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Werner Reichardt: the man and his scientific legacy

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CSAIL

Werner Reichardt:
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scientific legacy

Excerpts from a talk given by Tomaso Poggio in Tübingen on the opening of the Werner Reichardt Centrun für Integrative Neurowissenschaften, edited by G. Geiger and T. Poggio.

It is indeed a great honor – and responsibility – to speak to all of you at the opening of the new Werner Reichardt Centrun fuer Integrative Neurowissenschaften -- to speak to all of you about Werner Reichardt – the scientist and the man.

Werner Reichardt was born in 1924 in Berlin. He died on September 18th, 1992 a few days after a workshop celebrating his retirement. During his school years in Berlin, he worked in the laboratory of Hans Heinrich Hollmann, one of the pioneers of the electronics of the day.
At the beginning of World War II, Werner was assigned to work on radio projects in the air force. He was 19 years old when both of his parents were killed in an air attack on Berlin. He became a member of a resistance group, was arrested by the Gestapo; condemned to be executed, he was able to escape from jail. In postwar Berlin, Werner managed to set up a radio repair shop, and, with Kallmann's help, continue his studies and obtain his master and Ph.D. at the Technische Universitat in Berlin.

From 1952 to 1955, Werner was research assistant at the Fritz-Haber-Institut of the Max-Planck-Gesellschaft in Berlin, where he had among his teachers and advisors Dr. von Laue, who had received a Nobel prize for physics, and Dr. Ruska, who was later awarded the Nobel prize for the development of the electron microscope.
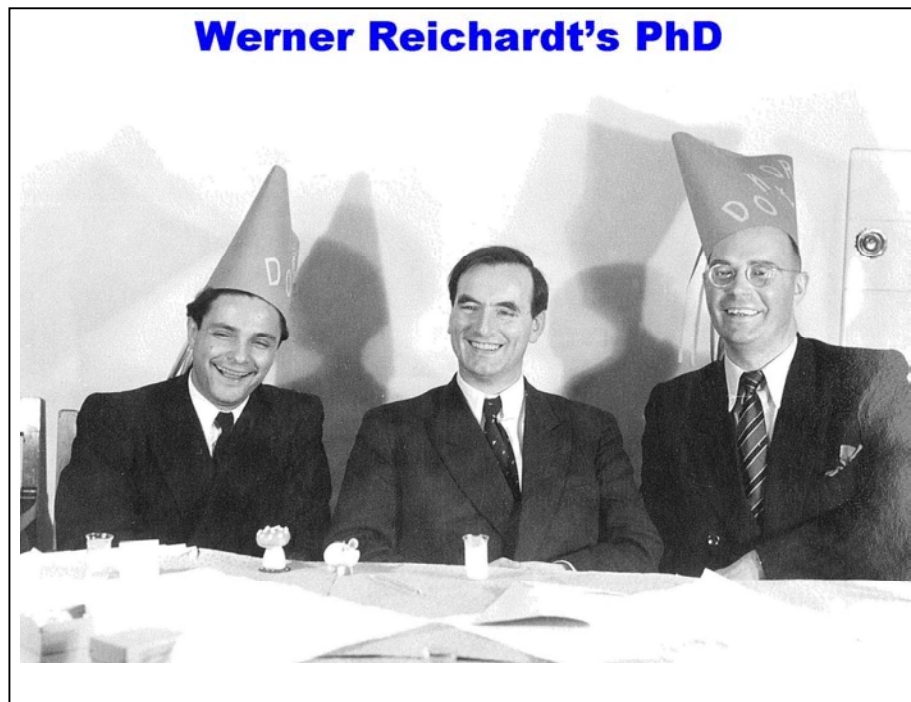
Figure 2. *A very young Werner is shown here with Dr. Ruska (in the middle). Photo dated Nov. 17, 1952 (courtesy B. Reichardt)*

At about this time – 1950 to 1952 --Werner started working with Dr. Bernhardt Hassenstein on the experiments and the theory of motion perception in the beetle. They had met during the war when Werner was on duty in a radio station monitoring the state

of the ionosphere. Werner – the physicist-- had met Berhard Hassenstein -- the future biologist -- who had a similar assignment. Those two kids – they were 20 years old or less -- decided then that they will someday start together a novel Institute in Physics AND Biology. This was clearly a very critical meeting for the future of both of them and even for the Centrun fuer Integrative Neurowissenschaften (CIN), the Center we are inaugurating! Dr. Hassenstein is here with us today, a great honor for which we are thankful.

