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In Memoriam Reprint of "In Memoriam" Henk Spekreijse (1940–2006) *



Henk Spekreijse suffered a fatal heart attack in Amsterdam on 20 October 2006. From 1991 to 2004 Henk was chairman of the board and editor in chief of *Vision Research*. Under his guidance the journal flourished and expanded to 28 issues per year. He worked with Elsevier to introduce and fund the pre-ARVO special symposia and initiated the publication of special issues of the journal, which bring together scientists from different disciplines to discuss questions of high interest in vision research.

In parallel with his life in research he played a major administrative role in the international development of vision research. Within Europe, he was instrumental in establishing the Netherlands Ophthalmic Research Institute as the focus of collaboration between sixteen ophthalmology departments in the Netherlands and Belgium, and served as director of research at that Institute.

Spekreijse has long been recognised as one of the outstanding visual researchers of his time. His was a large laboratory, scientific home over the years for many post-doctoral fellows and over fifty Ph.D. students. A remarkable number became well-known scientists with their own laboratories. In 1985 he was elected Fellow of the Netherlands Royal Academy of Arts and Science. In 2003 a

der Tweel. At that time the Dutch Ph.D. examination was an ordeal. Dressed in formal black tie and flanked by two supporters also in formal black tie, Spekreijse stood in a 17th-century church before several hundred attendees, including black-gowned professors from many Dutch universities. As an extra twist the Dutch system

Lion of the Netherlands.

from many Dutch universities. As an extra twist the Dutch system required the candidate to add to the thesis a list of several nontrivial "propositions" that had no relation to the thesis topic. The outstanding scientific merit of the thesis research having soon been established to everyone's satisfaction, professorial friends of van der Tweel relaxed by grilling Spekreijse on his propositions, including one on the strange mechanical properties of tomato ketchup and a second on what might be revealed by cleaning one of Rembrandt's most famous works; the edge to this grilling was that the supervisor was expected to resign his chair if his student failed the examination.

Festschrift organized by his ex-students was unexpectedly inter-

rupted by the entrance of a representative of the Queen who in-

ducted an astonished Henk Spekreijse as Knight in the Order of

der the inspiring supervision of late and much missed Henk van

After receiving his master's degree in experimental physics from Delft University, Spekreijse carried out his Ph.D. research un-

The wide distribution of over one thousand copies of Spekreijse's thesis, published as a book in 1966, immediately established him as a pioneer in the application of nonlinear systems

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analysis to electrophysiology and attracted the attention of several influential scientists: doors were opened. The importance of nonlinear analysis has been expressed by Reichardt and Poggio (1981) as follows: "every nontrivial computation has to be essentially nonlinear, that is not representable (even approximately) by linear operations".

Spekreijse spent 1967–1968 at the Naval Medical Research Institute in Bethesda, Maryland, where he learnt from H. Wagner and M. Wolbarscht the technique of recording single unit activity from the isolated fish retina and collaborated on several published studies on the colour coding of the intra-retinal action potential and (with Norton) on the colour coding and receptive field organization and dynamics of the retinal S-potential.

On his return to the Netherlands Spekreijse's progress within the distinguished and highly competitive biomedical community was rapid: from Ph.D. in 1966 to reader in 1971 and in 1977 appointed full professor of visual systems analysis in the Laboratory of Medical Physics at the University of Amsterdam.

In 1965 Spekreijse and van der Tweel had reported that, in humans, monocular stimulation with sinusoidally modulated light of frequency F Hz produced an electrically evoked response, recordable from scalp electrodes, and that the response was an almost pure sinusoid of frequency 2F Hz combined with a small F Hz component. By definition, the 2F component was produced by a nonlinearity. The addition of sufficient noise (an "auxiliary signal") to the monocular sinusoidal flicker abolished the 2F Hz response component, sparing the F Hz component so that the visual system behaved approximately linearly (the linearizing phenomenon). In his Ph.D. thesis, Spekreijse described the nonlinearity as an asymmetric rectifier. This proved to be an innovative concept: rectifiers feature in models of the visual and auditory pathways proposed by many laboratories over the following forty years. By using a sinusoid as the auxiliary signal in his thesis work, he introduced a two-sinewave approach to nonlinear systems analysis and was able to analyze the human visual system into two parallel pathways, each consisting of a sequence of linear and nonlinear stages. In subsequent work on goldfish retina and monkey LGN, Spekreijse and colleagues identified the rectifier-like characteristic with the behaviour of ganglion cells.

From his return to the Netherlands in 1968 until his retirement, Spekreijse continued to be active in research on visually evoked electric (and later magnetic) responses of the human brain, collaborating with Estevez, Dangelie, Regan, van den Berg, van der Tweel and van Dijk on a wide range of studies including interocular suppression, brain responses to luminance and chromatic contrast, stereoscopic depth, the onset and offset of motion, colour vision, colour blindness, texture segregation and audio-visual interaction. With Munck, Maire and van Dijk he published sophisticated mathematical approaches to the source location of evoked electrical and magnetic brain responses.

