



# The History of Neuroscience in Autobiography Volume 5

Edited by Larry R. Squire

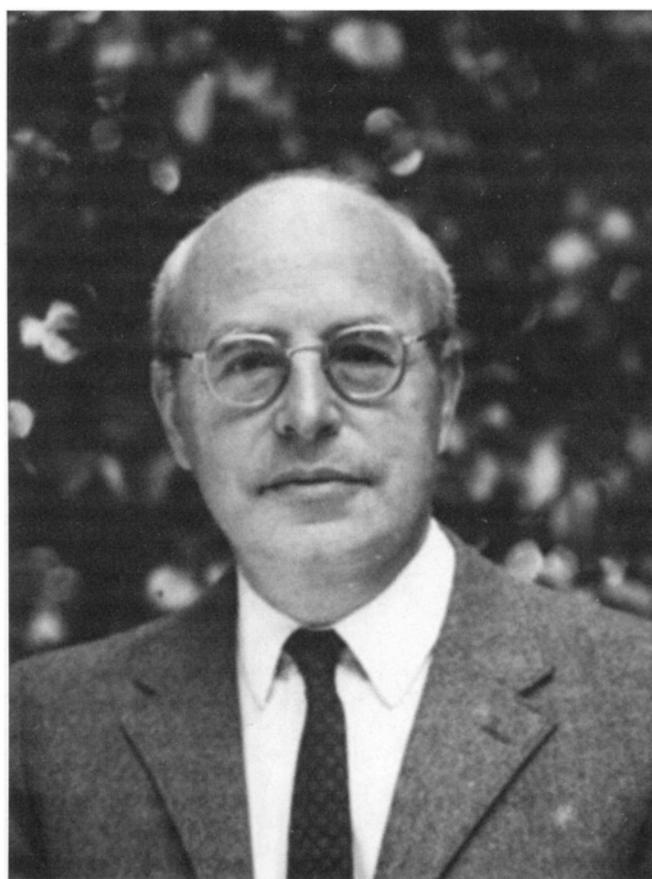
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Gerald Westheimer

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# Gerald Westheimer

## **BORN:**

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May 13, 1924  
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Sydney Technical College (Optometry Diploma, 1943)  
University of Sydney B.Sc.  
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Sydney Technical College, Fellowship Diploma,  
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Faculty Member, Schools of Optometry,  
University of Houston, Ohio State University,  
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Fellow, Optical Society of America (1963)  
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Tillyer Medal, Optical Society of America (1978)  
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Fellow, Royal Society of London (1985)  
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Ophthalmology (1986)  
Prentice Medal, American Academy of Optometry (1986)  
Bicentennial Medal, Australian Optometric  
Association (1988)  
Honorary D.Sc., University of N.S.W. (1988)  
Honorary D.Sc., SUNY (1990)  
Ferrier Lecturer, Royal Society (1992)  
Fellow, American Academy of Arts and Science (1994)

*After clinical practice as an optometrist in Sydney, Gerald Westheimer worked to attain a deeper understanding of human vision. He elucidated the neural control of eye movements and ocular accommodation by using the systems approach to map motor responses in the human and subsequently employed neurophysiological techniques to outline midbrain and brainstem circuits in the nonhuman primate. Measurement of the optical image of the eye led to the investigation of the retinal and cortical circuitry involved in the processing of spatial visual information, including the analysis of acuity, stereopsis, and contextual effects. In 1989 he set up and became the first head of the Division of Neurobiology at Berkeley.*

# Gerald Westheimer

**N**euroscience as a career option or even as an undergraduate or graduate major was not available to people of my generation; most gravitated to it after studying medicine or occasionally biology, physics, or psychology. For me, the path was even more indirect.

## Berlin

The critical juncture was a law enacted to take effect on April 7, 1933, a little more than a month before my ninth birthday. In it, the new German regime, no more than a few weeks old, mandated the removal from office of all academics and civil servants of Jewish descent, with almost no audible dissent from the rest of the university, legal, and professional communities. Having skipped a grade and been identified as promising, I had just been enrolled in the Goethe Gymnasium in the western part of Berlin, where our family—parents and a brother 2 years older—lived. Whatever schooling I might have, it was agreed, should prepare me to earn a living outside the confines of institutions. The subsequent emigration experience only served to reinforce this conviction.

Although my maternal grandfather, Sanitätsrat Dr. Moritz Cohn of Breslau, was a pediatrician, the family on both sides was almost exclusively business people. On my father's side, the family had been residents of a region near the Rhein in northern Baden for hundreds of years. On both sides they regarded themselves as Germans—all males had served in the Kaiser's Army during World War I—and at the same time consciously as Jews, fully aware of the limitations of their place in German society. Hence the growth of the Third Reich and its acceptance by the German people was a disappointment to them, but, deep down, not a total surprise.

I did not last long in the Goethe Gymnasium. My father's status as a veteran would have allowed me to stay but, even at this early stage of the Hitler regime, an atmosphere of anti-Semitism, albeit still genteel, pervaded the classroom teaching. Hence my parents decided to transfer my brother and me to the Mittelschule in the Grosse Hamburgerstrasse, a venerable Jewish institution. It required a half-hour train commute each way, but in those days, that was regarded as safe even for a 10-year old. Class size was large, up to 60 per form, teachers were barely competent, and there was little in the curriculum to enlarge the mind of the alert

pupil, let alone challenge it. I still have my semiannual reports, which show undistinguished grades, not because of lack of ability, dedication, or diligence, but because tests were haphazard and students were essentially anonymous. Even in subjects in which I showed proficiency later, such as music and mathematics, the grades were mediocre.

I have no happy memories of my preteen years: The shadow of the Hitler regime loomed and the middle-class upbringing did not expose me to the glittering atmosphere that is often identified with Berlin. However, we had music lessons, participated in sports, and during vacations were dragged through museums. I would not be surprised if it were shown that in those days Berlin had more specialty museums than any other city in the world. At home, my academic bent, although not exactly fostered, was at least mildly encouraged, especially because my elder brother seemed at an early age to acquiesce to carry on the family business, which in fact he did into his 80s.

As long as I can remember I was a rapid and avid reader and seem to have developed, without any overt encouragement from parents, teachers, or other role models, a knack for effortlessly absorbing and sifting printed material. Thus, by the time of my bar-mitzvah I had figured out for myself the differing rational contents of science and religion—the latter loomed large in the home and school environment—and had my mind made up to become a scientist. And naturally the ultimate boundaries of the cosmos fascinated me. Two more factors entered to seal my future career as a scientist. Even then I seem to have had an attraction for the empirical aspects of acquiring scientific knowledge, although actual handicraft or working with gadgets or tools played absolutely no part in my upbringing. Curiosity about telescopes and optical astronomy, and, in an entirely different sphere, the need for optical correction of my incipient myopia, combined to direct my interest to vision. When I was 12 or 13 and had to write a school essay about a famous person, I chose Helmholtz, having checked out his *Popular Scientific Lectures* from the school library.

By about the same time, my parents had understood the political trend and decided to emigrate. The range of destinations had become limited. Presciently they did not consider other parts of Europe. The United States was then no longer an option, because the avenues of entry—"affidavits" by relatives guaranteeing support—had been preempted by other members of the family. Middle and South America and Australia were possibilities. A most compelling chronicle of the topics around the dinner table of a middle-class German Jewish family at the time is given in Victor Klemperer's diaries but with the essential difference that our family had always been observant Jews, in both meanings of observant: obeying religious rules and remaining aware of the ever-present possibility of a dissonance arising from being both German and Jewish. Klemperer's trenchant account of the matters of concern in 1938 still resonate in my

mind: who emigrated where, to whom pets and house plants were passed on, what was said on terse postcards from ships or from Chile or perhaps the Dominican Republic, and what new regulations had been promulgated to make living conditions and emigration ever more difficult.

During 1937, my parents submitted an application for immigration to Australia and, in one of the pivotal days in my memory, in March 1938, the certificate arrived from Canberra, allowing us entry to Australia. There followed several frantic months, severing business and personal ties, liquidating assets, selecting what to pack and what had to be left behind, arranging passage, and trying to scrape together the £200 Australian currency that had to be shown on entry. When it was all over, there was the glorious moment in the morning of August 26, 1938 when we sailed into beautiful Sydney harbor on the *R.M.M.S. Aorangi* to start a new life.

## Australia

In the 1930s, Australia had a population of about 7 million who regarded themselves unreservedly a part of the British Empire. It differed from England in that a lack of aristocracy and upper classes made it an egalitarian, live-and-let-live society. The 5000 refugees from Germany and Austria were accepted, although without any particularly warm welcome. But the distinction between Berlin and Sydney in 1938 could not be starker: The weather, scenery, and living conditions, instead of being dingy, repressive, and cold, were inviting and stress-free. Still, a wrenching change took place in our personal life: From being schoolboys, embedded in a structured school and family situation, my brother and I, aged 16 and 14, were now the main conduit to our new world, especially because we were beyond compulsory school age. We quickly learned English and found employment, providing an important fraction of the family income before our parents could eventually establish themselves. One should imagine the situation in which the adolescent sons are the ones to whom a family's interpretations of the surrounding language and culture devolved!

