When we get right down to it, what do we human beings do all day long? We read the world, especially the people we encounter. My face in the mirror first thing in the morning doesn’t look too good, but the face beside me in the mirror tells me that my lovely wife is off to a good start. One glance at my eleven-year-old daughter at the breakfast table tells me to tread carefully and sip my espresso in silence. When a colleague reaches for a wrench in the laboratory, I know he’s going to work on the magnetic stimulation machine, and he’s not going to throw his tool against the wall in anger. When another colleague walks in with a grin or a smirk on her face—the line can be fine indeed, the product of tiny differences in the way we set our face muscles—I automatically and almost instantaneously can discern which it is. We
all make dozens—hundreds—of such distinctions every day. It is, quite literally, what we do.

Nor do we give any of this a second thought. It all seems so ordinary. However, it is actually extraordinary—and extraordinary that it feels ordinary! For centuries, philosophers scratched their heads over humans’ ability to understand one another. Their befuddlement was reasonable: they had essentially no science to work with. For the past 150 years or so, psychologists, cognitive scientists, and neuroscientists have had some science to work with—and in the past fifty years, a lot of science—and for a long time they continued to scratch their heads. No one could begin to explain how it is that we know what others are doing, thinking, and feeling.

Now we can. We achieve our very subtle understanding of other people thanks to certain collections of special cells in the brain called mirror neurons. These are the tiny miracles that get us through the day. They are at the heart of how we navigate through our lives. They bind us with each other, mentally and emotionally.

Why do we give ourselves over to emotion during the carefully crafted, heartrending scenes in certain movies? Because mirror neurons in our brains re-create for us the distress we see on the screen. We have empathy for the fictional characters—we know how they’re feeling—because we literally experience the same feelings ourselves. And when we watch the movie stars kiss on-screen? Some of the cells firing in our brain are the same ones that fire when we kiss our lovers. “Vicarious” is not a strong enough word to describe the effect of these mirror neurons. When we see someone else suffering or in pain, mirror neurons help us to read her or his facial expression and actually make us feel the suffering or the pain of the other person. These moments, I will argue, are the foundation of empathy and possibly of morality, a morality that is deeply rooted in our biology. Do you watch sports on television? If so, you must have noticed the many “reaction shots” in the stands: the fan frozen with anticipation, the fan ecstatic over the play. (This is especially true for baseball broadcasts, with all the downtime between pitches.) These shots are effective television because our mirror neurons make sure that by seeing these emotions, we share them. To see the athletes perform is to perform ourselves. Some of the same neurons that fire when we watch a player catch a ball also fire when we catch a ball ourselves. It is as if by watching, we are also playing the game. We understand the players’ actions because we have a template in our brains for that action, a template based on our own movements. Since different actions share similar movement properties and activate similar muscles, we don’t have to be skilled players to “mirror” the athletes in our brain. The mirror neurons of a non-tennis-playing fan will fire when watching a pro smash an overhead, because the non-tennis-playing fan has certainly made other kinds of overhead movements with his arm throughout his life; the equivalent neurons of a fan such as me, who also plays the game, will obviously be activated much more strongly. And if I’m watching Roger Federer, I bet my mirror neurons must be firing wildly, because I’m a big Federer fan.

Mirror neurons undoubtedly provide, for the first time in history, a plausible neurophysiological explanation for com-
complex forms of social cognition and interaction. By helping us recognize the actions of other people, mirror neurons also help us to recognize and understand the deepest motives behind those actions, the intentions of other individuals. The empirical study of intention has always been considered almost impossible, because intentions were deemed too "mental" to be studied with empirical tools. How do we even know that other people have mental states similar to our own? Philosophers have mulled over this "problem of other minds" for centuries, with very little progress. Now they have some real science to work with. Research on mirror neurons gives them and everyone interested in how we understand one another some remarkable food for thought.

Consider the teacup experiment I dreamed up some years back, which I'll discuss in considerable detail later. The test subjects are shown three video clips involving the same simple action: a hand grasping a teacup. In one, there is no context for the action, just the hand and the cup. In another, the subjects see a messy table, complete with cookie crumbs and dirty napkins—the aftermath of a tea party, clearly. The third video shows a neatly organized tabletop, in apparent preparation for the tea party. In all three video clips, a hand reaches in to pick up the teacup. Nothing else happens, so the grasping action observed by the subjects in the experiment is exactly the same. The only difference is the context.