Because of their '52 paper on the beetle – work that I will mention later -- Max Delbrueck offered Werner a postdoctoral position at the California Institute of Technology and convinced him to work as a physicist in biology. At about the same time, in 1954, Jim Watson and Niels Jerne were also post-docs with Delbrueck. With Jerne Werner made an adventurous coast-to-coast automobile trip at the end of his postdoctoral period punctuated by breakdowns of their car and impromptu lectures given at local colleges to help pay for gas and repairs. They offered a package of two lectures, one on horses on which Niels Jerne had done his experiments on the clonal theory of immunology (for which he received a Nobel prize) and one on beetles - the experimental subjects of Werner's theory of the optomotor response.

Back in Germany, Karl Friedrich Bonhoeffer offered Werner a position at the Max-Planck Institut fur physikalische Chemie in Gottingen – where Werner met his future wife Baerbel, who is here with us.

Figure 3. *Werner Reichardt with his son.*

Shortly afterwards, in 1958, Werner became head, together with Bernhardt Hassenstein and Hans Wenking, of the Forschungsgruppe Kybernetik within the Max-Planck-Institut fur Biologie in Tübingen. In the meantime, offers by CalTech, MIT and Bell Labs

triggered in 1960 a counteroffer by the Max-Planck-Gesellschaft that Werner accepted: in 1963 he started his own department in the Max-Planck-Institut fur Biologie. In 1968 this department became, with the nomination of three other directors' - V. Braitenberg, K. Goetz and K. Kirschfeld - the Max-Planck-Institut fur Biologische Kybernetik. So here they are….
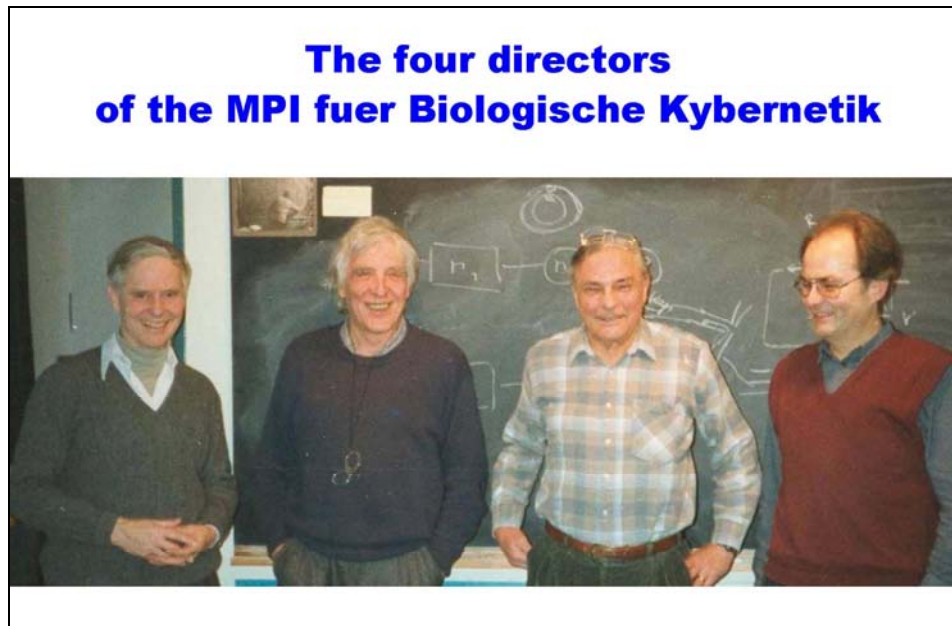
Figure 4. *From left K. Goetz, V. Braitenberg, W. Reichardt and K. Kirschfeld.*

For the new Institute, Werner had decided to choose a system for studying visual information processing that was neither too simple nor too complex. The choice was the fly's brain which, with its 10^6 neurons, is halfway on a logarithmic scale between unicellular organisms and man. From '68 to '92 Werner Reichardt made important contributions to the understanding of visual perception, using the fly as a model organism.

Werner was member of many academies in Germany, member of the prestigious order "Pour Le merite", foreign member of the National Academy of Sciences and recipient (with his friend B. Julesz) of the Heineken prize of the Royal Dutch Academy in 1985…many honors of which he was rightly proud.

Werner Reichardt's many experimental and theoretical discoveries add up to one of the most elegant contributions to neuroscience and represent one of the success stories of computational neurobiology. He -- and the Institute he founded -- had a profound influence in forming a new generation of researchers. Werner had old and deep connections with the main neuroscience laboratories in the US. He was an early member of Frank Schmitt's Neuroscience Research Program which had a lasting influence in shaping the emerging field of neuroscience and in bringing together some of its creators.