Gradually things settled and before long my violin lessons resumed. My father started anew in the leather business, but his health deteriorated and he succumbed to a heart attack in 1941 at age 57. My mother carried on as best as she could until my brother was discharged from the Australian army at war's end.

While working full time as an office assistant to supplement the family income, I enrolled in an evening course that, because I was left essentially to my own devices, allowed me to achieve high-school equivalency status at age 15. Full-time study at the University of Sydney, with its 3000 students in the faculties of Arts, Science, Medicine, Dentistry, Engineering, and Agriculture, was beyond reach then. But there was a less prestigious institution, the Sydney Technical College with evening courses in many

subjects. Its most advanced offerings were 4- to 6-year part-time diploma courses for high-school graduates who had to have concurrent employment in the area of their studies. Subjects ranged from chemistry and various branches of engineering to architecture and optometry. Nothing could have been a better fit to my then vista and intellectual aspirations. Here was an area that closely matched my interest in optics and vision. It also satisfied the firm conviction in my world that one's occupation should allow an existence independent of government and institutions, formed by the German law of April 7, 1933 and confirmed by the difficulties of former academics and professionals to establish themselves as immigrants in Australia.

Thus, although still 15, I enrolled in the optometry diploma course at the Sydney Technical College and sought the required employment as an optometric assistant. Mr. E.J. Jackson, who had a working-class practice near Central Railway Station in Sydney, hired me, and the course of my career was set for what could have been the rest of my life but turned out to be the next 11 years. I easily took to the study and practice of optometry, completed the diploma course with honors and the college medal, and was offered a partnership in the practice. This had to wait for 2 years until I became legally of age and was eligible for registration as an optometrist in the State of New South Wales, a status I have meticulously maintained ever since. In due course I was elected a Fellow of the Institute of Optometrists (FIO) and became active in the Australian Optometric Association, being named state delegate to the national convention in 1951. I still have the warmest recollection of my years building a successful clinical practice of optometry in Sydney, with its beautiful scenery, sunny climate, and quality of life. Mr. Jackson was not only a generous employer and later partner but also a dedicated rationalist and reader of Marxist literature. His analysis of social and political affairs provided valuable insights that were not available from standard news sources.

Below the surface of this smooth career path, however, agitated another element of my mind, the one that had led me to read Helmholtz's popular scientific lectures as a schoolboy. My day job was dealing with optometric patients in a far corner of the earth, but I kept on reading voluminously and wondering about science. One quickly recognizes that clinical literature, although at its best fully valid, is different from science. I felt that a full understanding of the eye and the sense of vision needed a deeper approach and not one that could be achieved by merely enlarging one's clinical repertoire through, for example, studying ophthalmology. But how to go about that? Australia in the 1940s was intellectually a backwater when it came to anything beyond undergraduate or first professional training, be it in the arts, sciences, humanities, or health professions. No resource person was available for counseling or as a role model; my scientific career had to be my own creation.

I had made a start by adding to the optometry curriculum, as electives, the mathematics and physics courses taught to engineers at the college. Then, while learning to be a clinician, I had what was no less than an epiphany. On an occasional visit to the Sydney Public Library, with its magnificent reading room, I came across the paper by Hecht, Schlaer, and Pirenne (1942) examining the limitations placed on vision by the quantal nature of light. In the transition from preclinical science to actual clinical work one has to come to grips with the fuzziness of the findings on patients. The highlight of the paper by Hecht et al. to a budding clinician was not so much that just a few photons sufficed to set off a visual response in the dark-adapted human retina, as the claim that the variations of thresholds were due to inherent variability, not of the biological apparatus, but of the physical stimulus itself; the Poisson distribution that a very small number of quantal events obeys. A vista of reductionism opened, although at the time the word was not used, and my career goal was set. It was encapsulated in the title of a talk I gave to the Institute of Optometrists "Physics, Physiology and Vision," and which later became the motto of the *festschrift* for my 65th birthday edited by Suzanne McKee and Ken Nakayama (1990).

What followed was the implementation of the program, as best as could be achieved in Sydney at the time and without disrupting, at the least for the next several years, the placid flow of developing and maintaining an optometric practice. I enrolled in the Faculty of Science of the University, studying part-time to graduate with a Bachelor's degree, majoring in mathematics and physiology/biochemistry. Then I completed the full sequence of diploma physics courses at the Technical College. There was the possibility of working toward a master's degree in physiology at Sydney University, but I was not accepted. On the other hand, one could submit a thesis to the Sydney Technical College for a higher diploma, the fellowship, and in due course I completed, without help from anyone, a 110-page thesis "Studies in the Optics of Contact Lenses," which duly led to the award of the first higher academic qualification in Australian optometry. Rediscovering the Gaussian theory of expanding multiple surfaces by a matrix formulation and then applying that to the contact lens/eye combination was a source of great satisfaction.

Then what? I had exhausted the research possibilities open to me. One did not know that in just a few years Australia would house world-class neuroscience institutions led by Eccles in Canberra and Bishop in Sydney. Eccles was still in Dunedin, and Bishop was at the point of returning from his postdoctoral studies at University College, London. The very best graduates in mathematics, physics, and chemistry of Sydney University were sent off to England, usually Oxford or Cambridge, for graduate study, but there was no such tradition in biology. There was no one to turn to for advice, let alone to provide an introduction to a research institution around the world.

Unlike most Australians, I was looking to the United States rather than Great Britain. But the many letters of inquiry to graduate schools yielded nothing positive; American universities were awash with graduate students under the GI Bill and admission officers found little indication of outstanding promise in my case. But there was one exception: Professor Glenn A. Fry, director of the optometry school at the Ohio State University, responded offering me admission and a teaching assistantship valued at \$1200 a year. Fry was on the map as a vision scientist, and I decided to accept. Consequently, I obtained a student visa to enter the United States, severed my connection with Mr. Jackson, booked a one-way flight to Columbus, Ohio, packed the violin, a few books and some clothes, and flew across the Pacific on a British Pacific Overseas Airlines DC-6 in September 1951. My fate turned out to be similar to many young Australian scholars, scientists, and artists for whom the challenges of taking on the wider world of their calling outweighed their nostalgia for the sunshine and beaches of their homeland and who returned only occasionally as visitors. For me at least, Australia has remained an anchor and a place of refuge from the terrors of central Europe in the 1930s and 1940s, and I have never relinquished the status of a naturalized Australian citizen.

## Ohio

It took some adjustment to fit into the subdivision of the physics graduate program that was devoted to physiological optics and run single-handedly by Fry. The emphasis was on construction of mechanical equipment. More space and money was devoted to the workshop than to actual experiments, but Fry was interested in and exposed us to a wide range of topics. Ohio State was, for those days, a very large university; many of the younger professors were well-trained, alert to the latest developments, and upwardly mobile in their career track. This meant that it was not too long before they moved to the East or West Coast or perhaps to Michigan or Chicago. Three members of the psychology department, in particular, made a strong impression on my scientific development. Phil Ratoosh offered seminars on the research directions he had participated in at Columbia, where Clarence Graham continued the traditions and emphases of the Hecht school. He and his wife Mildred opened up in their home a cultural alternative, widening my vista beyond the limits of mid-century midwest state university life. Donald Meyer, a student of Harlow's at Wisconsin, taught a course in physiological psychology in which he placed inordinate stress (in early 1952) on the recent, yet not fully published findings, by Hodgkin and Huxley. By far the greatest intellectual influence was a graduate course taught by Paul Fitts, who had just joined the faculty after spending several years at the Wright-Patterson Air Force Base on human factors in the design and

operation of aircraft. Within a couple of months in the fall of 1951, he introduced me to Wiener's cybernetics, Shannon's information theory, and the systems approach. Using differential equations to describe, analyze, and model human performance was grist to the mill for someone who had chosen to expand his study from optometry to mathematics, physics, and physiology!

My years as a graduate student at Ohio State University in the early 1950s were characterized by the convergence of several trends. The basis for this was a dissatisfaction with the softness of biological findings on the part of a clinician, who had therefore subjected himself to rigorous training in mathematics and physics and had subsequently struggled in vain to find a secure footing in the mathematical biology of Rashevsky and Luneburg. This was coupled with exposure to the uncomplicated, "can-do," "hands-on," farm-boy-who-became-pilot persona of the many fine scientists who populated midwestern universities. And finally, there was the impact of the post-World War II reductionist thrust of cybernetics, information theory, and the systems approach.

