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Carl Gustave Bernhard Lecture, Royal Swedish Academy of Science (1996)
Koetser Prize (1997)
King Faisal International Prize in Science (Biology) (2004)
The Tizard Lecture, Westminster School, London (2004)
The Edinburgh Lecture (2005)
Erasmus Medal, Academia Europeae (2008)
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Semir Zeki pioneered studies of primate higher visual brain areas and showed that a basic modus operandi of the brain is to process different features of the visual scene separately, in parallel, and asynchronously. His findings led him to investigate the nature of conscious vision and examine how we acquire knowledge through it, especially through its color and motion systems. His approach to the brain as an epistemic system led him to investigate what the products of artists can tell us about the organization of the brain and, ultimately, to enquire about the nature of beauty itself from a neurobiological perspective.

Semir Zeki

I breathed neuroscience at a relatively early age, when I listened to J. Z. Young's 1950 BBC Reith Lectures, entitled "Doubt and Certainty in Science." I cannot claim to have understood much, if any, of it and cannot now recall its details. Yet it stimulated me to want to study the brain. Years later, I applied to University College London (UCL) to read medicine with the hope of studying under Young (see volume 1), popularly known as JZ. I applied to the medical school but the subdean rejected me. I therefore applied to UCL to read anthropology instead, a topic in which I had a vague, but not profound, interest.

For my first day, UCL had chosen an "inspirational" lecturer who promised yawns; I went instead to another college of my university, the London School of Economics; they had invited Bertrand Russell, an altogether more enticing prospect. Of that lecture, I recall this advice: First, "do not waste your time going to lectures, which are relics of medieval times when there were no printing presses; spend your time in the library instead"; and, second, "if you want to be happy, you must come to believe that this is a very wicked world." I cannot remember now whether he added, "because things are not always as bad as you might expect," but that is the gist of what I retained.

I accepted the second piece of advice and have adhered to it ever since, developing a view of this world as a deeply wicked place, which has indeed made me a happier person. Not so the first, because I had entered an institution (UCL) that had brought under one roof some of the most formidable talents in the land—among them JZ in anatomy, Peter Medawar in zoology, Andrew Huxley (see volume 4) in physiology, Kathleen Lonsdale in chemistry, Bernard Katz (see volume 1) and Ricardo Miledi in biophysics, Nigel Barnicot in anthropology, A. J. Ayer in philosophy, Lionel Penrose (in what was then eugenics), and William Coldstream in painting; they were soon joined by Stephen Spender in English, Lawrence Gowing in art history, and A. J. P. Taylor in history; many were brilliant lecturers and, rather than skip their lectures, I instead waited impatiently for their next one.

Five among this extraordinary group (Barnicot, Young, Huxley, Katz, and Taylor) were to have a lasting influence on me; four were English, of whom two were from the high establishment and one from a dissident English family; one was a German émigré. All but one were scientists; all save Taylor were to become lifelong friends. They shared, or so I thought, three features—all were, to varying degrees, radical or revolutionary in their approach; all were supremely self-confident; and, yet, because of

their high intelligence, all seemed to be somewhat apart in their societies. These characteristics enhanced their appeal immeasurably. Their major influence, especially that of JZ, was not only to encourage radical thinking based on fact but also to cross disciplinary boundaries—even if they seemed apparently remote from each other. They were to be joined later by an American, Edwin Land; he was perhaps the most radical of them all in his thinking; he transformed my views of color vision, with profound implications. He too was to become a lifelong friend.

Continual discussion has been central to my education and thinking—an unanticipated word here or a sentence there, sometimes uttered casually and sometimes deliberately, often changed the course of my thinking significantly. I could not have hoped for more extraordinary interlocuters than the ones I found at UCL. I have written this autobiography to convey, as well as I can, this interdisciplinary interaction, from trivial to high levels, and the UCL environment that nourished it.

Early Influences

My great fortune during my first year was to know Nigel Barnicot, a highly sensitive and brilliant if self-effacing man, who was instrumental in lifting physical anthropology, quite literally, from the fossil age to the genetic level. He was also an accomplished artist with wide literary tastes who, I sensed, was somewhat estranged from society. He enlarged my horizons immensely. He had a dry, sardonic, and very English sense of humor. This was coupled with a profound contempt for the many people at universities who ostensibly are interested in the pursuit of knowledge, but who, in reality, are more interested in seeking high administrative posts and the relatively trivial power that comes with it. I inherited this contempt, which has increased significantly over the years. But, despite my distaste, I was myself much later prey to this power vanity. I started negotiations with three prestigious institutions for headship of departments; I rejected one and was rejected by the other two. These rejections did me a huge favor; otherwise, I, too, would have been stuck in the ever-worsening nightmare of administration. I once said to Nigel, "I will never yield to administrators." He replied, "But then you will become like them; you should instead say: 'I will sometimes yield to them!'"

Together with Nigel, I attended coffee sessions every Saturday morning in the Biophysics Laboratory with Ricardo Miledi and Bernard Katz. This was a high privilege at my stage, and, though reticent at first, I came to engage easily in the hour-long coffee sessions, from which I learned a great deal of scientific gossip in the good sense. Later, after Bernard retired, I sheltered him in my laboratory for 24 years, until his death; he used to bitch to me in the morning in his heavy German accent, often using colorful language; I returned the compliments in the afternoon, with more

guarded language. Whether what we bitched about was highly intellectual or very mundane, it was always made enjoyable by being laced with much, often coarse, humor. As well, Bernard, a refugee from Germany, had outdone the natives in mastering a style of clear, economical writing in English, believing that even the most complex phenomenon should be explicable in clear and simple language; he despised those who wrote otherwise. He made many stylistic improvements when I was writing my book, *A Vision of the Brain*, for which he translated for me many papers from the rich German literature. The discussions surrounding these translations became themselves a source of hilarity because many of their authors seemed to have elevated to perfection the art of bitchiness in describing their colleagues. But woven into these discussions was important scientific advice, to which I have tried to adhere with varying degrees of success.

These Saturday discussions had another favorable outcome; they led Nigel Barnicot to advise me to quit anthropology and switch to medicine instead, which relieved me immensely. He arranged it with JZ that I should get into medical school; JZ, who was then the dean, seemed only too keen to overrule the previous objections of the subdean, possibly to show the latter his evident contempt. JZ said to me: "Go tell the subdean to give you a place." I thus became a medical student in this roundabout way, through contempt. The subdean nevertheless took his revenge—he refused to give me a place for the clinical years—a revenge that ultimately worked to my advantage because I had by then concluded that, in medicine, once you have seen the first 100 patients, you have essentially seen them all.

JZ was my tutor during my undergraduate years and supervisor during my postgraduate years. A scientist and an educator to his fingertips, his charisma was much enhanced by a formidable lock of hair that he swept back at strategic intervals during tutorials. A descendant of Thomas Young, Britain's 19th-century polyhistor, he was blue-blooded to his fingertips, had an impressive scientific genealogy, and possessed supreme self-confidence. A polyhistor himself, he turned his private tutorials into delightful wide-ranging discussions, seemingly among equals, that revealed his deep interest in the humanities as well. For my first tutorial, he asked me to read Sigmund Freud's *Civilisation and Its Discontents*, which I in turn have since recommended to all my students. Eccentricity was part of his patrician manner; once when I approached him while he was walking, he said, "I can't talk to you now; I am thinking." On another occasion, Valentino Breitenberg, a neurobiologist, started his seminar with three slides, each showing the responses of neurons in tissue culture, analyzed by computer. JZ cut in: "Valentino, is this interesting?" he asked; Valentino said, "No, not really." That effectively ended the seminar. JZ was also a master at delivering the acerbic English comment with deadly precision, once confiding in me about a colleague: "Now that [his] English has improved, he has become rather irritating!"

I possibly learned more from JZ than from any other of my university teachers. He gave mesmerizing lectures by reading them all out, from beginning to end. His Wednesday morning lectures, entitled *Introduction to the Study of Man*, were exhilarating in their breadth and insight, inspiring generations of medical students. He was always radical in his thinking and provided me with insights that came to fruition years later, when I started my course in neuroesthetics at UCL.

Andrew Huxley, my undergraduate tutor in physiology, was altogether different. Descended from the Huxleys and married into the Wedgwood family, he had worked on developing radar control of anti-aircraft guns during World War II. The equal of JZ in self-confidence, he was master of all in his passion for calculation; like Charles Darwin, he had confidence in nothing save measurement. Some thought that he took this passion to unreasonable heights, even bringing his formidable intellect to measuring the cubic capacity of commercially available fridges when someone in his department asked to purchase one. He once used a measuring stick in the dead of night to ascertain the dimensions of a room that was to be shared between his department and anatomy, claiming his fair share next morning to the immense irritation of JZ who had thought the matter had been settled in his favor. Known as "hawk-eye" for the speed with which he detected the slightest error in any diagram or argument, he had put his formidable talents for quantification to one of the most formidable problems in neurobiology—the mechanism of conduction of the nervous impulse—a problem he had solved together with Alan Hodgkin (see volume 1), their work having been much eased by JZ's discovery of the squid giant axon. To achieve this feat, he had undertaken calculations on an industrial scale, perhaps as much as a quarter of a million, using a calculating machine that he had designed, which he demonstrated to me with pride in his rooms at Trinity College, Cambridge, long after he had retired from UCL. Having designed and built his own microtome as well, he cared nothing for scientists who purchased scientific instruments instead of building their own; like many of great ability, he overestimated the capacity of others. Ray Guillery, an anatomist, once sought his help to secure a grant for purchasing a microscope; Andrew said, "I can show you how to grind the lenses and put them together to make a microscope yourself. You need not apply for a grant." He was fearsome in the legendary UCL faculty colloquia, undertaking detailed measurements while some panicked junior member was discoursing. Andrew's *in situ* calculations often uncovered dramatically an error in a speaker's conclusions. Often, but not always; on one occasion, Andrew made furious calculations while a speaker was lecturing on the cochlea and, based on these, challenged the speaker's conclusions. The speaker, unlike most biologists, knew enough mathematics to question Andrew's intrusion. Andrew saw his error immediately and said, "Oh, I had been assuming that the cochlea is infinitely long!"

There was a downside to Andrew Huxley's obsession with measurement. Although he believed that the only two topics that could not be explained with clarity in 50 minutes were quantum mechanics and particle physics, he rendered his own physiology lectures impenetrable, by sandwiching his arguments between layers of incomprehensible mathematical formulae. Sometimes they became so difficult to follow that I imagined myself in the position of captive attendees during the reportedly long and boring recitals given by Emperor Nero; many feigned death to be taken out of the room, and some feigned it so well that they were actually buried!

Superficially, Andrew's talents made him unapproachable but in private, he was a charming and generous host; unlike what many supposed, he was well read outside science, and we shared a common interest in the writings of H. L. Mencken, the Sage of Baltimore, whose humorous and cynical articles, displaying impatience with "the charlatanry of the learned," were to have a lasting influence on me. Our relationship continued until his death and, when my son was studying at Cambridge, he made a habit of inviting him regularly to Sunday lunch.

Andrew taught me, like none other, the inestimable value of scientific rigor, down to the most minute detail but one whose level is strictly tailored to the problem at hand. He also veered me away from insoluble problems. One such problem was that of consciousness, which he found interesting but too complex. I accepted this advice and stayed clear of the problem, with minor incursions years later into whether activity in single visual areas can acquire a conscious correlate.

A. J. P. Taylor was not a scientist but a historian who has been described as "the Macauley of our age." He had come to UCL when denied a lectureship at Oxford, ostensibly because of controversial views expressed in his radical book *The Origins of the Second World War*, which has since been accepted as a masterpiece of historical writing; more likely, it was because of his iconoclastic brilliance and regular television appearances that brought him fame and reportedly significant earnings, thereby exciting the envy of many. I attended his lectures regularly but had only one personal, although highly entertaining, encounter with him, at a dinner organized by JZ. Wearing a flashy bowtie, he started his lunchtime lectures punctually at 1:10 p.m. and left precisely at 1:55 p.m. without using a single note from beginning to end, in contrast to JZ. His lectures were commonly crafted to start or end dramatically; one, on World War II, began thus, "Mussolini entered the war because he thought that the war was over and was fearful of losing a place at the top table." He was commonly radical in his thinking; he came up with the extraordinary, although cogently argued, view of the logistics of the Great War; he claimed that the long deliberations in the British War Cabinet—by men "mostly entirely ignorant" of their subject—changed suddenly when they were made aware that trains, unlike horses, could not change course

midway to their battle destinations. This turned generals into masters of railway timetables. It is a view that formed the basis of his book *War by Timetable*. His lecturing style influenced me deeply, if only because his brief, simple sentences were so confident; I was to find out later that each carried a huge wealth of knowledge, of which they were elegant summaries, the tip of the icebergs of knowledge.

These, then, were the five men who provided the intellectual basis for my formative years at UCL. Collectively, they gave me an education like no other.

My Beginnings in Research

My first year was, as one might expect, full of fun and parties with little time for studies. This was reflected in the miserable results I obtained, earning me a stern rebuke from the new dean but also acting as a wake-up call. Having been deprived of a place in the clinical years, I was desperate to do well and gain a bachelor's degree in science. I started working at 4 a.m. every morning; this effort earned me a university scholarship in the final preclinical examinations and the chance to spend an extra year studying a subject allied to medicine. I chose anatomy, principally because of my hope that JZ would be my tutor, which indeed he became, offering me immense opportunities. I never looked back except to write, years later, a flattering review of a book that the subdean who had rejected me for the clinical years had coauthored.

JZ left the choice of research topic to me and my choice was dictated by three factors: my interest in the workings of the cerebral cortex, my interest in vision, and my profound distaste for working in large groups. I was, and remain, a strong adherent of Jean-Paul Sartre's dictum that, "*L'enfer, c'est les autres*"! Most who were working on the visual brain then were doing so on the primary visual cortex (area V1), which receives the predominant visual input destined for the cerebral cortex. Much of this work was of little interest to me; the psychophysics linked to it was especially tedious. David Hubel (see volume 1) once remarked memorably that, "psychophysics is usually correct but boring and physiology is usually wrong but exciting." In fact, for me, David Hubel and Torsten Wiesel (popularly known as H&W), were doing the only radical and dramatically interesting work on V1. The pioneering work of clinicians and physiologists had determined the very precise way in which the retina is mapped onto its surface and how damage to it leads to blindness, which led most to assume, quite reasonably, that the cells of V1 respond to light. They were wrong. H&W showed that they respond to transformations in light energy between one small part of the field of view and its surrounds, a transformation that has a form and an orientation. They were, in brief, orientation selective cells; they had varying degrees of complexity, lead-

ing H&W to conclude that the visual brain "analyzes" the visual field in a serial, hierarchical manner at ever more complex levels. Since my (later) results emphasized parallel, rather than serial, processing as the major modus operandi of the visual brain, I was to disagree with them, not only about the processing strategy used by the visual brain but also eventually about whether the brain "analyzes" the visual field at all. The view I developed gradually was that the brain creates the visual image from the signals that it receives, rather than being a passive chronicler that simply analyzes the visual image. Given my huge admiration for H&W, I never contradicted them publicly; this perhaps worked to my disadvantage. But my intellectual disagreement with them never diminished my intoxication with their work.

