the gaze direction could be determined in a laboratory setting with the help of a magnetic coil system [58, 70]. Using the knowledge of the three-dimensional layout and wall patterns of the flight arena, the retinal image sequences were calculated at a high temporal resolution [47]. Under outdoor conditions, the flight paths and body orientations of free-flying blowflies were recorded with a pair of high-speed cameras. The retinal image sequences were assessed by moving a panoramic camera along the same path with a robotic gantry [4].

We used these behaviourally generated retinal image sequences as visual stimuli in electrophysiological experiments on HS and VS cells. On the basis of such experiments, the functional properties of these cells were interpreted in a different conceptual framework than in previous analyses: rather than being primarily viewed as sensors for determining rotational self-motion from the retinal optic flow patterns, they were concluded to provide also spatial information. Since blowflies keep their gaze virtually constant between saccades leading to prominent translational optic flow if environmental objects are sufficiently close to the eyes, the HS and VS cells can extract information about the spatial layout of the environment [4, 30–32]. For instance, the intersaccadic depolarisation level depends on the distance of the blowfly to environmental structures (Fig. 4.3). As we could show in recent experiments, the sensitivity of HS cells to retinal velocity increments caused by nearby objects is even enhanced by motion adaptation, i.e. after the fly is exposed to repeated optic flow patterns for sometime [46].

4.4 A CyberFly: Performance of Experimentally Established Mechanisms Under Closed-Loop Conditions

Given the ability of flies to perform extraordinary acrobatic flight manoeuvres, it is not surprising that there have been various attempts to implement fly-inspired optic flow processing into simulation models and on robotic platforms (for review [19, 51, 71, 75]; see also Chaps. 5 and 6). Although these approaches usually employed simplified model versions of the visual motion pathway, in all these studies the sensorimotor loop was closed. Most of them used optic flow information to stabilise the agent's path of locomotion against disturbances or to avoid collisions with walls. On the other hand, only few attempts in robotics make use of the fly's saccadic strategy of locomotion and of the implicit distance information present in translatory optic flow between saccades to implement obstacle avoidance [18, 55, 59, 75]. However, most of these agents generate very low dynamic movements compared to blowflies.

In a recent study we implemented a saccadic controller that receives its sensory input from a model of the blowfly's visual motion pathway and takes the specific dynamic features of blowfly behaviour into account. The model of the sensory system providing the input to the controller has been calibrated on the basis of experimentally determined responses of a major motion-sensitive output neuron of the blowfly's visual system, one of the HS cells, to naturalistic optic flow, i.e. the visual input of flies in free-flight situations [48]. Apart from an array of retinotopically organised spatiotemporal filters which mimic the overall signal processing in the peripheral visual system, the core elements of the sensory model are elementary motion detectors of the correlation type (EMDs; see Sect. 4.3). These are spatially pooled by two elements – one in

either hemisphere of the simulated brain – corresponding to the equatorial HS cell (HSE).

To simulate the behaviour of a blowfly, the output signals of the sensory model are transformed into motor signals to generate behavioural responses. The properties of the motor controller determine how these motor signals are transformed into movements of the animal. By simulating the system in a closed control loop, hypotheses about the functional significance of the responses of sensory neurons and different types of sensorimotor interfaces can be tested. So far, the main task of this CyberFly has been to avoid collisions with obstacles, one of the most fundamental tasks of any autonomous agent [49]. Coupling the differential signal of the sensory neurons proportionally to the generated yaw velocities does not lead to sufficient obstacle avoidance behaviour.

A more plausible sensorimotor interface is based on a saccadic controller modelled after the flight behaviour of blowflies. Here, the responses of simulated HSE cells in both halves of the visual system are processed to generate the timing and amplitude of saccadic turns. Timing and direction are determined by applying a threshold operation to the neuronal signals. The amplitudes of saccades are computed from their relative difference. The threshold used to initiate a saccade is very high just after the end of a preceding saccade, to prevent the CyberFly from generating saccades at unrealistically high frequencies. From this start value the threshold continually decreases, increasing the readiness for the generation of a new saccade with extending intersaccadic interval. Even with sideward drift after saccadic turns as is characteristic of real blowflies [58], the CyberFly is able to successfully avoid collisions with obstacles. The implicit distance information resulting from translatory movements between saccades is provided by the responses of model HS cells in the two halves of the visual system and appears to be crucial for steering the CyberFly safely in its environment (Fig. 4.4).

