Inside the
Fly's Onboard Computer

The brain of a housefly weighs around one-thousandth of a gram. Nonetheless, thanks to this miniscule control center, the insect can evaluate images in fractions of a second and steer its way through lightning-fast flight maneuvers. It was **Werner Reichardt**, Founding Director of the **Max Planck Institute for Biological Cybernetics** in Tübingen, who, more than 50 years ago, described how the motion detectors in the fly brain work.

TEXT **ELKE MAIER**

The hunting of flying insects appears to give wing to inventions. On the website of the German Patent and Trade Mark Office, the search term 'fly swatter' yields six patents, including one model specifically designed "for killing insects on the ceiling," and another in which a built-in mini vacuum cleaner means that "dead flies are easily collected without additional process stages."

However, even the most ingenious technology doesn't guarantee a successful hunt, as the reactive capacity of this particular prey is nothing short of astonishing. Werner Reichardt at the Max Planck Institute for Biological Cybernetics in Tübingen studied how these nimble insects register movements and transform them into course control signals.

Reichardt was born in Berlin in 1924. While still at school, he spent some of his free afternoons working as a lab assistant in the private laboratory of Hans Erich Hollmann, the developer of ultra-shortwave technology. Working on his own, the young researcher also familiarized himself with Maxwell's theory of electromagnetic waves and thus became an expert on the subject. This expertise was almost his undoing.

Due to his skills in this field, Reichardt was conscripted by the Luftwaffe to work as a radio measurement technician during the war. He met committed opponents of the National Socialist regime in one of the development labs and joined the resistance. He used his expertise to establish a secret radio connection with the Western Allies. Toward the end of the war, the resistance group was discovered. Reichardt was imprisoned and sentenced to death. During an aerial attack on Berlin, he managed to escape with a few of his fellow prisoners.

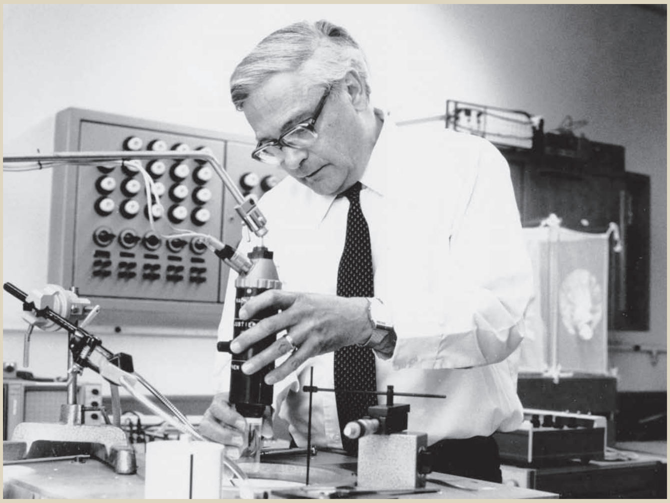
After the war, Werner Reichardt studied physics at the Technische Universität Berlin and completed his doctorate at the Fritz Haber Institute of the Max Planck Society. As his career progressed, however, biology became the increasing focus of his attention. A key factor in this development was the influence of zoologist Bernhard Hassenstein, whom Reichardt got to know in a detachment during the war, and who aroused his interest in biological questions. The pair decided at the time that, if they survived the war, they would establish a joint research program.

In 1950, the two scientists put their plan into action. Hassenstein was working as an assistant to Erich von Holst at the Max Planck Institute for Behavioral Physiology in Wilhelmshaven, and had told Reichardt about his experiments on the visual motion perception of the weevil or snout beetle *Chlorophanus viridis*. Reichardt realized that the small green weevil was particularly suitable for the development of a general model on visual motion perception.

Like all insects, *Chlorophanus* sees the world through compound eyes. These consist of hundreds of individual eyes, each of which perceives a small detail of the environment. The brain then computes the numerous individual shots into a comprehensive mosaic image. But how does the insect perceive movements and the direction of movements?

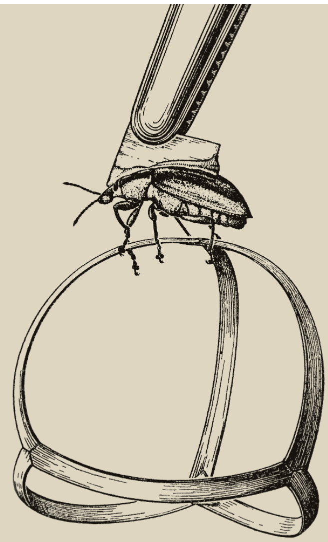
Werner Reichardt approached this question from the perspective of an engineer trying to work out how an unfamiliar machine works. Based on the experiments carried out on the weevil, he concluded how the structures that trigger a certain behavior in response to external stimuli must look.