Had I not hated crowded areas, I may well have worked on V1 because of my infatuation with H&W's work. But I sought my own, deserted, territory and opted instead to work on the cortex surrounding V1, often referred to as the prestriate or extrastriate cortex (since V1 is also known as the striate cortex). Because of this self-imposed isolation, I was the sole author of most of my papers until the early 1980s. The prestriate cortex was, at that time, a largely neglected cortical area, commonly referred to as "association cortex." My isolation had a silver lining; I was left largely, if not completely, alone—a blissful state that I came to yearn for later, when the influx of so many into the field made it much too claustrophobic. Just as the title of Patrick Howarth's book *When the Riviera Was Ours* suggests, I have often glanced back nostalgically on those blissful years when the prestriate cortex was largely mine, or so I felt.

Although JZ was my formal supervisor during my doctoral years, the day-to-day supervision was left to Brian Cragg, a wonderful and very critical colleague and, more remotely, to Jack Downer. Jack had established a monkey colony in the department and, though not really involved in experiments apart from teaching me and others how to operate on monkey brains, wanted to talk endlessly about the visual cortex; to him, this meant solely V1. These discussions always revolved around the position of the representation of the retinal fovea in V1 and always began with the statement, "Now that we know where the fovea is mapped in V1." This assertion surprised me because that was an issue that I believed had long been settled. Soon these discussions not only became tedious but also made it apparent that Jack was not well. I now very much regret that I was not able to, and did not, offer him the sympathy he deserved as a fellow human. Whatever his shortcomings, and although he faded quickly from my life and from academia generally, he played a central role in my research by providing the facilities of a monkey colony. And although the doctoral work done in his laboratory was not spectacular, it very much laid the foundations for my future work.

Modest Beginnings in Anatomical Studies

My doctoral thesis revolved around the topic of the effect of lesions in prestriate cortex on the visual capacities of monkeys. It was examined in September 1967 by JZ and Larry Weiskrantz, for whom I had developed a fondness until I came to blows with the Oxford school over the so-called phenomenon of blindsight with Larry as the leading, but unintended, casualty.

I spent my postdoctoral years as a research fellow in the United States and began my work by addressing the question of how the anatomical connections from V1 to the surrounding, prestriate, cortex are organized. The prestriate cortex was generally and indifferently spoken of then as "association" cortex, although no one had studied associational activity there; it was so named because the stern and eminent German anatomist Paul Flechsig had called it so. His nomenclature was based on the insight that he had derived from his myelogenetic studies. These studies had shown that, except for a small and significant subdivision (*Feld 16*, to be discussed), the cortex surrounding V1 was not fully myelinated at birth; rather, it myelinated gradually after birth, as if its maturation depended on the acquisition of experience. Flechsig saw in this pattern deep philosophical insights, dismissing all contrary views as being "totally useless from a scientific point of view." Without imputing any specifically visual functions to it, he referred to his association cortex as the *Cogitatsionzentren* and adopted grand ideas implied in this nomenclature; these ideas seemingly licensed him to explore major philosophical issues, one in an article that was somewhat grandiosely entitled "Gehirnphysiologie und Willenstheorien (Brain Physiology and Theories of the Will)." Speculative he may have been, but his nomenclature is testament to a profound insight. For it turned out that the activity within the visual areas of the prestriate cortex, described by me and others, is in significant measure the basis of visual experiences.

David Whitteridge, then professor of physiology at Edinburgh and known as a man with a "high IQ and a low pH," had been instrumental in encouraging me to undertake these anatomical studies when I started my postdoctoral work at the National Institute of Mental Health (NIMH) at Saint Elizabeths Hospital in Washington, D.C. Ezra Pound, principal mentor of my favorite English poet, T. S. Eliot, had been incarcerated there; this swelled my vanity into supposing that I could become a poet as well as a neurobiologist; a couple of weeks at Saint Elizabeths Hospital soon disabused me of the idea. This was all part of a youthful, if unrealistic, hope when looking forward to a romantic future, for I got married before leaving London. We left for New York on the magnificent *SS Le France*; before docking, it sailed majestically past the Statue of Liberty. That was a moving moment; I had arrived in the land that had provided so many with hope and opportunity; it promised to provide me with one too—and did.

I started my anatomical work at the National Center for the Prevention and Control of Alcoholism of NIMH. This may seem surprising; I was neither an alcoholic nor much interested in alcoholism. But I had been recruited by Nancy Mello, the effective director of the laboratory. Somewhat improbably in such a setting, she was interested in anatomical connections of pigeon brains, when she was not trying to get them, and monkeys, drunk. She wanted especially to determine the interhemispheric connections of the pigeon optic tectum; as she saw it, the topography of these connections would account for the mirror-image transmission of information between the hemispheres that her behavioral studies had suggested. The "deal" was that I would spend the first part of my year there charting these intertectal connections; once done, I could concentrate on my real interest—the anatomical connections between V1 and the prestriate cortex in rhesus monkeys.

It didn't happen that way; after studying some 20 pigeons, I could not find the anticipated intertectal pathways. Nancy was incandescent; she believed that I had deliberately sabotaged her work to pursue mine. After some banging of telephones and slamming of doors, it was decided that I could pursue the original plan minus the pigeon intertectal connections; this was largely because Max Cowan (see volume 4), who knew a thing or two about pigeon brain anatomy and could recognize the nonexistence of connections where there were none, had also been unable to find these connections. Thereupon my relations with Nancy thawed and remained cordial until I left to take up a second postdoctoral position, with Ray Guillery, at Wisconsin University.

Despite all the powerful irritations—on both sides—and of my strong disavowal of the motives that Nancy imputed to me, she nevertheless encouraged me to continue my work on monkey brain connections, which resulted in my first paper on the topic, in 1969. Although I lost contact with her after leaving Washington, D.C., I always remained grateful to her for providing me with the opportunity to undertake these studies, which laid the foundation for my future physiological work.

At that time, the only work on the connections between V1 and the prestriate cortex was the pioneering study published by Hans Kuypers and his colleagues; they had made large lesions in V1 to trace its connections to the large surrounding prestriate cortex; they had shown that large V1 lesions result in a distribution of degenerated fibers in a correspondingly large portion of prestriate cortex; and they named the latter the circumstriate cortical belt (CCB). The undoubted importance of their study nevertheless left me with the need to study the finer details of these connections. How could I refine their work? Given the precise representation of the retina in V1, I made small, separate lesions along the representation of the vertical and the horizontal meridians, as well as the fovea, in V1 and traced the anatomical connections from them to the prestriate cortex. The

results, when reconstituted, showed that there are, within the CCB, two areas in front of V1, with the representation of the horizontal meridian in V1 splitting to form a boundary between them. Such an arrangement was baffling because it was so unexpected; it absorbed me for weeks, and I consumed many packets of cigarettes, but I could find no other interpretation. Finally, throwing caution aside, I published the work in 1969. I referred to the two areas as 18 and 19. This was unfortunate; I had been uncritically influenced by the nomenclature of the German anatomist Korbinian Brodmann and of H&W. I later changed the nomenclature to V1 and V2. Results very similar to mine were published later by John Allman and Jon Kaas (see volume 9), in 1971. In fact, both were also working at Wisconsin but in the physiology department. I now regret that my interaction with both, when all three of us were working at the same university and on the same problem, was minimal. They are scientists whose work I came to admire, even staying with John Allman at his home in California, where one of the lemurs with which he shared his home surprised me by sneaking into my bedroom and making some very rude gestures.

There was another area that I highlighted in my 1969 paper; this was also located, separately, in the CCB, in the posterior bank of the superior temporal sulcus and thus relatively removed from V1; I later labeled this area V5. This same area was also highlighted by Allman and Kaas, in a separate paper published in *Brain Research* in 1971. V5 had an interesting history, unknown to me and indeed seemingly to anyone else then, presumably because no one had seen its significance then. Paul Flechsig had designated what turned out to be the equivalent area in the human brain as *Feld 16*; unlike the areas surrounding it, this area was partially myelinated at birth. Significantly, Konstantin von Economo and Georg Koskinas had, in their atlas of the cerebral cortex, labeled this area as *Augenbewegungen*, meaning eye movements. Imprecise though this terminology was, it seemed to fit loosely with my later discovery that this was a distinct cortical area specialized for detecting visual motion.

My anatomical studies continued in the University of Wisconsin, in Ray Guillery's laboratory; I much enjoyed Ray's sardonic sense of humor and cynically critical questioning of almost everything. There, I traced further anatomical connections between visual areas, including to an area I named V4; this, together with the area adjacent to it, which I was later to name V4a and include in the V4 complex, was to become significant in color vision studies. All these areas were located within the CCB, which therefore consisted of many visual areas. Although I later added other visual areas, such as V3A and V3B as well as V6, all my early theorizing about the operations of the visual brain is essentially centered around my studies of the anatomy and physiology of areas V1 to V5.

The mapping of these areas established the first principle I put forward—the multiplicity of visual areas outside V1. This was not entirely

novel. H&W had already recorded from visual areas outside V1 in the cat in the 1960s; they had postulated that the serial hierarchical strategy that they had discerned in V1 continued in them. These studies had not led to the same brilliant advances that their studies of V1 had. In a statement of disarming honesty, Wiesel was to write later that their explorations "of the properties of cells of higher visual areas beyond the primary visual cortex [was one] that each of us eventually regarded as a failure," hinting that this may have been a reason for ending their extraordinary partnership.

The novelty of my work and its significance thus lay less in my discovery of multiple visual areas outside V1 in the monkey and much more in coupling that discovery to the physiological characterization of the areas that I had defined anatomically. It is this that led me to propose, for the first time, that the visual cortex processes different visual features separately and in parallel (see the section "Recordings from Areas V3 and V4 and Establishing the Principle of Parallel Processing in Separate Specialized Areas of the Visual Brain").

Because the academic world has changed so much since those days, it is worth recording that none of those whose labs I worked in, and all of whom gave me invaluable help and advice, ever asked for their names to be on my papers, even though each, in today's terms, would have had a legitimate reason for doing so.

I returned to England in late 1969 and, in 1972, I began to present my results at meetings. In one of these, Hans Kuypers, later professor of anatomy at Oxford, approached me in a state of mild irritation; he said, "There is nothing that your small lesions have shown that our large lesions have not shown." I replied, "You are correct. But there is something that your large lesions have shown that my small lesions have not; therefore, my small lesions have shown something that your large lesions have not." If my response sank in, it must have been well after our conversation.

Callosal Connections and the Origin of Cortical Flat Maps

Ronnie Myers, then studying the connectivity in monkey brains in his monkey colony in Puerto Rico, had suggested an ingenious idea—that the pattern of distribution of degenerated fibers in the hemispheres following sections of the corpus callosum, which links the two hemispheres of the cerebral cortex, might be a useful guide to the manner of representation of the vertical meridian in the visual brain. This concept was based on the well-founded assumption that the corpus callosum links the representation of the midline across the two hemispheres. I extended this approach to study the pattern of callosal connections in large areas of the prestriate cortex; in some zones, the pattern was confined to narrow strips, suggesting an orderly representation of the vertical meridian and hence of the visual field; in others, it was more widespread, implying a less orderly

representation. Later, I started physiological recordings combined with anatomical tracings; these were designed to determine the receptive fields of cells recorded, to locate their position in the cortex, and to relate that position to the distribution of degenerated callosal fibers in the visual cortex and hence the representation of the vertical meridian, produced by sectioning the corpus callosum. It was, at that time, the most rigorous way of mapping the "representation of the visual field" in the visual areas of the prestriate cortex. The first of these studies was done with David Sandeman, a supremely enthusiastic undergraduate student who later became a neurosurgeon and has remained a good friend. Based on this pioneering study, I undertook further studies to better visualize the relationship of recorded points to the geographic distribution of the visual areas, determined through their callosal connections. This led to the preparation of the first flat two-dimensional maps of the visual cortex, which I published in 1977. I later developed this approach further with David Van Essen (see volume 9), who came to my lab as a postdoctoral fellow in 1975. These maps, which Van Essen was to develop greatly after leaving my lab, were very time-consuming to prepare; they seemed to me to be very valuable then. I became less sure of their value for my subsequent studies and did not pursue the effort.

In the 1980s, I studied the connectivity between the areas I had defined anatomically in more detail, with Stewart Shipp who came from Cambridge as a doctoral student and continued in my lab as a research fellow for several years. Stewart was second to none in his pursuit of the most minute detail, which at times frustrated my more mercurial and impatient personality. But he was one whose word was usually based on prodigious study and profound knowledge. Together, we combined anatomical tracing methods with the cytochrome oxidase (metabolic) staining technique, pioneered by Margaret Wong-Riley, to show regions of high metabolic activity in the cortex; we traced the detailed forward and backward connections from V1 to the multiple visual areas outside it, as well as the reciprocal connections between the latter areas. We related all these connections to the metabolic architecture of these areas. We were not the only ones to do so; similar studies were undertaken by other groups in the United States. We summarized our results in a 1988 *Nature* article entitled "The Functional Logic of Cortical Connections."

Early Beginnings in Physiological Studies

Long before charting with Stewart the more fine-grained anatomical organization of the areas I had defined, I wanted to characterize them functionally by recording physiologically from their cells. Being under the spell of H&W's work, I imagined that I could show how their proposed serial hierarchy progressed in the areas of the prestriate cortex that I had defined.

