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ANNUAL REVIEWS

Annual Review of Vision Science

Coming of Age in Science: Just Look?

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Annu. Rev. Vis. Sci. 2021. 7:1–17

First published as a Review in Advance on June 4, 2021

The *Annual Review of Vision Science* is online at vision.annualreviews.org

https://doi.org/10.1146/annurev-vision-100419-120946

Keywords

psychophysics, phenomenology, binocular vision, perception, surface representation, mid-level vision

Abstract

With Professor Patrick Cavanagh, I started the Harvard Vision Sciences Laboratory in 1990. Blessed with the largesse of a wealthy university, we occupied a very large common space. Here, students pursued their own projects in a uniquely cooperative and exciting scientific environment. The times were just right in the emerging and expanding field of vision science. With good thesis projects under their belt, most of the students went on to successful careers. However, my own coming of age in science did not have such a promising start. It only started well into my thirties when I joined the Smith Kettlewell Eye Research Institute in San Francisco. Providentially, it was there that I had the rare and unique opportunity to work closely and essentially only with peers (not students). Through these intense collaborations, I found my way as a scientist. Most of this account describes these formative years.

INTRODUCTION

I was born in early 1940, almost two years before the Japanese attack on Pearl Harbor. My father worked in a family business, a Japanese trading company in Manhattan. Largely unaware and shielded from these personally significant world events, which included the demise of the family business, I grew up in Leonia, New Jersey, a small, comfortable, all-white suburban town just across the Hudson river from New York City. My parents, atypically for Japanese-Americans, didn't push us kids to get top grades at school. So I worked hard at times but not at others. Besides, I always had greater interests outside of the school curriculum: astronomy, birds, and electronics and radio. In my senior year of high school, I became very curious about psychology, in particular, psychoanalysis.

I was good at math, but mostly, with the exception of ninth-grade algebra, which seemed such a wonderful advance over arithmetic, the other math courses didn't capture my interest or imagination. My last year in high school came just after the Russians launched Sputnik, and we were supposed to have a new, exciting modern math course for our senior year. It was a special course for the best students that included symbolic logic. As presented, the theorems we proved in symbolic logic weren't at all interesting or surprising. It seemed like the whole subject was so formulaic in a mechanical, uninteresting way. There was little sense of achievement, excitement, or discovery. Mistakenly, this soured me on mathematics for too long. Other science classes in high school were not particularly interesting, with the exception of chemistry; I was so taken with the idea of finite shells of electrons explaining so much about how specific atoms combine into molecules. A lot of this interest came from an unusually good high school teacher. I also remember so vividly a great lab exercise, the magical appearance of shiny metallic copper in my hands when heating the raw ore along with charcoal in a test tube, reliving the beginnings of the Copper Age.

HAVERFORD COLLEGE

A most exciting era of my life was leaving home and enrolling in Haverford College in the fall of 1958. Back then, Haverford was a very small liberal arts college, all male, with just over 100 students per class. The students were among the best, but being a Quaker college, the atmosphere was friendly and not fiercely competitive. In our day, we were not thinking much about grades or careers; rather, big ideas predominated. I, along with others, was interested in the central intellectual and moral problems of the day: What is true, and what is good? How can you have morality and social order without god or metaphysics? Discussions would go until the wee hours. But what to major in? Early on, I took a great course on the history of the West, tracking the rise of Christianity in Europe. To me, it was such a revelation to understand the roots of our common culture. History seemed to be *the* most important subject. However, as exciting and significant as it was to me, as I took more advanced courses, it was plainly evident that I didn't have the reading and writing skills in comparison to my more talented peers, so this was not to be.

I was interested in physics because here was something that seemed obviously fundamental. But there was too much math that I hadn't mastered and never would. Other sciences did not interest me, as they were not deemed foundational like physics. There was my high school interest in psychoanalysis. So, by default, I majored in psychology, but I really disliked experimental psychology. Behaviorism still reigned, and its methods and scope seemed so narrow and constraining. Furthermore, I never fully took to heart the contorted statistical formalisms (null hypothesis significance testing) that were considered so essential. I found it very hard to read the less than interesting assigned journal articles for class discussions, and my grades reflected this. A brighter spot, at least initially, was psychoanalysis, which claimed to reveal deep hidden and "forbidden" knowledge. However, it eventually became evident that there were so many diverse perspectives besides Freud, and there was no discernable common core. Being so young and inexperienced about life in general, I could find no way to evaluate the merits of each. In this fractured intellectual realm, I started reading and talking to friends about the philosophy of science. It seemed especially important to put psychology on a better footing. Eventually, I found and gravitated to logical positivism, reading A.J. Ayer's (1936) *Language, Truth and Logic*. This short manifesto seemed persuasive. With such rigid rules for science, which I accepted back then (but now question), psychoanalysis got moved to the margins.

Then, in my junior year, some famous neuroscientists arrived on campus, each for an extended visit. I was very impressed by Karl Pribram, who much later would become a guru and popularizer of the brain as hologram. However, back then, he was a respected neurosurgeon. He gave an evening talk titled something like "the neurology of Sigmund Freud," where he associated various Freudian concepts with specific brain regions. To me, this was a wonderful revelation. For the first time, I thought that studying the brain might be an option. The scope was almost as great as psychoanalysis but possibly grounded in something much more concrete.

Another visitor was James Olds, who discovered hypothalamic reward centers. He was a good showman, young and impish. Somehow, I found myself tasked to walk him around the campus; I even took him to a lecture by Arnold Toynbee, a world-famous historian. As we walked out, he said, "What a load of crap." That shocked me; he certainly was a different breed than the more restrained faculty at Haverford. Were scientists like this? As he finished his visit to Haverford, he told the psychology faculty that I was the one likely to be the scientist. On the strength of his remarks, not my middling grades, I got admission to the University of California, Los Angeles (UCLA) Graduate School in Psychology.

GRADUATE SCHOOL AT UCLA

Graduate school was a big shock to me. Los Angeles seemed like an alien place: Everything depended on having a car, and back then, there was always the smell of petroleum in the air. Smog was thick, and one rarely saw blue sky. In addition, the intellectual atmosphere of graduate school seemed to be a throwback to high school. The required courses were also, for the most part, uninteresting. Toward the end of my first year, I started to realize that brain science as covered by psychologists was a poor cousin to "the real thing." Maybe I was in the wrong field.