These influences found immediate and full expression in my thesis research, in which the eye movements of the normal human were subjected to what may be called the classical systems analysis. With the subject's head fixed, a light point was moved in the visual field with the instruction to keep looking at it. This was the input. The output was the eye position, recorded with millisecond time and half-degree position resolution. The input/output relations were then studied to steps, pulses, ramps and sinusoids, then the standard array of stimuli and allowed conclusions to be drawn about the neural control. The oculomotor apparatus utilizes what engineers call a sampled data strategy. Over a few tens of milliseconds the retinal image position and motion is being analyzed and then one of a small repertoire of response modes entrained; all this is followed by error feedback and correction. But, even at this early essay into a physiological control system, a couple of flaws in the approach became glaringly evident. The first step in systems analysis is to construct a model in which simple differential equations are fitted to the data; however, right here significant nonlinearities showed up. More important was a realization that even the very foundation of systems theory seemed inapplicable. A favorite analytical tool in this area is charting the amplitude and phase of responses to rhythmic stimuli of constant amplitude and frequency. In the first few seconds of such a record I saw that, whereas the response amplitude remained constant, the phase delay changed relatively quickly from a beginning value of 120 msec down to zero or quite often even to negative values (i.e., there was a response before the stimulus). The only interpretation was that human subjects, instead of responding in the manner of the physical systems that were our models, quickly learn to anticipate and to "voluntarily" introduce a negative delay so that the moving target always remained on the fovea.

The thesis work, for which the only outside help I received was in the construction of apparatus, was accepted and the Ph.D. in Physics: Physiological Optics duly awarded. Paul Fitts, who was not a demonstrative person, seemed to like it and made me prepare for him a couple of dozen copies to pass around in the human factors community. Two papers prepared for what I then regarded as the principal outlet in the field, the *Journal of the Optical Society of America*, were promptly returned by the editor as unsuitable but finally found a home in the *Archives of Ophthalmology* (Westheimer, 1954a,b). They shared a fate of quite a few of my subsequent papers in being ignored for several years before their impact on the subject became evident.

In retrospect, the two journeyman years spent as a graduate student transmuted myself from an armchair scientist to an experimentalist constituted an important developmental stage. What had heretofore been a purely theoretical and intellectual take on science had to confront and accommodate the imperatives of tackling nature via an empirical route. It was as significant a transformation as the one that I underwent earlier when my innately contemplative personality was faced with the task of adapting to the needs of handling patients in a clinical setting.

## Academic Career in Optometry Schools

The newly minted optometrist-Ph.D. had to make a difficult decision: return to practice in Australia or try to make a career in academia? The prospect for the latter was not particularly propitious. Postdoctoral studies were not routine in those days. Physiological optics at Ohio State was a springboard for faculty positions in an optometry school or an eye department, but only a few of these had the scientific stature that fitted my, actually quite modest, aspirations. As it happens, a former fellow Ohio State graduate student, Charles Stewart, had just become dean of the newly founded optometry school at the University of Houston and persuaded me to join him. I thought I would give it try and deferred the decision whether to go back to Sydney. The year I spent in Houston was by no means wasted. Research was, of course, out of the question; there were no facilities (much less set-up money or grants) and the grueling teaching load did not leave much time. I had to prepare lectures in most of the preclinical sciences of the optometry curriculum, including optics, physiology of the eye, visual processing, color vision, eye movements, and binocular vision and, in addition, was responsible for the construction and design of apparatus for the teaching laboratory. An enormous amount of material needed to be sifted, understood, and made palatable to the small class of good-natured and at that time quite tolerant Texas optometry students. I am not sure that I would recommend this trial by fire to others, but for me it helped build an

invaluable knowledge base for future research. Moreover, teaching undergraduate courses is exceedingly good training for clarity, concision, and relevance of presentation.

During that year in Houston, I recognized that this position was not the one for which I gave up optometric practice in Sydney, although I had advanced my visa status from student to "green card" resident alien, which I have maintained to this day. The question whether to return to Australia or whether to pursue an academic career in the United States was decided in the latter direction by an offer of a faculty slot at Ohio State. Although the teaching load was not much lighter, at least there was a tradition and some facilities for research. I was assistant professor from 1954 to 1957 and was promoted to associate professor with tenure in July 1957. In a very significant development of my career, the Office of Naval Research (ONR) (working on the basis "Don't call us, we'll call you!") approached me to submit a proposal and in due course awarded a contract for \$10,000 for research in human accommodation, which was renewed in various forms for the next 12 years. This allowed some independence in research directions and also constituted a validation of a certain standing in American science. The Physiological Psychology branch of ONR, in those pre-National Institutes of Health (NIH) days, was the principal source of support of all the major laboratories in sensory processes.

From my earliest days, I was interested in optical aids to vision. Hence the teaching of ophthalmic optics was not only no chore but also the impetus to publish many small-scale studies over a 20-year span in optometric and optical journals. These studies related to such areas as magnification, field of view, and aberrations of spectacle, telescopic and contact lenses, and microscopes. It prepared me for the future research in the optics of the eye and ocular accommodation and, quite directly, led to being recruited to Berkeley in 1960, where a vacancy occurred in the School of Optometry caused by the retirement of their instructor for ophthalmic optics.

More immediately, in the middle 1950s, I immersed myself in a couple of theoretical issues. Teaching the subject of eye movement made me aware of the lack in the literature of a rigorous treatment of the kinematics of the eyeball rotating in the orbit in the manner of a ball-and-socket joint. Rotations of rigid bodies are not vectors, and therefore I took up the topic by first studying the classical treatise on rotating tops by Felix Klein and Arnold Sommerfeld and then applying the theory to the eyeball by means of quaternions, a higher form of generalized complex numbers that allows the handling of rotations. The paper "Kinematics of the Eye" was accepted by the *Journal of the Optical Society* within 2 weeks without any revision, a situation almost unique in my career as an author of scientific papers (Westheimer, 1957b).

A second area that had also been left untreated in the literature, because it could not be handled without some mathematical preparation,

was the generation of the optical image on the retina in a special situation called the Maxwellian view. In this mode of illumination a light source is imaged in the eye's pupil. Any target in the beam generates a diffraction pattern there, requiring analysis of retinal imagery in terms of coherent light, a topic that was to gain much prominence with the advent of lasers a few years later. The calculations were needed to specify the retinal image in an out-of-focus eye, which constituted the stimulus for accommodation responses. The theoretical work led directly to the realization that one can create retinal images that were independent of the refractive state, in effect bypassing the eye's optics. To put the thought into practice it was necessary to generate twin coherent beams, whose separation in the plane of the pupil determines the spacing of interference fringes in the image space of the eye. Not too many years later this could be easily accomplished with a HeNe laser. But when I tried to do this in 1957, I spent months getting it to work. Light from a very bright arc source had to be focused on a pin-hole less than 0.1 mm in diameter and then passed through an interference filter. Gratings and variable magnification devices enabled the spatial frequency to be changed and modulation thresholds to be obtained on normal observers, including a measure of retinal resolution with 100% contrast. Thus, a true estimate of the resolving capacity of the retinal mosaic was arrived at. This disambiguation of optical and retinal factors of visual acuity had been a long-term goal in physiological optics; hence I proudly wrote this up for the *Journal of Physiology*, then the criterion outlet in neuro- and sensory physiology, where it was soon accepted (Westheimer, 1960), not without very insightful comments and suggestions from the referees (who I later learned to have been Bernard Katz and Eric Denton). One of the most prescient of these was the request for me to explain to the readers what I meant by the phrase in the discussion that "the results might foreshadow a Fourier approach to spatial vision." It made me think through the consequences of such an approach and explicitly reject it. Thus, when the Fourier theory of vision swept through the vision community a decade later I was immune to its temptations and could leapfrog to areas of spatial visual processing that it could not encompass.

Under the ONR contract I had studied fluctuations of accommodation and as a result I got together with Fergus Campbell and spent a sabbatical at the physiological laboratory at Cambridge University. Fergus, together with his then graduate student John Robson, had built an automatic infrared optometer, and we set about analyzing the oscillations that the instrument revealed. This involved many control experiments, such as opening the loop, examining odd and even errors, and comparison with pupil and finger tremor (Campbell, Robson, and Westheimer, 1959). The fluidity with which this lab would solve problems of instrumentation and procedure, utilizing off-the-shelf and war surplus components, was inspiring and a welcome counterweight to the elaborate and cumbersome metal

constructions featured in Fry's laboratory. John Robson, barely out of his teens, quick-witted and intellectually arrogant, had a deep intuitive understanding of electrical circuitry. Together with Fergus, more experienced in medicine, ophthalmology, and experimental physiology, there was no technical problem that could not be solved in an afternoon. The outcome of this collaboration was a series of papers in which the human focusing responses were subjected to much the same systems analysis that I had used in eye movements, Stark and Sherman (1957) in the pupil, Schade (1956) in human spatial vision, and DeLange (1954) in flicker perception. It was the decade of systems theory, and because new technical resources for generating, modulating, and recording light beams were employed, major characteristics of human focusing responses, such as latency and speed, were revealed for the first time (Campbell and Westheimer, 1960), although some of the details would soon be overwhelmed by the nonlinearities brought to light by more extended experiments. Our interest, however, was chiefly on the light the findings could throw on the neural control apparatus. As in so many similar situations, a necessary preliminary step to charting the internal physiological apparatus is the exposition of the actual capability of the organism. And here, also, a full understanding of the central neural circuits for the eye's accommodation is still a work in progress, almost 50 years later.

