

Giovanni Berlucchi



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BORN:

Pavia, Italy
May 25, 1935

EDUCATION:

Liceo Classico Statale Ugo Foscolo, Pavia, Maturità (1953)
Medical School, University of Pavia, MD (1959)
California Institute of Technology, Postdoctoral Fellowship (1964–1965)

APPOINTMENTS:

University of Pennsylvania (1968)
University of Siena (1974)
University of Pisa (1976)
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HONORS AND AWARDS:

Accademia Europaea (1990)
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Honorary PhD in Psychology, University of Pavia (2007)

After working initially on the neurophysiology of the sleep-wake cycle, Giovanni Berlucchi did pioneering electrophysiological investigations on the corpus callosum and its functional contribution to the interhemispheric transfer of visual information and to the representation of the visual field in the cerebral cortex and the superior colliculus. He was among the first to use reaction times for analyzing hemispheric specializations and interactions in intact and split brain humans. His latest research interests include visual spatial attention and the representation of the body in the brain.

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Family and Early Years

A man's deepest roots are where he has spent the enchanted days of his childhood, usually where he was born. My deepest roots lie in the ancient Lombard city of Pavia, where I was born 78 years ago, on May 25, 1935, and in that part of the province of Pavia that lies to the south of the Po River and is called the Oltrepò Pavese. The hilly part of the Oltrepò is covered with beautiful vineyards that according to archaeological and historical evidence have been used to produce good wines for millennia. My mother was born into a family that had a place of distinction in the history of Oltrepò wine-making. At the beginning of the last century, Luigi Montemartini, a member of the socialist party, a professor of botany at the University of Pavia, and an uncle of my maternal grandmother Serafina, founded an important *cantina sociale*, a wine cooperative of small landowners of the region. At vintage time, they took their grapes to the cantina, which had the enological expertise, the machinery, and the great barrels necessary for producing large quantities of good quality wine. Luigi Baraldi was the enologist who ran the cantina by organizing and surveying all the winemaking operations and then by distributing the product to wine shops in various northern Italian cities. He was also my grandfather; he had married Serafina Montemartini, and one of their four children (Elsa) was my mother.

I love the Oltrepò for several reasons, two of which are foremost in my mind. First, my enchanted childhood days were spent mostly with my maternal grandparents, in the villages of Montù Beccaria and Montescano (two of the sites of the cantina), from the late 1930s until 1948, the year of my grandfather's death. I enjoyed the country life enormously—the workings of the vintage and the many friends with whom I could practice our common passion of playing soccer. My grandparents were affectionate, down-to-earth people who enjoyed having children around and making them feel happy and loved. My grandmother Serafina was practically a second mother to me. My other very important reason for loving the Oltrepò is that 53 years ago, I made the smartest and luckiest decision of my life by marrying 19-year-old Maria Luigia (Luisa) Botta from Broni, one of the five towns of the region. As I once truthfully stated on an important public occasion, from our first day together, Luisa has enriched my life immensely by running it with the sweetest and wisest of iron fists.

My father, Carlo Berlucchi, was from Lodi, another Lombard city 30 km east of Pavia. His father, Giovanni, after whom I was named, was an engineer

who worked for one of the ceramics factories for which Lodi is known. I did not get to know my grandfather Giovanni because he died of pneumonia in 1922 during the great influenza epidemic. My father was an only child and his mother, Emma Madini, ruled his life with the typical attitude of the *reggiora* (lady boss), the central figure of the Lombard matriarchy. She had absolute control over the family money and had convinced my father to study medicine rather than philosophy, which he preferred, because she was positive that philosophers always ended up being impecunious. She lived by herself in her house in Lodi until her death at 93. Her beloved companion was a huge Brazilian parrot that she occasionally left free to roam the house or even the street, where its loud vocalizations often demanded the intervention of the city police or even the firemen. At times, Grandmother Emma could be capricious and overbearing, but she had a great sense of humor and self-irony and liked to play with me and tell me funny stories.

My father had started as a medical student in Pavia, where he had been taught histology and pathology by the famous Camillo Golgi. After interrupting his studies for service in World War I, he graduated in 1922 with a degree in medicine from the University of Parma, which then offered remedial courses for veterans. Before and after graduating, my father worked in Parma with Antonio Pensa—a pupil of Golgi's who was then professor of anatomy—and with the neurologist Luigi Roncoroni—who had been an assistant to the infamous criminologist Cesare Lombroso in Turin. In 1925, my father went back to Pavia to work as an assistant to Ottorino Rossi, another student of Golgi's who was then chairman of neurology and rector of the university. My mother lived in front of the hotel where the young neurologists took their meals. After a chance meeting on the street, my father fell in love with her at first sight and married her in 1930. Their marriage was a very happy one—blessed by the births of my sister Elena in 1931, myself in 1935, and my sister Maria Luisa in 1940—until my mother developed a severe cardiac valve disease that destroyed her life. She suffered from several embolisms, the last one of which left her in what is now called a vegetative state for over a month; she died at age 50 in 1956. If she had been born 20 years later, the now standard surgical procedure for valve substitution would have allowed her to live a full life, showering her unlimited capacity for love on her husband, children, and grandchildren. It was a tragedy for the whole family, but my father was literally shattered by the loss. Yet eventually he was able to recover by dedicating himself fully to the rest of his family and to his work. He retired at age 70 from the University of Pavia to live until he was almost 95 in a book-filled house in Brunate, a small village on a hill above the city of Como, overlooking the lake. Brunate's claim for a place in history is justified by a local lady who wet-nursed the infant Alessandro Volta. She was married to an expert builder of anemometers, and an earlier version of a commemorative inscription on a wall adjacent to the village's church hinted at an improbable connection between Brunate's

air, the nurse's milk, the husband's technical skills, and the invention of the electric pile. My wife, Luisa, our children (Filippo and Silvia), and I treasure the memories of the summer days spent in Brunate with my father, my sister Elena, her husband, Alberto Masciocchi, and their children, Laura and Alessandro. My father was such a good and loving grandfather that nowadays not only his grandchildren but also Luisa and I refer to him as *Nonno* (Grandpa) Carlo. I am deeply and permanently grateful to him for the constant support he gave to me and to my family and for providing such a good model of intellectual and moral values.

As a young man, my father's research work with Pensa, Roncoroni, and Rossi had been mainly in neurohistology and neurohistopathology. He would have been proud and delighted to see some of the color drawings from his old papers recently reproduced in *Cajal's Butterflies of the Soul* (De Felipe, 2010), a book extolling the almost artistic virtues of those who had illustrated the microscopic structure of the nervous system without the benefit of microphotography. Later, he devoted himself to problems of clinical neurology and psychopathology. Between 1936 and 1941, we lived in Parma and then in Padua, where my father was head of neurology. In 1941, he was called back to Pavia by Pensa, who had returned to his alma mater as professor of anatomy and dean of the medical school. As the director of the neurology clinic, my father had the right to live with his family in an apartment on the clinic's upper floor. During the air raids of World War II, the whole family went to an underground shelter along with the clinic's inpatients, including those from the psychiatric wards. I remember that sometimes I had to play ball with a very large woman in her fifties who believed she was a three-year-old girl. In the final years of the war, air raids took place almost every night—bombing the bridges on the Po and Ticino Rivers in or near Pavia. On many mornings, it was tough for children like me to have to go to school after a sleepless night in the shelter. One night I sneaked off to my bed instead of going to the shelter. After the end of the air raid, my mother—terrified by my unnoticed disappearance—gave me a well-deserved beating.

Education

I was educated in the public schools of Pavia, where I had some excellent teachers in grammar school and then in junior and senior high school. My senior high school was the *liceo classico* (humanistic high school) named for the bombastic poet Ugo Foscolo, who had briefly taught at the University of Pavia. The Liceo Foscolo was and is a rather haughty institution where, in accordance with the now almost centenarian public schooling reform of the philosopher Giovanni Gentile, the teaching of the humanities (including Latin and ancient Greek) must take a decided precedence over that of the sciences. For me, a strongly positive feature of the liceo was that it truly made everyone understand that learning requires dedication, time, and effort. In my liceo,

effortless learning did not exist. Nor did it exist in the medical school of the University of Pavia, where I enrolled in 1953 and graduated with honors in 1959, after six years of honest toil. In my high school and university days, as a relief from studying, my contemporaries and I enjoyed punting and rowing Venetian style in the slender, elegant, flat-bottomed Pavian boats (*barcé*) in the blue waters of the Ticino River. In that pre-air-conditioning era, swimming in those clean and fresh waters was the most effective respite against the sultry summers of the Po Valley. A respite, alas, that is no longer available because the most beautiful Italian river has been polluted beyond repair.

Pavia has always been proud of its university, founded in 1361, and its 16th-century Ghislieri and Borromeo university colleges. The university had enjoyed a splendid period as one of the greatest centers of learning in the late 18th century and the beginning of the 19th century. Just to mention a few names, Pavia could then boast among its professors the great anatomist Antonio Scarpa, the founder of experimental biology, Lazzaro Spallanzani, and the inventor of the electric pile, Alessandro Volta. After a period of decadence, the international prestige of the University of Pavia had been at least in part restored by the achievements of Camillo Golgi and his collaborators in the late 19th century—especially by the Nobel Prize in Physiology or Medicine awarded to him in 1906. (In that period of decadence, most of the descendants of Golgi and their colleagues were sadly aware that they could never attain the greatness of their teacher.)

About 10 years before I enrolled in the medical school, Emilio Veratti, Golgi's pupil and successor to the pathology chair, had publicly expressed his ruthless self-evaluation of his career during his last lecture before retirement. He surprised the students by recounting the parable of the czarina who had lost a precious ring during a grand ball at the czar's court. The czar had then divided the huge ballroom into a number of sectors equal to the number of gentlemen in attendance, and each gentleman had searched for the ring in the sector assigned to him. Obviously, only one gentleman eventually found the ring, but the czar rightly rewarded all participants because the success of the search was due to the lucky searcher as well as to those who had excluded the presence of the ring in their respective sectors. With this parable, Veratti wanted to convey the moral message that serious science is rewarding by itself even in the absence of major discoveries; but most probably he also felt that finding the metaphorical ring would have been a fairer reward for his competent and conscientious life in research. Ironically, he had found a ring without knowing it, when he had been the first to describe in a masterly way the internal structure of muscle fibers now known as sarcoplasmic reticulum. When, many years later, scientific authorities of the field such as H. Stanley Bennett, Andrew Huxley, and Keith Porter publicly credited him with the discovery, the octogenarian Veratti reacted with his usual modesty and understatement, along with some reservations about the soundness of the judgment of his newly found admirers (Berlucchi, 2002).

During my medical studies, I had a half-baked idea of becoming a clinical neurologist like my father, who encouraged me to start as a student by getting a good training in neurohistology. So I worked as an *allievo interno* (undergraduate research student) in the Institute of Anatomy headed by Gennaro Palumbi (the successor of the same Antonio Pensa, who in Parma had taught my father, and, as we shall see, the famous neurophysiologist Giuseppe Moruzzi). Pensa had retired years before, but he was still around as the nominal director of a National Research Council center for the study of the nervous system. Although he was well over 80, Pensa still took part in teaching and actually gave me the histology exam and part of the anatomy exam. The scientific atmosphere of the institute was not particularly stimulating, except for the presence of Elio Raviola, an exceptionally bright and enterprising student three years older than myself and now a lifelong friend. He was personally responsible for bringing electron microscopy to Pavia. Unfortunately, the conservative members of the faculty assigned him (correctly but without any vision) to the “dangerous” category of those who tend to rock the boat, and, as a result, he ended up becoming a professor not in Pavia but at Harvard University.

My MD thesis project was to describe the nuclear organization and the connections of the amygdaloid complex in guinea pigs, which I studied with the standard histological methods for the nervous system, including Golgi's black reaction. In those days, the amygdala was still thought to be mainly an olfactory structure, but I tried to distinguish the cortical nucleus, which receives direct projections from the olfactory tract, from other deeper nuclei with connections hinting at non-olfactory functions. The Anatomy Institute had a good library, including the entire collection of the *Journal of Comparative Neurology*, where I learned most of my comparative neuroanatomy and the English lexicon of neuroscience. About a year before graduating, I began to think about my future. I was still planning to become a clinical neurologist, and although in those days it was common for aspiring clinicians to do postgraduate research in basic science, I did not want to stay in anatomy. An alternative choice was neurophysiology. The research of the Institute of Physiology in Pavia was of high quality, but the only neurophysiology studied there (by excellent investigators such as Cesare Casella and Virgilio Perri) was restricted to the peripheral nervous system. Because I was interested in the so-called higher nervous functions, Pensa suggested that after graduating I should go to work in Pisa with Giuseppe Moruzzi. Moruzzi was a towering figure in neurophysiology—not only in Italy but in the entire world—because of his discovery with Magoun of the arousal system in the brainstem reticular formation (Moruzzi and Magoun, 1949). Pensa knew Moruzzi well; when he was in Parma, he had trained the young Moruzzi in neurohistology and had helped him publish his first scientific paper (an analysis of Golgi's neural network in the granular layer of the cerebellum) when he was only 20.