As I started my second year, to the rescue came Professor Theodore Holmes Bullock. Trained as a zoologist and comparative biologist, his undergraduate courses in zoology were, for me, transformative. The first was an introduction to the nervous system, and the second was a lab course as a sequel to the first. For me, each lecture of this sophomore undergraduate course was thrilling. As it spanned the range from ion channels to behavior, I could see that the study of the nervous system was a truly grand project. Most importantly for me personally, Bullock emphasized the key role of behavior as the main purpose for a nervous system. Ethology, of course, was thus highlighted. Stunning was his description of a behavioral study of motion processing in a beetle (Reichardt 1961). Here, simple choice behavior revealed the formal operations of adjacent ommatidia of compound eyes in terms of autocorrelation. Bullock's recognition of behavior was truly heartening and encouraging to me as a psychology graduate student. To this day, I still have my notes for Bullock's course after more than 50 years. They read well. For many years after this course, I would reminisce about something that I learned with, "was that before or after Bullock," as if I were saying, "was that before or after Jesus." One more thing about Bullock was his undergraduate lab course. We did some experiments on a variety of animals, mostly all invertebrates; the millipedes are what I remember the most. One thing he said stuck with me all these years. To paraphrase, he said, "Try to extract the most meaning out of the observations you make." To this day, these words are always in the back of my mind.

Research in the Psychology Department paled in comparison to the contents of Bullock's course. However, my duty was to sample various labs in the Department. After a few stints, I joined Donald Lindsley's lab because it was the biggest, seemed the most active with happy students, and was in the new shiny Brain Research Institute, not the Psychology Department. I admit that I was attracted to the glitter—racks of electronic equipment, as compared to a few syringes and cages in the Psychology Department labs. Lindsley's fame (decades earlier) came from early work on the reticular formation. His lab at the time I joined recorded evoked potentials in the visual system, something that I saw as a holdover of a bygone era. He was a renowned world traveler and was hardly ever seen, coming around rarely. Sometimes I saw him when I needed my study card to be signed and for other official things, like an oral exam and, finally, my thesis presentation.

Students in Lindsley's lab were studying visual masking, in particular, backward masking, which is when a second, brighter flash coming, say, 30 milliseconds later renders a first flash invisible. For a moment, this seems like a paradox: How could something come later and have such an effect? Of course, the second, brighter flash could have a much shorter latency, so that it could easily interfere with the response to the first flash. The lab was studying masking using evoked potentials in humans and monkeys and recorded these potentials when the two flashes came closer. They were looking for the times where one could not discern whether the first flash was there or not (Donchin & Lindsley 1965, Fehmi et al. 1969). They didn't see that this approach was doomed to failure because the gross compound evoked potential waveform didn't sample the real signals available to the brain to make the perceptual decision, *the activity of the individual neurons themselves.*

The only way to sample signals of use to the brain would be to record from single neurons and to see how they behaved under the same stimulus conditions that were used in human observers. Because the optic nerve is the only visual channel to the brain, I figured that recording from cat retinal ganglion cells would be the best approach. However, nobody at UCLA was doing proper visual neurophysiology, so I had to set up a single-unit visual physiology lab all on my own, relying to some extent on my teenage experience in electronics. All during this time, I remember poring over the Methods and Results section of Hubel & Wiesel's (1960) spider monkey paper many times. After spending at least a year building things [preamps (cathode followers), etching electrodes, visual stimulators, etc.], it all finally worked. To record my first action potentials was memorable, a thrill that I had been waiting for. Almost on the first day that I plotted my first retinal receptive field from fibers of the optic nerve as it entered the chiasm, I got the expected result. A second, brighter flash had a shorter latency biphasic response, completely obliterating the response to the first flash, thus "explaining" backward masking. That was my PhD thesis. However, I never published it because I was scooped by Peter Schiller at Massachusetts Institute of Technology (MIT), who published more or less the same results in the lateral geniculate nucleus (Schiller 1968). Professor Lindsley had really no understanding of my work, having never understood Hubel & Wiesel, and I had no other mentor around to advise me to publish. I regretted that my thesis work, abandoned and unpublished, was a totally wasted effort. Over the years, I realized that it was also disappointing for another important reason: It was such an obvious expected result that, at least to me, there was no real feeling of discovery.

BARLOW LAB AT BERKELEY AND BEYOND

While I was doing my thesis work, I was surprised to hear that Horace Barlow was not in England but in Berkeley. Compared to the scientists at UCLA and even with all other pioneers in visual neurophysiology, Barlow stood out as singular. As early as 1953, he made the prescient proposal that frog retinal neurons might be coding the existence of a fly in the environment (Barlow 1953). But as important in my mind were his imaginative speculations about redundancy reduction in sensory neurons (Barlow 1961). Then there was his insistence that quantal fluctuations and dark noise in the retina needed to be considered (Barlow 1956). This was way beyond the conceptual thinking of his contemporaries.

Through a personal family connection of his, I visited him and then later sent him the very clear results from that first neuron. He invited me to give a talk, the first I ever gave. For some reason, he accepted me as a postdoc. However, because of distracting family troubles, I never "caught fire" as a researcher in his lab. I got only one minor result, which was subsequently published (Nakayama 1971). Nevertheless, besides Barlow, I met top people who I regarded as real scientists, something that was rare at UCLA. These were people to respect and to learn from. Mike Land was a postdoc in Gerald Westheimer's lab. He discovered the reflective optical system of the scallop (like Newton's telescope), and his work at that time on the optical system and behavior of the jumping spider was elegant and outstanding (Land 1965, 1971). Mike was clever, innovative, someone who actually discovered real things about nature. We became friends, and he told me something in the form of advice that I didn't put into practice for a very long time but one that eventually became my lodestar. He said something like, "You psychologists have ideas that you pursue. We biologists find opportunity, some new subject waiting to be investigated, and we just study that."