But I did not know how to operate an oscilloscope to record from cells. Most who I approached for help were, reasonably, reluctant to teach me; rather less reasonably, they advised me to begin by reading the Tektronix oscilloscope manual in detail, a prospect as exciting as reading the Bible in ancient Bulgarian. Fortunately, my lab was adjacent to that of (Eu)Gene Merrill, whose high proficiency in electrophysiology was matched by his equally high irritability and thrombotic dislike of being disturbed. But we often had tea together, and I eventually succeeded in trying his patience so much that he accepted to teach me how to record from single cells. This game-changing moment, for which I am eternally grateful to him, was coupled to another one. Ron Dubner, from the NIH, had come to work with Pat Wall (see volume 3) and appeared to have much spare time. I asked him to join me in recording from the small area in the posterior bank of the superior temporal sulcus, which I had demarcated as a separate area in 1969; he jumped at the occasion.

The sessions spent recording with Ron were among the liveliest and happiest of my experimental career; they presaged memorable moments of recording excitement over many years, sessions during which the cells responded as if they were talking to me; I could not hear enough of their conversation. These modest beginnings were huge fun partly because results came in fast and early; they showed that the great majority of cells in that area are directionally selective and indifferent to both the form and the color of the stimuli—it was, in brief, a cortical area selective for detecting visual motion. This was surprising; it was a significant departure from my expectation of finding a continuation of H&W's serial hierarchical strategy well into the visual areas of the prestriate cortex. In fact, H&W had recorded from what many believe to be the homologous area in cat prestriate, the Clare-Bishop area; they, too, had found a preponderance of directionally selective cells there. But, wedded to their serial hierarchical doctrine, they were simply left "puzzled" as to what "further" processing occurs in that area. That puts into perspective Torsten's statement that he and David regarded their explorations in higher visual areas "as a failure." Our interpretation was otherwise—that it was not a "further" but a different and specialized processing that was occurring there. It showed me at once both the limits of the proposed serial strategy as a general one and the folly of adhering unquestioningly to inherited opinion. We published our results in 1971; it was the first demonstration of a specialized visual cortical area outside V1, an area that has since become one of the most studied of the cerebral cortex. It was a result that opened the door to a wider enquiry, for it implied that functional specialization may be a more general strategy used by the visual cortex. The rhesus monkey has excellent color vision. If in one of its areas all the cells are directionally selective and all are indifferent to the color and the form of the stimulus, then it follows that color and form must be processed elsewhere!

John Allman and Jon Kaas had used tungsten microelectrodes to record from clusters of neurons with the aim of determining the nature of the retinal representation in what has since become generally regarded as the equivalent area in the owl monkey, which they named MT; they did not study the properties of single cells there and did not determine its functional specialization. Today, many whose reading is restricted to titles, write of area MT as if the evoked potential study of Allman and Kaas had characterized this area in both the rhesus and owl monkey. My functionally specialized area in the rhesus monkey was later named MT by Van Essen, without any prior discussion with me. This makes it seem that, knowingly or unknowingly, one is being deprived of a unique finding, even if I have been given ample recognition for my functional characterization of that area. Van Essen remarks in his memoir that his nomenclature did not please me. And for good reason. As Peter Medawar wrote in a remarkable review in the *New York Review of Books* in 1963 on the discovery of DNA, "a scientist's discoveries are his only real possessions"; to deprive him of it, as giving it a new name invariably does, is to do him an injustice. Naming an area confers ownership; I had been the first to demarcate the area as a distinct visual area and, together with Ron, had been the first to characterize it functionally. It really "belonged" to me in terms of priority; my mistake was not to have claimed paternity by naming it V5 at once, as I later did. Many may applaud, and defend, their use of the term MT; let them put themselves in my position and consider how they would react if the same thing happened to them.

The dark side of scientific research was beginning to dawn on me.

Recordings from Areas V3 and V4 and Establishing the Principle of Parallel Processing in Separate Specialized Areas of the Visual Brain

After Ron left, I recorded from the other areas that I had defined anatomically. Area V4 cells were dramatically different from those in V5; all the ones I initially recorded from there responded to some wavebands and not to others or to white light, suggesting at once that they process signals related to color. The cells of V3, in contrast, were mostly of the classical orientation selective type; I took this to indicate that they are more concerned with the eventual elaboration of form. Taken together, these results led me to develop further the idea of functional specialization and add to it the principle of parallel processing in the visual brain. I presented these results and the ideas I attached to them at a meeting at Saint Catherine's College, Oxford, in September 1972. Of my description of a specialization for color, Hubel said: "You have discovered the philosopher's stone!" It was a prescient remark, for color is deeply conducive to philosophical enquiry and intellectual curiosity. It is also an area of research

that requires radical rethinking. But my elation at this compliment was soon deflated by another comment, made at the same meeting, by a very prominent (Italian) scientist; he thought that my description of the specialization of V5 for visual motion was "crap," pointing to the earlier description of directionally selective cells in the rabbit retina by Horace Barlow and his colleagues. The comment was water off a duck's back for me; I can laugh at it now because, in retrospect, it turns out to be of a piece with the account that Ezra Pound gives of an equivalent lack of insight by the tailor Blodgett, who prophesied that "sewing machines will never come into general use." It is fortunate for the Italian scientist that there was no one else within earshot.

I published two reviews, in 1976 and 1978 in the *Cold Spring Harbor Symposia* and in *Nature,* respectively, summarizing my view that functional specialization and parallel processing are the modus operandi of the visual cortex.

That I should have been the first to suggest that parallel processing between multiple, specialized modules is the modus operandi of the visual cortex might seem surprising. One might have expected computer scientists to have been the natural source for such an idea. In fact, they had sniffed at the idea of parallel computers sporadically but had not made it mainstream; above all, they had never suggested that the visual brain, or indeed the cerebral cortex, might employ such a strategy. Their ecstatic devotion to parallel, distributed processing only surfaced in the mid-1980s with the publication of a book by David Rumelhart and his colleagues entitled *Parallel, Distributed Processing*. Why were they so late in recognizing the importance of parallel computing? Perhaps because in the 1970s there were no mature programming languages, perhaps because most computers were single processor, serial machines; perhaps because computer scientists had not understood the power of parallel processing, as Marvin Minsky and Seymour Pappert were to claim later in their book *Perceptrons*; perhaps because, at that time, the most influential strategy for visual processing was the serial, hierarchical one proposed by H&W. Whatever the reason, the book did not refer once to my work, which led to the concept of parallelism, although they did so to other work derived from mine, which implies that they had understood the significance of parallel processing as a cortical strategy. This left me aggrieved, as it would anyone who feels so blatantly ignored.

Anyone who thinks that I am oversensitive in claiming what is mine is correct; I am indeed. And for the same reason as given in Peter Medawar's review. Nor am I the only one. Almost every scientist I have known is the same. Once, during a short-tempered discussion in my office with Francis Crick, I claimed priority over some discovery that he had attributed to others. Evidently annoyed, Crick replied with that loud laughter that had so irritated Sir Lawrence Bragg, "I am not interested in priorities." I was

indignant; I replied, "well, I am" and reminded him of the incident recounted by Jim Watson in *The Double Helix,* of Francis's fury at not being credited by Lawrence Bragg and Max Perutz for an important mathematical idea that he had propounded on polypeptide chain configurations. Watson relates that Francis had rushed in fury into Bragg's office to demand an apology. After this reminder, Francis and I continued our discussion more equably, and I developed an admiration for how quickly he backed down once he had realized the merit of my response, or so it seemed. In this basic instinct of ownership and possession, described by Peter Medawar "not as possessiveness but as pride of possession," the same rules seem to apply to all scientists, without distinction.

The Miasma of Color Vision

While visual motion was relatively simple and exciting, and visual form was (and still is) complex and difficult to study—the "philosopher's stone" of color vision offered a more challenging problem, both perceptually and philosophically. My interest in color had started with my recording from the cells of V4; in my early recordings, the great majority of these responded selectively to some wavelengths and not to others or to white light. My further results showed that there are subdivisions of the V4 complex where the concentration of wavelength selective cells is very high and others where it is lower, although even here there was a significant degree of bias for one set of wavelengths or another; among the latter were orientation-selective cells whose tuning curves were much broader than their counterparts in V1, V2, and V3. Overall, the results suggested that V4 cells were specialized in processing signals related to color and color in association with form (orientation), thus reinforcing my views on functional specialization. I published this evidence first in 1973. Exciting though it was to see a preponderance of such cells in an area close but separate from V5, much the most exciting moments in my color studies occurred later when I encountered truly color-coded cells, using the methods of Edwin Land (see the section "The Sixth Man: My Encounter with Edwin Land"); the responses of these V4 cells correlated with color as judged by humans and monkeys; they were independent of the wavelength-energy composition of light reflected from their receptive fields alone; and some of them responded to colors when produced by shadows (colored shadows). The excitement I experienced when encountering such cells was often attenuated because the recordings were largely done on my own; there was usually no one to share the excitement with during the long nights or to lift my spirits when the recordings were unproductive, as they commonly were.

I began to present my new results on color vision and the cells of V4 with enthusiasm at public meetings from about 1979 onward. Now dark moments began to intervene; it became evident that the hostility toward

Land and his theory was being transferred to me. I was not unprepared; Land, the seasoned recipient of color-related hate, had warned me of this eventuality. It first erupted publicly against me when, in 1980, I presented the results of my color studies at a Society for Neuroscience Symposium organized by Nigel Daw in Cincinnati. Someone sitting in the front row asked somewhat aggressively, "Who, besides you, has found heavy concentration of color cells in V4"? My response was ready; I said, "That is not an issue that will be decided by a democratic vote of the majority." My response has long been remembered by many who have forgotten everything else about my talk. In fact, I was giving the answer that Bernard Katz had taught me to use in such arguments, having used it himself on some previous occasions.

This hostility continued into 1983, when at a meeting of the Physiological Society (at Saint George's Hospital Medical School), I gave another talk on the responses of color cells in V4. Horace Barlow, in a state of high agitation, said, "You are pretending that color is done by magic; you are making propaganda." I asked, also in a state of agitation, "Propaganda for whom?" Horace replied, "for the color constancy boys." I replied, "Horace, they do not need any propaganda." His use of the word "magic" was interesting; it was the very same word that Gordon Walls had used earlier to stigmatize the work of Edwin Land. The incident is somewhat laconically recorded in the minutes of the Physiological Society of 30 March 1983, page 42 (now deposited at the Wellcome Trust London) as showing that "some agreement was reached in discussions between S. Zeki, H.B. Barlow, and D. Whitteridge as to the relationship between the wavelength of light reflected from an object and the colour that is perceived." I do not recall, however, reaching any agreement with Horace on color vision, either then or since (David Whitteridge merely intervened to say that the issue was an important one for discussion). The incident is worth alluding to because it reveals how out of the mainstream views in studies was the central issue of constant color categorization even as late as the 1980s.

This hostility was not unexpected. I had been warned of dark mutterings by Mathew Alpern, an eminent scientist, highly knowledgeable in color studies. He was a frequent visitor to my laboratory and surprisingly hospitable to my less than conventional views on color vision, given his own traditional outlook. Word also reached me of seminars at which my work on color had been trashed; in one, at MIT, it had been denounced so aggressively that Simon Levay had asked whether it was appropriate to attack in this way someone who was not there to defend himself. A request had even been made to Mat Alpern himself from Dr. de Monasterio, one of the authors of a forthcoming paper questioning my work, to acknowledge Mat's help in their paper, when Mat had apparently given none. Mat was displeased; in a response to de Monasterio dated July 13, 1981, and copied

to me, he wrote: "It seems quite inappropriate for you to acknowledge me in this way," since "I gave you no help except to listen politely … to your interesting results. … So, as flattering as the prospect of associating my name with yours in this case is, I cannot allow it."

Finally, in 1982, that paper appeared in the *Journal of Neurophysiology*. Reading it after an interval of over 40 years, there is not much in it to offend, apart from its title and its suggestion that the democratic rights of the majority count, even in science. Perhaps it seems innocuous today only because it actually turned out to be so innocuous in the longer term. But in the very short term, it nevertheless created a disturbingly hostile attitude toward me. Old and well-liked friends displayed their glee publicly at what they assumed was my discomfiture (see Kelly et al. 1982); others did so during personal encounters. They were correct in believing that I had been discomfited, but they did not know its extent; far more disturbing than their glee was that the Science Research Council (SRC), which had supported my research until then, decided to cut my grant in half, giving as reason the inability to confirm my findings on color. This rather shocked me and sent me into despair; how could the results from one lab, without corroboration from other labs, lead to such an extreme outcome? I thought: Bertrand Russell had been correct; this is indeed a deeply wicked world. But, as Russell had also implied, there is often a silver lining to these dark moments. The Wellcome Trust, richer and more powerful than the SRC, stepped in to support my work, on a far more generous scale; they continued to do so for the next 35 years. I hold them, and especially Sir Stanley Peart, then a senior trustee, David Gordon, then a director, and Ben Bembridge, then director of their ophthalmology program, in special affection and very high regard. When all around me was dark, they had courageously said, "Give him a chance." That remains a precious moment.

An equally unpleasant aftermath occurred when I submitted a paper to the *Journal of Physiology*, distinguishing wavelength selective cells from truly color-coding ones. The paper was rejected; one referee (I leave it to the reader to guess who that may have been) had sent in an improbable 19 pages of negative comments. The review began, "This is a long paper written in a pedantic style … [it is] not worth publishing even in a journal that does not require peer review." I vowed never to publish in that journal again and did not do so for another 25 years; my next substantive article there was when I was elected an honorary fellow of the Physiological Society in 2012 and invited to deliver the Paton Prize Lecture in 2021, which I devoted to color vision. This is worth recounting because it shows again, as Russell implied, that there is always a silver lining somewhere. A distinguished member of the Physiological Society (I believe it was David Whitteridge) was disturbed by the rejection and the way the paper had been handled. He had discovered that the handling editor had sent my paper to one of my adversaries for review. Deeming

it unbecoming conduct, the Physiological Society asked that handling editor to resign from the editorial board of the *Journal of Physiology*, for this among other reasons.

I eventually published my results in *Neuroscience* in 1983, to positive reviews. I dwell here a little longer on my misadventures in color vision, because they register a period of change in the approach to color vision, initiated, on the one hand, by Edwin Land's theories based on psychophysics and, on the other, by my physiological studies which used Land's stimuli and thus departed from traditional approaches. It is also partly because they mark, briefly, the only dark moments in my otherwise happy career, ones that increased my resolve. Finally, it is an interesting illustration of color vision as a traditional terrain for academic violence. Why this should be so is hard to tell; William Rushton, an eminent authority on retinal mechanisms of color vision, gave one plausible answer; he prefaced his Review Lecture on color vision for the Physiological Society in 1970 thus, "The trouble with colour vision is the mentality of those that write on it—and of those that read."