In the spring of 1958, armed with Pensa's letter of introduction, I approached Moruzzi with much trepidation at a meeting on sleep in Milan. In a calm, matter-of-fact manner he said that after graduating I could work in Pisa in his institute for a couple of years, during which time he and I could decide if I was fit for scientific research because, he explained, not everybody is. In the affirmative case, I could continue working in neurophysiology for another three years, one of which should be spent in a laboratory abroad. When I said that I wanted to become a clinical neurologist, he said that I was young, that I had plenty of time to learn to work with patients, and that five years in basic neurophysiological research could only do me good. Indeed, some of his pupils had become successful clinicians after several years in physiology.

Moruzzi and Pisa

Moruzzi was the first physiologist in Italy to fully devote his research to the nervous system although, for teaching purposes, he kept in touch with developments in all fields of physiology. He was a scientific descendant of the two British fathers of neurophysiology, Charles Sherrington and Edgar Adrian, who had shared the 1932 Nobel Prize in Physiology or Medicine for their studies of neurons (Berlucchi, 2008). Moruzzi's link to Sherrington was through Mario Camis, the professor of physiology in Parma whom he had joined after Pensa had left for Pavia. Camis had spent a few years in England working with Langley and Barcroft in Cambridge, and then with Sherrington in Liverpool, where he had discovered the phenomenon of occlusion in spinal motor centers. Camis had taught Moruzzi the techniques that had been the staple of Sherrington's neurophysiology—above all myography—and had also made him accept the Sherringtonian basic concept of the nervous system as an organized aggregate of specialized and selectively interconnected neurons. The link between Adrian and Moruzzi was a direct one. After working in the laboratory of Frédéric Bremer (another pupil of Sherrington) in Brussels, in 1939 Moruzzi had joined Adrian in Cambridge in an experiment providing the first demonstration that the spontaneous activity of single motor cortex neurons could be recorded from their axons in the bulbar pyramidal tract. Their findings implied that the frequency code discovered by Adrian for neuronal communication in peripheral sensory and motor neurons also applied to the highest level of the brain and that, at least in principle, the electroencephalogram (EEG) waves could be correlated with single neuron activities.

After World War II, Moruzzi's best-known work had been the discovery of the arousing EEG effects of the electrical stimulation of the brainstem reticular formation; he had undertaken this work with Horace Magoun at Chicago's Northwestern University in 1949. Upon his return to Italy, Moruzzi had founded the most successful Italian neurophysiological school at the University of Pisa, where he had created the material and intellectual

conditions for high-quality research and had made further pioneering studies on the physiology of the sleep-wake cycle. Moruzzi had an almost religious concept of scientific research and shared Primo Levi's belief that loving one's work is the best approximation to long-lasting happiness in one's life. On first acquaintance, his shy and rather withdrawn personality might make him seem cold, aloof, and awe inspiring, but everybody who knew him well can attest that he was a warm, caring, generous, altruistic, and altogether noble human being. My debt to him for my personal and scientific formation is so great that I cannot find the words appropriate to describe it.

After graduating in December 1959, I left Pavia at the beginning of 1960 to work in the Institute of Physiology at the University of Pisa, an imposing building located on Via San Zeno in front of a large garden bounded by the medieval walls. I did not know then that Pisa would become my home for more than 20 years, and that I would never return to live permanently in my native town. Pisa is similar in size and structure to Pavia, and like Pavia has some beautiful Romanesque churches—though their style is more ornate than that of the austere Lombard basilicas. As in Pavia, the academic institutions, including the university—in which the great Pisan Galileo had been a lazy student and a mediocre professor—and the Scuola Normale Superiore founded by Napoleon, are among the city's main cultural and economic resources. I lived for a few months alone in a small hotel near the train station, commuting by train between Pavia and Pisa on weekends in order to be with my fiancé in Broni. Following our wedding in July, Luisa and I set up our home in an apartment not far from the splendid Piazza dei Miracoli and the Leaning Tower. That we were not Pisan was easily revealed by our accents and by our restricted lexicon compared to the torrential verbal fluency of the Tuscans, but we were quickly integrated as bona fide citizens. We spent the happiest years of our lives in Pisa. Our two children were born there, Filippo in 1961 and Silvia in 1966. Bravely combining the chores of housewife and mother with those of a diligent student, Luisa was able to graduate with honors in biology at the University of Pisa and then teach science at junior high schools in or near the city. My research life at the institute, under Moruzzi's enlightened guidance and in the company of brilliant and friendly contemporaries, could not have been more satisfying. In the summer, the Mediterranean Sea and the beach at Tirrenia, a few kilometers away, were paradise. And above all, we were young and expecting to be masters of our lives.

Research Beginnings

At the institute, after learning some basic experimental procedures, I was assigned to do a project with Piergiorgio Strata, who had just graduated with honors in medicine after working as a student at the institute for six years. Other Italians of my age working in the institute at that time included Emilio Bizzi, Lamberto Maffei, Pier Lorenzo Marchiafava, Andrea Cavaggioni, and

a very young Luigi Cervetto, all of whom would become neuroscientists of international reputation. Moruzzi told me that Strata was brilliant and that we would get along well. He was truthful on the first count and foreseeing on the second. I quickly found out that Strata was sharp witted, superbly educated, exquisitely fit for scientific research, and that his verbal speed was astounding. He is from Liguria, the region around Genoa, the inhabitants of which are nationally known for their legendary reluctance to part with their money, called parsimony by Ligurians and stinginess by all others. Although on occasions I still cannot resist the temptation to tease Piergiorgio about the subject, more than 50 years of close friendship allow me to swear that if he is parsimonious, he is also one of the most generous persons I know.

The research task that Moruzzi assigned to Piergiorgio and me was inspired by an old study of Moruzzi himself and by a recent finding of Arnaldo Arduini, Moruzzi's first student who had followed him from Parma to Pisa to become his historical right arm. In pigeons, Moruzzi had found that each optic lobe contains upper motor neurons for opening the eyelids of the contralateral eye, and he had argued that pigeons can go to sleep with only one eye closed, if the corresponding optic lobe is deprived of facilitatory influences. Some of these influences were known to arise from light stimulation of the retina so that the eyelids of a blinded eye were expected to droop prior to those of the other eye at the beginning of sleep (Moruzzi, 1947). Arduini's recent work had shown that the spontaneous activity of retinal ganglion cells in the dark had an activating effect on the EEG of the cat (Arduini and Hirao, 1959). Strata and I were to investigate whether the retinal dark discharge had a similar arousing influence in birds. If we could detect an earlier drooping of the eyelids in a blinded eye of birds at the onset of sleep in complete darkness, the effect could be attributed to the absence of a retinal dark discharge, thus providing a behavioral confirmation of Arduini's EEG findings in cats.

We faced two experimental problems—how to inactivate the retina without producing other damage to the eye and how to observe sleep behavior in the absence of visible light. We chose to work on common owls because of their big eyes and because Piergiorgio had gained some experience in handling them during the preparation of his MD thesis. In the beginning, we planned to inactivate the retina by increasing the intraocular pressure so as to stop the retinal blood flow, but we found that the procedure was successful only if the high intraocular pressure was maintained for several hours. Then Piergiorgio, having seen during his medical studies that ophthalmologists used a photocoagulator for treating retinal detachments, had the idea that we could de-efferent the retina by photocoagulating the head of the optic nerve at the optic papilla. After securing the help of a young collaborative ophthalmologist, Giuseppe Salvi, and the permission from his boss to use the photocoagulator, we had to overcome the obstacles of our ignorance of the avian eye.

It took us some time to find out that, in order to dilate the pupil, you have to use curare rather than atropine because the pupillary constrictor of birds is a striated muscle and that the optic papilla is covered by a vascular structure, the pecten, which protrudes in the posterior chamber of the eye. But eventually Salvi was able to burn pecten and papilla through a curare-dilated pupil, leaving the eye otherwise intact. In a room sealed from light we restrained the owl in a position that would allow it to go to sleep without moving the head, and we “watched” it in the dark with an infrared sniperscope used by American soldiers during World War II for shooting at night. Our instrument was a war surplus that Leopoldo Nicotra, the ever-ingenuous head technician of the institute, had bought for us (almost certainly illegally) in the Leghorn flea market. By itself the infrared source of the sniperscope, made visible at the eyepiece by a wavelength multiplier, was completely invisible to our human eyes and most probably also to the only seeing eye of the owl. However, to comply with Moruzzi’s somewhat excessive requirements for complete experimental control, now and then we turned off the sniperscope and took random pictures with flashes too short to cause any physiological reaction within their duration. Thus we observed in several animals the expected palpebral asymmetry and documented it with impressive shots of “winking owls.” Of course, the asymmetry did not depend on an active eye closure such as a wink but rather, as we demonstrated by comparison with an actual blink, on a passive lid drooping in the blinded eye. Moruzzi was happy with our results and published the paper we wrote (Berlucchi and Strata, 1962) in *Archives Italiennes de Biologie*, the journal that had been founded in 1882 by the Italian physiologist Mosso and had been restarted by Moruzzi in 1956 after its suspension in 1937. Contrary to his modern stance and vision in most things scientific, Moruzzi was somewhat old-fashioned in relation to the reviewing process for *Archives*. If he felt competent to evaluate a submission, he did not send it out to independent reviewers, even when, as in the case of our owl paper, he could be suspected of being biased because he had inspired and closely followed our study. Because most of the institute’s studies were inspired and followed by Moruzzi, they were usually published in *Archives* without a regular reviewing process. Regardless, the journal was doing well because—as the most important publication specializing in sleep physiology—it received papers on the subject from important laboratories in Italy and abroad. When we became more experienced, Piergiorgio and I tried to convince Moruzzi that we should be allowed to publish in other international journals to receive independent evaluations of our work. He was not pleased but agreed, with the proviso that we should continue to publish some papers in *Archives*.

Sleep Studies

During the first 10 years of my research activity, I worked mostly on the physiology of the sleep-wake cycle within the Moruzzi tradition. In 1961,

Moruzzi's right arm (Arduini) was preparing to leave Pisa to assume the physiology chair at the University of Ferrara. Before Arduini left, Strata and I collaborated with him in a study on the degree of spontaneous pyramidal tract activity in free-moving cats during the full sleep-wake cycle (Arduini, Berlucchi, and Strata, 1963). Arduini was a first-class neurophysiologist with many experimental and surgical skills. In the 1950s, he had discovered the hippocampal theta rhythm during arousal with John Green at the University of California in Los Angeles. He was a knowledgeable, level-headed, and generous teacher from whom we learned the technique for chronic electrode implantation and for recording the electroencephalogram, the neck electromyogram, and the electrooculogram to distinguish the different stages of sleep. We recorded the overall pyramidal tract activity with macroelectrodes in the mesencephalon or the medulla as an index of a main cortical output during waking, slow-wave sleep, and fast or paradoxical sleep. The electrode placement was checked at the end of the experiments by Arduini's wife, Maria Grazia, an accomplished histologist. The main result was that tonic pyramidal activity decreased, as expected, from waking to slow-wave sleep, but in paradoxical sleep was as high as, or higher than, during waking. This was one of the first experimental pieces of evidence for vigorous and sustained activity of the motor cortex in paradoxical sleep, in spite of general muscle relaxation.