I really didn't discover anything significant about the natural world in Barlow's lab, and when it came to job hunting, the only thing I got was a position in a new medical school in St. Johns, Newfoundland, an island off the eastern coast of Canada. Jutting out into the North Atlantic, St. Johns is closer to Dublin than to St. Louis. Besides being a windy, bleak, and remote place, research opportunities were dim there, and my research work moved at a snail's pace. After two years, four years post PhD, I had only one small first-authored paper. The record so far did not look like the beginnings of a research career.

REBIRTH AT SMITH KETTLEWELL (1971–1990)

I recalled having heard about the tactile visual substitution system (TVSS) back when I was a postdoc in Berkeley. This system was designed for blind people, who would sit in a chair panning a TV camera such that the image would stimulate a 20×20 array of vibrators on the back (Bach-y-Rita 1967). Later, I read an exciting article by perceptual psychologist Ben White and his colleagues (1970) about the TVSS. I was astonished to read that people externalized the tactile stimulus outside of their body and that there was a 3D percept; expanding stimuli appeared even to loom, causing the subject to duck as if avoiding an approaching object. To me, this was amazing. This could not be attributable to somaesthetic perception in any way. That one could have "visual experiences" through the skin seemed incredible and hard to believe. Is the brain really that plastic? I was drawn to this, and I rather desperately needed a job because I had had enough of Newfoundland and resigned my Medical School position without getting another. I contacted Paul Bach-y-Rita, the director of the project at Smith Kettlewell (SK), and somehow persuaded him to hire me.

When I arrived in San Francisco, I asked Bach-y-Rita what it was like to use the device and what was his personal experience. I was surprised by his answer. He was never a subject. I immediately needed to try it out. Seated in the apparatus, my hopes were dashed as I realized that any claim that this was a substitution for vision was shamelessly oversold. Even the most elementary of claims, like spatial resolution, were suspect. I then quietly joined Paul's other research area, the neurophysiological study of eye muscles, especially the lateral rectus muscle innervated by the sixth cranial nerve. We worked together for a while doing the all-day surgeries and physiological experiments. After a while, he seemed to get bored, and he let me have the run of the laboratory in order to pursue other topics having to do with eye movements more broadly.

It was around that time that I realized that I had forgotten all of the little math that I had learned in school and that I needed to learn it all again; as the received wisdom went, "to do science, you need to know math." I also finally realized that I was terribly wrong about math itself. It was not just a tool. It was full of amazing "discoveries," and despite the received wisdom about math being inaccessible, I felt, perhaps naively, that some of it could be at least partially understood and appreciated by the nonexpert. Luckily, I was carpooling from Berkeley to San Francisco every day with Joe Schlesinger, a math graduate student at UC Berkeley, so I read math books at night and peppered him with questions during the daily commute. My goal was completely different than that of a regular math student. I wanted to understand, even if superficially, the greatest math hits of all time. Linear algebra and differential geometry were fair game. Theorems related to functions of the complex variable stood out as the most astonishing, far reaching, and surprising. Back then, I was smitten by Euler's identity theorem and Riemann's conformal mapping theorem. Today, I am still awed by the relation between the distribution of primes and the zeros of the Riemann zeta function.

More to the point, back then, I wanted to find some kind of math that would help me understand vision directly. I found a range of interesting books on projective geometry (e.g., Rosenbaum 1963). Because cross ratios along a line remain invariant under projective transformations, I thought it could be something that could unlock some secret aspect of vision. My thought was to extend the cross ratio idea to more than one dimension so that it could deal with the perceived invariance of a planar surface from different views. I kept thinking about this for at least a year. Needless to say, I failed to gain any traction and eventually abandoned this quest.

Being in Bach-y-Rita's eye muscle lab, I needed to learn about eye movements. I soon found out about the pioneering work of David Robinson at Johns Hopkins. Starting his career as an engineer, he set the agenda and was thus the acknowledged leader in a field bringing together systems analysis and neurophysiology (Robinson 1970). Robinson also had clinical interests, and because SK was a leading institution studying strabismus, one of the researchers gave me a huge printout of Robinson's physical eye muscle model of the eye written in Fortran. It enumerated the position of all the muscles of the eye and how each one would rotate the eye when contracting. I never learned to program in Fortran, but Robinson's code was extremely readable, and the mathematics (rotation matrices) behind it was surprisingly transparent. I began to fully realize [helped by papers by Boeder (1957) and Westheimer (1957)] that any object has 3 degrees of rotational freedom, but the eye fixation system has only two; this is determined by Listing's law (see equation in **Figure 1**). This I deemed very important given the inherent noncommutative nature of rotations in space. It meant that the nervous system had to solve a real problem, how to fix that third dimension.

So I got terribly excited by Listing's law. Few understood this amazing law, and nobody cared, but this was all the better because it seemed fundamental; maybe I could take advantage of this unique and otherwise hidden opportunity. I spent a lot of time reading the relevant mathematics and writing a technical article on how to measure the full three-dimensional rotational state of the eye using photography (see **Figure 1**). On the strength of this mathematical paper (Nakayama 1974), I suggested in my first grant proposal that these measurements could be used to study strabismus. I wrote my application, which, luckily, was funded. I wasn't primarily interested in strabismus, but I felt it was a practical way to understand the mystery of Listing's law. My love affair with Listing's law was intense and continued for quite some time. But it was in the long run a love unrequited. After a lot of effort and time, and to this day, I have never figured out the *why* or even the *how* of Listing's law, despite a string of related publications (Balliet & Nakayama 1978, Nakayama 1978, Nakayama & Balliet 1977). Yet on the basis of the math learned along the way, I got my first grant, which at least gave me a salary to stay at SK.

$$\psi = \sin^{-1}\left(\frac{\sin\psi\sin\phi}{1+\cos\theta\cos\phi}\right)$$

Figure 1

(*Left*) Apparatus to measure eye torsion for any gaze direction. The telephoto lens of a motor-driven camera is lined up with the eye. (*Right*) Eye torsion (ψ) is a function of azimuth and elevation according to Listing's law.