The Miasma Begins to Unravel

Dark though these moments were, they were also short-lived. Murmurings of a different kind began to circulate, in particular that new research had uncovered that wavelength selective cells in V1 are localized within small regions of high metabolic activity (the cytochrome oxidase blobs) in it; thus, a localization for color did not seem so absurd anymore. These studies became the prelude to many others from many laboratories that, together with my earlier work, began to turn the tide in my favor where a localization for color is concerned. All this has rendered the1982 paper by F. de Monasterio and his colleagues irrelevant. My response to their paper, in 1983, did not go into any eristic detail; it was a statement of facts, as I saw them. It is my belief that the resolution of scientific disputes depends on third parties; it is wasteful for a scientist to repeatedly reassert that she or he is correct. And, in the end, it was third parties who supported my work and my ideas on the localization of color, especially the work of Bevil Conway and his colleagues, which added significantly to our knowledge in other ways, in particular by showing the separation of form from color in terms of cortical localization. If I were given the opportunity to respond today, to both the critics of my work on color and on neuroesthetics (see the section "Toward Beauty and Neuroesthetics"), I would simply ask those interested in the debate to listen to the section entitled "The Hero's Adversaries," from Richard Strauss's tone poem *Ein Heldenleben*. My response would be found in that piece, sandwiched between the sneering chatter of the adversaries, appropriately represented by the woodwinds. But I do not consider myself to be a hero, far from it. It is just that the

music fits the critics and the outcome so well. And it is much more edifying than writing a response.

The Sixth Man: My Encounter with Edwin Land

The excitement generated by studying color vision physiologically had really started when I got to know Edwin Land, who had asked to visit me in London. Nothing if not a radical intellect, he was not only a brilliant theorist in color vision but also the inventor of the polarizing sheet and the Polaroid camera. His inventions had led him to drop out from Harvard early, to pursue an independent career in invention and business. The latter had turned him into a very rich man, thus exciting the envy of many in academic pursuits who were living on more meager earnings, or so I supposed. No visual physiologists had bothered with his work; most color psychophysicists despised him and had nothing but contempt for his theory; many thought that his color "Mondrian" demonstrations were unduly ostentatious. Gordon Walls had written: Land's results must seem "magical … to those who obtain their scientific information from popular magazines. This degree of verisimilitude secured so cheaply, by such simple means, is what piques the cupidity of those who now contemplate lower costs and higher profits in color photography, color television, and color printing, all as a result of Land's research." In fact, Land had started publishing his work on color in the *Proceedings of the National Academy of Sciences*.

The general contempt for Land interested me; the world of color psychophysics had not given me any remotely satisfactory account of how colors are generated. Could Land have better insight? Land became the sixth person to have a marked and long-lasting intellectual influence on me.

When Land first entered my shabby office in July 1978, accompanied by John McCann, his first words were: "I have known about your work since 1973 but have waited for it to mature before coming to see you." He began by explaining his Retinex theory. With the exception of W. S. Stiles, most authorities on color vision had warned me against that theory. Stiles, who Mat Alpern regarded as "the greatest colour scientist of the century," thought that I should restrict myself to using what he considered to be Land's important methodology. Otherwise, the largely unsolicited but well-meaning advice that I had received when embarking on color studies after my discoveries in V4 was to concentrate on colorimetry and related topics; this included a careful reading of *Color Science* by Wyszecki and Stiles and a good acquaintance with MacAdam ellipses, a prospect as enticing as reading a great novel in ancient Sumerian. Being vulnerable in my ignorance and incomprehension, I took a dreary course in colorimetry at the City University, more suitable for those interested in color photography. I also read as much as I could about fancy theories of color vision, an

enterprise so numbing that it would have been far easier to learn to read Chaldaic poetry in the original. I abandoned these studies when I began to realize their irrelevance to my purpose. The discovery of V4 cells had convinced me that classical theories and methods would lead to a dead end: A more radical approach was necessary.

The charismatic Edwin Land had therefore walked into an intellectual void in my life. He emphasized color constancy; this refers to the fact that colors remain stable despite the perpetual changes in the illuminant in which they are viewed. At that time, color constancy was a mere footnote in most texts on color vision, assuming it appeared at all; this was despite the fact that both Hermann von Helmholtz and Ewald Hering, two important figures in the history of color studies, had tried to account for it, albeit in unsatisfactory terms, at least to me. Helmholtz had sought for an explanation based on prior knowledge and the "unconscious inference"; the latter, he believed, leads the perceptual system to "discount the illuminant" and assign the true, "known" color to a surface. Hering had tried to explain, also unconvincingly, that we perceive colors through the filter of our memories for colors, and therefore perceive them differently from the way we should perceive them without these color memories.

In contrast, Land had proposed a radical departure; for him, color was the consequence of a computational operation by the brain; he believed that this process depended on using the one constant physical reality in the world outside, namely, the reflectance of surfaces for lights of different wavebands; through a ratio-taking process undertaken by the brain, the reflectance of different and adjacent surfaces for lights of different wavebands would be compared, a process that would lead to the generation of color. Using this approach, the brain would make itself independent of the constant change in the wavelength composition of the light reflected from surfaces; color then becomes a property of the brain, not of the world outside (although this is my language, not the language that Land used).

I found his exposition difficult to follow at first but deemed it instinctively exciting enough to invite both Land and John McCann to continue our discussion over lunch. Land, I thought, was presenting me with a fairly radical departure from the traditional way of describing color, as being merely the representation in the brain of something "out there." For Land, by contrast, the brain was registering, in terms of color, some kind of external reality, but a reality that was quite remote from that imagined by traditional color scientists. Nourished by the trichromatic and opponent-process theories, I was finding it difficult to absorb all this; sensing this, Land had an idea; he and John would go shopping in London at once to buy some high-quality color papers; they would return later in the afternoon to demonstrate his approach to me directly using a simplified version of his celebrated Mondrian experiments.

By the end of their demonstration, I had become convinced of the novelty and importance of Land's approach. I asked both to stay a little longer, to continue our discussion over drinks. We began speculating wildly as to how I might explore Retinex ideas physiologically. What had been intended to be a relatively brief morning meeting was gradually threatening to extend well into the night. Land became impatient; he would go to Cambridge (Massachusetts) with John tomorrow and return the following week with good Mondrian displays, along with all the measuring equipment. This would allow us to test Retinex ideas directly while recording from single cells in V4. I was not well pleased; I explained that experiments could fail. Land insisted; he understood, he was a scientist. He prevailed; the experiment was planned for the following week.

I spent anxious hours and many more packets of cigarettes preparing for it, as the excitement mounted. On the day, incredibly, the first cell encountered in V4 was genuinely a color cell, as opposed to the traditional wavelength selective one. In other words, it was one that responded to a surface of particular color irrespective of the wavelength energy of the light reflected from it alone. The responses of the cell and the applause in the room were recorded, not only on tape but also in the mind as a game-changing moment. From then on, Land was a regular visitor to my experiments, to which he contributed intellectually in a significant way. He and John prepared and shipped over a replica of his equipment for studying color, which I donated upon retirement in 2025 to the Royal Institution, where both Land and I had lectured on color vision. During his visits to my lab, Land also contributed gastronomically; he liked to eat well and, finding the food at the UCL refectory among the worst, he commonly ordered food from Harrods or Fortnum's, thus making the experimental sessions even more enjoyable.

The experiments on color were wildly exciting when they worked and depressing when they didn't, as commonly happened. In the end, I collected enough material to convince me that colors are not represented but constructed in a specific part of the visual brain, area V4. Color thus becomes a property of the brain, not the world outside. In fact, and perhaps surprisingly, Oscar Wilde had already been there before me, although more emphatically. In *De Profundis*, he had written that the eyes "are really channels for the transmission, adequate or inadequate, of sense impressions. It is in the brain that the poppy is red," a statement that is hard to improve on.

Land was never explicit about color being "constructed in the brain." He wrote instead of his Retinex system as being based, like traditional theories, on three channels; but he added the highly original computational process that the brain uses to generate colors. This made it, as he wrote, an extension and development of the classical color theories. But the classical theories are, in essence, representational ones; they assume that

color is "out there" and transferred to the brain by some representational mechanism, the color of a surface being determined by the dominant wavelength in the light reflected from it, as Isaac Newton had implied in his book *Opticks*. I, too, had adhered to this view. After recording from a sufficient number of color cells in V4, I submitted a paper to *Nature* (for which Land designed special color filters) on their properties; it was titled "The Representation of Colours in the Cerebral Cortex," a title that I now much regret. I should have instead recalled Newton's other and, significantly, more rarely quoted words in *Opticks*: "For the Rays to speak properly have no Colour; in them there is nothing else than a certain power and disposition to stir up a sensation of this Colour or that." I should have instead titled my paper "The Construction of Colour by the Cerebral Cortex." My search would then have been explicitly for the cortical locus that has the "power and disposition" to enable the brain to acquire knowledge of a constant and nonchanging property of the world, namely the reflectance of surfaces for lights of different wavebands, Critically, this power and disposition also stabilizes an unstable world, making the brain largely independent of the vicissitudes of flux in the wavelength-energy composition of the light reflected from surfaces. This stabilization brings us closer to incorporating into physiology and psychophysics both Eastern and Western wisdom. The former is encapsulated in the phrase, "Nothing is constant except change" and the latter in Plato's Heraclitan doctrine of flux, which essentially says the same thing. It also leads color physiology to a different path, that of understanding how the brain achieves the feat of establishing constancy in the face of perpetual change. The physiological study of color thus becomes a philosophical enquiry conducted by physiological means. David Hubel's prescient description of my work on color in 1972 as constituting the discovery of the "philosopher's stone" had therefore acquired a new philosophical dimension. That flattering opinion also threatened an uncomfortable future, when I might have to discourse with philosophers. At a party at Magdalen College, Oxford, JZ—ever the enthusiast—introduced me to the eminent philosopher Sir Peter Strawson, describing to him my studies on color and asking him excitedly what he thought of my view, but in his words, that color constitutes "brain knowledge." Strawson replied, "I'd say that it is interesting." There the conversation came to a dead end. I was relieved; it seemed that dialogues with philosophers need not be drawn out after all. In a significant way, this was a pity and a loss to me. I have always considered that one of the primary functions of the brain—including the visual brain—is the acquisition of knowledge. Since the problems of knowledge, of how we acquire it and how certain we are of what we know, lie at the heart of philosophy, studying the brain became something of a philosophical enquiry for me. My interest in philosophy was therefore profound but was not reciprocated by the philosophers' interest

in my work; when an interest existed, it was to trivialize what I was doing. In time, this ceased to matter to me.

Through the prism of Land's theory and my physiological recordings, I began to think of the construction of colors as leading to an experience. Thus, if there is any localization for the color in the cerebral cortex, which I consider to be in V4, it must be an *experience*, constructed in the brain, that is localized there. In other words, color must be understood as a brain-constructed experiential phenomenon rather than a mind–brain independent feature of the external world. A topic that I had been trying to avoid now reared its ugly head—consciousness, for one can only have an experience in the conscious state.

The Retinex Theory

Land was a master of the condensed utterance and therefore was often difficult to follow; whereas others used periphrastic phrases to explain an inexplicable idea, he rendered an explicable idea inexplicable by condensing it into a single sentence. My favorite was, "Color is always a consequence, never a cause," a statement so insanely contrary to the then-prevailing view of what color is that no one in the world of color bothered with it. This did not surprise Land; as he saw it, the world of color had "no second rate minds," implying that they are all third rate. Land had proposed a detailed transformative operation, dependent on defined processes; this involved the retina and the cerebral cortex (hence the term Retinex). My later imaging experiments showed that V4 is a fundamental stage in this computational process. This is not to say that V4 is the sole area involved in constructing constant colors, an accusation that the reductionists, forever clutching at straws, have used to question all specializations in the brain; nor does it imply that the wavelength selective cells in V1 and V2 that feed into V4 are not crucial to this process; nor yet that the visual brain uses a process identical to that outlined by Land.

I now use the term *constant color categorization* instead of *color constancy* to describe the foundation upon which Land's theory is built. This is because the hue (shade of color) of surfaces changes with changes in the wavelength composition of the illuminant in which it is viewed, as artists have constantly reminded me. The color category, in contrast, does not, within very wide limits. In the Bayesian-Laplacian context, Oliver Chen and I emphasized that color categories belong in the category of biological priors and are resistant to revision in light of knowledge and experience; hues, however, change according to viewing conditions and are thus experience-dependent priors from which posteriors can be generated (in the specialized Bayesian language).

Why did Land write that, in developing his theory, he was merely going beyond the trichromatic and opponent-process theories of color

vision? Was it modesty or fear of taking on the color vision establishment? Whatever the reason, I came to believe that, in basing his theory on three channels, corresponding roughly to the Young-Helmholtz channels, Land had not been radical enough; nor had he given a convincing reason why the channels should be limited to three; it is entirely plausible to suppose that there are many more —although a minimum of two is necessary. As well, I was surprised that he had not pursued his experiments to their logical conclusion, to show that the (opponent) color of the after-image produced by viewing a patch of a certain color not only is independent of the wavelength-energy composition of the light reflected from the viewed patch alone but also depends on what is reflected from its surrounds. I first demonstrated this in 1983 and in more detail with my colleagues in 2017. Hence, perceptual opponency followed the generation of color by the brain and did not precede it; in other words, the color of the after-image is generated after color is generated in the brain. Therefore, although opponent mechanisms can account for the sharpening of spectral response curves of cells after the earliest stages in the retina, they cannot account for the generation of color.

My work led me, ultimately, to question the status of the trichromatic and opponent-process theories as theories of color vision, and to reconceive them as general theories of vision, including but not specific to color. The brain, after all, can detect an object or a moving stimulus by registering the difference in the wavelength composition of the light coming from it and from its surrounds, without determining the color of the stimulus. A misunderstanding of this is at the basis of papers that, even in their titles, suggest they have detected cells that register color in, say, V5. In reality, all they have done is to describe cells there that can detect a moving object by registering wavelength differences between it and its surrounds, without ascribing a color to either (see also Thiele et al.,1999). But I delayed my disavowal of the classical theories as being specific to color vision until my Paton Prize Lecture of 2021, perhaps for the same reasons that I now impute as to why Land never disavowed theories of color vision and considered that he was merely going beyond them.