Moruzzi's interest in the phenomenology of sleep prompted a study in which Strata and I collaborated with him and with Giuseppe Salvi, the ophthalmologist who helped us with the retinal photocoagulator. We studied (by direct observation and filming) the movements of the eyes and the changes in the pupil diameter during natural sleep in cats. Piergiorgio brilliantly devised a contact lens with an attached cylinder that kept the eyelids apart without discomfort for the cat, so that we could film the pupil from a close distance in various physiological states. In some cases, the influence of visible light on the pupil was excluded by watching through the infrared sniperscope in the dark or after blinding the eye by photocoagulating the optic papilla. Deserting our puzzled wives, Piergiorgio and I filmed throughout the night, when the absence of the institute's diurnal din did not disturb the cats' sleep. We found that the pupil constricted in proportion to the depth of sleep but, during paradoxical sleep, the extremely constricted pupil underwent brief temporary dilations in concert with the bursts of rapid eye movements (Berlucchi, Moruzzi, Salvi, and Strata, 1964). The eye movements in paradoxical sleep, much faster than those observed in humans, were brisk, repetitive, conjugated, and ballistic, making it very unlikely that they served to scan the visual scene of a cat dream. Because pupil dilations during rapid eye movements also occurred after sympathetic denervation of the eye, we attributed them to transient inhibitions of the pupil's parasympathetic innervation.

The film we eventually put together was really good, and when Piergiorgio showed it at a meeting on the physiology of sleep organized by

Michel Jouvet in Lyon in September 1963 (Berlucchi and Strata, 1965), the international audience of sleep specialists was impressed. Moruzzi's classic distinction between tonic and phasic phenomena of paradoxical sleep, as presented in his Harvey Lecture (Moruzzi, 1963), was partly based on those observations of phasic pupillary dilations on a background of tonic pupilloconstriction. We lent copies of the film to many colleagues, but unfortunately, neither I nor Piergiorgio had the good sense to preserve the original or at least a copy. To my knowledge, a few frames of the entire film used in a video by Allan Hobson are the only survivors in circulation.

In another study, Strata, Lamberto Maffei, and I collaborated with Moruzzi to support his hypothesis of a functional antagonism between the activating mesencephalic and pontine reticular formation and the sleep-inducing structures of the caudal brainstem (Berlucchi, Maffei, Moruzzi, and Strata, 1964). By cooling the floor of the fourth ventricle, we showed that reversible inactivation could produce sleep or arousal in *encephale isolé* cats depending on which brainstem systems were inactivated. Sleeping *encephale isolé* cats were aroused by cooling the medullary floor of the fourth ventricle, and *encephale* cats that were awake were put to sleep by cooling the rostral floor of the fourth ventricle. Although the effects were dramatic, we have always had mixed feelings about this study because it was possible that the medullary cooling stimulated ascending pain pathways, rather than or in addition to inactivating sleep-inducing neurons. Certainly the experiment would not be permissible by today's ethical standards.

After the completion of these studies, Moruzzi suggested that Strata and I stop working together in order to prove our respective independent research abilities to the scientific community. We were sorry to give up a collaboration that had proven so congenial and fruitful, but we complied with Moruzzi's advice because we understood that it was offered for our own good. So we went our separate ways, though of course we kept in close contact and continued to exchange information, suggestions, and ideas, as we do by phone or e-mail almost daily today, half a century later.

The next line of research that I pursued had to do with the control of the peripheral auditory input during the sleep-wake cycle of cats. In 1963–64, I collaborated with Moruzzi and Walter Baust, a hard-working and competent German physiologist from the Heidelberg school of Hans Schaefer, one of the discoverers of the muscle end plate potential. In addition to protecting the cochlea from loud sounds, the contraction of the two middle ear muscles—the tensor tympani and the stapedius—can also occur in other physiological conditions. Moruzzi wanted to find out whether the middle ear muscles are specifically used to dampen the auditory input for protecting sleep from disturbing sounds, similar to the way visual inputs are excluded during sleep by closure of the eyelids and pupil constriction. We were to record the auditory input at the cochlea in free-moving cats during waking and the various stages of sleep. One major experimental problem was the

variability of the stimulation that occurs because of the changes in the position of the animal's head within the free field of a sound source with a fixed position in space. We wanted an acoustic stimulus of unvarying intensity throughout the entire sleep-wake cycle of a freely moving cat, and this was provided by an earphone fastened to the cat's head so that the distance from it and the tympanic membrane was the same regardless of any movement on the part of the cat. The plan was to record the cochlea's electrophysiological responses to clicks of fixed intensity before and after removing the action of the middle ear muscles. It was then that I made my acquaintance with the wonderful Zeiss binocular surgical microscope, which (after a considerable amount of time and effort on our part and the sacrifice of an equally considerable number of cats from the institute's stabulary) allowed us to record microphonic and neural responses to clicks at the round window of the cochlea, as well as to cut the tendons of the two tiny middle ear muscles or to stick recording electrodes into the muscles themselves.

Eventually, we were able to show that the amplitude of microphonic and neural responses to clicks of the cochlea were reduced during the stage of sleep with rapid eye movements—particularly in association with the latter movements, but that these reductions disappeared after tenotomizing the middle ear muscles. Accordingly, electromyographic recordings showed that the middle ear muscles contracted synchronously in many physiological conditions, including sleep with rapid eye movements, and their contractions corresponded with and actually caused the reduction in the cochlear response amplitude during paradoxical sleep. Our electroacoustic and electromyographical recordings were really beautiful, and sometime after we published our results (Baust, Berlucchi, and Moruzzi, 1964), we were gratified to read a report from a very important sleep laboratory at Stanford University that described results very similar to ours and that acknowledged the priority of our publication (Dewson, Dement, and Simmons, 1965). Bill Dement, one of the discoverers of paradoxical sleep and an author of the Stanford paper, told Moruzzi, not so light-heartedly, that we had “scooped” them. Because histology was not necessary for our studies, and as a partial compensation for all the cats we had killed while learning to approach the middle ear muscles, I removed the electrodes from a cat that over several days had regaled us with beautiful records, sewed up the skin, and gave her to my mother-in-law, who kept her as a pet for years.

I briefly returned to the auditory system in sleep right after a stay at Caltech (which will be discussed later in this chapter). Giacomo Rizzolatti—another friend who was to become a permanent fixture and influence in my life—John Munson—a student of Bob Doty with superb experimental training in chronic electrophysiological recordings—and I confirmed the role of the middle ear muscles in the control of the auditory input in sleep and studied the central modulation of the transfer of auditory information to the cortex and the cerebellum (Berlucchi, Munson, and Rizzolatti, 1967).

Three studies I did by myself during my time at Caltech also belong in this section because in them I tried to combine my experience with the sleep-wake cycle in the cat with the split-brain studies that Sperry and Myers had started at the University of Chicago and continued at Caltech (Sperry, 1961). I showed that section of the corpus callosum disrupts the fine bilateral symmetry in the EEG but not the synchronous appearance of signs of sleep or arousal in the two hemispheres (Berlucchi, 1966a); that the overall activity of the corpus callosum is low in sleep compared to waking, particularly in paradoxical sleep, except during the bursts of rapid ocular movements (Berlucchi, 1965); and that EEG signs of arousal and waking are still observable in a hemisphere isolated from the rest of the cerebrum (Berlucchi, 1966b). The latter study involved a really difficult surgery, in which I combined a deep midline split with a midbrain hemisection so that the hemisphere on the side of the hemisection was completely disconnected from the brainstem. I think that these were sound pieces of research but not particularly original. The role of the callosum in the bilateral coordination of the EEG had long ago been suggested by Bremer and collaborators, though only in acute preparations. The return of EEG and behavioral manifestations of arousal after destruction of the reticular formation, and its dependence on the hypothalamus, had been demonstrated by Adametz, Batsel, Chow, Villablanca, and others (see Berlucchi, 1970), though my preparation had the advantage of a direct comparison between the EEG of the isolated hemisphere with that of the hemisphere still connected with the brainstem. Finally, my callosal activity findings were very likely due to the fact that I was recording from callosal fibers belonging to large cortical neurons, which Evarts had shown to produce bursts interspersed with periods of complete inactivity during paradoxical sleep (Evarts, 1964). Interest in a reduction or modification of callosal activity during sleep, and particularly during paradoxical sleep, has been resurrected by studies of unihemispheric sleep in aquatic mammals (Mukhametov, 1984) and by recent evidence of a decrease in transcallosal activity in man during awakenings from paradoxical sleep (Bertini et al., 2004). In retrospect, the studies I did at Caltech were most useful to me from a technical point of view because after my previous experience with the middle ear I learned to use the surgical microscope for operating on the brain. It was at Caltech that, under the bright light of the microscope, I learned to expose brain structures such as the corpus callosum, the anterior commissure, the optic chiasm, and the superior colliculi, and to use that ability in many subsequent studies throughout many years.

My Farewell to Sleep Studies

My last experimental effort regarding sleep physiology was connected with a project that Moruzzi had agreed upon—a collaboration with Woodburn (Woody) Heron of McMaster University in Canada. Heron, a pupil of the

famous psychologist Donald Hebb and a world authority on the effects of sensory restriction and perceptual isolation, was to spend a sabbatical year in Pisa in 1967. At that time, Moruzzi was trying to obtain evidence for his belief that sleep was necessary for the functional recovery of synapses and circuits that had been used for learning during waking, a hypothesis that he had forcefully put forward at the famous 1964 Vatican conference (Moruzzi, 1965). He wanted to know whether the disconnected hemispheres of split-brain cats would develop different sleep-wake cycles if only one hemisphere was used for learning.

I was to split the optic chiasm and the forebrain commissures in cats that would be deprived of vision in one eye and in the corresponding hemisphere by an opaque contact lens, while the other eye and the corresponding hemisphere were used for various kinds of visual learning and experience. Moruzzi's expectation was that, at the beginning of sleep, EEG slow waves would appear in the exercised hemisphere sooner than in the deprived hemisphere. Heron's expectation was the opposite because he had found a slowing of the alpha rhythm in humans submitted to a restricted environmental stimulation. I kept a neutral position and worked hard to prepare the cats. The results were far from clear cut, but if there was a tendency it was in favor of Heron's expectation. Eventually no publication came out of all that work because Moruzzi noticed, and did not like, some occasional abnormal EEG waves that (not surprisingly) appear in split-brain cats after such a major brain manipulation.

That was a hard period for Moruzzi because of the political unrest that had begun in the Italian universities, with the attendant occupation of classrooms, libraries, and laboratories by students fascinated with the Chinese Cultural Revolution, which was then in full swing. Although it was true that many aspects of the university system were deeply unsatisfactory, the disruption of the institutions and structures of authority advocated by the Maoist revolutionary movements was hardly the solution to the problem. The dogma that all branches of human learning were directly or indirectly ideological in nature undermined the respect for and the trust in science, and even teaching physiology was accused of being influenced by bourgeois and capitalistic prejudices. Moruzzi saw the dangers of the situation, which would tragically degenerate into years of bloody terrorism, and was not afraid to appear at some of the students' riotous meetings to defend reason, scholarship, and freedom of learning. Usually, he was regarded with respect, if not with sympathy, by most.

For this and other reasons, he did not have much time to devote to our experimental project, which—in spite of Woody's brave attempts to do quantitative analyses on the EEGs that were acceptable to Moruzzi—eventually collapsed. For me, one compensation for this failure was that Woody and I struck up a very good friendship after surmounting the hurdle of his legendary shyness (he was known for having sneaked out of a classroom where he

was supposed to give a seminar because the audience was too big). I learned much from him about many subjects, from Hebbian psychology to American and Canadian politics. Eventually, he participated in the reaction time project that Umiltà, Rizzolatti, and I had started on interhemispheric transmission in humans, and his silent disapproval of my driving style did not keep us from having many interesting discussions while we rode on the *autostrada* to Bologna to perform the experiments. After going back to Canada, he kept in touch by writing amusing letters about the changes then affecting universities throughout the world, including the then fashionable habit of professors growing long sideburns. Woody died a few years ago, and his former student Doreen Kimura (of dichotic listening fame) wrote affectionately and humorously about him in an autobiographic sketch (Kimura, 2006).