Collaboration with Fergus Campbell was so successful that I asked him to work with me on the corollary of the retinal image experiments that had just been published. If in ordinary vision we cannot bypass the eye's optics, why not use the optical and electronic know-how between us to characterize the quality of the retinal image? The question was urgent because the literature was deeply divided on the issue. Direct image quality measurements in animal eyes gave results that were totally at variance with the single human study, by Flamant, in which the ophthalmoscopic image of a slit was analyzed by a rather cumbersome photographic technique. So Campbell and I, using narrow filament lamps, a photomultiplier and oscilloscope, obtained a good estimate of the eye's line-spread function (Westheimer and Campbell, 1962). It validated Flamant's results, accorded rather well with expectations from visual acuity and the retinal mosaic, and formed the basis of later work in Campbell's lab, which provided definite data on the optical image on the retina that held up for decades. In the early 1990s, I returned briefly to the optics of the eye in collaboration with Junzhong Liang, the most gifted of the new generation of researchers in ocular optics. We developed an ingenious method of conditioning the wavefront of light from a laser source entering the eye to generate patterns for measuring retinal resolution more sophisticated than interference fringes (Liang and Westheimer, 1995). Liang went on to found the new discipline of adaptive optics, which is about to replace all the traditional approaches to the optics of the retinal image (Westheimer, 2006).

## Cambridge

Nothing I experienced in Australia, then a traditional British country, or in American universities, had prepared me for the cultural climate awaiting me when I arrived in Cambridge in early January 1958 and stayed in St. John's College. The buildings were ancient with high ceilings and thick walls, dreadfully cold in winter, and the bathrooms were across the courtyard; yet there were servants, waiters at meals, porters with top hats at the narrow entrance gates; fellows, usually bicycling everywhere, wore academic gowns and ate sumptuous meals at high table but only after a Latin grace was recited. Afterward there was port in the Combination Room where I could, and occasionally would, sit next to Paul Dirac, Fred Hoyle, or Harold Jeffreys, conversing on topics of mutual interest. In the physiological laboratory in Downing Street there was a traditional afternoon tea, separately for the academic staff and for the technicians, many of whom were excellent but who knew their place. Except for Fergus, a gregarious Scot, and Horace Barlow, whom I had known before and whose social grace is a natural attribute, I was totally ignored, people barely acknowledging a greeting on the corridor. This changed rather suddenly a few months into my stay. John Robson was the Michael Foster scholar and responsible for organizing the Michael Foster Club, a once-a-term function involving a more elaborate afternoon tea and a scientific seminar. John had forgotten to invite a speaker and in a last-minute decision asked me to do it. So I dug out the slides of my systems analytical treatment of eye movements and talked for 45 minutes. Somehow this resonated with the group, which included most of the well-known names in neurophysiology in Cambridge, many of whom had been active participants in war research utilizing this approach. There were numerous questions and a spirited discussion. My case was helped because in a naïve attempt at brevity I skipped over many slides with confirmatory evidence that I then proceeded to reveal in answer to specific queries. Campbell complimented me on what he thought was the clever subterfuge of keeping the best slides in reserve to drive home the major points in reply to the expected searching questions from the critical audience.

Within the hour my status in the physiological laboratory had changed from an outsider from America (it was fashionable then in Cambridge circles to be disdainful and patronizing to Americans) to a member of their circle. Someone had described the *Journal of Physiology* as the "Cambridge Physiological Laboratory and friends" and up until then and a few more years, nothing was regarded as firm knowledge unless and until it was published there. (There was the famous retort by William Rushton when confronted with a discrepancy in the peak absorption of a cone pigment, that the first publication was only in *Nature* and not yet in *Journal of Physiology*) My acceptance into the circle had several consequences.

Whereas before the sole aim had been to satisfy my curiosity and try for a coherent understanding of a few phenomena that attracted my attention, I now began to subject myself more consciously to the rigid intellectual discipline I saw around me and to focus on areas where the expected scientific yield would have impact on the development of the subject.

The second consequence was that rather than being a remote acquaintance I developed personal friendship with many whose intellectual power I respected and with whom I shared a variety of cultural pursuits, music in particular. The Brindley's, Horace Barlow, and I often played quartets and many a Sunday afternoon was spent with William and Marjorie Rushton at *Shawms*, including the only time in my life that I played the Brahms Horn trio, with Marjorie and Adrian, one of their sons. It was an environment unlike any I had experienced before.

One of the fall-outs of this development was a lively intercontinental exchange. I spent many summer terms in Cambridge, and in turn hosted many English visitors in my lab, which soon moved from Columbus, Ohio to the University of California in Berkeley. One of the most cherished was Cyril Rashbass, with whom I studied the human eye vergence apparatus. The paper is one of the most satisfying of all those that came out of this period, featuring a new method of recording eye rotations free from translational artifacts, an analysis of open-loop vergence responses, and the demonstration of the inapplicability of standard engineering rules such as Bode's law of minimum phase (Rashbass and Westheimer, 1961). Cyril was one of the most gifted scientists I ever knew, quiet and somewhat shy, the son of an orthodox rabbi who made him study the Talmud and insisted on a career in medicine rather than mathematics. Cyril obeyed kosher dietary laws, yet smoked heavily although not on the Sabbath. Late on a Saturday afternoon he would go outside and look for the earliest possible manifestation of the requisite three visible stars that signaled permission to resume smoking. Although it was indirectly responsible for good visual performance through these exercises of attention and concentration in the aid of detection thresholds, this cigarette habit also, unfortunately, caused his early death of a heart attack.

During the 1960s, the optometry school in Berkeley was a veritable *dependence* of the English physiological establishment. I have mentioned Campbell and Rashbass already. They were followed, in due course, by William Rushton who utilized my expertise in retinal image quality to demonstrate that spatial summation of retinal signals could not be ascribed to passive optical image spread (Rushton and Westheimer, 1962): a validation, if ever there was one, of my motto "Physics, Physiology and Vision." Giles Brindley had two sojourns in Berkeley. In the first he demonstrated unequivocally that there were no centrifugal fibers in the cat optic nerve, in the second I acted as an amanuensis in his electroretinogram research. There were many casual visitors, notable W.S. Stiles and on many occasions

John Robson, but the most lasting impact on the local scene was made by Horace Barlow. During a year Barlow spent on a sabbatical in Berkeley, Gordon Walls, who had made an uneasy perch for himself in the optometry school, died suddenly at a relatively young age. Walls, whose “The Vertebrate Eye” remains a permanent classic in the literature, was a very knowledgeable and opinionated naturalist, a conversationalist who reveled in the intellectual yeastiness that these visitors introduced to the more formal and restrained atmosphere there. To everyone’s surprise, Barlow expressed an interest in becoming Walls’ successor as the resident scientist in the School of Optometry and took up the position in 1964, bringing along Bill Levick, who had been trained in retinal physiology by Peter Bishop in Sydney. Barlow had a different take from Rushton’s on the origin of the pooling of retinal signals in the dark-adapted eye. The crucial test was the threshold elevation when the rods were bleached with a polka-dot pattern, and much depended on the retinal light distribution of disk-shaped targets, for which both parties had to turn to me. Thus, I was dragged into a series of dark-adaptation and increment threshold experiments to decide who was right. The back-and-forth lasted a couple of years and is entombed in several *Journal of Physiology* papers but for me it had a significant fall-out. The data-oriented attitude won rather than the theory-oriented attitude, into which the limited success of trying to shoehorn oculomotor responses to systems theory had molded me, and I withdrew from the battlefield. Instead I sank my teeth into an oddity that William Rushton and I had encountered while measuring increment thresholds in the dark-adapted retina and with which William naturally wanted nothing to do because it pointed to neural processing in the retina rather than passive summing of rod excitation.

## Visual Neurophysiology in Berkeley

The trajectory that started with an early interest in optics and astronomy, led to the study and practice of optometry, continued on with the training to become a researcher, then extended to investigating the role of the eye’s optics and intraocular and extraocular musculature in generating the image to the retina, now neared the point where it merged into neurobiology. In Berkeley, a very active group had assembled itself in the School of Optometry with many graduate and postdoctoral students, but it was hemmed in by the limitations of the space and teaching program of a small professional school. We made one attempt to break out. The recommendation of a faculty committee to replicate in the neural sciences the success 15 years earlier in establishing molecular biology as an independent academic discipline in Berkeley was unfortunately shelved. Relief, however, came in the form of a move to the Department of Physiology-Anatomy and more adequate space in the very large Life Sciences Building. A wider teaching program in the neurosciences was instituted and a couple of new faculty

slots opened up. One of them was occupied by Michael Land, whose work on the optics of the scallop eye had made me secure for him a Miller Fellowship to come to Berkeley, where he began studies on the spider eye. These were also the days when one could count on that indispensable research aid: steady NIH funding. It provided the financial support for not only the eye-vergence research with Cyril Rashbass, but also for the rest of my research for more than 40 years. The university covered only 3/4 of one's annual salary in return for the teaching activities. Although the NIH indirect costs ("overhead") provided some compensation to the institution, the cost of all research, including even telephone calls and postage, came from funds that the principal investigator had to apply and account for, explain, and justify.