Despite these small reservations, I consider Land's theory to be the only viable theory of color vision, which I therefore imported into neurophysiology, with such experimental and theoretical modifications as I deemed necessary; in particular, I substitute a multichannel input into its computational stage rather than the three classical channels. That turns it, for me, into the radical theory that it is.

Land was a frequent visitor to my lab to watch recordings from V4, often staying late into the night, although we never published together. He remained a friend until his death in 1991. In 1986, he was elected a foreign member of the Royal Society but was unable to travel to London to sign its Charter Book. In 1991, I asked the Council of the Royal Society to

allow me to take a page of the book to Cambridge, Massachusetts, so that he could sign it. When the Royal Society agreed, I took a page, signed by Paul Langevin, the French physicist, to Land's home in Cambridge. I read the citations for both Edwin and for Ed Purcell, the US physicist and friend of Land, who had also been unable to go to London to sign the Charter Book. Hugh Huxley (no relation of Andrew), the British scientist who had worked at UCL but was then a professor at Brandeis University, admitted both formally to the Royal Society. As far as I can ascertain, it was one of only six occasions when the signing ceremony for admission to the Royal Society was conducted outside the house of the Society in London—the first two being Sigmund Freud and Winston Churchill. It was also the last time I was to see Edwin.

Our Golden Years

The years from 1983 until my retirement in 2025 were golden years, characterized by high-octane energy and high-voltage intellectual enterprises conducted with exceptional colleagues, who are mentioned under the relevant sections. I have remained friends with all of them. Among them were two with whom I published little or nothing, although they were major contributors to the work of the laboratory: Wolfgang Fries and Ludovica Marini (now Lumer). Wolfgang had come to London with a German scholarship. An accomplished neurologist and musician, he was also an outstanding intellect who understood the implications of functional specialization at once, and before many others; we had prolonged discussions and shared many ideas. While in the laboratory, he published an important paper; along with a similar paper published in Japan, he showed that the output from the lateral geniculate nucleus (LGN), through which the predominant visual input into the brain reaches the cerebral cortex, does not connect with V1 only; instead, it has direct outputs into the visual areas of the prestriate cortex as well, ones that bypass V1. This work was to have an important influence on my later thinking about the relative autonomy of the prestriate visual areas and the consequent "disunity" of consciousness (see the section "Paranoia Strikes Again"). Our discussions continued later when he moved to the Ludwig Maximilians University in Munich, eventually specializing in neural rehabilitation, and I was an occasional visiting research fellow there.

Ludovica came to the lab after a chance encounter at a meeting in Turin on color vision. Her presence electrified the laboratory—possessed of formidable energy with an intellectual curiosity to match, she assisted in many electrophysiological experiments and joined me in imaging studies on color vision. She animated the lab to an unusual extent.

There were two other colleagues: A dominant figure in the lab, and one who was in a sense a critical backbone, was John Romaya, the computer

programmer; he was also a severe critic, whose ability to spot weaknesses was of invaluable assistance to all in the lab. He contributed immeasurably for a period of 30 years to improving our experiments.

Finally, Grant Wray contributed in sterling ways to ensuring that the physiological experiments were successful and that the laboratory generally was functioning smoothly.

The magic moments we spent in the lab during those years were supplemented by retreats to France and to Tuscany where we once asked local poets to read for us, and explain, the *Rime* of Michelangelo, who had come to play a dominant role in my thinking about neuroesthetics; his. concepts of art and beauty are often most explicitly exposed in those sonnets. The locals found these sonnets as difficult to understand in the original Italian as we had found them to be in translation.

From Monkeys to Humans

Ever since the Wellcome Trust started to fund me after my color misadventure of 1982, I became increasingly involved with its affairs, ending up as chair of the Vision Working Group at the Trust for six years. In this capacity, I got to know Sir Stanley Peart, its senior scientific trustee, quite well, and we lunched together once a month to discuss biological problems. Stan was searching for ways to deepen the Trust's involvement in neurobiology, a development much aided by the involvement of David Gordon, then a director at the Trust. I, in turn, was becoming increasingly interested in the then very new field of brain imaging and saw the chance to establish a new imaging research center in London. The director of the Trust, Peter Williams, jumped at the idea when we put it to him. The Trust eventually allocated £24 million to the project, for which it purchased a building. Who should be the director? I wanted nothing to do with directorships; so we approached Richard Frackowiak, who turned out to be an outstanding director; he brought to fruition the dream that Stanley and I had had for years, through his absorption in every detail of the construction and operation of the new center. It was 10 years in the making, the first formal meeting regarding it having been in 1984, at the Neurosciences Institute in New York (where I was then a fellow), and its inauguration by Andrew Huxley taking place in 1994. I became the codirector of the Wellcome Imaging Center; in truth, this was only an honorific appointment. It was Richard who oversaw the establishment of the first and most exciting brain imaging center in the world, which has made an incalculable contribution to neurobiology. It also allowed me to transfer my work from monkeys to humans.

I had become restless working with monkeys, having developed a close relationship with several of them; two especially always seemed to be as overjoyed to see me as I was to see them. Because of this closeness,

I became increasingly reluctant to work on them, and I terminated my experimentation with them after an experiment, which, to me, was highly significant. This was undertaken with Makoto Kusunoki and Konstantinos Moutoussis; we recorded from single cells in awake, behaving monkeys while they were experiencing color. The experiments showed a strong relationship between single cell responses in V4 and the experience of color. It was a demonstration of capital importance for me, but it was also the end of my experimentation with monkeys. From then on, I decided to transfer all my experimentation onto humans, using imaging techniques coupled to psychophysics.

Imaging experiments with humans opened up new possibilities, especially related to the study of human visual experience. My first step was to demonstrate that the human visual brain also consists of several, distinct, specialized visual areas that process different visual attributes in parallel and to determine their positions. These experiments, published in 1991, were undertaken with John Watson, who had come from Australia principally to work in a clinical setting with Richard Frackowiak but who had sufficient interest in visual problems to devote considerable effort to working with me. It was a wonderful collaboration.

Next began a set of experiments designed to show that, as with color, the brain constructs what we attribute exclusively to the outside world instead of being merely a chronicler of outside visual occurrences. For this, I turned first to human V5 whose position coincides with the area demarcated as *Feld 16* by Flechsig and damage to which causes the syndrome of akinetopsia, the inability to see visual motion. This offered us the opportunity to study the experience of visual motion in the absence of physical motion (i.e., motion generated in and by the brain). Starting in the late 1980s, when I had become increasingly interested in weaving art into my studies, I had become friendly with Isia Leviant, whose studio in Paris I visited several times for prolonged discussion; he had turned from being a director of the Bechtel Corporation to becoming a successful artist, interested in geometric illusions. Our discussions led me to convince him to write an article for the *Proceedings of the Royal Society* on one of his best-known creations, *Enigma*. Many, if not all, see rapid, reversing motion in the rings of *Enigma* although the painting itself is completely static. Would V5 be active in subjects who perceived movement where there is none? Our imaging studies said: "Yes, it would." We published the paper under the title of "Going Beyond the Information Given," a phrase lifted from the title of the book by Jerome Bruner.

Having determined the position of V4 in the human brain, we wanted to learn whether it is critical for generating color experiences. This amounted to learning whether V4 is the critical site for the ratio-taking, color-generating mechanisms, as our earlier work with monkey V4 had hinted, or whether V1 and V2, which feed signals into V4, are also involved in the

color-generating experience (as opposed to processing chromatic signals). My collaborator in the fMRI study was Andreas Bartels, who had come to my lab as a doctoral student after a stay in Terry Sejnowski's (see volume 14) lab; he stayed on for two years after completing his doctorate; his contribution was throughout central to the success of the lab. A sharp intellect with a well-developed sense of humor, my collaboration with him was among the most enjoyable of my career. We approached several problems, of which color was one. We adapted Land's Retinex Mondrian experiments for these imaging studies. The results showed that when the colors remained stable despite changes in the wavelength composition of the light reflected from them, the activity was confined to V4; V1 and V2, which feed V4 and contain wavelength selective cells, were not especially active. When the same subjects looked at actual objects, instead of abstract scenes, under the same conditions, an area lying just in front of V4 was recruited, which we named V4a, thus constituting the human V4 complex. The correspondence with monkey brain was convincing.

With this demonstration, my experimental physiological and imaging work on color vision virtually ended. I would have loved to have continued but knew that this was beyond my capacities. The next step, to understand the precise implementation used by the brain to construct color, would have required a highly sophisticated technology, which would enable recording from hundreds of cells simultaneously and subsequently analyze their responses in relation to each other; even Andrew Huxley may have baulked at the idea, although I am not so sure of that. For me, it was the end of the road in color physiology, but I was to continue with some psychophysical experiments. Time had come to turn my attention elsewhere.

Dynamic Parallelism

The experiments on color, and the view that I was beginning to develop of it as an experience generated in the brain, led me ineluctably but timidly to consider the issue of consciousness, something that I had generally wanted to avoid, partly because it excited the interests of philosophers—a dangerous sign, given their addiction to insoluble problems. But I pursued the issue in the context of my discovery of V5 and its functions. A brilliant but truculent postdoctoral fellow in my lab, Georg Beckers, suggested that visual signals may reach V5 before reaching V1. This excited me; it was radical thinking of high order and promised the temporal separation of V5 from V1 experimentally; this, in turn, led to the question of whether activity in an area that is isolated from its main source of visual input could acquire a conscious correlate if it had another visual input that reached it without passing through V1. If visual signals that reach V5 through V1 and those that reach it by bypassing V1 do so asynchronously, then one could, perhaps, isolate the two inputs spatially and temporally, by studying

patients with damage to V1 or by manipulating the speed with which signals reach V5 separately; ideally, I wanted to do both.

We set about studying this first with the transcranial magnetic stimulation (TMS) technique, of which Georg was a master. The results showed that his intuition was correct, with the added inestimable bonus that it is fast-moving signals that reach the cortex of V5 before that of V1, whereas slowly moving ones reach V1 first. Georg was jubilant; I was more conservative; we poured over the results argumentatively. But, in the same year, our conclusion was confirmed by similar results obtained in EEG and MEG (electroencephalographic and magnetoencephalographic) studies that I undertook with another brilliant research fellow, Dominic ffytche.

I could now extend the concept of parallel processing in the visual brain and add to it *dynamic parallelism*, since the parallel inputs to an area do not deliver their signals simultaneously; the speed with which signals are delivered to an area depend, instead, on the stimulus. As I later found out, it also depends on the task that the subject is instructed to undertake. Asynchronous convergence of parallel pathways, judged by the evidence below, is likely to be a fundamental organizing principle of visual perception.

Together, these results were a game changer; I now began to look forward to studying visual consciousness with moderate enthusiasm.

Parallel Processing, Perceptual Asynchronies, and the Binding Problem

Fortunately, I was joined by Konstantinos Moutoussis, who was an outstanding doctoral student and stayed on as an outstanding postdoctoral fellow. Konstantinos liked, as he put it, "to think philosophically about the brain," and his originality was second to none. We began by thinking in depth about the fundamental problem of binding and its relationship to conscious experience. Binding refers to how the separately processed and registered attributes of the visual world are united to give us our apparently seamless, holistic, and unified experience of it. The common view then was that the processing of different signals in the parallel pathways was simultaneous and in perfect temporal alignment; this temporal alignment allowed for the simultaneous unification of the results of the parallel processings, or so it was believed. There was a general supposition, too, that binding must involve some kind of direct physiological interaction between cells signaling different attributes. But how? No one knew then and no one knows now. There had been numerous experiments, extending over some 30 years, to address this issue; many were ever more sophisticated iterations of the same experiment; none has resolved the issue. Had they been asking the wrong question, perhaps because of an understandable hebetude in thinking? Here Francis Crick entered the arena with a

grand idea; his entry was ecstatically welcomed by the many who supposed that he would rescue the study of consciousness from the disreputable state into which it had allegedly sunk, making it scientifically respectable. Francis was a master of the dramatic utterance; the grand idea that he had developed with Christoph Koch proposed that binding is the basis of the unified conscious experience. By making the unresolved binding problem the basis of consciousness, they had added a new and dramatic dimension to its study, adding one unsolved problem to another. Could this be so, considering the results that I had obtained with Georg and Dominic, which suggested an asynchronicity in the arrival of signals in V1 and V5. Nor is this asynchrony unique to V1 and V5. My later work with Yoshihito Shigihara using MEG showed that many prestriate visual areas, even extending to "higher" areas such as those critical for the perception of faces and houses, receive dual visual inputs—one through V1 and one that bypasses it. How would this play out in daily perception and what implications did asynchronous processing have for the ever-elusive problem of binding? Konstantinos and I pondered the problem. We asked: How certain is it that different features, processed in parallel pathways, reach a perceptual end-point at the precise same time, as was current thinking? It seemed to us more plausible that, maybe, they do not process signals at the same speed. As well, we reasoned that, if the central binding question had not been credibly answered after so many years of intense and often technically demanding work, it becomes legitimate to enquire whether the right question was being asked. We began by asking a different question: Are all features processed at the same exact speed and, if not, how does binding occur? This was my entry point into the field of consciousness.

My psychophysical experiments with Konstantinos, published in 1977, showed that two simultaneously presented attributes of a stimulus (e.g., its color and direction of motion) are not perceived simultaneously; rather, we become conscious of color some 80 ms before we become conscious of directional motion, and 40 ms before we become conscious of the orientation of lines. There is, in other words, a perceptual asynchrony in visual processing. This asynchrony is stimulus dependent; its extent can be modified by manipulating the characteristics of the stimulus. It is also task dependent; if the task is not to identify the characteristic of the two stimuli (i.e., the color and direction of motion) but only whether a change has occurred in the state of the two stimuli, there is no asynchrony. In summary, the attributes of two simultaneously presented visual stimuli are not bound at brief time windows after their appearance; instead, they are mis-bound. This led us to an ineluctable conclusion: There is no brain area that "waits" for the different parallel systems to terminate their processings before binding the results of these processings together; instead, the brain binds what has already been processed and, given asynchronous processing between areas and the consequent asynchronous awareness of different features, it mis-binds.