My non-experimental adieu to the field of sleep-wake physiology was a chapter I wrote in English but that was translated into German by my former coworker Walter Baust. He included it in a book that he edited and published in 1970 (Baust, 1970). During my stay at Caltech, I had learned of Strumwasser's discovery of circadian activities of single neurons in the parieto-visceral ganglion of *Aplysia*. This led me to suggest that similar pacemaker neurons, endowed with a capability for autonomous activity, but open to exogenous synaptic control from sensory organs and other nervous centers, might engender sleep and waking in mammals. At that time, I was under the influence of Hebb's and Kleitman's views of sleep as an endogenous cerebral organization alternative to wakefulness and by Moruzzi's theoretical and experimental arguments in favor of an active production of sleep by brainstem mechanisms. My chapter was totally neglected in the neuroscientific literature, except for a citation by Moruzzi in his monumental review in *Ergebnisse der Physiologie* in 1972. Recently, in writing about Moruzzi's contributions to sleep physiology, my colleague Marina Bentivoglio and her collaborator Gigliola Grassi Zucconi (Bentivoglio and Zucconi, 2011) unearthed my review and concluded that I was the first to postulate the possible importance of pacemaker neurons for the genesis of sleep and waking. Although thankful for their generous evaluation of my old review, I remain skeptical that I was then proposing a particularly new theory; in a commentary at the end of their paper, I pointed out that Kleitman and Hebb had already suggested an endogenous generation of sleep.

Sperry and Caltech

Moruzzi was a strong believer in the idea that working for at least one year in a laboratory abroad was essential for the formation of a young scientist. Accordingly, in the summer of 1963, he started to arrange for Piergiorgio Strata and myself to work in the laboratories of two great scientists: Piergiorgio was to go to Australia to work with John Eccles and I was to go to California to work with Roger Sperry. Neither Eccles nor Sperry had as

yet won a Nobel Prize, but those who knew something about brain science had no doubt that sooner or later they would be called to Stockholm, as indeed they were. I knew Eccles personally because in 1961 he attended the meeting of the International Brain Research Organization that Moruzzi organized in Pisa. Many outstanding neuroscientists of the time, including Magoun, Granit, Brazier, Grey Walter, Anokhin, Bremer, Brookhart, Jung, Fessard, Buser, Naquet, and others were present at that conference, and Strata and I and other young members of the institute had to drive them from their hotels to the meeting venue. However I had never heard of Sperry, and Moruzzi directed me to his most important discoveries. These were summarized in a chapter in Stevens' *Handbook of Experimental Psychology* (Sperry, 1951) and an article in *Scientific American* on the formation of brain circuits (Sperry, 1958) plus a review of the effects of sectioning the corpus callosum in cats and macaques (Sperry, 1961). I thus learned, in 1963–64, that Sperry had demolished a pet theory of his two teachers Paul Weiss and Karl Lashley. This was the “blank slate” theory, according to which the developing nervous system starts out as an essentially random network to be shaped into a functionally adaptive structure by use, practice, and elimination of inappropriate connections. In ingenious and deceptively simple experiments, Sperry had instead shown that in replicating embryogenesis, central nerve regeneration in adult cold-blooded vertebrates rebuilds a preordained pattern of connections that persists even when forced by experimental manipulations to sustain completely maladaptive forms of behavior. Complementary experiments on the effects of peripheral nerve crossing in mammals had led him to conclude that the mammalian nervous system also possesses a high degree of inborn self-organization, prior to and independent of any environmental influence. In accord with Cajal's largely conjectural chemotropic hypothesis, Sperry's chemoaffinity hypothesis postulated, on the basis of indirect but convincing experimental evidence, that populations of nerve cells acquire and retain individual chemical identification tags, such that lasting functional synaptic connections are established only among neurons that are selectively matched by inherent chemical affinities.

The other, more recent line of Sperry's research, which would win him a Nobel Prize, had to do with the functions of the corpus callosum. Sperry had always been in disagreement with Lashley about the role of long intra- and inter-hemispheric connections, which Lashley regarded as mere “skeletal structures” because the evidence then available suggested that they could be cut without causing any major behavioral loss. Instead, Sperry and his collaborators, especially Ronald Myers, had shown by selective lesions and appropriate behavioral tests in cats and macaques that the corpus callosum, far from being a mere mechanical link between the two hemispheres, is the essential route for the exchange of sensory, motor, and higher-order information between the two cerebral hemispheres. But I was most impressed by Sperry's paper that was published in a book that I found in the rich library

of Moruzzi's Institute of Physiology. *Basic Readings in Neuropsychology*, edited by R. L. Isaacson (1964), included 16 articles culled from scientific journals. The final paper, entitled "Neurology and the Mind-Brain Problem" and written by Sperry had appeared in *American Scientist* (Sperry, 1952). Sperry was declaredly influenced by the essay "How to Make Our Ideas Clear" in which the pragmatist philosopher Charles Peirce had argued that "the whole function of thought is to produce habits of action" (Pierce, 1878). Sperry maintained that the core of the cerebral process underlying the perception of an object is neither isomorphic with that object nor in the form of a motor pattern. It is instead premotor or pre-premotor in nature, preparing and adjusting the motor system for selecting among a number of possible reactions to the object itself. This view has long anticipated modern theories according to which perceiving is equivalent to being set to act on the basis of actual or remembered environmental affordances. I still recommend this paper as a gem in the history of ideas about cerebral organization in cognition and behavioral control.

I was thrilled by the possibility of working in Sperry's lab. Moruzzi wrote to him, and he agreed to accept me as a postdoc provided I obtained an international fellowship from the U.S. Public Health Service. Such fellowships were granted by the National Institutes of Health (NIH) in Bethesda, Maryland, to provide "specially selected and qualified foreign scientists" with research and/or training opportunities in health research laboratories and institutions throughout the United States. On April 1, 1964, I was informed that I had been selected to receive one such fellowship (no April fool, fortunately), and in June, Lee Dubridge (then president of California Institute of Technology in Pasadena) notified me that I had been appointed research fellow in biology for one year, effective September 1, 1964. I knew that Caltech was an outstanding international scientific university, which had grown out of a small technical school mainly due to the efforts of the physicist George Millikan; only later did I read that, according to another of its presidents, Marvin Goldberger, there are no good appointments at Caltech—only superb ones (Goodstein, 1991). I doubt that I am equal to that statement, but certainly I can only define my stay at Caltech as a superb experience in my life.

My wife Luisa, our three-year old son, Filippo, and I were granted visas by the American consulate in Florence and, at the beginning of September 1964, we embarked on an Alitalia flight from Milan Malpensa to the recently renamed John F. Kennedy International Airport. It was our first flight, but in my natural predisposition to fret in anticipation of the challenge that waited for me in the United States, fear of flying was the last of my worries. After a couple of days as very provincial tourists in New York, we went on a tour of laboratories suggested by Moruzzi, which gave me the opportunity to give talks to select audiences (as well as causing me a lot of additional anxiety). In Baltimore, we stayed in the home of Janet and Moise Goldstein—who

had previously spent a year in Pisa, and at Johns Hopkins University, I met the legendary physiologist Vernon Mountcastle and my amusing countryman from Genoa Gian Franco Poggio. At NIH, I was a guest of Ed Evarts, in whose laboratory I met Emilio Bizzi, who had come from Pisa via Saint Louis, and a young Bob Wurtz, both of whom were on their way to splendid careers in neuroscience. At Harvard University, I visited the laboratory of David Hubel and Torsten Wiesel, who were already famous for their work on the visual cortex. They impressed me greatly not only for their science but also for their friendly, unassuming manners. Hubel was still interested in the physiology of sleep and was proud that Moruzzi had published his work on single visual cortical neurons during sleep in *Archives Italiennes de Biologie*. Because of my recent work on the auditory system, I also visited the laboratories of two great men in the field: Bob Galambos at Yale and Hallowell Davis at the Central Institute for the Deaf in St. Louis, both of whom were kind enough to listen to my account of the activity of middle ear muscles in sleep. We then flew from St. Louis to Los Angeles, and Sperry later met us at the Pasadena bus terminal and drove us to a motel near Caltech. He told Luisa that she could rely on the advice of an Italian member of the Caltech wives' circle, Inuccia Dulbecco, being careful not to mention her former husband, Renato (the future Nobel awardee), because he had just divorced her and moved to La Jolla with a new wife. Inuccia was indeed a great help for our settlement in Pasadena and our familiarization with the local opportunities and ways of living.

My stay at Caltech allowed me a continuous contact with a group of young gifted scientists working under Sperry, including, among others, Chuck Hamilton, Mike Gazzaniga, Emerson Hibbard, Evelyn Lee Teng, and Richard Mark. In addition to Sperry, Caltech's biology division boasted eminent professors such as Wiersma, van Harrevel, Delbrück, Owen, Sinsheimer, and others, all of whom participated in seminars and informal discussions during which there was always something important to learn. The neurosurgeon Joe Bogen, who had been instrumental in reviving the callosotomy treatment of epilepsy, frequently visited the lab and told me amusing and instructive stories about his hemispherectomized cats. My interactions with Sperry were infrequent but uniquely formative and illuminating. Although I could confirm his reputation for being at times withdrawn, taciturn, and even sullen and grouchy, I was also able to enjoy the moments during which he exhibited his great sense of humor and his propensity for a good laugh. He was always nice and helpful to me, though I was awed and somewhat inhibited by his obvious genius and dry Socratic attitude. I had met American university professors in Italy and had been impressed by their general easy-going, amicable manners. By comparison, Sperry looked to me more like an austere European professor, keeping some distance from his students. Many years later, I heard that when one of his former students—after becoming a full professor in another California

university—asked Sperry if as a colleague she could call him Roger, he replied: “Gee, I don’t know, I never called Doctor Lashley Karl.” But even at a distance, he was a superb teacher. He did not particularly like the electrophysiological approach to studying the brain, and he claimed (wrongly, as we now know) that learning does not involve the addition or subtraction of any actual fiber connection but only physiological (electrical) changes, probably at the synapses. I asked him to coauthor the three papers I completed at Caltech but he refused, possibly because he did not completely trust electrophysiology. Nevertheless, he discussed those papers with me in a profoundly illuminating way and corrected my drafts and greatly improved them. I had learned the importance of clear writing in science from Moruzzi, but I think it was from Sperry and the reading of his papers that I had a direct experience of the closest approximation to perfect scientific writing, along with the distinct feeling that I would never be that good.

In 1964, when I was at Caltech, Sperry had begun to claim that the most important task for the neurosciences is to try and understand the patterns of cerebral organization that underlie the human mind. At the famous Vatican conference of that year, he had caused some commotion in ecclesiastic circles by claiming that if you split the brain you also split the mind (Sperry, 1965). In the following years, he perfected his philosophical conception of an interactionist monism, whereby mind is considered an entity emerging from brain activity that reacts back on the brain without breaking the causal closure of the physical world. I may misrepresent his philosophy here because I must confess that I have never been able to understand it fully. In the late 1980s, *Sfera*, a beautifully illustrated cultural Italian magazine, asked me to solicit a story from Sperry about the brain and the mind. Sperry suggested that I prepare a draft by combining a description of the classical split-brain experiments with some tentative “consciousness” material that he had sent to me earlier. I prepared the draft in English and submitted it to him with the understanding that I would translate it into Italian after his approval. He approved the draft and added that he trusted that I would appear as joint author because “he could not see himself as authoring alone an article in Italian.” The article eventually appeared with our two names in *Sfera* magazine (Berlucchi and Sperry, 1990), the elegance of which was much admired by Sperry’s wife, Norma. The final sentence of the article argued that the rejection of the old “mind does not move matter” belief was the most important outcome of split-brain research. On many occasions over the years, I returned briefly to Caltech to talk with my old friend Chuck Hamilton and with other “Sperryists” who had joined the lab after I had left in 1965, especially with Eran and Dahlia Zaidel. If Sperry were around on those occasions, he always told me that as a neurophysiologist I should support his view of consciousness as a main ingredient of brain functioning. He died in 1994 and was commemorated shortly thereafter by many of his former students, friends, and colleagues at a Caltech meeting organized

by the psychologist Toni Puente, which I attended with Mitch Glickstein. When I was editor-in-chief of *Neuropsychologia*, I asked Chuck Hamilton to organize a memorial issue of the journal dedicated to Sperry. The issue appeared in October 1998 with a moving preface by Sperry's wife, Norma, who wrote: "Roger would have been delighted to see these papers of his former coworkers, surprised by the breadth and quality of their endeavors and in particular gratified that he had passed on a sense of excitement and pleasure in searching for answers to important questions" (Sperry, 1998).

Return to Pisa, Choice of a Career, and the Fortune of Excellent Collaborations

When we returned to Italy, everything looked quite small after our experience with the immensity of the California spaces, from the huge Los Angeles metropolitan area to the High Sierras, from the living Mojave Desert to the wasteland of Death Valley, from the wonderful Yosemite and Sequoia National Parks to the wide beaches of the Pacific Coast. There was one problem, however, that appeared far from small. Clinical neurology no longer attracted me because I wanted to continue to work full time in research. I talked to Moruzzi, and he said that he would be glad to help me pursue an academic career in physiology. I could continue to occupy the National Research Council position that I had before going to the United States until a post at the University of Pisa became available. The problem was thus promptly solved, and we resumed our life in Pisa, with the prospect of a welcome addition to the family. Luisa and I wanted a daughter after our son Filippo, and with her characteristic determination, she delivered Silvia on September 26, 1966.