The experimental setup was as ingenious as it was simple: "The laboratory animal's carapace is glued to a small piece of card-



The fly brain in his sights: Werner Reichardt in his laboratory at the Max Planck Institute for Biological Cybernetics in Tübingen.

Photo: Ingrid von Kruse



The weevil as a guinea pig: A simple experiment investigates the motion perception of *Chlorophanus viridis* with the help of the Y-maze globe.

board that is held by tweezers. In this situation, an object made of straw, the Y-maze globe, is presented to the insect, which it grasps voluntarily." This Y-maze globe was a round object made of six curved pieces of straw arranged in such a way that three of them intersect at four points and form Y-shaped junctions.

When the weevil made walking motions, the straw globe rotated under its feet. It appears that this gave the insect the impression that it was walking upside down along a branch. And, as would probably occur if it were walking through branches, after a few steps, the weevil kept encountering a junction at which it had to decide which direction to take.

The insect usually opts to go right and left with equal frequency. However, this changed when the researchers fixed their test participant in the middle of a rotating hollow cylinder on which vertical black and white stripes were painted. When the striped carousel turned to the right around the insect, it tended to choose the same direction. The strength of this innate optomotor response could be influenced by varying the width of the stripes and the speed of rotation. With the help of numerous experiments, the researchers were able to quantify the optomotor turning behavior of the weevil. Their results formed the basis for a theoretical model describing the principle behind the functioning of the elementary motion detectors in insects.

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» Using elegant, ingenious experimental setups, Reichardt succeeded in tracing sensory processing from the lowest to ever higher levels. The further he and his colleagues penetrated the secrets of the minute fly brain, the clearer it became what a marvel nature had created here.«

According to this model, a moving object generates differences in brightness, which are registered by the photosensitive cells in the insect's compound eye. A motion detector consists of two such cells that receive these light stimuli in sequence and transmit their information to a shared switching point. This postsynaptic neuron compares the interval between the two stimuli, and the brain calculates the direction from this information. Similar to the way in which two light barriers can be used to determine the direction a human went, this is how the insect brain registers motion.

Hassenstein and Reichardt published their model in 1956 in a paper with the rather unwieldy title: *Systemtheoretische Analyse der Zeit-, Reihenfolgen- und Vorzeichenauswertung bei der Bewegungsperzeption des Rüsselkäfers Chlorophanus* [A systems theory analysis of time, sequence and sign evaluation in the motion perception of the weevil *Chlorophanus*]. Two years later, together with electronics expert Hans Wenking, they were appointed Directors of the Cybernetics research group at the Max Planck Institute for Biology in Tübingen. This group went on to form the nucleus of the Max Planck Institute for Biological Cybernetics, which was established in 1968. Bernhard Hassenstein moved to Freiburg in 1960, and Werner Reichardt carried on working in Tübingen until his retirement in 1992. He died the same year.

At the new institute in Tübingen, the common housefly *Musca domestica* took the place of the weevil in the striped carousel. Not only was the housefly extremely fertile and easy to keep, its outstanding flying skills meant that it proved to be a very rewarding research object. Using tiny waxed discs, the researchers fixed their six-legged test subjects in the middle of their flight simulators so that the insects would beat their wings without moving. This enabled the scientists to record the reactions of the fly to different visual stimuli under controlled conditions.

Through numerous experiments, Werner Reichardt and his colleagues revealed fascinating details about visual motion perception, such as how the insect manages to distinguish between figures and background and steer directly toward objects. Based on this, the scientists in Tübingen established important foundations for the understanding of higher visual functions. They also succeeded in penetrating further into the fly's cockpit at the cellular level. For example, using very sensitive measurement probes, Martin Egelhaaf and other researchers from the group examined which neurons are active when the insect reacts to certain visual stimuli.

But the precise appearance of the motion detectors described by Reichardt and Hassenstein remained a mystery. Were they the cells that the famous Spanish neuroanatomist Santiago Ramón y Cajal had discovered as early as 1915 and described as "curious elements with two tufts"? For over 50 years, this question was something like the Holy Grail of fly research.

The tufted cells are far too small for their electrical signals to be extrapolated using measurement probes. The mystery remained unsolved until the scientists had special fluorescent proteins available to them that light up when the cell is active. Alexander Borst, Director at the Max Planck Institute of Neurobiology in Martinsried, and his colleagues made the tufted cells of the fruit fly *Drosophila* visible with the help of such proteins and measured their activity. It actually emerged from their tests that the mysterious cells were, in fact, the elementary motion detectors described by Werner Reichardt and Bernhard Hassenstein in 1956.

Moreover, many years ago, French researchers developed a "fly robot" that perceives motion based on the principle proposed by Reichardt and Hassenstein. Using its electronic compound eyes, the fly robot maneuvers through a labyrinth on three wheels. "However, the machine cannot fly and is capable of only comparatively pathetic movements," noted the Frankfurter Allgemeine Zeitung in 1994. The skills of its much smaller winged model remain unequalled to the present day.