It follows that binding cannot be the basis of the unified conscious experience; visual consciousness is instead distributed in time and space because geographically separate areas process different attributes. This idea was also reflected in other psychophysical experiments with Andreas Bartels. In these, we studied the times required to perceptually pair spatially separate pairs of stimuli consisting of color or motion. The results showed that cross-attribute binding between color and motion took longer than within-attribute binding. Taken together, these results seemed to me to have profound implications for understanding critical aspects of visual consciousness. A conscious, unified view of the world is constructed, not detected, by post-perceptual and post-initial conscious processes because there may be many separate consciousnesses distributed in time and space. I started dividing consciousness of the attributes of a stimulus after its appearance in the field of view into two phases—the micro- and the macroconscious phases. The justification for this subdivision is obvious. But it created a problem: Over longer periods we *appear* to perceive all the different attributes simultaneously; whether this is mere appearance has yet to be determined. It also remains to be determined whether there is a transition between the two states, assuming them to be two states rather than two different manifestations of the same state, revealable only in a laboratory setting. As significantly, it seemed to us that the entire question of binding had been wrongly framed and its relationship to consciousness had been wrongly configured; features processed at different speeds are not bound; instead they are mis-bound, at least at very early stages after the appearance of visual stimuli. That changes the approach to the problem of binding and of consciousness.

It now seems to me that we have still not quite integrated the principles of dynamic parallelism and asynchronous perception, which depend on task and stimulus, into our thinking on the operations of the cerebral cortex. Those who have promoted the idea of binding by synchrony have, unfortunately, never addressed the issues of asynchronous transmission of signals and asynchronous perception; both call into question not only the nature of binding but also the nature of consciousness even if confined only to early stages after exposure to visual stimuli. Additionally, those who have promoted the idea of a single hierarchy throughout the cerebral cortex have never addressed the issue posed by the earlier arrival of signals in some "higher" areas than in "lower" ones, which calls into question the hierarchical edifice of the organization of cortical connections. I suppose complete silence is one response—and we can read whatever we want into it.

Paranoia Strikes Again

Konstantinos and I thought that our results on asynchronous perception were important; accordingly, we sent our paper to *Nature*; they dithered

and wanted it rereviewed after modifications in light of their reviewers' comments. When we resubmitted, one of the reviewers updated his earlier review; he wrote, "I have now been to the library and think that this result could have been predicted." Another, wiser reviewer, responded, "I don't care if it could have been predicted, it wasn't." This threatened to descend into an eristic discussion between referees, with us as the victim. To me, a paranoiac by necessity rather than temperament, this even carried the makings of a ruse to delay the paper indefinitely. What could we do? I had an idea: Paranoiacs like me had found refuge and release from their habit for centuries in the system installed by the *Académie des Sciences* in Paris in 1666; the system, implicitly recognizing scientific paranoia, accepted sealed letters (*lettres cachetées*) in which results could be deposited. The Academy undertakes to keep it under seal for 100 years, unless the depositor asks for it to be opened publicly, to establish paternity of the work or ideas contained therein. It was not an unpleasant way of protecting oneself, given my experience with V5—it only involved an enjoyable trip to Paris. Fortunately, I have had no reason so far for the letter to be unsealed.

These results, then, raised profound questions, especially about the presumed "unity" of consciousness. While I was pondering that question, I received an invitation to a meeting in Brussels. The meeting was entitled "The Unity of Consciousness." I accepted and sent in my title: "The Disunity of Consciousness."

I should like to emphasize that I am not doubting that, at a certain level—the level at which I become aware that I am the source of an experience—a plausible argument can be made for that "unity." But I have considered consciousness to have hierarchical stages and, at early perceptual stages, I am not at all convinced of any kind of unity considering the experiments on asynchrony described earlier. My view perhaps corresponds better with Daniel Dennett's multiple drafts theory; although Dennett derives his conclusions from formulations in philosophy and cognitive science, and I derive mine from experimental neurobiology, the basis of both of our views lies in a parallel, distributed system. That this system is distributed in time and space can be dramatically illustrated through an experiment that I undertook with Andreas Bartels, perhaps the first of its kind. In that experiment, we explored the activity in the brain when subjects viewed an action movie (we chose James Bond's *Tomorrow Never Dies*), in which many events occur at once. We analyzed the results using independent component analysis, which Andreas had imported from Sejnowski's lab; the results showed that activity in the brain is not only segregated in space, as might be expected from our previous studies, but also in time, each area seemingly having its own independently varying temporal sequence.

This led us to introduce a new concept into brain studies, that of *cerebral chronoarchitecture*. This could be thought of as the manifestation of

the asynchronous signaling between areas. I think that it will acquire a greater significance in the future, although I should not be surprised if others try to attach a different name to it.

All this can be summarized as follows: that the operations of the brain, or at least the functionally specialized visual cortex, are governed by massively parallel, asynchronous, activity that, in viewing natural scenes, is reflected in its chronoarchitecture. The demonstrated perceptual asynchrony, which is governed by stimulus and task as well as the speed of connections between visual areas, is a pointer to processing areas being also perceptual areas. This makes phenomena such as the degraded but conscious vision of the blind more comprehensible.

The "Blindsight" Affair

The demonstration of separate and asynchronous inputs into the brain and into area V5 in particular, and my increasing conviction that what is localizable in these specialized areas is the experience generated by their activity, began to suggest new ideas to me. In 1973, Ernst Poeppel and his colleagues had demonstrated that patients blinded by lesions in V1 could detect visual motion accurately. In the following year, Larry Weiskrantz and his colleagues took this discovery to a dramatic new level; they demonstrated, or so they supposed, that patients blinded by lesions in V1 could discriminate visual stimuli with high accuracy even though they declared not having seen anything; they came to believe not only that discrimination of a visual stimuli was perceptually separate from its conscious experience but also that different neural mechanisms were engaged; as they saw it, correct discrimination in patients with a total loss of visual awareness because of a damaged V1 could be attributed to subcortical activity. Weiskrantz termed the phenomenon "blindsight"; I, unfortunately and thoughtlessly, wrote about it approvingly even as late as 1993, in my book *A Vision of the Brain*. The purported syndrome was paradoxical enough to excite the interest of philosophers. It was, therefore, something to be avoided. But my results, summarized earlier, propelled me into it ineluctably. It raised the question of whether signals reaching a visual area such as V5 directly, without passing through V1, can result in visual processing with conscious visual experience as its correlate.

V5 became once again central to my enquiries. Blindsight experiments had concentrated on studying visual motion discrimination. Did this mean that there was little or no activity in V5 when blindsight subjects could discriminate correctly the direction of motion without being aware of it? Exploring consciousness in this limited way had another advantage; I had been mulling for some time about how to neutralize the Oxford group, who had been making snide remarks of insidious intent, although never by Larry, about my work on color; these had been conveyed to me by reliable

sources and were in any case evident in some of their writings. How should I respond? I was interested in something more serious and heavy weight than Oxford style tittle-tattle. I warned Larry in 1988, when he came to UCL to deliver the Royal Society Ferrier Lecture, that my response would come in time and that it would not be mild. Larry had shrugged it off by saying that his group at Oxford knew what they were doing. Within five years, I kept my promise, through a study that had two aims: to study the minimal requirements for eliciting a conscious experience of visual motion, using V5, and to give Oxford a taste of its own medicine. Hence, the motivation was only partly scientific. But one motivation is as good as another if it advances science. I approached Keith Ruddock; patient GY, the most celebrated and well documented of the blindsight patients, was his patient; Keith readily agreed.

My first study of the phenomenon was undertaken with John Watson and John Barbur. Our results showed that, contrary to what Larry and his teams had emphasized for years, the V1 bypassing input to V5 was potent enough to elicit a crude but conscious experience of visual motion. This was not surprising. Tom Albright and his colleagues had previously shown physiologically that, in monkeys, directional selectivity in V5 survives lesions in V1, with the strong implication that a V5 disconnected from V1 could still signal the direction of motion in the field of view. This survival accounts for why a patient like GY was able, in the great majority of presentations, to discriminate correctly and report (consciously) the direction of moving stimuli. But, as our studies with GY were to show, he was only able to discriminate and become consciously aware of the stimuli if they were of high contrast and moved at speeds in excess of 5 degrees per second; stimuli moving at slower speeds were not discriminated correctly, and there was no reported awareness of them. In simpler terms, V5 was processing high-contrast, fast-moving signals, which Dominic Ffytche, Georg Beckers, and I had demonstrated reach V5 selectively before reaching V1, and that processing had evidently resulted in a conscious correlate, presumably without the need for further processing. The term "without further processing" requires an explanation. I argued, in a 1999 review on consciousness with Andreas Bartels, that it is improbable for a visual area not to retain some of what it has processed, which should then acquire a conscious correlate. If all that an area A has processed has to be reprocessed in its entirety in area B, then the result of the processing in area A would be lost to conscious experience—the mark of a most inefficient system, which the brain is decidedly not. There is, in any case, no "final," highest area in the cerebral cortex—cortical connections are massively reciprocal and all areas receive and send signals.

We prepared a paper, for which I gave—to my later regret—first authorship to John Barbur, because of his acquaintance with patient GY. Barbur was reluctant to use the term conscious, which we therefore

omitted from the initial manuscript submitted to *Science*. I later referred to one of the referees at *Science* as a "swine" because she or he had concocted a miasma of trivial reasons for rejecting our paper. But within that miasma was a gem: The reviewer expressed surprise that we had not used, even once, the term "conscious." This was insightful; the swine thus turned out to be a savior, which is why I said, in my Presidential Lecture at the Society for Neuroscience in 1993, that one "needs a swine to show you where the truffles are"—a phrase lifted from Edward Albee's *Who's Afraid of Virginia Woolf*. In light of this "truffle," we had an ill-tempered meeting in my office at which I insisted that the term "conscious" should appear prominently in the paper, indeed in its title. It was published in *Brain* in 1993, under the title "Conscious Visual Perception Without V1."

Displeased, Larry asked to come to London to give a talk at our Imaging Center. Being its codirector, I chaired the meeting; perhaps intimidated by my presence, no one asked any questions and there was no discussion after his talk. If Larry had been angered by our results, he showed no sign of it. He delivered his seminar with self-assurance. The anger surfaced later, in his papers and in his book. To me, there was something odd about these papers, coauthored with John Barbur among others; their only reference to our papers was to the extent of the lesion in GY's V1 as determined from our scans; there was no mention that our findings contradicted theirs—an eloquent admission, perhaps, that we were right, or so it seemed to me. Five years after publication of our results, Weiskrantz rebranded blindsight by dividing it into two categories, Type 1 and Type 2, of which only the first corresponded to the classical blindsight promoted by the Oxford group, namely high levels of correct discrimination of visual stimuli without conscious awareness. Type 2 blindsight was what we had demonstrated in our experiments—namely, a crude but conscious experience of the appropriate visual stimuli when presented to the blind field. Larry's subdivision amounted, in brief, to a major retreat by the Oxford group, even if rarely explicitly acknowledged as being so. I described Larry's new subdivision as a "damage limitation exercise." Larry responded by writing that I had been "destructive and snide." I shall remain silent on the other defenses mounted—first, that GY, in spite of discriminating accurately the direction of motion of visual stimuli and reporting them correctly, was not having any visual awareness at all but merely a "feeling" of something having happened; or, second, that what he was conscious of was not the visual stimulus that he could discriminate correctly and report on, but rather an awareness that his pupils had dilated.

Given how ingrained this phenomenon had become in the popular mind, I wanted to pursue this finding in more granular detail and did so with Dominic, nothing if not an original thinker and a stickler for detail. And for good reason; the stakes were high, and we were "trespassing" into someone else's territory. But our detailed reading of the blindsight litera-

ture had revealed its weak spots. Correspondingly, our more detailed study showed that (1) there is, in general, a good correlation between GY's capacity to discriminate stimuli presented in his blind field and his conscious awareness of the same stimuli; and (2) GY's performance on some tasks is characterized by a marked variability, both in terms of his awareness for a given level of discrimination and in his discrimination for a given level of awareness. This led us to propose a simple model of the relationship between visual discrimination and awareness: the two independent capacities are very tightly coupled in normal subjects (gnosopsia); the effect of a V1 lesion is to uncouple them, but only slightly. This uncoupling leads to two symmetrical departures; on the one hand, to gnosanopsia (awareness without discrimination) and, on the other, to agnosopsia (discrimination without awareness). Perhaps the most interesting aspect was our imaging study of the activity in V5; this showed that V5 is always active when moving stimuli, whether slow or fast, are presented to GY's blind field. This allowed us, for the first time, to titrate conscious awareness against brain activity and show that there is a straightforward relationship between awareness and V5 activity, both in individual cortical areas, in this case area V5, and in the reticular activating system. The strength of activation in V5 correlated with whether or not motion was experienced consciously. The imaging evidence, together with the variability in GY's levels of awareness and discrimination, manifested in his capacity to discriminate consciously on some occasions and unconsciously on others, led us to conclude that agnosopsia, gnosopsia, and gnosanopsia are all manifestations of a single condition. In essence, this had been described by George Riddoch in his 1917 paper in *Brain* following his examination of British soldiers who had succumbed to brain wounds through enemy fire in the Great War; that paper had shown that patients blinded by lesions in their V1 could discriminate motion in their blind fields but could not discriminate the form or color of the moving stimulus. Riddoch repeats several times that his blinded subjects were "conscious" of the motion. His paper thus turns out to have been remarkably accurate for its time; but its thesis of a special representation of motion in the visual brain had been rejected emphatically by Sir Gordon Holmes, then the doyen of British neurologists, who had written that Riddoch's observations were "certainly incorrect." Riddoch's work had consequently been almost totally and unjustly neglected. Dominic and I decided, in our review of what we had found and published in *Brain* in 1998, to refer to this syndrome, not as blindsight, but as the *Riddoch Syndrome* in recognition of the man who had first described its critical feature, namely the conscious experience of a moving stimulus presented to the blind field produced by damage to V1.

In the end, we managed to convince ourselves that there was something critically mistaken in the phenomenon referred to intriguingly as "blindsight," a term that had started to conjure up for me visions of a bad

Hollywood movie, in which a blind witness is able to identify a criminal with certainty but without having ever been able to see him. I even imagined that I could write a detective story based on the phenomenon, leading to untold riches. But I desisted when I decided that such a book would probably not sell many copies.

An unintended but nevertheless welcome casualty of our work on the Riddoch Syndrome is the probably widely held supposition that the return connections back to V1 from V5 are the ones that generate conscious visual experience rather than the forward projections from it; welcome because that is one suggestion that is not worth pursuing further, at least in terms of the relationship between V1 and V5 and the necessary conditions for conscious vision. Clearly, if V1 is damaged, both the output from it and the return inputs to it are no longer operative. This refined a central thesis: that input into V5 that bypasses V1 can result in a conscious, if crude, visual experience without the necessity of a return, feedback input into V1. Konstantinos and I were later to demonstrate, through psychophysical and imaging experiments, that visual areas other than V5, processing other visual attributes, are also involved in their conscious perception, without necessarily involving the need for further processing.