The scientist and his honors

1970, Honorary Professor University of Tübingen; Akademie der
     Wissenschaften und Literatur in Mainz;
1971, Deutsche Akademie der Naturforscher Leopoldina in Halle;
1972, American Academy of Arts and Sciences in Cambridge MA;
1977, Koninklijke Nederlandse Akademie van Wetenschaapen in
     Amsterdam;
1984, Member of the MPG Senate
1985, H. P. Heineken-Prize of the Royal Dutch Academy, awarded
     with B. Julesz;
1988, National Academy of Sciences in Washington;
1989, American Philosophical Society in Philadelphia and
     Academia Europea in Cambridge, England;
1989, Honorary Doctor of Engineering from the Technische
     Hochschule Aachen.

Table 1. *Sample of the honors bestowed on Werner.*

Figure 5. *43rd Stated Meeting of the NRP Associates, March 14-17, 1982.*

Because of him all the people who mattered in neuroscience at the time, many of them his friends, all came to Tübingen and we learned to know them personally, one of the greatest gifts that Werner could make to young researchers. One great friend of Werner and of the Institute was sir Berhard Katz. Many of the others are shown in the photo of the NRP Associates of 1982, which include David Hubel, Max Cowan, Eric Kandel, Thorston Wiesel, Chuck Stevens, Alan Hodgkin.

One key lesson I learned from Werner's scientific approach is his emphasis on coupling experimental and theoretical work in the neurosciences: without close interaction with experiments, theory is very likely to be sterile. This is a lesson that I never forgot. Closely related is what I regard as Werner Reichardt's main scientific legacy – the belief that we ought to study the brain at *different levels of organization, from the behavior of a whole animal to the signal flow, ie the algorithms, to circuits and single cells*.

Integrative Neuroscience

Werner's argument for starting the Max-Planck-Institute fuer Biologische Kybernetik (see Hengstenberg, 1997):

"…we ought to study central nervous systems at different levels of organization, from the behavior of a whole animal to the signal flow, i.e. the algorithms, to circuits and single cells."

- Marr's book *Vision* (Marr, 1982) had a great impact on computational neuroscience: a system as complex as the brain must be understood at several different levels:
  -- computation
  -- algorithms
  -- biophysics and circuits

- The argument came from "From Understanding Computation to Understanding Neural Circuits", Marr and Poggio, 1977…

- …part of which comes from Reichardt and Poggio, 1976 (Q. Rev. Biophysics, Part I)…

- **…which is a follow-up of Werner's argument for starting the Max-Planck-Institute fuer Biologische Kybernetik!**

Table 2. *Werner Reichard's scientific legacy.*

This approach of Integrative Neuroscience is usually attributed to David Marr but in fact originates with Werner! I was the link (see the Epilog of the last edition of Marr's Vision Book). Furthermore, he believed that insights gained on higher levels help to ask the right questions and to do experiments in the right way on lower levels. And above all he was sure that it would be necessary to study nervous systems at all levels simultaneously!

The integrative work continued after Werner died, at the same Institute with 3 new directors, Heinrich Buelthoff, Nikos Logothetis and Bernhardt Schoekopf. It is now going to continue in the heart of University at the new CIN which we are inaugurating today. It is a great honor for Werner – as many of us will recognize -- especially since it comes from the University.

I will now mention some examples of his scientific work at these 3 levels, drawing mostly from my collaboration with Werner from '72 to '81, since I was fortunate enough to participate at a quite early stage in the work on the fly in Reichardt's group.

Let me open a brief parenthesis here – a more personal one. I came to Tübingen in '71 because of this 1-year offer from Werner shown in the letter below.

Table 3. *A copy of Werner's offer.*

I stayed in Tübingen for ten years in the Institute shown in the slide -- as it was back then ☺. It was a very happy period of my life
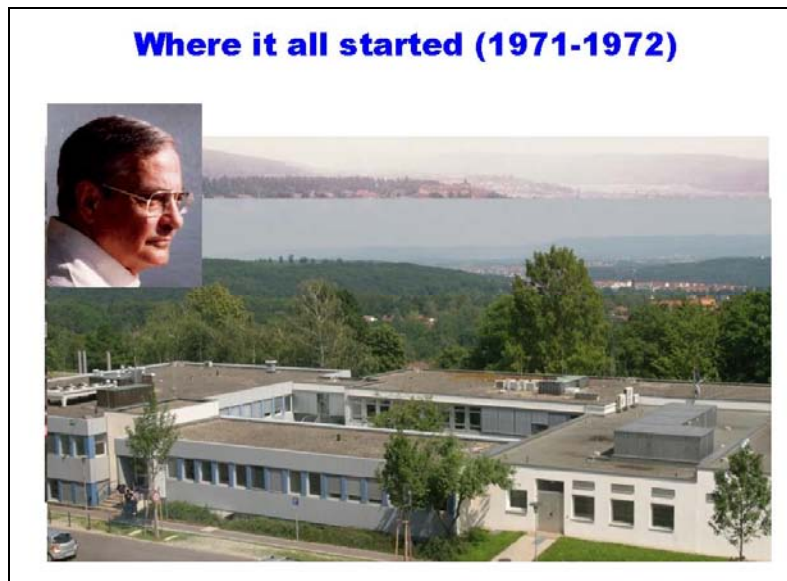
Figure 6. *The Max Planck Institute for Biologische Kybernetik at that time.*