A limitation of this simple mechanism is its strong dependence on the textural properties of the environment. A strong pattern dependence is also suggested by behavioural experiments of flight behaviour of *Drosophila* ([21]; see also Chap. 17). Currently, we are analysing in combined electrophysiological and behavioural experiments on blowflies as well as by model simulations the reasons for the sensitivity of the CyberFly to changes in the textural properties of the environment. Moreover, the current CyberFly, which operates so far only in the horizontal plane, is being elaborated to a fully three-dimensional model and implemented on a robotic gantry platform. These elaborations will be based on the recent knowledge of prototypical movements comprising all three degrees of freedom of rotation and translation as well as by
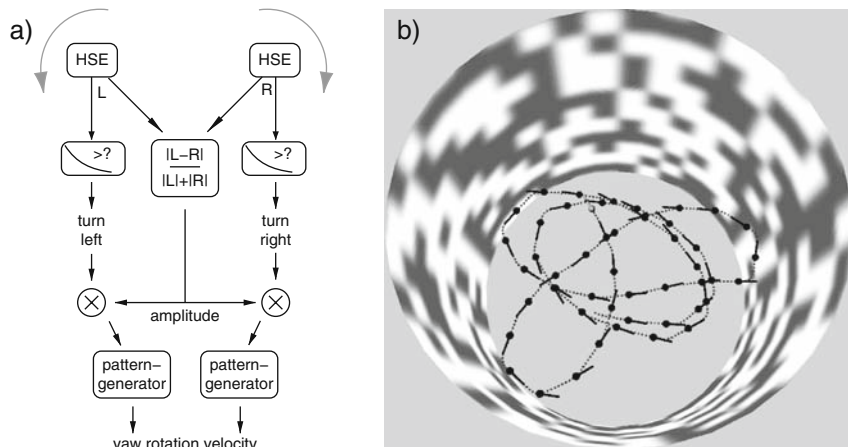

Fig. 4.4 Structure and performance of CyberFly: (**a**) Responses of simulated motion-sensitive neurons (HSE) are processed to generate the timing and amplitude of saccadic turns. Timing and direction are determined by a threshold operation, and amplitudes are computed from the contrast of the neuronal signals. A pattern generator replays yaw velocity templates computed from behavioural data. (**b**) Example for the trajectories generated by CyberFly (*grey marker*: start). The big markers indicate position (spheres) and viewing directions. The texture of the cylindrical simulation environment is shown with reduced contrast to enhance perceptibility

taking larger populations of motion-sensitive tangential cells (HS cells and VS cells) into account. One aim of these modelling studies is to assess which aspects of the saccadic flight and gaze strategy of blowflies and of the underlying neural mechanisms will turn out to be particularly relevant and advantageous for flight performance and, thus, might prove suitable for implementation in micro-air vehicles.

4.5 Conclusions

Although blowflies and many other insects are only equipped with a tiny brain, they operate with ease in complex and ever-changing environments. In this regard, they outperform any technical system. It is becoming increasingly clear that visually guided orientation behaviour of blowflies is only possible because the animal actively reduces the complexity of its visual input and the mechanisms underlying visual information processing make efficient use of this complexity reduction. By segregating the rotational from the translational optic flow generated during normal cruising flight, processing of information about the spatial layout of the environment is much facilitated. By adapting the neural networks of motion computation to the specific spatiotemporal properties of the actively shaped optic flow patterns evolution has tuned the blowfly nervous system to solve apparently complex computational tasks efficiently and parsimoniously.

Biological agents such as blowflies generate at least part of their power as adaptive autonomous systems through efficient mechanisms acquiring their strength through active interactions with their environment and not by simply manipulating passively gained information about the world according to a predominantly predefined sequential processing scheme. These agent–environment interactions lead to adaptive behaviour in environments of a wide range of complexity. By cunningly employing the consequences of a closed action–perception loop animals' even tiny brains are often capable of performing extraordinarily well in specific behavioural contexts. Model simulations and robotic implementations reveal that the smart biological mechanisms of motion computation and of controlling flight behaviour might be helpful when designing micro-air vehicles that may carry an on-board processor of only a relatively small size and weight.

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