As a consequence of the soft money nature of SK, getting grants was essentially all that mattered, so if my ill-conceived mathematically informed projects failed, it was largely irrelevant. Because all of our salary came from our own research grants, there was no teaching, and there were few administrative duties. As long as you could support yourself in something related to SK's mission, you were fine. This also meant that, to a much larger extent than in most academic departments, rank or achievement mattered much less than money. If you could support your research projects, you could stay. Although this "free market" system seemed to be stressful, it was far less so than was the case for junior faculty, as I learned from my experience as chairman of Harvard's Psychology Department—here the stress level for tenure-track junior faculty, as I later learned from my experience, seemed to me almost unbearable. At SK, you just got grants, and essentially everybody was on the same footing. We were all "second-class" citizens. As such, there was a great spirit of cooperation in terms of scientific exchange, and researchers often loaned money and equipment to colleagues for interim funding, because all of this was mutually beneficial in the long run. Arthur Jampolsky, the founder extraordinaire; Alan Scott; Suzanne McKee; Christopher Tyler; Erich Sutter; Tony Norcia; and Ed Keller, among others, contributed to this rare community of independent scientists.

THREE IMPORTANT PEOPLE

Furthermore, the beauty of SK was that life there was otherwise unstructured and not overfilled with daily responsibilities. Because of this, I had the time to work with many other established scientists (and rarely with students). Three collaborators in particular made a huge difference, and each transformed how I operated as a researcher. I worked with each of them in turn: Jack Loomis (1971–1974); Christopher Tyler (1974–1985); and, finally, Shinsuke Shimojo (1986–1989). Each relationship lasted at least two years, and the interactions with each collaborator were the most fruitful formative parts of my life as a scientist.

Jack Loomis and I arrived in San Francisco in the late summer of 1971. We both came to SK for the same ill-conceived reasons, to work on the TVSS. Both of us were greatly impressed by the written article describing the TVSS so glowingly (White et al. 1970). As I indicate above, I made my escape and got into eye muscles and eye movements. Jack fully understood the failure of the TVSS but used the opportunity to do fundamental work on touch (Loomis 1974). However, because we both were students of vision, we would spend a lot of time together, days and hours, just talking. Our conversations had a lot to do with science and mathematics, and with classic vision experiments, what they revealed, and what experiments to do in the future. In so many ways, we were very much in sync, and that enabled us to talk effectively. However, there was one area where I just couldn't fully understand him: his longstanding interest in phenomenology or, what he called at that time "experience." We didn't use the word consciousness in those days. He was classically trained in color psychophysics at the University of Michigan, but that did not reflect his core and deep abiding interest. Phenomenology or experience, his main preoccupation, was something actually rather new and initially alien to me.

I then was more sympathetic to the emerging field of classical threshold psychophysics melded with neurophysiology and considered conscious "experience" to be just the indicator, like a needle on a voltmeter. I didn't really think about the "qualia," the experience itself. My mission was to leverage the newly emerging discoveries about the receptive fields of visual neurons to understand perception, for it was here that I believed answers would lie. With this approach, one could measure behavioral thresholds in a human observer, cat, or alert monkey and compare this with the threshold of a neuron. Later, this approach would bear fruit and became a milestone in the history of visual neuroscience (De Valois et al. 1982, Newsome et al. 1989).

Jack held his ground, and slowly, I started to soften. Mainly through Jack, I got to visit the Exploratorium, a new science museum nearby, and to meet Frank Oppenheimer, its director. The museum was unusual in that, in addition to physics, perception was one of its major themes. From what I could get from Oppenheimer's writings and conversation, he had a vision and a mission for a science museum that would later be copied by other museums. As I understood him, he felt that modern science was becoming inaccessible to the general public, something that could only be understood by experts. By having "experiential" demonstrations, the museum allowed the visitor to engage with science directly and unmediated. In physics, two exhibits were especially memorable and spectacular: a cloud chamber, where you could just sit and watch the tracks of the cosmic rays that bombard us at all times, and a "real" image of a copper coil afforded by a parabolic mirror, which was so much more realistic than a hologram in that you could shine a light on it and see the specular reflection from it. The perceptual demonstrations included the classics: a real Ames Room, binocular rivalry, and the Cornsweet step, among others. The museum and Jack's interest in phenomenology had a very strong effect on me. It took a very long time, but over the years, I took to heart Frank Oppenheimer's credo, and it has had a major influence on my subsequent work, which continues unabated.

While Jack loosened me up toward experiences, I influenced him as well. Our common meeting ground was the work of J.J. Gibson who we both were familiar with. However, my own take was very different from that of Gibson's disciples, who ignored the brain. I felt that his insights could be directly related to the neurophysiological concepts of the day (see Nakayama 1994). After a lot of discussion, I persuaded Jack that this was a viable perspective. In particular, we laid out the intuitive and formal mathematics of the optical flow fields of a moving observer undergoing translational, rotational, and curvilinear motion. Given this analysis, we speculated that hypothetical center-surround motion cells could provide the observer with key information regarding the boundary of surfaces in the environment (Nakayama & Loomis 1974). Many years later, I worked with Barrie Frost at Queen's University in Canada, and we found center-surround motion cells in the pigeon optic tectum (Frost & Nakayama 1983).

After Jack left to take a job at UC Santa Barbara, there was no longer a vision scientist that I could converse and collaborate with. What was I to do? By some stroke of luck, even as the most junior newly minted Principal Investigator at SK, I was able to persuade the directors of SK that

Christopher Tyler should be hired. I had heard a talk by Tyler at a meeting. He did something unusual: measuring the spatial frequency sensitivity of higher-order variables such as binocular disparity. Besides working with such quirky stimuli, he was extremely productive. Given my near-zero publication rate and scientific loneliness at SK, he seemed like a good bet.