It is difficult for me to speak about Werner Reichardt only as a scientist. He was the most influential person in my life, both scientifically and personally. He was first and foremost my scientific mentor. Werner was a man of integrity and courage who stood behind his convictions and was always ready to sacrifice his personal interests. He was a loyal friend whose word could always be fully trusted. He was a gentleman of science educated in the tradition of the great German schools. I always admired his intellectual honesty and his courage; he was somebody you could trust in the small and great needs of life. I will never forget the dinners with him and Baerbel at their house next to the Institute. I will never forget the long discussions with him in his office and at his home mainly about scientific work and sometime about his passion to make a difference in the politics of science and in the Max Planck Society – about which he cared deeply. Later, when I went to MIT, he became like a father for me. He was ""Uncle Werner" to my children, and his visits to Boston were always an occasion for happiness.

During the time I collaborated with Werner between '71 and '81 the experimental work on the fly's visual system, using behavioral and physiological techniques, led to experiments and theories and models at three levels of integrative neuroscience: the *phenomenological* theory of flight behavior, the *algorithms* for detection of motion and relative motion, and the underlying *neural circuitry*. I will describe briefly each one.

Table 4. *Examples of Werner Reichardt's work.*

Werner had discovered that flies fixate, in other words they fly towards small dark objects. He had used a sophisticated flight simulator in which a flying fly could be held fixed while its torque, measured by a very sensitive device, developed by his longtime friend and colleague Karl Goetz, controlled the visual environment, thereby simulating a free flight situation. In this way Werner was able to experimentally study and quantify the fixation behavior. He had also developed a model of it which we further extended into a quantitative description capable of accounting for the main features of fixation, tracking and chasing in flies.
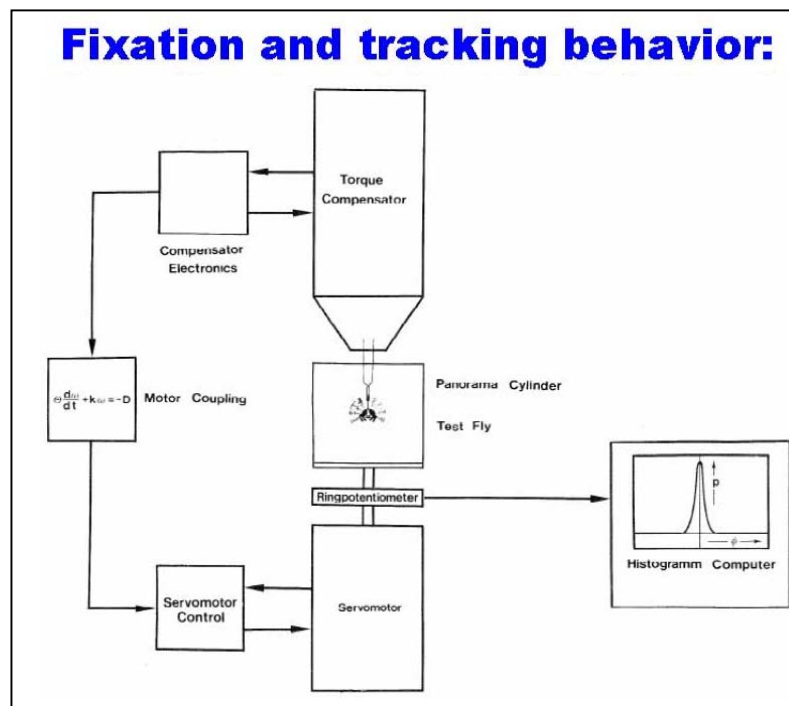

Figure 7. *Reichardt's closed loop flight simulator.*

- Fly can fixate and track small dark objects such as other flies.
- Werner discovered this behavior using a flight simulator developed by Karl Goetz and wrote equations to describe it
- Together we developed a quantitative theory of this visuo-motor control system based on stochastic differential equations that explained and predicted several of the experimental data.
- The equations could even approximatively predict the trajectory of a male fly chasing another fly (see Land and Collett, 1974; Weherhahn, 1979; Buelthoff, Poggio and Wehrhahn, 1980)!

The equations – derived from the experiments in the stationary setup I showed earlier -- could, in fact, predict in a satisfactory way the free-flight trajectory of one fly chasing another!