Building on his experience in the Bethesda laboratory, Spekreijse established in Amsterdam a laboratory for retinal research that was soon noted internationally for its combination of productivity, high level of scientific insight and technical skill. There he collaborated with colleagues, including van den Berg, van Norren, Schellart, van Dijk and Kamermans. In single-unit studies of goldfish retina and on monkey LGN they introduced to single-unit electrophysiology the concept that for strongly modulated flicker stimulation the addition of an auxiliary signal can cause the essentially nonlinear stage expressed at ganglion cell level to mimic linear behaviour and found that even neural noise can produce this linearizing phenomenon for near-threshold stimuli. This concept is important, not only for a deeper understanding of information processing at cellular level but also in general for the interpretation of psychophysical data in humans. Spekreijse and colleagues developed a realistic model for the feed forward/feedback pathways between cones and horizontal cells in goldfish retina, showed that this organization provides a physiological basis for the perceptual phenomenon of colour constancy, and found that the phenomenon is established already at the level of the cone pedicle.

During the last few years Spekreijse and colleagues Lamme, Super, Roelfsema, Khayat, Landman, Scholte, van der Togt and Witteveen published in the highest-impact journals a remarkable number of papers on higher visual processes in primates. By combining electrophysiology with psychophysics in alert behaving monkeys they made the important discovery that object-based attention expresses itself by increased neural firing at the level of the striate cortex. They showed how the synchrony of firing in V1 neurons relates to visual detection and contour grouping, and discovered neural correlates of the visual stability of the perceived world across saccades. By recording the magnetic field of the human brain (MEG) they found a putative physiological basis for awareness, and by combining MEG with fMRI discovered neural correlates of scene segmentation.

Spekreijse himself wrote that his main research interests "concern the introduction of findings from basic research into ophthalmological and neurological practice" and indeed from the moment he became a professor of medical physics the formidable scientific expertise and technical facilities of the department were available to support and strengthen clinical research carried out in the Faculty of Medicine on patients with a wide variety of ophthalmological and neurological disorders. He was closely involved in clinical diagnosis, largely through his supervision of the Electrophysiology Laboratory of the Amsterdam University Eye Clinic. He had a long-term interest in the development of non-invasive techniques for monitoring the visual status of patients, especially of pre-verbal infants who are notoriously difficult to test. To that end his research group's lengthy and laborious work on the development of visual evoked potentials from the age of a few weeks up to ten years provided physicians with a normal baseline of infant and child development. Without that baseline the technique would not have enjoyed its current level of clinical use. More recently Spekreiise worked to attract the large funding and technical support required to apply the non-invasive brain imaging techniques of functional MRI and magneto-encephalography to the assessment of neonates and premature babies-truly an example of the most advanced technology and scientific skills being applied to the benefit of ophthalmological and neurological patients.

Over the years, Spekreijse's laboratory was host to many visiting scientists, only some of whom were already well established. He helped to establish the reputation of many young researchers whose home country provided only slim support for science. In addition to research experience, the generous after-work hospitality of Henk and his wife, Yvonne, was a practical realization of the internationalization of scientific research that has been appreciated by many throughout the world.

Spekreijse played an important role in enhancing the international visibility of Dutch biomedical research, and to that end introduced innovations in research training. Within the Netherlands he was active in many administrative and planning issues concerned with scientific facilities and funding. He was forceful and determined in bringing about changes that he considered to be for the future good of neuroscience and biomedical research in the Netherlands. But sadly, and to the dismay of his friends, some changes were not achieved without lasting personal cost. Without the unfailing support of Yvonne Spekreijse–van der Heyden through difficult times it is unlikely that he could have made the outstanding contributions to science and to his country for which he was widely respected and admired.

Henk and Yvonne had two daughters, Stephanie and Dieuwertje, who gave him many reasons for his quiet pride in them. During the last few years he and Yvonne took delight in their new roles as grandparents.

"What is most impressive about Henk's work apart from its consistent high quality is its breadth. He has made contributions at the highest level to retinal biophysics, human psychophysics, infant development studies, mathematical modeling, electric and magnetic evoked potentials, and single-unit recording in the visual pathway of anaesthetized and awake behaving animals" (Colin Blakemore). "... in 1969 I heard Dr. Spekreijse talk about his new use of nonlinear analysis. Over the years I have been continually amazed by Spekreijse's mathematical and scientific genius applied to many diverse problems in vision research. He is internationally recognised as one of the most outstanding vision scientists of his generation" (Bob Shapley). "I do not know any other person whose scientific contributions follow so closely the idea of ARVO to bring together basic neuroscience of vision and clinical ophthalmology" (Heinz Waessle).

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