Given the new environment, my own research became more overtly physiological. I had spent the summer of 1957 in the nerve-muscle program organized by S. Kuffler, C. Ladd Prosser, and A.S.V. Burgen at Woods Hole and had become familiar with the neurophysiology practiced there on cold-blooded animals. But my interest was in the human visual system. As a student in Sydney I had thoroughly immersed myself in the one available compendium that attempted a complete coverage of the nervous system of higher animals, Fulton's *Physiology of the Nervous System* (1943), without finding in it promising research directions within the avenues available to me then. Things had changed in the meantime. Mammalian single-unit studies in the laboratories of Eccles, Kuffler, Mountcastle, Hubel and Wiesel, Bishop, and others brought insight into processing modules within the central nervous system. And at the front end, because stimulus artifacts from optical and optomotor sources could be convincingly ruled out, signals could be traced right through to the neural stages of vision.

The work in my laboratory now followed two separate tracks and in rooms on different floors of the Life Sciences Building. Downstairs we proceeded to outline the processing of spatial visual stimuli in the human by psychophysical experiments. At first the research was directed frankly at the retina to determine how the anatomical and physiological apparatus that had been discovered (by e.g., Hartline in *Limulus* and frog, Kuffler in the cat, and Dowling, Boycott, and Werblin in *Necturus* [see Dowling's chapter in Volume 4 of this series]) is being deployed in the human. (I was, and still remain, immensely impressed by the solid grounding given by the *Necturus* studies to our understanding of the retina, and was able to bring Frank Werblin to Berkeley, first as a postdoc in my lab and then as a faculty member.) It took the form of examining and outlining the neural circuits for the center-surround antagonism that had been in the way of William Rushton's models of photoreceptor signal pooling (Westheimer, 1965) but that have since shown to be an excellent bridge between processing deep in the retina and the eventual visual percept emerging from retinal and cortical circuits. It found overtones in color vision, as demonstrated in the

thesis of Suzanne McKee (1970), in the diagnosis of retinal dysfunction as shown by the convincing work in Jay Enoch's lab over the years (Enoch, 1981), and in the differential diagnosis of amblyopia as proposed by Levi. The differentiation of its retinal from its cortical components continues to challenge current workers (Westheimer, 2004). The research merged into the more ambitious visual hyperacuity studies to be related later and the relationship with these collaborators has firmed into close friendship over the years.

## Primate Oculomotor Studies

The 1960s were the times when single-unit neurophysiology held the greatest promise. Much had been learned already and many investigations were in progress all over the world. The most spectacular results came from tracing sensory signals because this approach could utilize the traditional physiological experimental procedure of keeping the organism in a neutral state and observing the responses to stimuli controlled by the experimenter.

The motor system posed a different set of problems. The knowledge base at the time had come down from Sherrington and was linked to single-cell physiology by the Eccles school, who had, however, soon found more fertile ground in synaptic physiology. The more global questions of motor control, of preprogramming of action pattern so convincingly described by W.R. Hess (1941), of extrapyramidal and cerebellar circuitry, remained wide open. Familiarity with the human oculomotor system made me aware that it featured routinized, ballistiform movement patterns (the saccades), involving sophisticated but innate switching circuits that keep 12 extraocular muscles working as a unit. Also, unlike skeletal muscles, extraocular muscles operate under constant load conditions and are not seriously affected by muscle-spindle feedback. And as an added bonus, I had a great deal of experience with the target movement stimuli needed to elicit the saccadic, smooth pursuit, and vergence response patterns.

However, unlike the majority of the contemporary studies on the sensory system, motor control research could not very well be conducted on an anesthetized organism. One was looking at the alert, behaving non-human primate preparation. This required an entirely different laboratory set-up and equipment. Facilities—space, animal rooms, veterinary care—could be found on the fifth floor in the vast Life Sciences Building, and NIH funding allowed the purchase and construction of the requisite equipment for surgery, head gear, and electrode-holding implants, monitoring of physiological functions, stimulus presentation, eye-movement and electrophysiological recording, and subsequent histological analysis. I was exceedingly fortunate in having associated with me in all this work, first as a graduate student and then as research associate, an extraordinarily capable medical graduate, Sidney M. Blair, who could meet every possible

challenge in all areas of this research. In addition, a series of excellent and dedicated postdoctoral associates (Rolf Eckmiller, Barry Frost, Alex Skavensky, Rich Marocco, Ron Rempel, Essie Meisami, Meredith Wallace, Mary Gavin) helped keep up the momentum in this demanding research enterprise, which remained active between 1968 and 1981. Although I was intellectually engaged, most of the day-to-day work was conducted by this group and one or two technicians, while I divided my research time about equally between this laboratory and the psychophysical one on a different floor of the building.

The aim was to elicit oculomotor responses to visual and vestibular stimuli in the primate and relate them to single-unit activity in the brainstem with the hope of charting the underlying neural circuitry. After less than a year, the technical difficulties had been ironed out and recording began. Right away we found that cells in the third nerve nucleus discharge at constant rates that depend on eye position. This finding accorded well with the proposition I put forward 15 years earlier that a saccadic movement was the rapid change of the oculomotor apparatus from one set state to another. The neural correlate of the state was, obviously, the set of maintained impulse rates in the 12 muscles, all carefully calibrated to maintain the requisite steady eye position. (This formulation was subsequently modified to include transients in the impulse rate, to allow a faster repositioning.)

When it came to claiming credit for this finding, however, we were out of luck because this "position coding" of oculomotoneurons had just appeared in the literature in three different publications (Fuchs and Luschei, 1970; Robinson, 1970; Schiller, 1970). We had obviously started a year or two too late. The oculomotoneurons are what Sherrington called the final common path, the last neuron in the long interconnected series of pathways and they receive many thousand synaptic connections onto their extensive dendritic tree. So onward and inward was the motto: What signals might there be in near-by or related neural regions that have tight correlations with observed eye movements—the logically reverse process to finding firing correlates in higher sensory neurons to visual stimulation? One candidate problem, obviously, is the circuit that holds the maintained discharge at the designated rate, what became the search for the "neural integrator." From the point of motor organization, the more interesting question was the origin of the signals for making a saccade, and the code containing instruction for its direction. Here one quickly ran into a morass. Recordings show several candidate classes of neurons, those that burst before or during saccades, those that stop during saccades, and a variety of related ones, but their codes, if any, remained elusive (Westheimer and Blair, 1972).

One question we tackled was whether there is a hierarchy of firing within the ensemble of the nuclei of the 12 extraocular muscles. It had been

suggested, on neuro-ophthalmological grounds, that third-nerve activity was secondary to sixth-nerve activity. So we set about simultaneously recording from cell pairs in the alert behaving primate using separate electrodes, one cell in the third and the other in the sixth nerve nucleus, in what may readily have been the first use of this heroic procedure (Eckmiller, Blair, and Westheimer, 1974). It did not reveal that the sixth nerve cells fired earlier than those in the third nerve.

It may be mentioned parenthetically that the research was located in the strategic intersection of several disciplines. It is obviously motor physiology, and also part of the wider problem of oculomotor control and eye movement responses. But hints about normal functioning come from clinical observations of dysfunction and abnormal development. Neuro-anatomists have always played a major role, witness Ann Graybiel's 1974 delineation by the marker horseradish peroxidase of several structures not previously suspected as part of the oculomotor complex. For awhile, also, there was much activity involving engineering and computational models. The inescapable kinematics of ball-and-socket joints has already been mentioned.

Considerable insight into motor organization was afforded by Hess's focal stimulation experiments of the 1930s, which demonstrated midbrain locations in which quite complicated and biologically relevant preprogrammed motor routines could be elicited. Sidney Blair and I made some efforts to map brainstem sites in which stimulation can trigger oculomotor responses. By this means we were able to describe in the monkey at least two syndromes whose counterpart can appear in clinical neuro-ophthalmological patients and whose neural substrate had therefore been located. One was saccadic inhibition (Westheimer and Blair, 1973a), in which for the duration of the stimulation all saccadic activity ceases; the other was the ocular tilt reaction (Westheimer and Blair, 1975), a unitary syndrome involving head and eye rotations.