Here you can see the observed 3D free flight trajectory of a male fly chasing another fly (first studied by Land and Collett). Here you see the stereo pair of 2 seconds chase with the simulation of the chasing fly (arrows). It agrees very well with the real chase trajectory shown above.
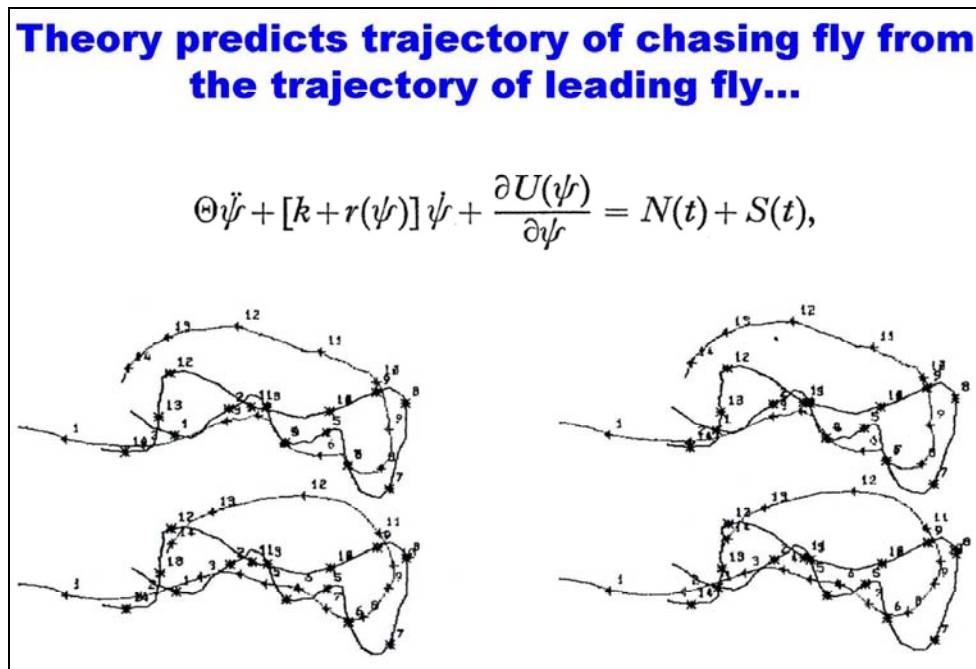

Figure 8. *Stereo plots of 3-D flies trajectories. The top traces show a chase of flies. The bottom traces show its simulation. They could be viewed with standard stereo-glasses. From Buelthoff, Poggio and Wehrhahn, Z. Naturforsch. 35 c, 811-815 (1980)*

Early on, long before I arrived in Tübingen, Werner, together with B. Hassenstein and D. Varjú, had worked out the properties of motion detection in the beetle. This early work is his best known contribution to science. It has been described beautifully by Bernhardt Hassenstein – I highly recommend Hassenstein's paper -- and others. The optomotor response of the beetle *Cholorphanus* is the animal's tendency to follow the movement of the visual surround to compensate for it. The beetle was glued to a rod so it could not

move its body, head or eyes relative to the surround, but could express its behavior by rotating a 'Y-maze globe' under its feet. The rules of the optomotor behavior are summarized in a precise, quantitative way by the correlation model on the right, by now known as Hassenstein-Reichardt model or simply as *Reichardt detector*. The strict mathematical treatment of this model led to many <u>counterintuitive</u> predictions, which were, one by one, experimentally verified. They hold true in many species and in many types of neurons. The theory's influence can hardly be overestimated. It inspired work on motion vision in many animals, including humans. Thus, the Hassenstein-Reichardt model set the standard for how researchers thought about visual motion detection and how they designed experiments. In a more general sense, it introduced mathematical techniques and quantitative modeling to biology.