I was not disappointed. We collaborated enthusiastically on a range of projects, publishing 10 papers together. However, it wasn't the papers that we did together that were the most important for my future. Tyler's approach to science was completely new to me, a unique strategy and attitude for doing research. Whereas my largely failed work to date was exclusively theory and idea driven, his was *opportunity* driven, pure and simple. He had a terrific yet powerful strategy: Just measure the temporal and spatial frequency sensitivity of any or all higher-order visual variables. This was his "opportunity." The results were early high-profile papers in *Nature* and *Science* (Tyler 1971, 1973, 1974). While people were using the Fourier approach to study the temporal and spatial frequency response to luminance (Blakemore & Campbell 1969, De Valois et al. 1982), Tyler saw *any* visual dimension as fair game, including disparity, motion, and color. This provided a systematic way to measure visual functions over an extremely wide range of conditions because one could often vary frequency (spatial or temporal) over several orders of magnitude. He and I did this for moving stimuli, which allowed us to determine that some moving stimuli were detected by a velocity-sensitive mechanism, whereas other moving stimuli were best detected by a position system (Nakayama & Tyler 1981). I got a first-hand lesson that frequency analysis, Tyler style, was a powerful way to dissect and isolate visual mechanisms.

However, there was something else about Tyler that proved to be perhaps even more important, an attitude that I sorely, perhaps even desperately, needed to cultivate: He was just so terribly efficient. He cut corners legitimately like no other that I have met. For example, rather than bothering with a stereoscope, he free fused the stimuli (see **Figure 2*a*,*b***), which later led to his invention of the "Magic Eye" autostereogram (Tyler & Clarke 1990). And rather than displaying the stereogram on a screen or printing it out, he would just draw a stereogram free hand on a piece of paper and free fuse it. Also, he taught me intuitive and instant Fourier analysis, i.e., just mentally or visually superimposing sinewaves on a waveform or stimulus.

SHINSUKE SHIMOJO AND VISUAL SURFACE REPRESENTATION

The spirit of efficient and open exploration that I learned from Chris Tyler and the phenomenology advocated by Jack Loomis were miraculously combined when I took on Shinsuke Shimojo as my first postdoctoral student. Shimojo received his PhD at MIT studying visual function in infants. I was not interested in infant vision and barely understood Shimojo's work in this field. However, there was something appealing about Shin when I first met him. He had a kind of raw energy and enthusiasm that I rarely see, and that was enough for me.

Shimojo spent less than three years with me at Smith Kettlewell, not a long time. However, it was the most exciting and significant collaboration of my entire scientific life. Even though he was junior to me by 15 years, he brought to the relationship a lot of experience that diminished this age difference. First, at age 23 he had completed a first-class master's thesis at the University of Tokyo before going to MIT, including a heroic study (with himself as a subject) using reversing prisms to study the plasticity of stereopsis (Shimojo & Nakajima 1981). As such, he was much more experienced at doing fundamental vision research than his PhD in infant vision might imply. Second, he brought with him the gospel of vision according to David Marr. Recently deceased, Marr was a legend, and his students and collaborators were still at MIT. Having taken a course on Marr's work taught by Whitman Richards, Shimojo was thoroughly briefed, indoctrinated, and inspired. As such, Shin's arrival to my lab provided the occasion for me to more fully understand Marr's work. Most important, it made me more fully realize that the scope of visual science was

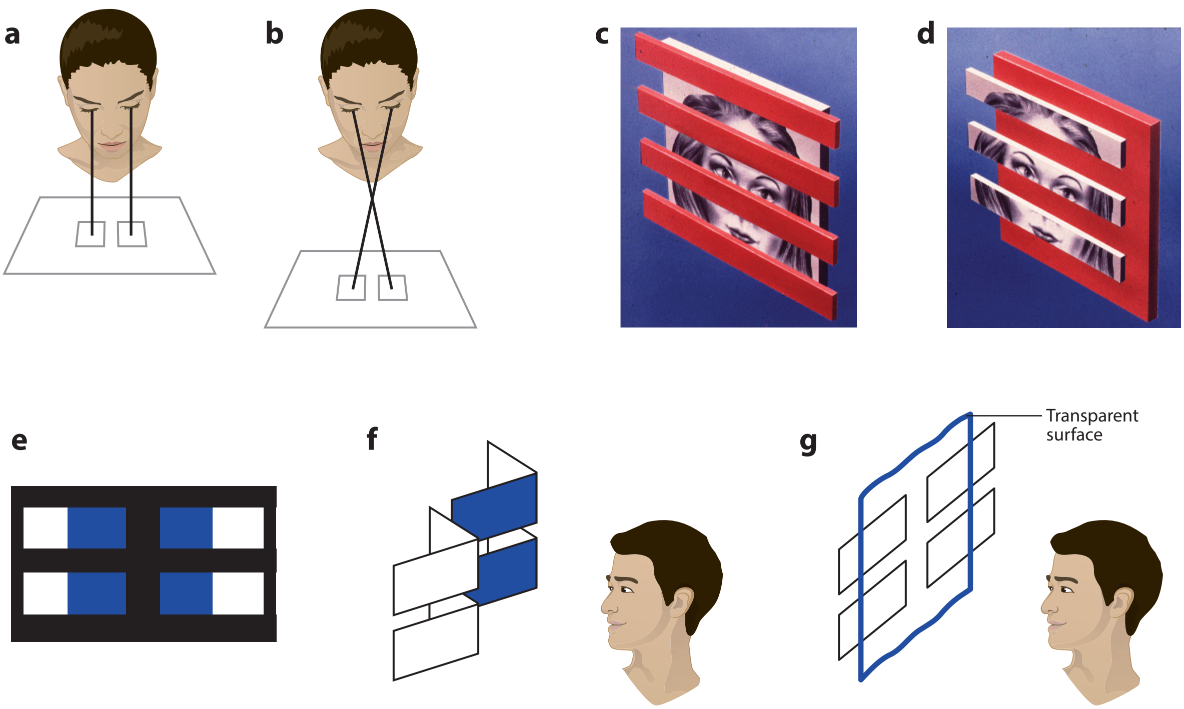

Figure 2

(*a*, *b*) Method of free fusion where practiced observers can either (*a*) diverge or (*b*) converge their eyes such that images in stereo pairs can be swapped. This dispenses with the need for a stereoscope, allowing quick inspection of binocular images. (*c*, *d*) Artist's depiction of relative depth in stereograms when right and left images are swapped. Surprisingly, the face is much more easily seen when it is behind. (*e*) 2D depiction of a stereogram with no monocular depth cues. (*f*) Artist's depiction of predicted depth from classical stereopsis given binocular disparity cues, where the blue–white boundary of each element is in crossed disparity and should be seen in front. (*g*) Unexpectedly, no such configuration is seen. Rather, the observer sees a transparent surface in front, with blue color bleeding into the dark regions.

much grander than what I had been exposed to. Most of the vision science of my day was preoccupied with the image and with how cortical neurons, with their receptive fields, encoded the image. Thus, the language was one of Fourier analysis, wavelets, and Gabor functions. Marr, more familiar with the tradition of computer vision and artificial intelligence and stealing concepts from J.J. Gibson, indicated that operations on the image were only part of vision and that the system needed qualitatively different processes to encode properties of the world, not just to process the image.