The function of the cerebellum had long been the object of speculation. One conjecture, by H.H. Kornhuber (1971), assigned to it the role of a clock, in particular in counting down impulses to control the extent of saccades. The idea did not fit the picture that had by then emerged about the neural apparatus for generating saccades. Although its intimate internal circuits were receiving detailed attention (Eccles et al., 1967), the specific functions of the cerebellum remained uncharted. In discussing various ways of testing Kornhuber's proposition with Sidney Blair, he was quite willing to go the way of late 19th century experimental brain research and just ablate the whole of the cerebellum to determine whether this leads to an absence of saccades. No sooner said than done; when the monkey awoke from anesthesia next day, it had a full set of normal saccades. So much for Kornhuber. We saw, however, an entirely different syndrome: inability to make pursuit movements and, in addition, gaze-holding nystagmus, namely

smooth centripetal drift toward the primary position followed by compensating outward saccades (Westheimer and Blair, 1973b). The pointer to a smooth eye movement component in maintaining eccentric fixation was unmistakable. Vergence movements were unaffected. Here, again, there were many clinical overtones, because this particular symptom complex is known in neuro-ophthalmology.

At the time, one of the most innovative contributions to the oculomotor physiology was published by Gonshor and Melville-Jones (1973) of McGill University. These workers demonstrated that the vestibulo-ocular reflex, long thought of as one of the most basic and neurologically simplest motor routines, evolutionarily conserved over hundreds of millennia, was subject to quite specific learning. The finding was very influential in that it pointed to the likelihood that the brainstem, pontine, and cerebellar neural circuits being studied were not only complex, interwoven, and just about impossible to decipher by any of the means available but were plastic to boot. It also put into better perspective the then popular attempts to describe the oculomotor system by engineering models.

As gripping as all this research was to Sidney Blair, with his background and board certification in neurology, and to me, so used in an earlier stage to look at patients' eye movements—daily we were reminded and encouraged by its clinical implications—the effort to maintain such an active primate lab became too much. The research being carried out in parallel on the other floor, to be described presently, was intellectually more attractive, and I began to turn all my attention to it. Dr. Blair rejoined the Navy to assume a sequence of important slots as Capt. S.M. Blair, MC, USN. The remaining primates were turned over to my colleague Russ DeValois in the psychology department.

## Fine-Grain Visual Processing

If I had been forced to restrict my interest to a single topic in vision it would have been visual acuity. Resolution depends in the first instance on optical factors, but they had now been characterized in sufficient detail. The experiments bypassing the optics with Young's interference fringes had convinced me that the conventional wisdom about the match of the optical limit and the grain of the receptor mosaic held up. The focus, so to speak, now was on the central nervous system. The single-unit recordings from the primary visual cortex, insofar as they were available in the primate and could be extrapolated to the central fovea, however, did not reveal a grain fine enough to match the known resolving capacity. Because "wet" neurophysiology was not ready, guides to neural circuitry had to be provided by psychophysics.

The attention of the vision community in those days was riveted on sinusoidal gratings as stimuli, but these extend over long retinal distances

and hence do not match the predominantly local neural processing in the retina and primary visual cortex. In addition, the application of systems theory in the 1950s had alerted me to the nonlinearities lurking on or just below the surface in biological phenomena. Where linearity holds, all complete basis functions are equivalent, but where it does not, the stimulus set must be chosen to fit the structure of the apparatus. The referees for the *Journal of Physiology* paper, in immunizing me to Fourier approaches to vision (although of course not to optics) gave me the advantage of being able to ignore the voluminous literature that for 20 years sponsored and for the following 20 years distanced itself from the "Fourier Theory of Vision" (Westheimer, 2001). Moreover, awareness of the pitfalls resulting from nonlinearities when using inappropriate basis sets allowed me to skip over all the claims for linear neural "filters" and computational models that employ them.

Driving my experimental program was the realization that the high foveal visual acuity, right at the edge of the maximal capacity of the eye's optics and retinal anatomy, places such high demands on neural processing that, when stressed, it would exhibit deficits whose nature might point to the strategies used in the nervous system to extract this fine information. The first study, showing that visual acuity deteriorated with shortening exposure time much more seriously than simple light detection (Baron and Westheimer, 1973), validated the suspicion of the importance of cortical neural factors. It also made me face up to the technical challenge of performing rigorous psychophysical experiments in this area. Randomizing stimulus presentations in many trials and recording responses would have to be automatized.

When this was accomplished, the next acuity experiment was performed with my former graduate student Suzanne McKee, who became the most significant research collaborator in this area before going over to Arthur Jampolsky's Smith-Kettlewell Eye Research Institute in San Francisco. Examining the effect of target motion across the retina, we found that quite prominent velocities and excursions leave acuity unaffected (Westheimer and McKee, 1975). The ability of cortical mechanism to resolve the orientation of a 1 arc minute gap in a letter now was shown to require more than 100 msec, but during this interval it was robust to location shifts of up to 50 times the size of the detail! The kind of mechanism that can accomplish this has not yet been laid out in neurocomputational detail, let alone been discovered by recordings from the cortex.

The advent of computers opened up an even larger and more challenging area of inquiry. Vernier and stereoscopic acuity had been known for a long time to be in the range below the width of a single foveal receptor. Hering (1899), realizing the difficulty of explaining this, had proposed that it was due to averaging of local signs along the length of the stimulus lines or edges. In a little-known paper, Ludvigh (1953) had undermined

this idea by claiming that dots could be aligned as well as lines. Ludvigh, one of the ablest thinkers of his generation of vision researchers, did not, however, have any track record as an experimentalist and I was prepared to discount his claim, but not without subjecting it to a test. It turned out to be a difficult experiment to implement. Don Mitchell, Bill Baron, Ralph Freeman, and I found a space in the attic of the optometry building long enough to allow the positioning of two dots down to a precision of a few seconds of arc of visual angle. The procedure was tedious: Stimuli were positioned by hand with a micromanipulator using tables of random numbers, experimenters and observers communicated over the 30-meter distance by intercom, and data were graphed on Gaussian probability paper. The results, however, supported Ludvigh's claim and eliminated Hering's theory of averaging local signs.

Because the misalignment threshold in the vernier task is well below the resolution limit, it was necessary to dispel doubts that a law of physics was being transcended. Resolution, or separation of two feature elements, is indeed limited by the diffraction laws that any optical system, including the eye, must obey. But an object can be *located* with arbitrary precision, provided there is enough light (Westheimer, 1976). Suzanne McKee and I were able to demonstrate that the task devolved to identifying the centroid of a light patch on the retina, quite a feat of neural computation (Westheimer and McKee, 1977a). It is of the kind to which Georgopoulos pointed in the population vector summation model in the motor system. We showed that vernier acuity is just one of a whole class of relative localization abilities, where differences in location of two objects can be discriminated with high precision. Because the word visual acuity had been preempted, for at least 150 years, by its application to resolution, with its dependence on optical laws and retinal anatomy, I coined the term hyperacuity for this class of discriminations (Westheimer, 1975). I deliberately eschewed the word superresolution because it was being used in radar for quite a different process, viz., the identification of a target whose spatial-frequency components within the cut-off spatial frequency match those of a targets about whose total spatial frequency spectrum there is prior information.

A variety of findings—wide latitude for the shape but need for tight temporal synchrony of all components of the configuration, summation of some of the properties and masking of others by flanking stimuli in time and space—pointed to processing even more central than the primary visual cortex. Simple linear spatial filters could not be invoked to handle the range of target configurations and relative positions. Finally, aspects of learning and attention could not be ignored. The research that started with optical images and then led to retinal spatial interaction had unequivocally arrived in the central nervous system and the transition from optometrist to neuroscientist was complete.

In association with a steady sequence of graduate students and post-doctoral colleagues (Gert Hauske, Suzanne McKee, Keiko Shimamura, Tom Butler, Dennis Levi, Bertil Lindblom, David Badcock, Mike Fendick, Graeme Mitchison, Bob Bennett, Armand Abulencia, Manfred Fahle, Christian Wehrhahn, Mark Pettet, Wu Li, Eric Ley, Tina Beard, Scott Brincat, Angela Gee) I have investigated over the last 25 years many aspects of the neural processing that underlies the discrimination of such spatial attributes of visual features as location, orientation, and stereoscopic depth. Although the pattern components are sharply delineated and quickly identified by any observer, they are not easily characterized in the Fourier domain and hence not encompassed by the research routines of the many single-cell and psychophysical investigators who restricted themselves to the use of sinusoidal grating or Gabor targets. But even in electrophysiological explorations of the retina and cortex that were not so limited, elucidation of the neural substrate of spatial visual processing has evolved slowly, presumably because one is dealing with higher circuits involving representation of activity more widely distributed than can be captured by the analytical procedures of the day. Altogether, this research enterprise continues to strengthen my conviction that analysis of behavior has a primary role in a search for understanding neural functioning. In my investigations, we employ psychophysical procedures in human observers, which can yield results as sharp, repeatable and universal as anywhere else in biology. Tschermak (1947) used the term "exakter Subjektivismus" to address and counteract the impression that data based on human judgments necessarily lack general validity.