For a number of years after our return to Pisa, I had the great fortune of collaborating with gifted scientists from Italy and abroad who were attracted to Pisa by the fame of Moruzzi's institute. I have already mentioned Woody Heron and, briefly, Giacomo Rizzolatti. Giacomo, a medical graduate of Padua, had gone to Pisa on the advice of his mentor Hrayr Terzian, a brilliant clinical neurologist who had spent a couple of years in Moruzzi's institute in the 1950s (more about him later). While I was in California, Giacomo had already worked with Maffei and Moruzzi in an important study on the modulation of visual input to the cortex during the sleep-wake cycle. During our study in collaboration with Munson, which I have mentioned before, I had had the opportunity to appreciate that Giacomo loved science and culture in general, was extremely well read, and was a keen observer of social and political events in Italy and the world. He had strong and often highly debatable opinions about many subjects and defended them with the same ferocious resolution that he put into his research work. The discovery of the mirror neurons, which has brought him international fame and many well-deserved accolades, is no doubt the best product of that resolution.

Like me, he was interested in the functions of the corpus callosum and wanted to test them electrophysiologically. The occasion for such a study presented itself in the fall of 1966 when Mike Gazzaniga came to Pisa with a postdoctoral fellowship from the U.S. Public Health Service. My deep friendship with Mike started at Caltech in 1964 and continues uninterrupted at this time of writing, in spite of some old disagreements over his responsibilities in his split (no pun intended) with Sperry. Recently, Mitch Glickstein, another great friend from Sperry's school with whom I share many interests, and I have contributed to the book, *The Cognitive Neuroscience of Mind*, a tribute to Mike edited by his former students and collaborators. As I wrote in that book, I do not laugh easily, but Mike can make me laugh at will at any time (Glickstein and Berlucchi, 2010). I am sorry that I remember only a few of the million jokes that he used to crack on our way to and from the Caltech cafeteria, where he ate enormous hamburgers at any hour of the day.

My collaboration with Mike and Giacomo focused on a direct electrophysiological identification of the visual information transmitted by the corpus callosum. The behavioral experiments of Myers, Sperry, and others on monocularly trained split-chiasm animals had shown that such transfer occurred through the back part of the corpus callosum. Theoretically, the callosum could either convey a basic visual input to the untrained hemisphere, allowing the parallel formation of memory traces in both hemispheres during learning, or it could convey higher-order visual information encoding a memory trace formed exclusively or predominantly in the trained hemisphere. By recording the responses of single callosal fibers to simple visual stimuli, we could at least learn whether the corpus callosum can transmit basic visual information. Indirect electrophysiological evidence to that effect had been recently published by Whitteridge and coworkers at Oxford University (Choudhury et al., 1965). Using cats as subjects, they had deprived one hemisphere of its direct visual input by cutting its optic tract and had found that it still contained visually responsive neurons in a cortical strip 1–2 mm wide between the primary and secondary visual cortical areas. The receptive fields of the responsive neurons were all in the vicinity of the vertical meridian of the visual field, and their responses were abolished reversibly by cooling the splenium of the corpus callosum, and permanently by cutting it.

Gazzaniga, Rizzolatti, and I decided to use the midpontine pretrigeminal preparation because it does not need pharmacological anesthesia and has an almost continuous “waking” cortical activity. Under microscopic control, we exposed the back part of the corpus callosum by separating the two hemispheres, and we inserted tungsten microelectrodes into it. Various single units that were so isolated responded briskly to static or moving lines presented in their elongated receptive fields, which—in agreement with Whitteridge and coworkers—were invariably located close to or on the

vertical meridian of the visual field. The response characteristics of these single units allowed us to assign them to the simple, complex, or hyper-complex classes recently described by Hubel and Wiesel. Thus there was no doubt that the callosum could provide basic visual information to either hemisphere, though from a restricted portion of the visual field.

Although our experimental effort proved successful in a relatively short time, it did not proceed without disturbances. As is usual in this kind of experiment, we monitored neural activity by ear, by transforming action potentials into acoustic clicks. One disturbance that we had to overcome was the tendency of our microelectrode recording system to pick up music broadcast by local radio stations. Mike was much amused by these nuisances. According to his (most probably embellished) account, on one particular occasion, the loudspeaker blared the Beatles' song "Yellow Submarine" instead of the rattling sound of action potentials. Giacomo's prompt and dry reaction was that this is what is transmitted by the corpus callosum. Be that as it may, we eventually were able to collect many beautiful recordings, in spite of other unexpected difficulties. In the fall of 1966, when we were in the middle of our research project, Florence, Pisa, and other Tuscan cities were badly flooded by the Arno River, which had been swollen by an unusually persistent rain fall. There was water at human height in the main streets, the electricity was cut off, and we had to interrupt our experiments and live for a few days in our houses without illumination and heating. Mike and his family had rented Strata's apartment (at that time, Strata was working in Australia with Eccles) and the flood certainly did not make their stay in Pisa a pleasant one. I was not surprised when Mike announced that he was going back to the United States because he had to immediately take up a position he had been offered at the University of Santa Barbara in California. Fortunately, we had collected sufficient material to make up a reasonable story, so that he was able to present our joint results at the meeting of the Federation of American Societies for Experimental Biology. The abstract that was published in federation proceedings in the spring of 1967 was almost destined to scoop the two best visual neuroscientists of all times, Hubel and Wiesel, who had (completely unbeknownst to us) started to record from the cat corpus callosum more or less at the same time as ourselves. With characteristic fairness, they added the following note to their March 1968 paper in *Journal of Neurophysiology* (Hubel and Wiesel, 1967): "Since this paper was submitted, Gazzaniga, Berlucchi and Rizzolatti have published a preliminary report on single-unit recording in corpus callosum (Federation Pro., 26: 1864, 1967). Their main findings are in agreement with those reported here." Our full paper (Berlucchi, Gazzaniga, and Rizzolatti, 1967) was published in *Archives Italiennes de Biologie* toward the end of 1967.

Galvanized by our success and by the confidence that we could work profitably together, Rizzolatti and I thought that we could demonstrate that

the callosal input could not only build up visual receptive fields of neurons in the receiving cortex, as Whitteridge and coworkers had shown, but also interact with the visual input transmitted to them through the geniculocortical pathway. We reasoned that, following a splitting of the chiasm and the restriction of the projection of each eye to the ipsilateral hemisphere, binocular receptive fields could be built up in principle by the convergence of a geniculocortical visual input from one half-field and a callosal visual input from the other half-field. In split-chiasm cats, we did indeed find binocularly driven neurons in visual areas 17 and 18 whose “callosal” and “geniculocortical” receptive fields matched each other not only as to the position occupied at the vertical meridian but also with regard to size and preferred stimulus orientation and movement direction. In brief, the convergence of the callosal input and the geniculocortical input appeared to build up homogeneous receptive fields spanning the vertical midline. The laws of optics and the organization of the optic pathways from retina to cortex impose a sharp separation of the projections of the two halves of the visual field onto different hemispheres. The convergence onto common neurons of geniculocortical and callosal visual inputs that we had shown could provide the continuity of the cortical visual field map across the interhemispheric gap. We submitted the paper to *Science* (Berlucchi and Rizzolatti, 1968) where it was accepted and published with few modifications on January 19, 1968. A few weeks later each of us received an identical letter from the Montreal Neurological Institute, dated February 12 and signed in elegant handwriting by the famous neurosurgeon Wilder Penfield. Mine read

Dear Dr. Berlucchi: Many congratulations on the beautiful article which you and Dr. Rizzolatti have written in the January number of *Science* on “Binocularly Driven Neurons in Visual Cortex of Split-Chiasm Cats.” When I saw it, it stirred a chord of my memory and I turned to an article which two of my associates and I wrote in the April number of the *Archives of Neurology and Psychiatry* in 1935. . . . In Figure 16, you will see that we hypothesized a crossing tract from the left geniculate ganglion to the right calcarine cortex. Does this correspond to your finding in the cat? . . . Yours sincerely, Wilder Penfield

On one hand, we were amazed and flattered that such a great man could take an interest in our work, and on the other, we were puzzled and preoccupied because we thought that our findings by no means suggested a crossed geniculocortical pathway. Our somewhat tongue-in-cheek reply, after profuse words of thanks, stated that

Our findings and those of Choudury et al. and Hubel and Wiesel seem to indicate that a cortico-cortical callosal pathway, rather

than a crossed geniculo-cortical connection, is involved. However Glickstein et al. have presented anatomical evidence that a crossed geniculo-cortical pathway, like the one you suggested to account for macular sparing in your patients . . . does indeed exist in the cat. The issue is controversial and requires further investigation.

Jim Sprague and Philadelphia

In 1966–67, James (Jim) Sprague, from the department of anatomy of the University of Pennsylvania, was an illustrious visitor to the Institute at Pisa. He was a longtime friend of Moruzzi and had worked with Magoun at Northwestern University in Chicago shortly after the discovery of the arousal function of the reticular formation. He had done fundamental work with Chambers, Liu, and Stellar—first at Hopkins and then at Penn—on the effects of cerebellar and brainstem lesions on motor, attentive, affective, and adaptive behavior in the cat. His recent work had centered on the visual functions of the superior colliculus, and when he arrived in Pisa, he had just published in *Science* his now famous paper on the Sprague effect in cats, whereby a hemianopia following an extensive ablation of contralateral visual cortical areas is “cured” by a lesion of the superior colliculus on the intact side (Sprague, 1966). He quickly established an easy-going and constructive personal rapport with Marchiafava, Rizzolatti, and with me, treating us as peers in spite of the difference in academic rank and a two-decade separation in age. He did electrophysiological studies on cortico-tectal relations in awake midpontine cats with Marchiafava and Rizzolatti, while he taught me to train cats in a two-choice visual discrimination apparatus (custom-built in the institute to match the one in use at Penn) with the aim of testing the importance of the superior colliculus in form vision. The view prevalent at the time was that form vision was the job of the visual cortex, whereas the superior colliculus was mainly for oculomotor control and visual orienting. Our approach was to make a large lesion, as complete as possible, in one superior colliculus of cats with a section of the optic chiasm, the corpus callosum, and the anterior and posterior commissures. We knew from Myers’ and Sperry’s findings that, in these split-brain cats, visual pattern discrimination learning proceeds independently in the two hemispheres, such that there is no interhemispheric transfer of discrimination learned with only one eye open. We were thus in the position to compare (in the same animal) the performance in visual learning and memory of a visual system having an intact superior colliculus with that of a visual system without a superior colliculus. I did the brain splitting surgery, for which I had a lot of experience; for the collicular lesion, Jim guided me by watching my actions through a second view-sharing microscope. I performed the collicular ablation after removing the overlying bony tentorium and by aspirating

the tectal gray matter until Jim decreed that I had made “a nice crypt” in place of the superior colliculus. For good measure, as often as possible, the lesion was extended into the pretectum. Four of the cats so prepared were tested in Pisa and then flown to Philadelphia for further testing and the final histological control.

In the summer of 1968, I went to Philadelphia on a Fulbright fellowship and was followed after a month by Luisa, the children, and my maternal aunt Liana who taught high school English in Pavia and who took the opportunity to visit the United States. We lived in Merion, a northern Philadelphia suburb, where we rented a nice house belonging to an architecture professor at Penn who was on sabbatical in Bologna. In the lab, it was reassuring to see that the preliminary findings from Pisa were fully confirmed by the Pisan cats themselves and by the additional cats that we prepared and tested at Penn. Jean Levy and the Italian-American Angela DiBerardino were essential contributors to the study with their expert technical help in surgery, training and testing, and histology. In brief, we found that the collicular lesion severely interfered with the learning of visual pattern discriminations but not with the retention of discriminations learned before the collicular lesion. In an extensive monograph published in the *Journal of Comparative and Physiological Psychology*, we supported the hypothesis that the pretectum and superior colliculus form an important link in the complex neural mechanism for learning to recognize and discriminate visual figures (Berlucchi et al., 1972). Another analysis of the effects of selective cortical ablations showed that, in the cat, the primary visual cortex (the striate cortex, or area 17) is not necessary either for learning or for retention of pattern vision, at least when high acuity is not required. By contrast, pattern vision was severely impaired by lesions of extrastriate areas, and we put forward the hypothesis that a midbrain-pulvinar-cortical pathway reaching these areas independent of the geniculo-cortical pathway could provide the first stage in simple, coarse form perception and discrimination (Sprague et al., 1977). The visual abilities of cats deprived of the primary visual cortex were then studied in detail by Jim with Mark Berkley (Berkley and Sprague, 1979), while I also conducted some studies in which I made select cortical lesions, and Professor Werner von Seelen and his collaborators, first at the University of Mainz and then at the University of Bochum, devised special tests to assess residual visual abilities (Krüger et al., 1986, 1988; Kiefer et al., 1989).