Sophisticated visual stimuli were presented to the beetle Chlorophanus, held by its back in a fixed position while climbing on the grass-like ribs of y-maze globe. The frequency of left/right choices revealed its intended turns. This way it could be shown that its motion detector required at least two input sensors looking into slightly different areas of the visual field. These sensors are excited in sequence by pattern edges moving by. If one input signal is delayed appropriately the two signals become synchronous for the "preferred direction" of pattern motion but strongly asynchronous in the opposite direction. Multiplication of the two signals and time-averaging of the result yields a direction-specific motion signal irrespective of the polarity of the change of brightness achieved by a moving object. This process corresponds formally to an autocorrelation of the input signal. Hence the name "correlation-type motion detector". Since the beetle responds also to motion in the opposite direction, two antisymmetric detector subunits must be combined and their outputs subtracted. This step eliminates unspecific signal components of the subunits and thus increases directional selectivity of the motion detector.
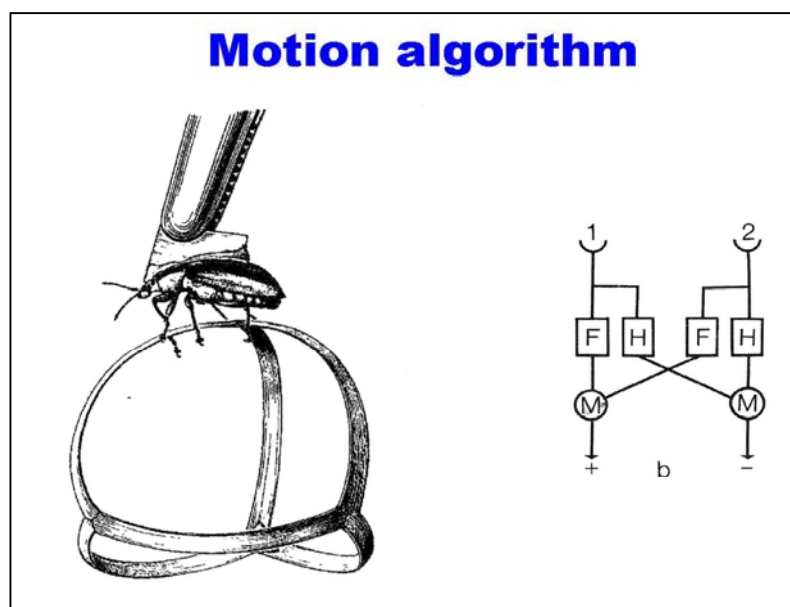
Figure 9. *The beetle Clorophanus and **b**. Reichardt's motion detector.*

Thus this older work described the algorithm for motion used by the beetle and other insects such as the fly and also primates. Beautiful work on motion perception was done at different levels of neuroscience by Kuno Kirschfeld and Karl Goetz and Valentin Braitenberg.

Motion algorithm: the beetle and the fly

- The beetle follow the motion
- Each photoreceptor sees only an alternation of dark and light: how is motion computed?
- Reichardt and Hassenstein (and Peter Kunze) found the rules used by neural circuits. The algorithm (refined by D. Varju) explained many data : *Reichardt detector*.
- The same model describes motion perception in flies: beautiful papers on anatomy, optics and organization of motion perception by Braitenberg, Kirschfeld, Goetz.
- An equivalent ("energy") model describes motion cells in primate cortex.
- A form of it has been used by Matsushita in the first chips to stabilize videocameras (see also Buelthoff, Little and Poggio, Nature, 1989)

Table 5. *The second level of integration: Motion algorithm.*

In 1977 Reichardt discovered that flies use motion discontinuities in the visual surround to distinguish objects from the background. Flies turn towards a single, randomly textured stripe in front of an equally textured background, but only as long as it moves relative to the ground.

Part of the theoretical and experimental work between 1974 and 1978 was devoted to characterizing the properties of the algorithm used by the fly's visual system to detect relative motion in a way similar to what Werner had done 35 years earlier in the case of motion detection. The interplay of experiments and theory led to a class of model which could be characterized as a form of nonlinear lateral inhibition between motion detectors.

I will not speak about our work on characterizing the algorithm for relative motion detection. Instead I will focus on the effort after '77 at the level of circuits of neurons. Together with Klaus and Werner we derived a skeleton model of a neural circuitry and refined it further through quantitative experiments. I will not explain it but for the experts it is a lateral inhibition network that finds and enhances discontinuities in the motion field, such as the discontinuities generated by an object moving relative to the background.
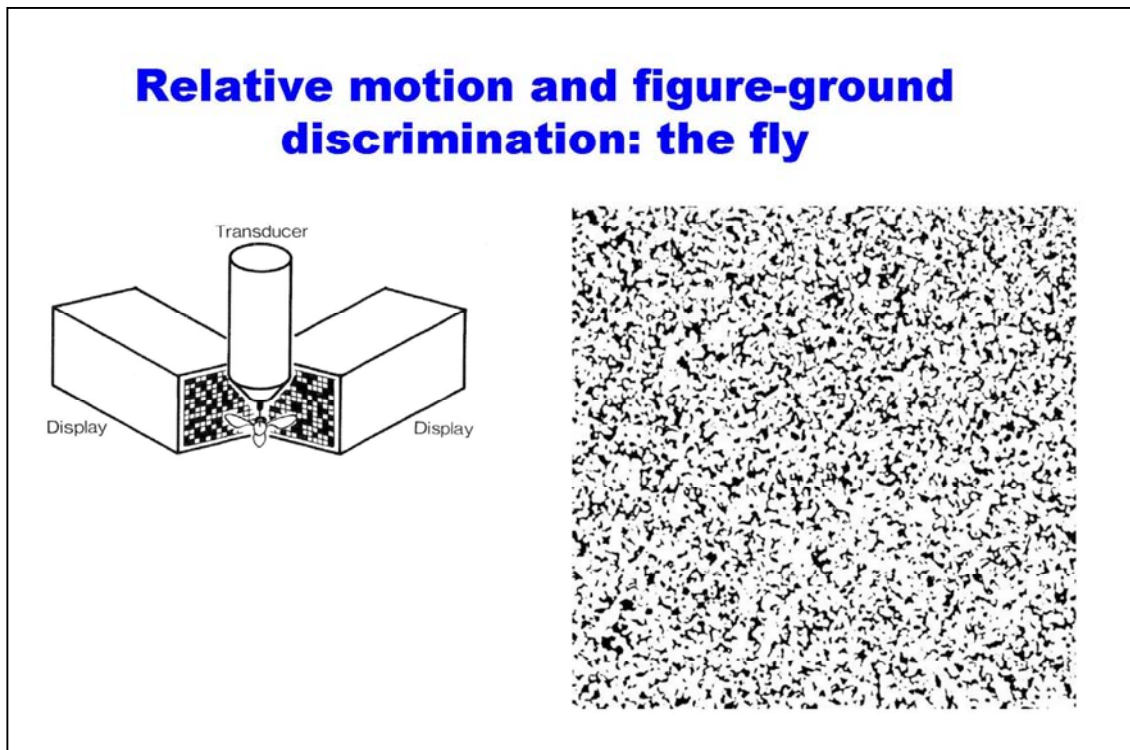
Figure 10. *Work by Werner Reichardt (with T. Poggio, K. Hausen and later with M. Egelhaaf and A. Borst).*