All along, binocular and stereoscopic vision fascinated me. As an optometry student I had made my own stereograms to use in orthoptic training of strabismics and vividly remember noting, about 1945, a phenomenon that later gained great prominence. In a monocular view of a tree one would see just a disordered array of foliage, but in stereoscopic viewing this would immediately arrange itself into separate, clearly articulated branches. Hence when random-dot stereograms became popular they contained no great surprise for me. In any case, the early claim that they contained no monocular clues was never fully accurate: They contained a great many monocular clues. The task, as was clearly defined by Marr and Poggio (1979), was the disambiguation and the suppression of conflicting pairings. Over most of my career I have intermittently returned to research in stereoscopic vision (Westheimer and Tanzman, 1956; Westheimer, 1979; Mitchison and Westheimer, 1984) and when selected as the Royal Society Ferrier Lecturer in 1992, I chose this as my topic (Westheimer, 1994). Over the ages, the two most controversial attributes of vision have been color and depth. The disputatious tone permeating color vision and its theories, starting with Goethe, I have always found unappealing, but depth perception with its roots in three-dimensional geometry had from the start

exerted an intellectual attraction. Not that color vision does not harbor its own fascination for sophisticated geometry, witness Silberstein's (1943) elaboration of a Riemannian color space. However, during my most impressionable years as a beginning scientist, the literature was abuzz with what was widely claimed to be "the most important contribution to binocular vision since Helmholtz." Luneburg, a mathematician, put forward in 1947 the proposition that perceptual visual space has the metric of a hyperbolic space of constant curvature. Because I did not understand what that meant, I had to go back to the mathematics books and learn about non-Euclidean geometry. After some time, much reading in differential geometry, and working through the experimental findings that the theory began to generate, I developed a skepticism not only about Luneburg's clever conjecture but about attempts in general to find anchor points for spatial vision in geometrical scholarship. The episode was paradigmatic of a tendency on my part to be intrigued by a mathematical model of visual perception when first encountered and then on further study to reject it as inadequate.

Serendipity played a part in alerting us to the plasticity that characterizes the functions we were studying. One of our good undergraduate student observers performed very poorly in a stereoscopic situation when transferred from a vernier to a stereoacuity acuity task. We were, of course, familiar with the fact that new observers, or seasoned observers starting a wholly different task, required a few hundred responses before settling into a steady response state, and had always made it a practice to discard the first couple of runs. So this particular observer was allowed to continue in the stereo task; it took 10 days of practice for him to reach a 10 arc seconds threshold. We were thus alerted to the role of perceptual learning (Fendick and Westheimer, 1983; Crist et al., 1995).

A second lesson was learned when Bertil Lindblom, an ophthalmologist from Goeteborg, came over to try to develop a clinical stereo test akin to the pseudo-isochromatic color vision plates. Preliminary results made it clear that an observer's stereo threshold—as also other spatial thresholds—depends critically on prior expectation. Thresholds rise directly with the degree of uncertainty (Lindblom and Westheimer, 1992). Both the perceptual learning and the uncertainty findings revealed that the cortical circuits involved have parameters that are not permanently fixed, even in the adult.

In the early 1990s I started active collaboration with the Neurobiology Laboratory at the Rockefeller University, which was at the time gradually being relinquished by Torsten Wiesel and taken over by his long-term associate Charles Gilbert. Charles saw in my psychophysical results not only evidence of cortical processing but specifically the operation of interaction of horizontal connections within the ensemble of neurons in the primary visual cortex. The response of individual neurons to even the optimal stimulus in its classical receptive field was seen by him to depend on context, learning, attention, and expectation. This cortical plasticity, for which there

was no dearth of possible anatomical pathways, needed, however, to be demonstrated and moreover, if adequate comparisons were to be drawn to the human psychophysical findings, in the alert behaving primate. Charles, unusual for someone trained in medicine and neurophysiology, was quite prepared to accept that even Gestalt phenomena of good figures, grouping, continuous and contiguous arrangements, and so forth might have their neural counterpart in the primary visual cortex. A sequence of parallel studies, human psychophysics and primate single-unit recordings, was entrained, in which Mitesh Kapadia's enthusiasm and drive were particularly invaluable. And indeed, for suitably selected spatial configurations, the behavior of single neurons in the primary visual cortex of the primate matches those of a human observer in psychophysical tasks (Kapadia et al., 1995). This research is ongoing with Wu Li, who was trained by Prof. C.Y. Li in Shanghai, now playing a leading role.

Over the last dozen years, a steady visiting coworker has been Christian Wehrhahn, based in the Tuebingen Max-Planck Institute founded by the late Werner Reichardt. In one of Christian's enterprising collaborations, we teamed up with Barry Lee in Goettingen to conduct parallel studies in human hyperacuity and recordings from monkey retinal ganglion cells. These studies heavily implicated the magnocellular stream and revealed how additional cortical processing is needed to extract the relevant information from the retinal signals, which after all are the primary source (Lee et al., 1993).

Both from my musical activities and from the early observation showing accurate eye movement predictions for rhythmic stimuli, I had been curious about the fine grain in the perception of the sense of time. Suzanne McKee and I had shown that temporal asynchronies of just a few milliseconds could be correctly judged in the onset of adjacent visual stimuli (Westheimer and McKee, 1977b). A few years ago I took the question up anew, investigating the discrimination of the duration of intervals demarcated by visual, auditory, and tactile pulses. It seems that good time-interval discrimination is not achieved locally in the immediate cortical projection for each of the sensory modalities individually but by an apparatus that is common to all (Westheimer, 1999a). Unfortunately, I have to leave its further elucidation, along with the search for the neural substrate of motor anticipation, and of indeed motor programming in general, to the next generation of investigators.

## Computers

An autobiographical sketch would not be complete without reference to a life-long fascination with computers. It was presaged by the interest engendered by material on numerical methods that were included in the lectures for the mathematics major in Sydney University—numerical integration

and solution of differential equations, interpolation, etc. When measurements of the refractive state of the eye showed fluctuations, I wanted to analyze them and worked my way through the Wiener-Khinchine procedure of autocorrelation and Fourier transformation for the purposes of harmonic analysis. Ohio State had an IBM 650 computer and I proceeded to program and run the data through it. Thus, my first research using electronic computers was published in 1957 (Westheimer, 1957a). When I got to Cambridge in 1958, we generated a lot more data and fortunately were granted access to EDSAC, the computer for which Maurice Wilkes was responsible and which was in constant use by the molecular biologists analyzing electron diffraction patterns (leading to the identification of protein structure). Within the small and friendly community of computer mavens, colleagues helped each other by freely sharing programs. I remember Teddy Bullard and Peter Swinnerton-Dyer competing to have us use their harmonic analysis programs.

In Berkeley there was an IBM 704 card-programmed computer, and I had to learn FORTRAN to have it run the Fourier analysis needed for deconvolution of the measured line-spread function and the characterization of the contrast transfer function of the eye. Later we used it extensively to map image spread for all kinds of target patterns employed in the retinal interaction, acuity, and hyperacuity studies.

I was always keen to learn computer languages: FORTRAN, BASIC, FORTH, COBOL, PASCAL, and finally C, which I now have used almost exclusively for the last 20 years.

In 1970, on a visit to Mat Alpern in Ann Arbor, Bill Uttal showed me how he was testing visual perception by displaying patterns with a PDP-8 computer. I was sold on it instantly, and proceeded to request one in my next NIH grant renewal. Funding started on October 1, 1972 but in the mean time the PDP-11 had been released. There were long discussions in Berkeley with Horace Barlow and Bill Levick, who had been won over by the competing NOVA and wanted me to join that trend. But I was more impressed with the DEC system, which I had seen in action as early as 10 years before when the LINK was being developed and placed in neurophysiological laboratories.

When the PDP-11 finally arrived and was put into operation in May 1973 my life changed. I had taken on the charge of being my own systems manager and so had the responsibility for all aspects of understanding and maintaining it. The first task was to learn to program it, which had to be done in those days in assembly and sometimes even machine language. It gave me a unique insight of what is actually going on, program step by program step, when stimulus patterns are being generated and responses registered and sorted. Gaining familiarity with the computer bit by bit, so to speak, was an extremely time-consuming activity—there were almost no resource people to consult—but it has also given me unsurpassed versatility

and assurance in the organization and control of experiments. For more than 30 years now I have felt secure in my grasp of stimulus generation, in terms of seconds of arc of visual angle and milliseconds. In time the PDP-11 was replaced by a LSI-11, then by a Microvax, and finally by a series of INTEL computers using first 286 and eventually Pentium processors.

My first home computer was a 1979 Northstar Horizon S-100 bus computer, using a Z80 processor, whose instruction set I also learned. But by the middle of the early 1980s the IBM machines had for all practical purposes replaced the much better S-100 bus architecture. Needless to say, I started e-mail in 1985 and my user name "gwest" reflected the then requirement to stay within 6 letters.