During that stay in Philadelphia and many subsequent ones, Jim and his wife, Dolores, were magnificent hosts to me and to my family. They were in love with Italy and with its geographic, architectural, cultural, and culinary riches, and we tried to reciprocate their hospitality on the occasions of their numerous visits to Pisa and then Verona. As a result, a tradition of reciprocal visiting exchanges between Philadelphia and Italy, initiated in 1966–68, extended through nearly 30 years, with mutual enjoyment and scientific

gratification. In Pisa, the Spragues made friends with some of our friends, especially with the plastic surgeon Paolo Santoni and his Swedish wife, Gerd, as well as with Italian and American academics working in the university or the Scuola Normale Superiore. In the summer, the beach at the Lido in Tirrenia was the best place for the Spragues and ourselves to meet and chat with friends, to swim and to enjoy the exquisite fish dishes prepared by the manager of the Lido, Pina Ammannati Giannessi, allegedly a descendant of the family of Galileo's mother, Giulia Ammannati. I like to remember Jim Sprague as a member of an old generation of gentlemen scientists who knew how to mitigate the natural hubris of the investigator with the dispassionate integrity of the scholar. Contrary to the attitude prevailing today, he was convinced that science can benefit more from cooperation than from competition, and, like Moruzzi, he believed that doing good science is aided by having broad cultural interests apart from science itself. Someone, probably Thomas Kuhn, said that the history of science is written by the winning side. For Jim Sprague, all scientists (barring perhaps a few conceited peacocks) were, or ought to be, on the same side. He died in 2002, and I am grateful to Alan Rosenquist, Larry Palmer, and their colleagues of the Mahoney Institute of Neurological Sciences at the University of Pennsylvania for kindly inviting Luisa and me to Philadelphia in April 2010 on the occasion of the 25th anniversary of the James M. Sprague Lectureship (I had given the sixth Sprague Lecture in 1990). I shared the honor of remembering Jim and his work with two other of his collaborators, Murray Sherman and Guy Urban. I had known Murray in 1965 when he was an undergraduate at Caltech and had re-encountered him in 1968 when he was a PhD student at Penn in the department of anatomy, chaired by Jim Sprague. We share many fond memories.

Collaborations with Other Good Friends in the 1960s and 1970s

Two of the persons who came to work in Pisa in the late 1960s, Carlo Alberto Marzi, a medical graduate from Florence, and Henry (Gus) Buchtel, a psychologist with a PhD from McGill University, became close lifelong friends of mine. Carlo has spent most of his academic career as a physiological psychologist alongside me, first in Pisa and then (after a period in Padua) in the medical school of Verona, where he is presently a full professor of psychology. He and I have many experiences, interests, ideals, and passions in common; his wife, Brigitte, and daughter Tessa are very close to my family; and we all have shared many events (good or bad) over the years. I am sure that Carlo, along with our companion for adventures in Pisa and Verona, Alberto Cangiano, knows my mind better than most, and that I know their minds better than most. Carlo has worked in Oxford with Larry Weiskrantz and Alan Cowey. He is well known for his original contribution

to the demonstration of blindsight, based on the influence that visual stimulation of a blind field exerts on the responses to visual stimuli in a normal field, as well as for his work on interhemispheric transfer. Gus left Pisa many years ago to work in Parma, London, Montreal, and finally in Ann Arbor where he works in the departments of psychiatry and psychology at the University of Michigan. In spite of our physical separation from Gus, Carlo and I feel that he is still with us because we have kept in constant contact throughout the years. Of course, e-mail is a great help and so are our yearly encounters at the meetings of the International Neuropsychology Symposium, the Web site of which is under Gus's very efficient control. Gus brought his deep knowledge of Hebbian and Skinnerian psychology to Pisa, as well as his love for and expertise in experimental control and his mastery of the English language. Moruzzi entrusted him with the correction of the English text of his latest papers. Gus and I share a strong interest in the history of scientific thought in the neurosciences, and I daresay that in 2009 we published the definitive account of the genesis of the term and of the concept of neural plasticity (Berlucchi and Buchtel, 2009). Gus knows and speaks Italian well, and we owe the English translation of the biography of Camillo Golgi by Paolo Mazzarello from Pavia to him and to Aldo Badiani.

Two other close friends who came to work with me in Pisa belonged to emigrant Italian families. Gian Mascetti came from Chile and Franco Lepore came from Canada. They were involved with Buchtel, Marzi, and with me in various behavioral and electrophysiological studies that were partly inspired and coauthored by Jim Sprague. In the 1980s, Gian returned to Italy as a professor of psychology in Padua, where he has done interesting studies on unihemispheric sleep in birds, the research subject of the young Moruzzi. Franco is a professor of psychology at the University of Montreal where he leads a very productive research group studying various aspects of cognitive neuroscience, including hemispheric interaction and specialization.

Antonella Antonini was a PhD student of the Scuola Normale when she joined my laboratory to prepare her thesis. She was a valued presence in the lab because of her sharp mind, collaborative personality, and superior technical abilities, including performing difficult brain surgeries in cats. She was part of the group who followed me from Pisa to Verona, but after her marriage to Alan Stein, whom she had known in Jim Sprague's department at Penn, she emigrated to the United States, where she proved herself a very gifted scientist working first with Carla Shatz at Stanford and then with Mike Stryker at the University of California at San Francisco.

The research topics that I pursued with Antonella, Buchtel and his former wife Elise, Lepore, Marzi, Mascetti, and Sprague all had to do with various aspects of the organization and functional significance of the cat's visual pathways, including the callosal connections mediating the interhemispheric transfer of visual discriminations. We showed that, in contrast

with the primary visual cortex, where callosal connections are limited to the vertical meridian region, the callosal connections of extrastriate visual areas cover a much larger extent of the visual field because of their wider receptive fields. However, even these wider receptive fields abut the vertical meridian to ensure the continuity of the cortical representation of the visual field across the midline. This has justified the claim that the visual callosal connections obey the so-called midline rule—a notion still debatable but reasonably worthy of support. Our lesion-behavioral studies provided evidence for attributing a primary role in interhemispheric transfer of visual discriminations to the callosal connections of extrastriate areas conveying information from wide visual field areas. Our single unit electrophysiological recordings furnished evidence for a complex interaction between cortex and superior colliculus in the representation of the visual field within and across hemispheres, including participation of the corpus callosum via cortico-tectal pathways. We also studied the abnormalities of this representation in Siamese cats (which, because of a genetic defect, have almost completely crossed visual pathways) and the alterations induced by immobilizing one eye. We used the split chiasm preparation in many experiments, and I always remember the extraordinary feat of Antonella and Franco Lepore when they were able to cut the corpus callosum while maintaining the contact between a cortical neuron and the recording electrode. Thanks to them, I could photograph the response of that neuron to stimulation of both eyes before the callosal section and the loss of the response to stimulation of the contralateral eye following the section (Antonini, Berlucchi, and Lepore, 1983). The thrust of those years of work is summarized in a number of papers and reviews (Berlucchi, 1972; Sprague et al., 1973, 1981; Berlucchi et al., 1978, 1979; Berlucchi and Sprague, 1981; Berlucchi and Marzi, 1982; Berlucchi and Antonini, 1990).

Reaction Time Studies

In 1967, Giacomo Rizzolatti moved to the Institute of Physiology of the University of Parma, which was then headed by Arduini. At that time, Carlo Umiltà, a psychologist from Bologna, who had been encouraged by his professor, Renzo Canestrari, to collaborate with physiologists, was also working at the Parma Institute. Carlo was already a sophisticated experimenter with a solid cultural background. A few years later, after working at the University of Oregon with psychologists of note such as Mike Posner and Steve Keele, he was responsible for bringing a refined experimentalist attitude back to Italy and for training a generation of psychologists interested in the brain. He, Giacomo, and I got together to discuss the possibility of testing the functions of the corpus callosum in humans. I had read somewhere, possibly in a paper in *Brain* (Efron, 1963), that the American psychologist Poffenberger had estimated the interhemispheric transfer time to be about

5–6 msec in a reaction time experiment involving a simple visuomotor task (Poffenberger, 1912). Nowadays you can download Poffenberger's paper from the Internet as a free pdf, but in 1967, I could not find the volume of *Archives of Psychology* containing that paper in any library in Italy. My friend Pier Lorenzo Marchiafava from Moruzzi's institute, who was then on a sabbatical at Yale University with Robert Galambos, lent a crucial hand by air-mailing photocopies of the paper's 73 pages to Pisa. On the last of them, he had written in large letters: *Mi dovrai invitare a cena per almeno una settimana*. (You will have to invite me to dinner for at least a week.)

We read that Poffenberger had investigated several factors of simple reaction time to a light stimulus, but the part of special interest to us was that he had found that the right hand is slightly faster than the left to react to a right visual stimulus, and the left hand is slightly faster than the right to react to a left visual stimulus. His interpretation of the finding was that a stimulus lateralized to the right or left visual field is projected through the optic pathways to the contralateral hemisphere. Because the motor pathways are crossed, if the reaction is to be made with the hand on the same side of the visual stimulus, only one hemisphere is needed for the response. If the response is to be made with the hand contralateral to the visual stimulus, the hemisphere in charge of the response is different from the one receiving the visual stimulus. Hence, an interhemispheric transfer is required, and reaction time increases due to added conduction and synaptic delays. Poffenberger had envisaged the callosal connections of the motor cortices as the likely pathway for the transfer, but we thought that the interhemispheric transfer might also occur through the callosal connections of the visual cortex. If so, the transfer should be faster with stimuli projected to visual cortical sites representing the vertical meridian region (which has rich callosal connections) than with stimuli projected to cortical regions representing the far periphery (which have few or no callosal connections). The plan then was to replicate Poffenberger's study with visual stimuli presented at different eccentricities from the vertical meridian.

We performed the experiment at the University of Bologna's Institute of Psychology where Umiltà had available a homemade apparatus for visual stimulation and for recording reaction times. We engaged Woody Heron, who had much experience with extrafoveal visual stimulation, and Ray Hyman, a psychologist from Oregon University who was then spending a sabbatical in Bologna, as collaborators. Ray had a deep knowledge of statistics and was already famous in psychology for the Hick-Hyman law of choice reaction time, but soon he would become even more famous for his ability to debunk claims of paranormal or supernatural powers by illusionists such as the then very popular Uri Geller. Performing the experiment on ourselves and on a group of students, we confirmed Poffenberger's interhemispheric transfer time and found that it did not vary with the stimulus eccentricity. Therefore, we concluded that the callosal connections of the primary

visual cortices are unlikely to be involved in the particular type of interhemispheric transfer, which is then best attributed to the callosal connections of other cortical areas.

The idea that one could use simple reaction times to measure interhemispheric latencies appeared repellent to a number of people. When I presented our results at a meeting in 1970 in Oxford, the venerable professor of physiology David Whitteridge, the first discoverer of the link between the callosum and the visual vertical meridian, looked outraged. On the other hand, in 1969 in Australia, Malcolm Jeeves had found that interhemispheric transfer time tested with the Poffenberger paradigm in two subjects with callosal agenesis was more than 10 times longer than in normal controls (Jeeves, 1969). At a 1969 meeting on interhemispheric relations in Smolenice near Bratislava in what was then Czechoslovakia, Rizzolatti and I met Jeeves, who had then become chairman of psychology at Scotland's University of St. Andrews, and we set up a collaboration that eventually also involved Umiltà's and Jeeves' collaborators David Milner and Mick Rugg. The main results on interhemispheric transfer with the Poffenberger's paradigm in observers with intact brains or partial or total callosotomies have been confirmed over the years in several laboratories, including my own in Pisa and Verona (Milner et al., 1985; Berlucchi et al., 1995; Marzi, 1999).