At this time, K. Hausen and the late R. Hengstenberg had developed the techniques for intracellular recording and staining of motion-sensitive neurons in the fly brain. These neurons correspond to some of the boxes in the previous diagram of our model of the neural circuitry. Here are two such neurons in a paper by Axel Borst. Thus the original model and experiments led to a series of remarkable physiological experiments by Werner, Martin Egelhaaf and Axel Borst, which were broadly consistent with the gross outline of the model while revealing its precise anatomical and biophysical features. So… they could study the *actual* neural circuitry of motion perception and figure/ground-discrimination.
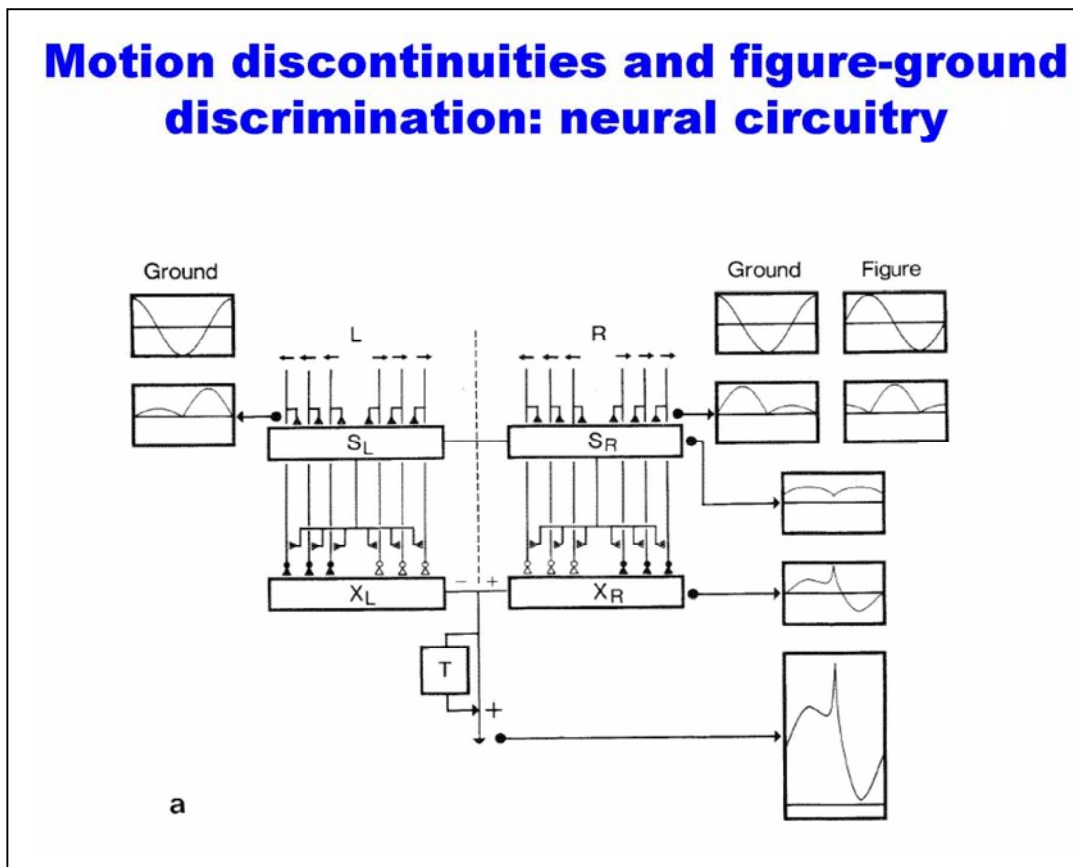
Figure 11. *From the original paper by Reichardt, Poggio and Hausen, (1983).*