We celebrated the publication of our 1998 review in *Brain*, entitled "The Riddoch Syndrome," with a wonderful lab dinner, prepared under the supervision of the indefatigable Ludovica; when the main course arrived, it was appropriately entitled *Spaghetti all'awareness*!

Although I have published more papers on the topic since, the substance of my modest excursion into consciousness had been accomplished and my account with Oxford settled. It was a pleasant way of settling a festering account, for it gave new knowledge about the brain.

Dominic and I decided that we could stay clear of the topic of blindsight for a good ten years, because the literature would by then be flooded with papers either defensive of blindsight or accepting our new view but still calling the phenomenon blindsight. This is precisely what we did and precisely what happened: We revisited the issue about a decade later, using different patients; the results were the same. By that time, the literature had indeed been flooded with many papers. It now surprises me how many of those papers acknowledge the presence of a crude, conscious element in the motion vision of patients blinded by damage to V1 but continue to refer to the phenomenon as blindsight—a demonstration of the enduring power of early naming, however inappropriate the nomenclature may later turn out to be.

The terminology that Dominic and I had used to describe different manifestations of the Riddoch Syndrome was cumbersome enough not to have been widely adopted, if adopted at all. But it had the merit of not sacrificing truth for simplicity of nomenclature. We referred to one of the Riddoch Syndrome manifestations as *gnosanopsia*, admittedly quite a mouthful; it

refers to the conscious discrimination of the direction of motion of nonexistent visual stimuli—that is, in the absence of vision, something resembling a visual hallucination. The terminology, although cumbersome, is—I believe—close to a description of one of the variable manifestations of the Riddoch Syndrome. As a variant, it gained further support from later work that I did with Samuel Rasche and Ahmad Beyh. We showed that patients could discriminate the direction of motion of stimuli that were not there if they had previously been presented with directionally moving stimuli—yet another example of the brain constructing an experience. This reinforced my view that these specialized areas are loci of visual experiences, a view that finds further experimental evidence in work that Konstantinos and I did, which hinted strongly that processing sites in the visual brain are also perceptual sites. The latter is an idea that in any case emerges strongly from my previous work on color and on visual motion.

Toward Beauty and Neuroesthetics

JZ Young had instilled in me the importance of a humanistic approach in neurobiology. I sniffed at this at various times with little outcome, until the mid-1980s when I met Jean-Pierre Megnin, an enologist who had established the *Prix Science pour l'art* at Louis Vuitton Moët Hennessy (LVMH) in Paris. From then on, my interest took a more serious turn, traceable to a widened circle of acquaintances whom Jean-Pierre introduced me to; these included many from the humanities who showed a keen interest in engaging with neurobiologists. I became increasingly interested to search, neurobiologically, for something in art and beauty that is universal, not tied to any culture or ethnic group, an approach closer to the quest of philosophers of aesthetics than that of art historians, whose concern is often restricted to special periods. I inaugurated a new field, that of neuroesthetics, which really is a direct extension of my work on the visual brain; the common theme is the acquisition of knowledge through vision and through art and beauty. Neuroesthetics is of course a wider field, in the sense that it includes the study of experiences that are allied to beauty, such as those of love, desire, and sublimity, all topics that I tackled in imaging studies.

Establishing the field of neuroesthetics earned me the hostility of some art historians and philosophers. Roger Scruton, the philosopher, joined forces with other philosophers, of lesser eminence, to denounce my new discipline as "neurotrash"; other, even stronger, adjectives were used to stigmatize this new field. The charge of reductionism, always a last resort and always ready to hand, was prominently deployed. At a meeting at the Getty Center in Los Angeles in the early 2000s, Vilayanur Ramachandran and I were publicly criticized by the then director of the center, Tom Crowe; he did this, he claimed, to initiate a dialogue at the meeting. To me, it all

sounded like a lot of *massage parlare* and I did not respond at all. Instead, I wanted to run, as fast as possible, far, far away, and fall into a dream-like trance, like *Alice in Wonderland*, to digest the absurdity of it all and wake up in a world that resembled more closely my early years at UCL where, in an intellectually brilliant environment, hospitality to new ideas was the rule. It was perhaps a case of *reculer pour mieux sauter*.

But when the time came to jump in again, what they had or had not said became irrelevant. I wondered whether they had deceived themselves or tried to deceive their audiences into thinking that the pursuit of so interesting a topic as the brain's involvement in affective, aesthetic experiences would succumb to such criticism when the technology for doing so was available? But by then, I could in any case afford to ignore what I believed were trite comments. Circumstances had changed; unlike that hapless period when I stood vulnerable and alone in what I felt was a largely hostile world, now my intellectual environment was different. I was more secure not only in the large grants I was receiving but also in the strong support I received from the scientific community and from prominent artists and art historians as well. In addition, I was receiving invitations to lecture at some of the world's leading art galleries and museums, as well as many art festivals, especially in Britain, Italy, Japan, and India. At these meetings, I met and had public dialogues with many eminent artists who were hospitable to new ideas that linked neurobiology and art. In such an environment, the name-calling by hostile philosophers and art historians became harmless. Perhaps paradoxically, this more hospitable environment was, internally, also the more dangerous one. Success is more insidious and treacherous than failure; taken seriously, it risks pulling one in a perilous direction—of sleepwalking into a state of contentment and self-satisfaction through the illusion that one has achieved something of lasting value. Fortunately, I was always aware, or so I think, of how imperfect my achievements have been.

The artist with whom I had the lengthiest discussions was the French painter Balthus (Count Klossowski de Rola) whom I met at a reception in Paris in the mid 1980s; I often stayed with him and his wife, Setsuko (also a painter), at their beautiful *Grand Chalet de Rossinière*, by Lake Geneva. As our friendship and discussions developed, Balthus came to appreciate increasingly my argument that beauty is not "out there" independently of mind and brain but, as with color vision, the brain actively constructs it partly according to neurally inherited laws. This may seem obvious to some; I was surprised when so many had never considered it, although the idea can be traced back to Plotinus, the neo-Platonist philosopher, and from him to Schopenhauer and to Cézanne, among others. What developed into this common understanding nourished my dialogues with Balthus, the last one of which was held on April 20, 1993, in the sumptuous setting of the Palazzo Farnese. Designed during the High Renaissance in part by

Michelangelo and now the French Embassy in Rome, the invitation to hold our last dialogue there came from the French ambassador, M. Philippe Cuvillier. It was a hugely inspiring setting. After my long discussion with Balthus, the ambassador had invited the Chilean-French surrealist painter, Roberto Matta, to join us for lunch. Matta had been influenced by Salvador Dali and by concepts of "psychological morphology" and "inner psychological space" to produce some stunning canvases. My conversations with him, in Rome and at his home in London, laid the germs of the article I was later invited to write, on the neural sources of ambiguity in Dali's work, to commemorate the centenary of Dali's birth at Figueras in Spain in 1904. The ambassador had also invited Federico Fellini, the film director and friend of Balthus who, like me, was fascinated by inner, subjective, perception but from a different angle. Unfortunately, Fellini could not make it because of ill health, to my great regret; I am sure that he would have inspired me enormously in a further undertaking. The French Embassy had evidently been meticulous in their choice of guests, bringing together diverse men with a shared passion. For me, this signified the new reality of interdisciplinary discourse between artists and neurobiologists. Or perhaps it was just another rebirth, of the time in the High Renaissance when vision was a central epistemic problem and discourse between scientists and artists was the norm.

My dialogues with Balthus were published in 1995 in a book entitled *La Quête de l'essentiel*.

Three other events in 1992 and 1993, all unplanned, increased my resolve to pursue neurobiologically a study of art and beauty. Of these, the most immediate trigger was an encounter in 1992 with Jean-Louis Prat, the celebrated director of the Fondation Maeght at Saint Paul de Vance, in France. I was expressing to him my interest in how the brain perceives movement when he surprised me by inviting me to the exhibition that he had curated at the Foundation on *l'Art en mouvement*. The exhibition exhilarated me; it contained all that I needed to prepare for an article on the involvement of the brain's system for detecting visual motion; this, I thought, should be centered on V5 and the steps taken by kinetic artists to tailor their work to its physiology. The exhibition confirmed my conviction that artists are also scientists, dissecting brain activity but with techniques unique to them; a careful examination of their works may therefore reveal important insights about the functioning of the brain, a topic that I addressed at greater length in my book *Inner Vision* (1999). Soon thereafter, in 1993, I attended a retrospective exhibition at the Palazzo Grassi in Venice on Marcel Duchamp, "the Frenchman who dissects sensations" and who had turned views on art upside down with his radical thinking, by writing about "art without an artist" and coining the term "readymade." He had long tinkered with making movement part of the work of art but had only done so to a limited extent, movement being represented

statically in most of his work. Finally, on a visit to New York in 1992, my ex-research fellow, Mathew Lamb, convinced me that we should visit the superlative exhibition, *The Great Utopia*, at the Guggenheim Museum on a dreary Sunday morning. And it was with Mathew Lamb, whose interest in the artistic side of neurobiology was second to none, that I wrote the article entitled "The Neurology of Kinetic Art," which was the first neuroesthetic article I wrote for a journal of neurology. Writing it was tremendous fun; we prefaced it with a "Credo" or "Manifesto of Physiological Facts"—in line with the "Futurist Manifesto" of Filippo Marinetti and the "Realist Manifesto" of Naum Gabo and Antoine Pevsner. We submitted the article to *Brain*, whose readership consists mainly of serious clinical neurologists, mostly in gray pin-striped suits; we were shocked when *Brain* accepted it. But Ian MacDonald, its then editor, was an enlightened man who was himself deeply interested in the arts. The paper had been reviewed, he later told me, by an eminent art critic, although he never revealed the name. It was another affirmation that times had changed; one could ignore the idle human chatter so admirably represented by the woodwinds in *Ein Heldenleben*.

A New, Neurobiological, Definition of Beauty

Although I had published a few papers on art and neurobiology before, the publication of the article in *Brain* ignited my desire to stray into even more dangerous territory—to study the brain mechanisms that are engaged during the experience of beauty. This was a daunting undertaking, beauty itself being so difficult a topic, discussed without adequate resolution or definition since the time of Plato. Here, another unexpected opportunity arose. Peter Day, director of the Royal Institution in London, asked me to address the topic of art and beauty neurobiologically in the Woodhull Lecture, which he invited me to deliver in 1995—a scientific rite of passage toward the forbidden territory of beauty. My new direction was greatly eased when I much later received a Strategic Award exceeding £1million from the Wellcome Trust to pursue my studies in neuroesthetics. Thus encouraged, I began approaching the question with two enthusiastic Japanese colleagues, Hideaki Kawabata and Tomohiro Ishizu. The question we addressed was inspired by my reading of Clive Bell's book *Art* (1914). Bell, an English art critic, had raised a visionary and sweeping question in aesthetics. He had written that if we can determine what is common to all objects that arouse the aesthetic emotion, then we would have essentially solved the problem of aesthetics. I transcribed this into a scientific question: If we can find a neural mechanism that is always engaged during aesthetic experiences, regardless of source, then we would have solved Bell's question on aesthetics neurobiologically, if not philosophically. The results were clear, that the experience of beauty derived

from a variety of visual and musical sources correlates with quantifiable activity in a specific part of the brain, field A1 of the medial orbito-frontal cortex (A1mOFC). This finding went a long way, I believe, toward resolving the question posed by Bell.

It also led me to give a new, though strictly neurobiological, definition of beauty: that beauty is an experience that correlates with quantifiable activity in field A1 of mOFC. But beauty is also linked to desire, and Hideaki and I thought it important to learn whether the cortical area active in states of desire is linked to A1mOFC. The result was better than that: The quantifiable activity that correlates with desire occurs in the very same cortical area, raising the issue of whether there are subdivisions of different, but linked, specialization within field A1. Equally, in later imaging studies with Japanese colleagues under the direction of Yasuyoshi Watanabe at Kobe, we showed that the medial orbito-frontal cortex is strongly active during the experience of romantic love, presumably because lovers experience beauty when viewing their partners.

Because of my early belief that artists are in some measure neuroscientists, studying the brain with techniques unique to them, I started delving into the work that some had produced; I wrote articles on Dante, Michelangelo, Wagner, Dali, Francis Bacon, and Clive Bell, none completely satisfactory and the first three less so than the last three. I addressed the work of many other artists in my book *Inner Vision.* By then, I had authored three books alone; my favorite was *Splendors and Miseries of the Brain*, though it was not nearly as successful as the first two. If asked to (as I was for the first book), I would not prepare another edition of any of them now. It will be a lot easier to write new ones.

Commissioning and Producing Art (On a Modest Scale)

I was fortunate enough, during this period, to acquire two new colleagues. One was my new research assistant, Anton Burdakov, a graduate in science from Cambridge who had strong artistic tendencies and has since gone on to become a successful full-time artist in Berlin. The many discussions I had with him were invaluable, and I liked his art sufficiently to commission drawings from him for my book *Splendors and Miseries of the Brain.* He executed these with flare and imagination, and I still own the originals.

My close association with the Slade School of Art at UCL, where I lectured occasionally, brought me into contact with Vijay Patel, who was studying there and was intensely interested in neuroesthetics. Together, we prepared many abstract installations, inspired by Malevich's painting entitled *White on White*, which Malevich thought of as the end of representational painting and the beginning of Suprematism; the latter he described as "nonobjective art" and "nonobjective sensation," themes that rhyme well with my views; his attitude to art is summarized brilliantly

in his statement that "Art wants nothing further to do with the object as such." I took this to mean that the artist will create what is in his brain, without reference to the outside world. Whether I am in error or not does not matter; the Suprematist approach was inspiring and, for Vijay and myself, became another departure into a world of abstract installations illuminated in a new way. Using my knowledge of colored shadows and Vijay's artistic abilities, we jointly designed these installations so that they could be illuminated to produce shapes with a variety of colors on the walls behind them. This was a great collaboration; it illustrated for me the huge difficulty of producing works of art that satisfy one's concepts. Eventually, we were both satisfied enough with what we had produced; more significantly, what we produced satisfied the Pecci Museum of Contemporary Art in Milan sufficiently for them to organize an exhibition of our works at their gallery in 2011, with the help of Ludovica. We named the exhibition: *Bianco su bianco: oltre Malevich* (White on White: Beyond Malevich). Neuroesthetics was no longer solely a theoretical and experimental study; it had become an artistic endeavor as well.