## Institutions, Organizations, and People

Parental injunctions and early career planning notwithstanding, I have spent most of my life within universities, predominantly lecturing to undergraduate or professional students. In the optometry schools, there was a great deal of teaching, up to 10 lectures a week on occasions, as well as organizing laboratories and sometimes even clinical duties. Research had to be done in one's spare time and I developed the life-long habit of working in the laboratory on Saturdays. Only when I transferred to the Department of Physiology-Anatomy in Berkeley did the time and facilities make the position at least an approximately half-time research slot. During several time spans, however, I could devote full time to research: the academic year 1952 to 1953 as a predoctoral fellow at Ohio State, most of 1958 at Cambridge, England, and the academic year 1972 to 1973 when I received an appointment as Miller Research Professor. From then on the teaching load became progressively lighter as I had various sabbatical leaves and then took over administrative tasks. In 1994 I entered retirement status as professor in the graduate school with some duties in graduate teaching and the provision of some modest laboratory space. Altogether, the expansion of research funding and resources in the biomedical field in the United States during the second half of the 20th century made it progressively easier to be a life scientist. I was also fortunate in doing most of my work before the explosion of multiauthored publications and increased cost and complexity of instrumentation and procedures left those of us behind who look at science as a predominantly scholarly, intellectual activity and who enjoy the challenge of fast, even day-by-day, turn-around in the cycle of planning and performing experiments and interpreting their results.

It was only in the 1980s that I became involved in academic administration. Under Dan Koshland's leadership, a major initiative was started to reorganize the whole of the large biology community in Berkeley. After almost a decade of continuous meetings and conferences, we had something to show: two new laboratory buildings, a complete renovation of the

old enormous Life Sciences Building, and a new departmental structure that allowed flexibility in accommodating changes in disciplinary boundaries. As a result, neurobiology became a division in the Cell and Molecular Biology “megadepartment” and we finally had neurobiology in the title of our appointments. After several years on various planning committees, I assumed the roles of both administrative head of one of the buildings, the Life Sciences Addition, housing the laboratories of 46 faculty members, and head of the new academic Division of Neurobiology, which I had organized. Because I was then in my 60s, with a good deal of experience in academic affairs, I was not overwhelmed by these tasks and took them in my stride. By the same token I had no regrets when passing them on to the next generation of administrators, Corey Goodman, Carla Shatz, and Geoff Owen.

For over 30 years I regularly commuted to Washington to serve on committees of the National Research Council and the National Institute of Health, as member and several times chairman of study sections, training committees, and then the Board of Scientific Counselors of the National Eye Institute. From the late 1960s to this day I have been associated with editing many scientific and professional journals, in particular *Vision Research*, *Experimental Brain Research*, *Journal of Physiology*, and during the last few years *Proceedings of the Royal Society B*. I have never minded the several hours every week that I have routinely spent preparing reports on grant and promotion proposals, refereeing manuscripts for publications, and writing letters of recommendation for what must have been a couple of hundred undergraduate, graduate, and postdoctoral students who have rotated through my laboratory.

I have always accepted that membership in scholarly and professional organizations is a part of belonging to the scientific community. The nearest thing to a vision society was the Optical Society of America and I became a member in 1948, when I was still a practicing optometrist in Sydney. To these were added various other organizations, including the Society for Neuroscience, when Ted Bullock recruited me the year after it was started.

Attending scientific meetings is an integral part of participating in the enterprise and in the early stages I did my full share. In the 1950s and 1960s I regularly attended the annual conventions of the American Academy of Optometry in early December, and the twice-yearly meetings of the Optical Society of America. They were modest affairs by contemporary standards with rarely a conflict due to parallel sessions. The vision community was relatively small and allowed good opportunities for personal interaction. The same applied to the less frequent international meetings. Between these events and the occasional visitors from abroad, it was possible to keep in touch with developments. In the last couple of decades, the number of organizations has grown enormously, and so has the size of their meetings and the number of presentations. I do not find these occasions

particularly attractive, especially because my mind is not well matched to oral presentations and lectures. Over time I have developed the capacity of quickly capturing the essence of an experiment and the implication of its results. Hence the cost/benefit ratio is not in favor of the time spent in listening to a lecturer, compared to viewing an abstract or a publication. Rapidly walking along a row of posters and quickly taking in what is informative is not always appreciated by the eager exhibitors.

All this does not mean that I would shun getting personally acquainted with fellow scientists or hearing them give a lecture at least once; very much to the contrary. But on the whole, I subscribe to the description once presented to me by Stanley Stiles, one of the ablest and wisest vision researchers of the 20th century, of the practice of science as arriving at "the residue." By this I took him to mean the distillate in the attempt at a rational description of natural phenomena, succinct, concentrated, and free of contradictions. On the other hand, the role that personality characteristics of scientists, beyond their abilities and opportunities, play in the creative nature of their contributions has long fascinated me. In visual science, the two polar opposites are Helmholtz and Hering.

Helmholtz single-handedly made more contributions to visual science than anybody before or since. Endowed with great mathematical ability, an orderly mind, and a calm and steady personality, he logically, linearly, and sequentially worked through the optical and anatomical stages to reach as full a description of the visual process as could be achieved at the time. When he reached the limit, he made unprovable propositions about cortical processing (the concept of unconscious inference) and proceeded to seek clues in the foundations of geometry. Being thoroughly embedded in 19th century thought, he regarded this as a natural progression. It was only a couple of generations later that the intuitional basis of mathematics and geometry was laid bare. Although Helmholtz helped secure a Berlin chair for Planck, one cannot help sympathizing with the dilemma he would have faced had he lived to be confronted with quantum mechanics and Goedel's theorem.

When it comes to inspired leaps of imagination, closing a gap not bridgeable by simple incremental steps, the outstanding figure is Ewald Hering, most notably when he examined a few psychophysical phenomena and enunciated the opponent theories of spatial and color vision. It took almost a century to uncover their neural substrate and integrate them into the body of visual science. More often, however, such conjectures remain open-ended, witness the compelling demonstrations of Gestalt groupings by Wertheimer of 1923. Despite assiduous study of the provenance of such formulations and the personal history of their proponents, the workings of these minds remain mysterious to me (Westheimer, 1999b).

In practice, of course, very many human traits are in play when doing science. Most of the ones on display during a lecture or on social occasions

are not relevant. In assessing the personal attributes of a scientist, to me by far the most important trait is integrity. Carelessness, oversight leading to errors of omission, and failure to properly research the antecedents or to be sufficiently rigorous in analyzing the outcome of an experiment, these can perhaps be excused, although they can needlessly hinder progress. But I have no tolerance for the deliberate shaping of results in support of a preconception or the creation of the illusion of a phenomenon.

On the other side, there can be enormous rewards in personal contact with colleagues. Here are just a few of the many examples that I have encountered and that engendered admiration and the wish to be able to emulate: Francis Crick would grasp, in what seemed only a microsecond, all the ramifications of an experimental result related to him, a period that when he got into his 80s lengthened to perhaps a millisecond; Roger Penrose's mind similarly bores down instantly to the core of an issue—when shown my paper on the kinematics of the eye, he barely glanced at the expression in terms of quaternions, of which I was inordinately proud, but homed in on the fact that the eyeball moved as a ball in a socket and that Listing's law was, of course, a good possible mode of its operation; Glenn Fry, on the other hand, had such a remarkable geometrical intuition that it was obvious to him, without recourse to quaternions or other mathematical formulations, that the axis of the equivalent to two consecutive eye rotations does not lie in Listing's plane; Torsten Wiesel is unique in being a top scientist who always brings, unfailingly and quite naturally, a genuine empathy to interactions with his fellow scientists and with any one else, even the most junior; Jack Eccles, was a master at what would now be called multitasking—when I visited him in Canberra in the 1950s, he ran four laboratory set-ups concurrently and could explain in detail what was going on in each; Horace Barlow has a mind so well furnished and finely honed that he can contribute something interesting and insightful to any physiological or psychological topic; Dan Koshland was unmatched in his ability to bring divergent disciplinary agendas to a consensus in the interest of overall advance of the academic environment.

Overviewing my experiences in a variety of settings during a good fraction of the 20th century makes it obvious how much social and political conditions provided an inescapable framework beyond any individual's control. There is a great deal to be grateful for in a trajectory through the century's science that included an upbringing in Berlin, college and professional training during the darkest years of the century in sunny Australia, exposure to high-caliber intellectual atmosphere in Cambridge, and the opportunity to carry out scientific work with adequate NIH support in the inviting setting of the University of California in Berkeley. I remain enthusiastic about the future of the discipline. For me, the aim of illuminating the structure of the visual apparatus by catching it between the twin beams, one pivoted in the physical sciences, the other on a patient-centered

clinical approach, yielded a satisfactory outcome when applied to the optics of the eye and the functioning of the retina. But the gap between our current knowledge of the operation of the cortical apparatus of vision and the ultimate performance of the human in visual perception and object recognition remains vast and not as simply bridged by optical physics and rigorous psychophysics as was the case for the more primitive visual tasks. This is the challenge of the road immediately ahead; I wished I could participate building it, much as it has been my privilege to help with its construction so far.

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