The interplay of theory and experiment laid the groundwork for the development of a whole class of models characterized by special forms of non-linear lateral inhibition between motion detectors. This work took the problem of motion discontinuities to a further stage and described the neural circuitry and biophysical mechanisms responsible. This has led to a series of remarkably productive physiological experiments by Martin Egelhaaf and Axel Borst, substantiating several of the basic predictions of the model while revealing its precise anatomical features. In particular, M. Egelhaaf discovered figure-detection neurons that are inhibited by wide-field motion of the visual background. Thus we could study the actual neural circuitry of self-motion perception and figure/ground-discrimination. The close interplay between behavioral analysis, theory and neurophysiology guided this work very efficiently and led to a profound understanding of these perceptual processes, very much as Reichardt had suggested way back in 1965.
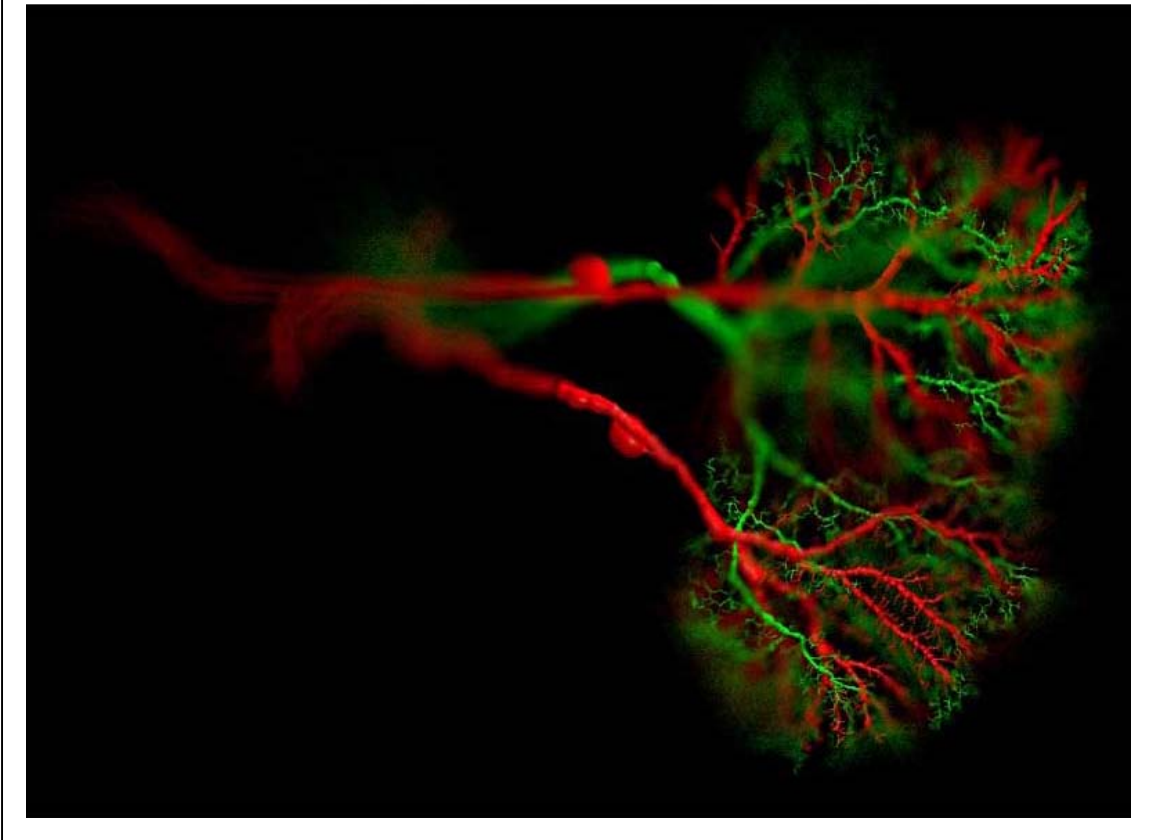
Figure 12. *The photograph shows a vCH cell (green), connected to an HSS and an HSE cell (red). (From H. Cuntz, J. Haag and A. Borst, 2003)*

In summary, the close interplay between behavioral analysis, theory and neurophysiology – integrating all levels of neuroscience -- guided this work and led to a profound understanding of these visual perceptual processes, very much as Reichardt had suggested way back in 1965.

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