Measured as a difference in simple reaction times, the Poffenberger effect can be explained by reference to a go-signal conveyed from the visual cortex to the motor cortex along fixed inbuilt connections, with added conduction and synaptic delays when an interhemispheric transfer was required. Rizzolatti, Umiltà, and I began to discuss the possibility of measuring the time for responding to lateralized stimuli that did not merely provide a go signal but that had to be interpreted before deciding to react. That the right and left hemispheres were differently specialized for the recognition of various stimulus categories was well known from classic studies of the effects of unihemispheric lesions and from the recently demonstrated differences in performances of the disconnected hemispheres in split-brain patients (Sperry, Gazzaniga, and Bogen, 1969). There was no doubt that the left hemisphere was dominant for the recognition of verbal material, and there was less-documented but nevertheless convincing evidence that the right hemisphere was dominant for the recognition of faces. We decided to measure choice reaction times to letters and faces presented separately to the two hemispheres, and we found that reaction times to letters were systematically faster with the stimulus in the right compared to the left field and vice versa with face stimuli, independent of the hand used for responding. An obvious interpretation was that the material presented to the non-dominant hemisphere had to be transferred for recognition to the dominant hemisphere, and that this putative interhemispheric transfer was much longer than that connected with the Poffenberger effect and most probably different in kind from it. Subsequent research showed that

other interpretations are possible, but this is not the place to deal with this complicated subject.

Our two papers on interhemispheric transfer, one on the Poffenberger effect and the other on the opposite hemispheric superiorities, were published in *Brain* (Berlucchi et al., 1971; Rizzolatti et al., 1971). They were among the first studies to demonstrate hemispheric interactions and functional asymmetries in normal human observers using simple, inexpensive methods and were received with considerable interest. They contributed, along with a few other pioneering publications, to launching the trend of the so-called divided field studies of hemispheric functions. The trend flourished in the last decades of the last century, filling the pages of various neuropsychological journals, and is not dead yet—even in this era of big and expensive neurotechnology. Of those times, I remember with pleasure and some nostalgia the long hours of heated arguments with Umiltà and Rizzolatti during which each of us learned a lot from the others—although at the same time raising serious doubts about each other's intellectual competence.

Of the reaction time work done subsequently in Pisa, I remember two studies that have been highly cited: the differentiation of the Poffenberger effect from spatial compatibility effects (Berlucchi et al., 1977) and the influence of unimanual and bimanual responding, and the use of proximal or distal arm muscles, on the Poffenberger effect (Di Stefano et al., 1980). The senior author of the latter paper was Marirosa Di Stefano, a medical graduate from Naples who, after collaborating extensively with Carlo Marzi and me in Pisa, did interesting work on vision in cats with Concetta Morrone and Dave Burr in Australia and in humans and cats with Maryse Lassonde, Franco Lepore, and Maurice Ptito in Canada.

With regard to the collaborations among Pisa, Bologna, and Parma, I also like to remember the demonstration that attention orienting could not explain the opposite hemispheric superiorities for letters and faces found by Rizzolatti, Umiltà, and myself and the analysis of the importance of verbal and non-verbal coding of physically similar stimuli in determining the prevalence of the left or right hemisphere. In addition to Umiltà, Rizzolatti, Marzi, and myself, one student of Umiltà from Bologna, Daniela Brizzolara, participated in the first study (Berlucchi et al., 1974) and two other students of Umiltà (Carlo Franzini and Giovanni Zamboni) and Marcello Camarda (then in Parma with Rizzolatti) participated in the second study (Umiltà et al., 1974). I presented a summary of these results at the Third Study Program in the Neurosciences organized by Frank Schmitt and Fred Worden in Boulder, Colorado (Berlucchi, 1974), where I spent two very pleasant weeks with Luisa and our children. In a subsequent divided field study that was well received by the scientific community, Carlo Marzi and I showed that the left hemisphere may take the lead in recognizing familiar faces by utilizing distinctive characteristics and details (Marzi and Berlucchi, 1977).

From Pisa to Verona

Professor Moruzzi retired in 1980. It was easy to predict that without his enlightened chairmanship, based on a highly idealistic conception of research and scholarship, the Institute of Physiology could never be the same. However, the situation turned out to be even worse than the worst predictions. Efficient academic research and teaching in a large institution comprising small different groups is based on the assumption of mutual trust and on the sharing of values by like-minded scholars. Because the institute's climate was becoming increasingly bitter and polemical, I did not want to spend my energies on irrational clashes over personal prestige, academic weight, and egotistic demands rather than on scientific research and for the promotion of merit. These completely unneeded clashes had already cost the institute the loss of my close friend and coworker Carlo Marzi, who had moved to the University of Padua as a full professor of physiological psychology. During that troubled period, I benefited from strong support from Alberto Cangiano, another close friend who had been working in Pisa since the late 1960s, and who had built up a group doing original and innovative work on the neuromuscular junction. His thorough analysis of the situation convinced me that we both should leave Pisa for a place where we could create the conditions suitable for our own research work and that of our collaborators.

A convenient solution was offered by Hrayr Terzian, the neurologist who had worked in Pisa with Moruzzi in the 1950s and later in Marseille and Padua. He had made important contributions to basic and clinical neuroscience, including the description with Dalle Ore of a human Klüver and Bucy syndrome with deep amnesia (Terzian and Dalle Ore, 1955). In the late 1960s, the medical faculty of the University of Padua had started a branch in Verona, and Terzian had been appointed chairman of its neurological clinic. The year 1982 saw the separation of the University of Padua from Verona and the inauguration of an independent University of Verona, of which Terzian became the first rector. With his generous help, I moved to the chair of physiology in 1983, soon followed by Cangiano and our collaborators from Pisa—Antonella Antonini, Mario Buffelli, Efrem Pasino, and Giancarlo Tassinari. In 1988, Carlo Marzi moved from the University of Padua to the chair of psychology in the medical faculty of Verona, so that we were able to reconstitute the original research group that we had started in Pisa. Terzian's pet idea was to create a department of neuroscience comprising basic and clinical disciplines, but unfortunately, he died too soon to see an at least partial realization of his aspiration.

The move from Pisa to Verona was not without costs for my family, and I am most grateful to my wife and children for the good will with which they agreed to leave the city in which they had lived happily for most of their lives. Fortunately, Verona is a beautiful city with many cultural attractions,

and it did not take long for us to feel at home there. Although, as I have already said, my deepest roots are elsewhere, I have now lived in Verona longer than in any other city in my life, and I consider it my home. Our son Filippo and his wife Daniela Provasi live in a small town on Lake Garda, but he works as a financial promoter in Verona. Our daughter Silvia and her husband Giacomo Pavesi are both busy neurosurgeons who work and live in Modena, but they keep frequent contacts with their respective families in Verona. Their two children, Elsa and Vittorio, whom Luisa and I adore, were born in Verona and are strongly attached to the city and especially to its soccer team (Hellas). I am sorry for them that Hellas has no chance against my beloved Inter team from Milan.

Research in Verona

In Pisa, while gathering evidence for defending the interpretation of the Poffenberger effect as being due to a simple callosal transfer, we had stumbled on a phenomenon that would occupy us for some time in Verona (Berlucchi, 2006). Believing that a lateralized stimulus always engages the attention of the contralateral hemisphere, with a resulting functional advantage for any response controlled by that hemisphere, Kinsbourne has long regarded the Poffenberger effect as an attentional effect (Kinsbourne, 1975). For him, a left visual stimulus yields a faster response from the left hand than from the right hand, not because a callosal transfer is needed, but because the left stimulus would arouse the right hemisphere more than the left. In Pisa, we tested Kinsbourne's assumption by presenting a pair of successive peripheral light points, both on the same side or one on the right and the other on the left. The first light point required no response and only informed the subject that the second light point was about to appear with equal probability on the same or the opposite side. The subject's task was to press a key as fast as possible in response to the second light point. If Kinsbourne was right, the reaction time should be faster with stimuli on the same side because the second stimulus goes to the hemisphere where the attention has been engaged, according to him, by the first stimulus. It turned out instead, and exactly contrary to Kinsbourne's expectation, that if the two stimuli appeared on the same side, reaction time was considerably longer than if the stimuli appeared on opposite sides. The effect did not interact with the Poffenberger's effect. I tried to concoct a rather fuzzy attentional hypothesis for the effect we had found, and I discussed it with Michael Posner sometime between 1979 and 1980 when he was visiting Rizzolatti and Umiltà at the University of Parma.

Mike was the right person to consult because he had resurrected the reaction time method for studying attentional effects with great success. We started a correspondence and the following quote is from a letter that he wrote me on July 2, 1980.

When I visited Parma last summer I discussed with you some experiments that you had been running in which inhibition effects related to attention were found. The experiments were rather vague in my mind from the oral report, but during this year I have obtained a similar phenomenon and have been working on understanding its source. If a subject pays attention to a position in space and shifts attention away to a new position, he shows relatively less sensitivity to the position to which he has attended than to the position on the opposite side, or at some other location away from the original source of attention. The effect does not seem to be due to the direction of movement away from the attended area, but rather to inhibition at the attended area. I think this work is most interesting and may be closely related to the phenomenon that you observed.

Mike's view was that a peripheral visual cue in an empty field summons attention to the cued position, improving efficiency until attention is withdrawn, with a consequent reduction of efficiency. Evidence for this view was provided by an early facilitation of reaction time at the cued position, followed by reaction time (RT) inhibition. I had an opportunity to tell Mike, on another of his visits to Italy, that most often we found inhibition without a preceding facilitation. His answer in a letter of September 24, 1982, was as follows.

It occurred to me before the seminar on attention that your results and our own results might be linked in the way I mentioned briefly in my presentation. In your paradigm, the first stimulus (cue) and the second stimulus (target) are similar and subjects must respond only to the second. Because the subjects are highly trained, they may be able to prevent orienting to the first stimulus, thus preventing any evidence of facilitation while producing a larger inhibition effect than we usually get. This would fit your result and ours together with the additional point that the facilitation effect is more voluntary (under the control of the subject).

Later on, Posner and collaborators (1985) coined the term "inhibition of return," meaning that once attention has been directed at a location, it is refrained from returning to that location in favor of other potential sources of information. I think that that term disagrees with Posner's original intuition that inhibition stems from reduced sensitivity rather than from the absence of attention at the cued location; indeed, we showed that reaction time can be increased by previous stimulation at a volitionally attended location (Berlucchi et al., 2000). Probably many of the effects published as instances of inhibition of return, including some from my lab, have little

to do with attention, and I tried to expose some of the contradictions of the field in a review a few years ago (Berlucchi, 2006). Although I have recently published a small paper on the so-called inhibition of return with Sonia Mele, a former doctoral student, and Andrea Peru, associate professor of psychology in Florence (Mele et al., 2012), my interest in the topic has almost completely abated. Andrea may perhaps rekindle it when he acts as my favorite sparring partner in discussions on soccer and politics.

My main autobiographical reason for mentioning “inhibition of return” from Verona at some length is that I take pride in the fact that two coauthors of those papers have become international stars in the field of attention, entirely on their own merit (Chelazzi and Corbetta, 2000). One of them is Leonardo Chelazzi, a medical graduate from Florence, who came to work in Verona due to his interest in the higher nervous functions. After doing first-rate work with Bob Desimone at NIH on the neural mechanisms of attention in macaques, Leonardo has developed several original lines of research on the subject—working with monkeys and humans—in Verona, where he is presently a full professor of physiology. The other star in the field of attention is Maurizio Corbetta, a medical laureate from Pavia who worked in Pisa and Verona with Carlo Marzi on blindsight and in Verona with me and with others on spatial attention. After a splendid scientific and clinical career with pioneer contributions to the brain imaging of various cognitive functions, Maurizio went to work with Marcus Raichle at Washington University in Saint Louis where he is now a professor of neurology. Anyone caring about the meritocratic interests of Italian academics and research can only hope that he can return to one of our universities as a professor.