However, none of this would have happened without two essential things. One was a new gadget (the Amiga computer); the other was Christopher Tyler's skill (or trick) of free fusion, which meant that another gadget (the stereoscope) could be dispensed with.

Before Shin's arrival, my research assistant, Jerry Silverman, told me of a rumor about the Amiga, a new personal computer that was being developed by the Commodore Computer Company. Different from all others, it had special video hardware that allowed it to present visual images much more quickly and efficiently. Jerry suggested that we get on a waiting list to buy one. Just as important was an amazing program called Deluxe Paint, from a company called Electronic Arts. Costing very little, maybe $100, it allowed the user to create an incredible variety of stimuli, including moving ones, very quickly and without a programming language. By today's standards, however, the video quality was indeed primitive. It was a very low-resolution bit-mapped system (full screen 320 × 200 pixels) and only 8 bits deep. Up close, you could easily see all the individual pixels, far from the magazine quality that we demand today. For example, you couldn't make a low-contrast sinewave grating or Gabor patch, the stimulus de jour. However, for our purposes, it was good enough, and the low bandwidth was a blessing in disguise because it allowed fast video processing with the slow chips of the day. Deluxe Paint gave us an unusual opportunity to do something entirely different.

Recall that I was very taken by museum director Frank Oppenheimer's emphasis on "experience." Frank said that modern science was mostly inaccessible. His antidote was to allow museum visitors to experience science directly via demos. I recognized then that, with this cheap new technology, we had something really new. We could create so many diverse images in a matter of minutes with the Deluxe Paint program. With this in mind, I made an unusual open-ended "educational" suggestion to Shin: Let's not make any fixed plans for our own research. Instead, because we have such a wonderful tool, let's just make demos of as many published findings as we can find. In my own mind, by seeing all the reported visual phenomena first-hand with our own eyes, we could have a unique "personal and subjective" perspective on the whole field of visual perception. We could assess how strong the various claims really were that this could lead to something. In practice, we did reproduce many classic demos, but more importantly, we found we had the capacity to make new ones easily.

Most important were various binocular vision phenomena. The whole process was speeded up by our well-trained ability to free fuse image pairs, to either diverge the eyes so that the left and right image were seen by the left and right eye, respectively (**Figure 2*a***), or to converge (cross) the eyes so that the left image was seen by the right eye, and the right image was seen by the left eye (**Figure 2*b***). For us, it meant that anytime we were at home or anywhere else beyond the lab, a pair of images could be produced and viewed binocularly as a stereogram without a stereoscope, and we could swap the left and right eye images just by uncrossing or crossing our eyes.

We spent much of our time together in one large windowless room, for hours and days, almost side by side, each with our own computer, just creating and looking at new pictures, trying to find something interesting to show to each other, often chatting and laughing. Each of us was using Deluxe Paint. In making demos, our hands often worked faster than our thoughts, and some discoveries just happened as we were making so many images, seemingly at random. In essence, this furnished to us something unique and unprecedented, which one might call "high-throughput phenomenology" and which was so important for our work together.

Shimojo and I published about a dozen papers, and almost every one hinged on the simple fact that reversing disparity had dramatic and clear consequences that were obvious just by looking. All we did was create image pairs in the Amiga Deluxe Paint program and just look. And look we did.

We found so many surprising and unexpected qualitative changes as we fused these very simple pairs of images binocularly. Three examples will suffice. First, I removed alternate strips from a face and placed what was left of them either in front of or behind the non-face interleaved strips by changing the sign binocular disparity (**Figure 2*c,d***). My vague hunch was that it would be easier to see the faces if they were in front. I was dead wrong. Just looking at the two alternatives, it was immediately obvious that the face behind was so much more recognizable. The face strips in front were seen as separate entities, a series of fragments. Just looking (free fusing) was enough to apprehend this striking phenomenon; no experimental apparatus (stereoscope), no experiment, and no statistics were required to see this dramatic effect.

However, in seeing this, I had little idea of how to think about the result. What was going on? It did seem like the face strips behind might be virtually connected to each other behind the other occluding strips. Gradually, we started to develop a theoretical perspective based on the idea that occlusion of one object by others in front presents a very specific problem for object recognition.

If something in front obscures part of an object behind, that rear object is bounded by a contour that is spurious, containing wrong information about its shape. So the visual system must make the distinction between intrinsic contours, related to object shape, and extrinsic contours, something that would have to be ignored if we were to recognize objects (Nakayama et al. 1989). Later, Shin started reading Koffka's (1935) *Principles of Gestalt Psychology*, and we were pleased to see that he mentioned the "one sided nature of contours," that a contour "belonged" to one or the adjacent image region (pp. 181–84). This then led to the development of the term border ownership, which is now a well-recognized term describing a phenomenon that has been documented successfully by neurophysiologists, thanks largely to Rudiger von der Heydt and colleagues (Zhou et al. 2000) and, more recently, the laboratory of Doris Tsao (Hesse & Tsao 2016). The virtual connection behind, earlier dubbed as amodal completion and amodal continuation by Michotte & Burke (1951), would be the topic of many additional papers by us. Our conclusion was that this continuation, although invisible, was a specific visual phenomenon, likely occurring very early in visual processing.

However, a second demonstration, depicted in **Figure 2*e*–*g***, widened the whole enterprise and eventually led to a much broader conception of what we had uncovered. A fairly innocuous stereogram was presented (see **Figure 2*e*** for its 2D image). The disparity arrangements are set so that the transitions between the blue and white areas of each of the four panels is in crossed disparity, and thus, the apex of a convex fold should be seen in front, as depicted in **Figure 2*f***. Surprisingly, something completely new and unexpected is seen. Rather than the folded surfaces, as seen in **Figure 2*e***, we see something qualitatively different in several distinct ways. Instead of the folded cards, we see a blue planar transparent surface in front; so vivid is this that the blueness even spills over into the black center region between the two pairs of stacked panels (Nakayama & Shimojo 1992).