Biological and Artefactual Beauty and the Bayesian Hierarchy

Color, which had dominated my outlook for so long, now became the path toward more questions about beauty. My 2020 paper on the Bayesian-Laplacian brain with Oliver Chen had approached the question of the extent to which percepts or opinions can be updated and modified through knowledge and experience. We had proposed that the extent was limited when it came to color categories. It was now time to apply our views, that there is a hierarchy in the facility with which opinion can be updated, to beauty. The question to consider was encapsulated in the Latin phrase: *De gustibus non est disputandum*; this is rendered somewhat more palatable in its common English form as "beauty is in the eye of the beholder," a leaden phrase deadly enough to bring any discussion on beauty to a screeching halt. How true is it?

We decided to divide beauty into two very broad categories—biological and artefactual, inspired by, although different from, Immanuel Kant's philosophy. Kant had said, "percepts without concepts are blind." We agreed with that but divided brain concepts into two broad categories, with subdivisions within each: We suggested that biological stimuli such as faces, bodies, and landscapes are interfaced through inherited brain concepts and artefactual ones such as buildings through acquired concepts. It follows that inherited, biological concepts should be much more resistant to Bayesian revision through external opinion or new experiences than artefactual ones, which can be subject to continual revision and updating throughout life. Broadly speaking, our psychophysical experiments

confirmed this by showing, first, that human faces judged to be very beautiful in some cultures are likely to be also judged as very beautiful in others; this is presumably because the aesthetic status of faces depends to a significant degree on correct proportions and relations of parts of the face to one another, which is universal, as the ancient Greek sculptor Polykleitos had proposed. This is not true of artefactual beauty where opinion is much more diverse and divided. Such a division is uniquely visible in the artistic output of Francis Bacon, whose self-proclaimed aim had been "to give a visual shock." In an article on him with Tomohiro Ishizu, we argued that Bacon did so by mutilating on canvas the inherited concepts of faces and bodies but did not mutilate objects or did so to a far lesser extent. With other colleagues, I showed, in studies in which subjects of different racial and cultural backgrounds assessed the beauty of human faces belonging to different races, that the assignment of aesthetic status to a biological stimulus is less hostage to revision through experience and peer opinion, compared to artefactual stimuli. I was beginning to acquire a new outlook on beauty in a broader sense. Taken in conjunction with our work on color, Chen and I concluded that there is some kind of hierarchy in the Bayesian system. At one extreme is color vision where no amount of knowledge or experience is likely to modify one's perception of the color category of a surface, although its hue may be subject to Bayesian revision. Next to it comes mathematical beauty, which, if not as resistant to revision as color, is high up the scale, following which comes biological beauty where stimuli are more resistant to revision than the final category, that of artefactual stimuli, whose aesthetic status is much more pliable.

My studies on the neurobiology of beauty excited the interest of Sir Michael Atiyah, one of the greatest mathematicians of the 20th century. His view, shared by other mathematicians, including Bertrand Russell, Paul Dirac, and Hermann Weyl, was that there is a strong aesthetic and artistic element in mathematics; indeed, that the guide to the veracity of a mathematical formulation lay in its beauty rather than its simplicity. Michael often recounted how beauty had triumphed in Weyl's mathematical formulations that had reconciled the electromagnetism of James Clerk Maxwell with Einstein's theory of relatively, despite Einstein's earlier objections to Weyl's formulations. He wanted me to enlarge my aesthetic studies to include mathematics. This was fraught with difficulty; it amounted to studying the most extreme example of beauty, one that is heavily dependent on culture and learning; no one who is not trained mathematically would be able to experience beauty in a mathematical formula. But it was also a radical departure, because it explored the extremes of aesthetic experience. The study was long in the making; Michael objected to many of the formulae that we collected, often because he felt they included too much physics or were not abstract enough. Sensing the importance of the experiment, my highly demanding research assistant, John Romaya,

suddenly also upped his demands and made a major contribution to the study by going through every single formula and every single result with his mathematical pitchfork, until I asked him to stop, *stop*—the results were too obvious and clear cut; they showed that, as with varieties of visual and musical beauty, the experience of mathematical beauty also correlates with quantifiable activity in A1mOFC. This added a highly cognitive element to solving Bell's problem of aesthetics; we had now come full circle in showing that the brain abstracts for beauty since activity in the same area correlates with the experience of beauty, regardless of its source. Kant had enquired into what mathematical beauty consists of; he thought that our reasoning faculties rather than a mind-independent truth "out there" leads to it, that "it makes sense." But sense to what? My answer has been: to the logical inductive and deductive systems of the brain, which is the same for all human brains and which is, in turn, why I put mathematical beauty in the biological category.

Given my earlier experience with philosophers, I was surprised how hospitable renowned mathematicians were to our incursion into their field of mathematics.

We sent the paper to *Nature*, *Science*, and *Current Biology*; all rejected it within 48 hours; all the rejections were accompanied by prissy letters advising us to send the paper to more specialized journals. We sent it to *Frontiers in Human Neuroscience*. At the time of writing this autobiography, it had been viewed 229,000 times, including from war-torn countries and regions like Libya, Yemen, the Gaza Strip, Syria, Myanmar, and Nigeria, as well as remote islands like French Polynesia, Samoa, and Tonga. The little confidence that I had in the judgment of most scientific journalists, with some remarkable exceptions, as to what topic is of general interest could now be justified.

There is, indeed, a biological, perceptual imperative even in mathematics, which is why Mikhail Filippov and I emphasized the importance of importing neurobiology into mathematical studies. This approach bore fruit later when my colleagues and I showed that perceptual axioms are irreconcilable with, and trump, Euclidean geometry. In its way, it was also a demonstration of the brain constructing its own perceptual realities stubbornly, even when they lie in opposition to the cognitive axioms whose origins can also be traced to the brain. It is, I hope, the beginning of new enquiries into the dominance of brain-generated immediate experiences over cognitively acquired brain knowledge.

And Love?

Beauty is linked to romantic love, another difficult topic; I addressed it in a limited way, through experimentation and through considering the world literature of love. The latter was critical and constitutes a perfect example

of why neurobiologists should take the output of the artists (in the broadest sense) seriously when formulating their questions, for works of art are themselves products of the human brain and regulated by its capacities. In terms of love, my readings of the world literature of love showed that a central—I believe biologically based—concept that emerges is that of the "unity in love," or the desire for it. This is true not only in romantic love but also in spiritual love. Whether one looks at the writings of the Azeri poet Nizami, or those of the Sufi poets Rumi and Hafiz, or Michelangelo, or the Indian legend of Radha and Krishna, or Wagner's *Tristan und Isolde*, or Emily Brontë's *Wuthering Heights*, the theme of unity in love emerges prominently. It emerges powerfully, as well, in writings of romantic love that have a strong sacred element, as in those of Petrarch's *Canzoniere*, or the writings of Saint Theresa or Saint John of the Cross, among others. Such a concept does not emerge from neurobiological studies themselves. But my imaging studies on love suggested possible neural explanations for this concept as well as for the phenomenon of the "madness of love" celebrated by poets from Plato onward. I undertook these studies with Andreas Bartels (on straight romantic love) and with John Romaya on homosexual love (both gay and lesbian). I had been reluctant to broach the latter subject; if the results were to show that there are significant differences in the pattern of brain activity when homosexual men and women view their partners compared with their straight counterparts, then this would provide just the kind of evidence that those who consider homosexuality to be an aberration need to strengthen their view, thus leading to the possibility of further oppression. I pondered the question for a long time. In the end, I decided to do the experiments and live with the consequences.

Given my studies of the literature of love, which reveals a similarity in the desire for unity in love regardless of the orientation of those experiencing it, it was not surprising to find that the results for both groups were broadly similar, if not identical (a reminder that we were studying the basis of romantic love, not sexuality). Prominent among these was the deactivation of large parts of brain areas obtained in both studies, especially in areas of the brain reported by others to be important in distinguishing between self and others; this possibly constitutes a neural basis for the unity in love in which the distinction between self and the beloved is blurred. The other interesting observation, in both groups, was of a significant deactivation in areas of the brain that are considered to be involved in judgment, when lovers look at the pictures of their loved ones. This raised two interesting questions—namely, that the suspension of judgment when in the amorous state is restricted to the loved person; it does not, for example, extend to a suspension of judgment about mathematics in a mathematician or music in a musician; it is, in other words, very specific. The other question relates to marriage. Unknown to me, the importance of this specific suspension of judgment had been recognized

by the Catholic Church long ago, in the context of human behavior. It was Myriam Tinto, a jurist at the Vatican, knowledgeable in ecclesiastical law, who pointed this out to me. The Catholic Church, which does not accept divorce, will nevertheless consider the lack of a "discretion of judgment" as a reason for annulling a marriage, if it can be proven that the marriage was entered into when one or both had lost their faculty of judgment. The relevant passage is to be found in the *Codex Juris Canonici* (Code of Canon Law; Can. 1095, n. 2); it reads as follows: "The following are incapable of contracting marriage: [ ] those who suffer from a grave lack of discretion of judgment concerning the essential matrimonial rights and obligations to be mutually given and accepted." And when are humans rendered incapable of exercising the discretion of judgment? When they are passionately in love of course. This shows very forcefully how even law and jurisprudence can be used to gain insight into how the brain functions; they are, after all, products of our brains.

There were two other dimensions to love that I really wanted to study. One was religious love, a study that I actually embarked on but found difficult; the results were baffling and I never published them. I discussed my work with priests and priestesses, who persuaded me that my approach was misguided. I abandoned the effort as too complex for me. I unfortunately never embarked on the third category of love, namely passionate love in old age, which I deem is necessary—along with straight and same-sex love—to really understand romantic love neurobiologically. I hope that someone will think it a worthy enterprise to pursue.

The Mapping of Experiences in the Cerebral Cortex

I have emphasized strongly that a common conclusion that arose from my studies, whether of the organization and functioning of the visual brain or of neuroesthetics, is that what is mapped in the brain is experience, which is the result of specific brain operations. I perhaps reached that conclusion somewhat indirectly and only relatively recently. I had, many years ago, emphasized that what is represented in the visual brain is neither the retina nor the visual field because, even though one may find that in some areas these are mapped in an orderly and in others in a disorderly way, one can nevertheless only elicit activity from them if one activates their cells in a particular way, according to their specialization. I now move a step beyond to the notion that what is localized in the cerebral cortex are apparatuses for generating specific experiences. At one end of the brain, quite literally, is the apparatus for generating the experience of oriented lines, and it is perhaps no accident that the oriented line became an autonomous element depicted in works of art, which Rodchenko, the Russian Constructivist artist, insisted he had introduced into art. If oriented lines are a physiological reality, they are also a visual experience,

just as visual motion, depicted in kinetic art, is. Both are dependent on specialized cells inhabiting specialized areas. At the other, front, end of the brain, the apparatus for the experience of beauty is localizable in the sense that, whatever its source and whatever activity in specialized areas its activity correlates with, activity in A1 of mOFC always correlates with the experience of beauty. Before the chorus of excoriation starts, of how dare I localize the cortical apparatus for experiences, especially ones such as beauty, to particular brain areas, let me say at once that I am not advocating that these areas act alone but only that activity in them is central to the relevant experience. Some philosophers, and particularly those trained in metaphysics and mereology, might disagree. I accept that.

My interest in neuroesthetics triggered in me a desire to start an undergraduate course in neuroesthetics at UCL. I had always tried to avoid formal teaching, concentrating on tutorials instead. When I was forced to do so for a period of two to three years at the very beginning of my career, I chose to teach topographical anatomy, something despised by most except by young aspiring surgeons. I did so because topographical anatomy does not change from year to year and therefore does not require updating. With neuroesthetics, it was different—updating annually became a pleasure, a pleasure much enhanced by the enthusiasm with which students embraced the course. My task was made that much more enjoyable through the help and insight that I received from my teaching assistant, Taylor Enoch.

The Summing Up

I gave of my best, such as it is, to my chosen subjects; I pursued my career at UCL for almost 65 happy years, ending it just one month short of my 85th birthday; when I stepped down, I was perhaps UCL's longest serving and, chronologically speaking, most senior professor. I served under nine provosts, several heads of departments, and many deans. Throughout, UCL never brought any pressure on me to retire, quite the contrary; I salute my institution for that. I did not retire because of infirmity or ill health, nor because of waning enthusiasm. I did so because I had almost imperceptibly entered a different world, quite remote from the brilliant one I had experienced when I first entered UCL 65 years ago. It is a world to which I am increasingly ill adapted; a world in which educational institutions are gradually losing their purpose of seeking knowledge and are becoming corporations instead. I do not blame any individuals or institutions for this. It is just that times have changed, and I have not changed along with it or perhaps not changed to nearly the same extent. As well, lacking the virtuosity of an Andrew Huxley, I am also ill-suited to learn the increasingly complex and rapidly changing technology necessary to handle experiments; should the need arise, I would require the assistance

of multitudes, which I dread. My only solution is to create a brave new world of my own, one that will nourish what I have lived for professionally, the seeking of knowledge through new ideas. Together with a few colleagues, I have addressed this void; we have created our own informal academy that meets regularly to exchange ideas. Ironically, this is made possible by what has also made me withdraw from experiments—a sophisticated technology that enables us to talk across countries and continents.

Exiguum Reliqui, Sed Satis Mihi Fuit[1]

During this long career, I have contributed a little, but not much, to understanding how the visual brain operates and a little but even less to understanding beauty and love. That little was made possible only by what those who had preceded me had bequeathed before I played my part. In words reminiscent of Evelyn Waugh's *Brideshead Revisited*, I see myself as having built a new and imperfect house from the stones of the old castle. I learned much from the builders who came before me; I also learned, though in lesser measure, from the darker intent of adversaries. The little that I have achieved would not have been possible without both.

I do not pretend that the stones of my new house will not be used to build another, better one. I hope that they will. I do not treat any of my hypotheses as dogmatic. As Ramón y Cajal, one of our greatest, said when addressing the issue of consciousness in his *Histologie du système nerveux de l'homme et des vertébrés*: "We do not wish to give our hypotheses a dogmatic character. We know too well that a hypothesis can be reversed, from one day to the next, by unforeseen facts. The best we can hope for is that there should remain from our hypothesis something of the facts on which it is based."

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[1]I left little, but it was good enough for me.

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