Another field of research in which I was involved in Verona concerns the neural mechanisms of corporeal awareness, as expressed in the ambiguous terms body schema and body image. I owe this interest to Salvatore Aglioti, who graduated in medicine from Pisa and then moved with me to Verona. He did work in clinical neurology with Terzian in Verona and with De Renzi and Faglioni in Modena, and he played an essential part in the studies on spatial attention and interhemispheric transfer in Verona. His collaboration with Mel Goodale in London, Canada, resulted in a now famous experiment showing that visual illusions deceive the eyes but not the hands (Aglioti, et al., 1995). Salvatore is a first-rate researcher and scholar, and I would be proud to be considered even minimally responsible for his development as a scientist. His interest in phenomena and mechanisms of phantom sensations after amputations and mutilations led him to make the important discovery that phantom sensations develop very early after mastectomies, indicating that the removal of a body part unmasks silent functional connections already present in the brain (Aglioti, et al., 1994). These early phenomena precede those attributable to long-term processes of reorganization. The studies we did on his initiative on aspects of bodily awareness

and perception in brain damaged patients or in intact observers submitted to transcranial magnetic stimulation are summarized in two reviews that appeared 13 years apart as “The Body in the Brain” and “The Body in the Brain Revisited” (Berlucchi and Aglioti, 1997, 2010). Salvatore is currently a professor of psychology at the Sapienza University in Rome, where he has gathered a very active and successful group of young investigators who explore various areas of the cognitive neurosciences with very original approaches. One of my regrets is that I was unable to obtain a position for him at the University of Verona, but I take consolation in his great success in Rome and in his fast-growing international reputation. He and I share the conviction that if the immanent philosophical problem of knowing ourselves can be solved at all, the solution will have to include knowledge of our brains.

Aglioti was also involved in experiments we did in Verona, Rome, and Ancona on patients with total and partial callosal sections regarding various aspects of interhemispheric communication. We performed the first study ever of gustatory lateralization in a completely callosotomized patient in Verona and inferred from the results that the gustatory pathways from tongue to cortex are bilaterally distributed with a predominance of the uncrossed component (Aglioti et al., 2000). By comparison with intact observers, we also inferred that the corpus callosum equalizes the strength of the crossed and uncrossed components, as previously hypothesized by Pritchard et al. (1999) on the basis of results in patients with unilateral insular cortex lesions. Mike Corballis from Auckland, New Zealand, was then spending a sabbatical in Verona and took part in the research, bringing to it his great expertise with laterality studies and commissurotomy patients. Mike’s stay in Verona enriched us all with his profound knowledge of the human brain and its evolution. I remember with nostalgia his discussions with Alberto Cangiano, Carlo Marzi, and myself at lunch in the medical school cafeteria when he shared with us his vast erudition, spiced with sophisticated humor. Subsequently, we replicated the gustatory split-brain study with our physiological colleagues in Ancona, Mara Fabri and the late Tullio Manzoni, who made it possible for us to study two more partially callosotomized patients from their split-brain population. The additional surprising result was that the posterior rather than the anterior callosum was responsible for the suggested equalizing function (Aglioti et al., 2001).

Teaching Activities, Involvement in Scientific Societies, and Awards

In my career, I have consistently regarded research as my real occupation, but I have always accepted, even if sometime grudgingly, forgoing my research to fulfill other obligations toward the university and the national and international scientific community. I do not rank administrative work

as a major obligation and shied away from it as often as I decently could. On the contrary, I regarded teaching as a major obligation and have devoted myself to it with enthusiasm, especially when I was younger. Physiology of the nervous system was obviously my favorite teaching subject but throughout my career I have taught courses on most aspects of physiology. Moruzzi had taught me to present physiological facts in light of how they had been discovered, and I have always been fascinated by the history of the search for the mechanisms of the bodily machine, whether neural or otherwise. I taught physiology and physiological psychology in Pisa in the 1960s and early 1970s and physiology at the University of Siena between 1973 and 1976, where I was promoted to full professor. My family remained in Pisa during my years in Siena, and every week I worked three days in Siena and three days in the lab I kept in Pisa. I updated much of my knowledge of physiology on slow trains traveling through the Tuscan countryside, with the advantage that when I lifted the eyes from my books I could see some of the most beautiful landscapes in the world. I was fortunate enough that one of my colleagues in Siena was Giancarlo Carli, who had worked in Pisa and gave me all the help he could, but I was unhappy because I felt that I was not pursuing research work as I should. The teaching load had been made unbearable by granting an unlimited access to medical schools, so that I and my colleagues had to teach and give exams to many hundreds of students several times every year. The mental and physical demands of those efforts and the sheer boredom of repetitious explanations and discussions began to weaken my enthusiasm. When I was able to go back to the University of Pisa, the number of medical students was still unacceptably high, and I remember that for some exam sessions we worked uninterrupted for several hours every day for a week or more. At the University of Verona, we were blessed by a law that reduced the number of medical students to about 100 per year, but some colleagues responsible for the organization of the courses were obsessed with the idea that the teaching of the basic sciences, including physiology, should be reduced in content and duration to make more space for the clinical disciplines and for practical work in hospital wards. Unlike in my student days, an early contact with fundamental research is no longer regarded as a building experience in the formation of a medical doctor. So after teaching too much, we physiologists ran the risk of teaching too little. Fortunately, the arguments that my colleagues Alberto Cangiano and Carlo Marzi and I put forward in defense of teaching physiology and physiological psychology were at least partially accepted. Now that I am retired, the opportunity for satisfying my residual drive for communicating scientific knowledge is furnished by occasional lectures or seminars to selected and specialized audiences. I am gratified when I meet some middle-aged doctor who tells me that I taught him or her physiology and that they loved my lectures, but I am well aware that those praises may be ascribed to a distorted memory or to an act of personal courtesy.

The papers on hemispheric transmission and on functional hemispheric specialization in normal humans gained me an entrance into some international groups that were forming in those years with the specific aim of dealing with the nervous system, behavior, and psychology. Alan Cowey enrolled me in the European Brain and Behaviour Society founded by Larry Weiskrantz, and I served on one of its first councils with Larry as president and Elizabeth Warrington as secretary. When the European Neuroscience Association (ENA) was founded in the mid 1970s, Konrad Akert, as president of the nominating committee, informed me that I had been elected to represent behavioral neuroscience on the first ENA council alongside the famous neuropsychologist Alexander Luria from Moscow, who disappointingly was never able to attend the council sessions. I would have been thrilled to meet such a legendary figure in neuropsychology. The first ENA council was chaired by János Szentágothai (later replaced by Leslie Iversen) and included Changeux, Hökfelt, Kuypers, Lundberg, Thoenen, de Wied, and myself. I was audacious enough to undertake the organization of the second ENA meeting in Florence in September 1978, at a time when Italy was badly afflicted by political terrorism (the Christian democrat leader Aldo Moro had been assassinated by the Red Brigades just a few months before) and by frequent and unforeseeable strikes of workers in public transportation, the mail, and other essential services. The Fondazione Menarini supported the meeting organization after negotiations with the ENA executive secretary Hugo Zweg and me. I have canceled from my memory most events connected with that meeting because the objective difficulties of its organization, amplified by my constitutional anxiety, cost me a protracted period of suffering. After the meeting, I took pleasure in destroying the enormous mass of paper that I had accumulated (in that pre-electronic communication era) during the meeting's preparation. I only kept the notes of congratulations that very few kind souls took the trouble to send me after the meeting. Konrad Akert, ever the gentleman, wrote: "Dear Berlucchi, I would like to write to you in my own name and in the name of my collaborators by expressing to you our sincerest thanks for all your efforts you made on behalf of ENA. In our view the meeting has been a great success and certainly has helped a lot in establishing the new society. I hope that you have already recovered from the enormous stress that was put on you before and during the meeting." Enormous stress indeed!

The support of Brenda Milner and Herbert Jasper got me into the Neuroscience Research Program of Frank Schmitt, and I participated in one of their intensive programs in Boulder, Colorado, and in one or two smaller meetings in Boston and Woods Hole. An invitation by Hans Lukas Teuber helped me join an informal discussion group called International Neuropsychology Symposium. This group, started by the French neurologist Henri Hécaen, had been the crib of neuropsychology, officially born

in 1963 as an autonomous discipline with the foundation of the journal *Neuropsychologia*.

Although I consider myself a neurophysiologist rather than a neuropsychologist, I was on the editorial board of *Neuropsychologia* for several years and was part of the group of researchers from various disciplinary fields that formed in my country around the charismatic and intellectually catalyzing figure of Ennio De Renzi, a neurologist of international renown and the father of Italian neuropsychology. In 1994, quite unexpectedly, I became *Neuropsychologia*'s editor-in-chief. After *Neuropsychologia*'s editorial management by its founder Hecaen and then by his successor, Marc Jeannerod, the journal had passed into the hands of Malcolm Jeeves, the St. Andrews psychologist with whom Umiltà, Rizzolatti, and I had collaborated for years. A sudden illness forced Jeeves to give up many of his commitments including the handling of the journal. He asked me to replace him in that capacity, and after an unfruitful search for other possible and more appropriate candidates, I had to say yes and to commit myself to a difficult five-year job. I had already served as panel editor for journals such as *Experimental Brain Research* and *European Journal of Neuroscience*, participating in the foundation of the latter journal with the editor-in-chief Ray Guillery and other colleagues from the ENA, but I had never managed a major journal by myself. Nevertheless, the journal and I survived, though with a cost for my research; altogether I have a positive memory of that experience in which I had the unfailingly wise support of Paul Carton, Elsevier's senior publisher for neuroscience. In general, I much prefer working as a reviewer to serving as an editor, and nowadays I am still evaluating a fair number of papers for various scientific journals. Immodestly, I believe that reviewing papers is one of the very few things I am really very good at.

Of the awards that I received during my career I will mention the ascription to the Accademia Nazionale dei Lincei and the honorary degree in psychology received from my alma mater, the University of Pavia in 2007. The Accademia, founded in 1603 by Federico Cesi and boasting Galileo as one of its first members, is the most important cultural institution in my country. Its present president, Lamberto Maffei, is a friend from over a half century ago, when as fledgling neurophysiologists in Pisa we started our career under the big wings of Giuseppe Moruzzi. I am involved in the organization of some activities of the Accademia, including scientific meetings and conferences that keep me in contact with the national and international scientific community. The honorary degree from Pavia was a generous gift from the psychologists from that university, Gabriella Bottini and Tomaso Vecchi, who convinced the academic authorities to bestow the honor on me in connection with the inauguration of an undergraduate course in psychology. My dear friend Carlo Marzi did a marvelous job of orchestrating the scientific events connected with the ceremony. The ceremony itself was attended by many who came from Italy and abroad to show

their friendship with a gesture of affection, which touched my heart deeply. Carlo, Gabriella, and her husband, Eraldo Paulesu, put together a scientific meeting in which 25 friends who had been fellow travelers in my scientific career presented lectures on their work, flavored with their reminiscences about me (Marzi et al., 2009). The list included Emilio Bizzi, Gus Bachtel, Mike Corballis, Alan Cowey, Ulf Eysel, Richard Frackowiak, Mike Gazzaniga, Mitch Glickstein, Mel Goodale, Mickey Golberg, Charlie Gross, Peter Hoffmann, Marc Jeannerod, Giorgio Innocenti, Franco Lepore, Lamberto Maffei, David Milner, Morris Moscovitch, Elio Raviola, Giacomo Rizzolatti, Wolf Singer, Piergiorgio Strata, Carlo Umiltà, Leslie Ungerleider, and Bob Wurtz. When I read this list today, I am still amazed and moved—as I was then—by the generosity of such important scientific personalities who came to Pavia to show their friendship and esteem for me. And it gives me much sadness to think that two wonderful persons on that list, my long time close friends Alan Cowey and Marc Jeannerod, are no longer with us.

Epilogue

I have no profound thoughts to express or lofty messages to deliver to close this autobiography on a solemn note. I hope I have made it clear that I have been very fortunate to do work that I liked, to have the unstinting support of my family, and to benefit from the affection, friendship, and intellectual stimulation from many people from every walk of life. I also hope that what I have written about them can convey my deeply felt sense of gratitude. I owe my sincere thanks to Larry Squire, the editor of *The History of Neuroscience in Autobiography*, for deciding that my autobiography could be interesting enough to appear alongside those of the many eminent neuroscientists who have contributed to the publication. I resisted Larry's invitations for a few years, until his kind prodding convinced my old brain to go back in time and relive and recount some of the experiences of a long life in neuroscience. Memory is known to be fallible and memories can be fabricated, but my old brain believes that what is written here bears a reasonable correspondence to the truth. And my old brain also believes that the completion of an autobiography in neuroscience does not have to coincide with the end of a life in neuroscience, and that there is still a lot of interesting work to look forward to.

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