This is a dramatic result. The contradiction between what is seen and the predictions of classical stereopsis is plainly evident. Not only does it create a new unexpected surface in front, it also gives rise to a different material property of this surface, transparency. These dramatic results, along with many others, demanded a much larger framework. These stereo demonstrations (and there were many more) indicated the existence of a distinct level of visual analysis, that of surface representation. Rather than simply measuring and scaling disparity readings to arrive at the relative depth in a scene, the visual system is looking for the best interpretation of the layout of surfaces. The visual system will opt for an interpretation that is the generic view of a given surface configuration, not an accidental one. This we interpreted as the likelihood term in a Bayesian formulation (Nakayama & Shimojo 1992). Later work with Zijiang He (Nakayama et al. 1995) and Barbara Gillam (Gillam et al. 1999) would add significantly to this picture.

The third demonstration indicated that such surface processing was not some kind of higher function, but was instead likely to begin very early in the visual system, at cortical area V1 or V2. Back then, we were heavily influenced by the discovery of cortical cells, each sensitive to different amounts of binocular disparity, along with the issue of the matching problem to determine how points in one eye get correctly matched to corresponding points in the other. The general supposition was that, once this binocular matching process was established, depth in a scene could be determined. However, only a few researchers were concerned with something that is always evident in binocular natural images: the fact that to the sides of the edges of things in front are regions visible in one eye and not in the other (Gillam & Borsting 1988, Kaye 1978). Left-eye-only regions are seen to the left of a surface in front, and right-eye-only regions are seen to the right of such surfaces. Our contribution was to simply show such unpaired points without the front occluding surface (see **Figure 3**). Lo and behold, what was clearly seen was a surface in front delineated by vivid subjective contours. The surprising de novo subjective surface is not surprising if we think of the visual system as making reasonable inferences from image data. The whole range

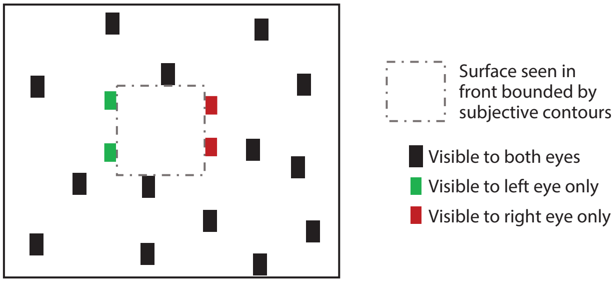

Figure 3

In real life, occluding surfaces in front usually give rise to binocularly unpaired points in regions behind. When such unpaired points are presented to viewers in stereograms, one sees the "recreation" of a phantom occluding surface. The surface is bounded by vivid subjective contours. Because left eye and right eye neurons are present only in the early stages of visual processing, surface processing likely begins in those stages as well.

of phenomena seen with unpaired points we dubbed Da Vinci Stereopsis, honoring Leonardo. In his famous essay on painting, Da Vinci suggested that unpaired image regions likely serve as a cue for enhanced depth (see Nakayama & Shimojo 1990). Because left eye versus right eye information was only really evident in V1, we made the claim that visual surface processing must begin there or soon thereafter.

Finally, I should not fail to mention that we began to carefully scrutinize the works of the earlier pioneers of perceptual psychology, in particular, authors such as Edgar Rubin, Gaetano Kanizsa, Kurt Koffka, and Albert Michotte. Each had discussed some of the processes that we had encountered, and we adopted their vocabulary when appropriate. Later, in a long review chapter, we indicated that surface representation represents a necessary level of visual analysis, beyond the image itself but before other higher visual functions, object recognition being one of these (Nakayama et al. 1995).

OTHER WORK AND "JUST LOOKING" AT SMITH KETTLEWELL

The work that I did with Shimojo I deem to be the most important of my career, but he was with me for only two years and eight months. I was at SK for almost 20 years. What else did I do? Well, it's embarrassing to say that quite a bit of time was spent on failed projects. Besides the kinematics of the eye mentioned above and other forays into mathematically inspired work, one spectacular failure was my attempt to find the origins of the surface visual evoked potentials to visual stimuli using current source density (CSD) analysis in cats and monkeys. This I did with my collaborator, Manfred Mackeben. We were led foolishly into this field after a study section site visit. The members of the study section picked up on a comment that I made that such a project could be undertaken and that I had made some preliminary efforts along the way, having had a visit from Ulla Mitzdorf, who successfully traced synaptic cortical currents in the monkey visual cortex using electrical stimulation of the optic nerve (Mitzdorf & Singer 1979). They didn't like the project stated in the grant, but on the spot said that we should propose this new CSD project and send in the proposal within a week. So we got trapped by the grant reviewers. This overly ambitious project was funded, and we did not have sufficiently good multi-array electrodes to make satisfactory measurements with any consistency.

Fortunately, I also initiated a project that was even less systematic than "just looking;" instead, it involved "just noticing accidentally." This took place when I was a subject in a modified visual search experiment with postdoctoral student Mary Bravo, in which the odd-colored target and distractor color switched on a random basis (Bravo & Nakayama 1992). I just happened to notice, as a subject, that when the same colors repeated, I responded much faster. Years later, when I got to Harvard, I remembered this. There, it became Vera Maljkovic's PhD dissertation and is the most widely cited of all my papers (Maljkovic & Nakayama 1994), but it had very humble origins, something I "just noticed." Thus, in the practice of science, almost anything goes when it comes to origins (Feyerabend 1993, Koenderink 2002).

What is the moral of the story? I am not advocating "just looking" for others, but it seemed to be the best approach for me, and I took it to heart, remembering the words of people like museum director Frank Oppenheimer and Ted Bullock and Michael Land, both zoologists. It was an approach that I became more sensitive to because my early instincts and training were to do just the opposite. I was taught to look at some literature exhaustively and carefully and have a deep theoretical perspective, perhaps even a mathematical one. I did this on repeated occasions, and the approach mostly failed. Eventually, I was able to unlearn this strategy.

Maybe "just looking" worked for me because of my extremely broad (and superficial?) interest in the "best stuff" about the brain and about math and science more generally. Maybe my mind was attuned differently than my peers and was able to pick up on odd random observations. I really do not know. Again, I don't advocate it for others, but it's clear that it worked for me.

Along these lines, perhaps the most extreme example of "just noticing" in modern science is the discovery of Lucy, a four-million-year-old skeleton of a proto-human, noticed just lying on the surface of the shifting sands of the Ethiopian desert by Donald Johansson, UC Berkeley Professor and Director of the Institute for Human Origins (Johanson & Edey 1990).

HARVARD, 1990–2016

The bulk of my scientific career was spent at Harvard. However, space in this article does not permit doing justice to a most obviously rewarding and very different part of my scientific life. Some of this life was not due to my own work alone, but was instead the result of a collaborative organizational project with Professor Patrick Cavanagh. We were both offered jobs at the same time, with the notion that we together were to start something significant. I think we did. It's our intention and hope that Patrick and I will tell this story more fully at another time.

So I include just a few words on how this began. Sometime around 1988, I was unexpectedly offered a job in the Psychology Department at Harvard along with Patrick, then at the University of Montreal. For some reason, I didn't jump at the chance. Sure, it was a wonderful thing to get an offer from the top-rated university in the country. However, at that time, I had hardly heard of anybody in the Psychology Department. I was disappointed by the first visit, I didn't really engage with any of the psychology faculty, and the graduate students seemed to be a dispirited and depressed lot. I got the same negative read on the Department when I visited Professor Richard Held at MIT. I wasn't exactly fishing for advice, but he must have sensed my uncertainty. He said, in a deadpan voice, something like, "If you invited a great speaker of your choice, who would be there to listen?"

Eventually, I came to my senses and more fully realized I only had a soft money job at SK with no real security. Pointedly, Richard Andersen, then an MIT Professor, said, "Ken, they are not going to ask you again, if you turn this down." Well, maybe another reason why I made the right decision was that I would have the opportunity to set up a new huge lab in cooperation with Patrick Cavanagh. I didn't know him well, but I did hear a talk he gave at SK many years earlier, likely invited by his friend Christopher Tyler.

His talk was on the confusability of letters. If I remember correctly, he formulated the problem in terms of overlap in the 2D Fourier spectra. He was much more technically advanced than me, certainly a plus. However, this was nothing in comparison to what I learned of his most recent research. In essence, it was a truly brilliant phenomenological demonstration, later published in *Science* (Cavanagh 1992). He created a rotating circular display where the observer saw one direction of motion if viewed passively, whereas the opposite direction of motion was perceived if the observer mentally tracked a pair of visible sectors. This was something truly wonderful to just "see." Such a huge difference in motion perception was astounding. Most important, it illustrated an important conceptual distinction about motion that is yet to be fully appreciated by some researchers, even now. In one single display, he allowed the observer to experience the workings of a low-level motion system, as studied by neurophysiologists, and something completely new, a higher "attentive tracking" system, maybe the one we use even more frequently in real everyday life. This was the clincher that really helped seal the Harvard deal for me. He shared my respect for visual phenomenology and its role in obtaining a fundamental understanding of the visual system.

Sometimes, tiny snippets of a conversation can have a huge impact. I just happened to be chatting with MIT professor Tomaso Poggio in Professor Lucia Vaina's Cambridge kitchen. He said something that made a big impression on me back then, something like, "Ken, if you change your work environment several times in your life, when you are old, you will have memories of a much richer life." Looking back over 30 years later, I was so very lucky to get this position, as it was so bountiful in its effects in so many unforeseen ways. Tommy Poggio's prophecy was certainly correct.

I had not been in a real psychology environment for a very long time because in graduate school, I was in UCLA's Brain Research Institute. Richard Herrnstein, then a professor in the department, indicated that I could be designated as a professor of psychophysics, not psychology. Ten years earlier, that would have sounded just right. However, by then, I was less loosely tied to the tradition of classic vision and politely indicated that being a professor of psychology was just fine for me. I saw the job as an opportunity to really connect to the discipline of psychology, and looking back now, this was truly the case. As one small example, I had the opportunity to teach an undergraduate seminar on consciousness many times. This was an amazing way to reconnect to the whole field of psychology in countless ways, for which I am still reaping the benefits.

The department was extremely generous with space, giving us a whole floor of William James Hall. Patrick also had a real talent for spending goodly amounts of money in a flashy yet tasteful way, which I fully approved of. Given this unusual opportunity, we had so much fun designing the whole space from scratch. This included very large common areas, including a functioning kitchen with a good-sized refrigerator, a dishwasher, two microwaves, and a table for eating and a very large open laboratory space, plus our own dedicated seminar room, which could expand into the library, allowing for a very large audience when needed. Most importantly, we both decided that we were going to have a *single* laboratory: Students advised by Patrick and I would be fully intermingled spatially.

Because we were relatively well established, we seemed to agree implicitly not to exclusively promote our own past research agendas, but instead to allow students to develop their own under our guidance. As such, the range of research, in terms of methods and content, was sufficiently wide that students were not in competition and cooperated surprisingly well; some of them got little input from us, others more. As such, we ourselves weren't competing with them either as they started their new careers elsewhere. As Patrick said, "We don't want to eat our young." The result was that a surprising proportion of our students worked on their own projects, not ours. Thus, over the years, more than 80 graduate students and postdocs enjoyed a unique interactive environment under our watchful guidance. In addition, we had many senior visitors as well. Most important, we were able to have Charles Stromeyer join the lab as a Harvard Senior Research Fellow. In sum, it is with some pride and pleasure that I note that many of these young people were able to take their place as successful independent scientists in a variety of institutions far and wide.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

I am grateful to Jack Loomis, Christopher Tyler, Shinsuke Shimojo, and Gerald Westheimer for reading and commenting on an earlier version of the manuscript.

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Annual Review of
Vision Science

Volume 7, 2021

Contents

Errata

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