Do mirror neurons in the brains of our subjects note the difference in the contexts? Yes. When the subject is observing the grasping scene with no context at all, mirror neurons are the least active. They are more active when the subject is watching either of the scenes and most active when watching the neat scene. Why? Because drinking is a much more fundamental intention for us than is cleaning up. The teacup experiment is now well known in the field of neuroscience, but it is not an isolated result: solid empirical evidence suggests that our brains are capable of mirroring the deepest aspects of the minds of others—intention is definitely one such aspect—at the fine-grained level of a single brain cell. This is utterly remarkable. Equally remarkable is the effortlessness of this simulation. We do not have to draw complex inferences or run complicated algorithms. Instead, we use mirror neurons.

Looking at the issue from another perspective, labs around the world are accumulating evidence that social deficits, such as those associated with autism, may be due to a primary dysfunction of mirror neurons. I hypothesize that mirror neurons may also be very important in imitative violence induced by media violence, and we have preliminary evidence suggesting that mirror neurons are important in various forms of social identification, including "branding" and affiliation with a political party. Have you heard of neuroethics, neuromarketing, neuropolitics? You will in the years and decades to come, and research in these fields will be rooted, explicitly or otherwise, in the functions of mirror neurons.

This book tells the story of the serendipitous and groundbreaking discovery of this special class of brain cells, the remarkable advances in the field in just twenty years, and the extremely clever experiments now under way in several labs around the world. Quite simply, I believe this work will force us to rethink radically the deepest aspects of our social rela-
MIRR ORING PEoplE

tions and our very selves. Some years ago, another researcher suggested that the discovery of mirror neurons promised to do for neuroscience what the discovery of DNA did for biology.¹ That’s an extraordinarily bold statement, because essentially everything in biology comes back to DNA. Decades in the future, will everything in neuroscience be seen as coming back to mirror neurons?

BRAIN SURPRISES

For fifteen years I have lived in Los Angeles and worked in my laboratory at UCLA, but as my name suggests, this story should rightly begin in Italy, and I’m happy to report that it really does—specifically, in the small and beautiful city of Parma, famous for its fabulous food, particularly prosciutto di Parma and Parmesan cheese, and for its music. Now we can add neuroscience to the list of Parma’s world-class exports; it was at the university here that a group of neurophysiologists, led by my friend Giacomo Rizzolatti, first identified mirror neurons.

Rizzolatti and his colleagues work with *Macaca nemestrina*, a species of monkey often used in neuroscience labs worldwide. These macaque monkeys are very docile animals, unlike their more famous relatives, rhesus monkeys, who are highly competitive alpha-male types (even the females). Research on monkeys in a lab such as Rizzolatti’s is predicated on its inferential value for understanding the human brain, which is generally considered the most complex entity in the known universe, with good reason. The human brain contains about one hundred billion neurons, each of which can make contact with thousands, even tens of thousands, of other neurons. These contacts, or synapses, are the means by which neurons communicate with one another, and their number is staggering. The distinguishing brain feature in mammals is the neocortex, the most recently evolved of our brain structures. Now here’s the key “inferential” point: the macaque brain is only about one-fourth as large as ours, and our neocortex is much larger than the macaque’s neocortex, but neuroanatomists typically agree that the structures in the neocortex of macaques and humans correspond relatively well despite these differences.

In Parma, the Rizzolatti team’s pertinent area of study was an area of the brain labeled F5, located in a large region called the premotor cortex—that part of the neocortex concerned with planning, selecting, and executing actions. Area F5 contains millions of neurons that specialize in “coding” for one specific motor behavior: actions of the hand, including grasping, holding, tearing, and, most fundamental of all, bringing objects—food—to the mouth. For every macaque, as for every primate, these actions are as basic and essential as they come. We *Homo sapiens* are grasping and manipulating objects from the moment we fumble for the snooze button on the alarm clock until we adjust our pillows at bedtime, eighteen hours later. All in all, we each perform hundreds, if not thousands, of grasping actions every day. In fact, this is precisely why the Rizzolatti team chose area F5 for the closest possible investigation. All neuroscientists want to understand the brain for
understanding's sake, but we also have an eye on more practical goals, such as discoveries that may eventually drive new treatments for disease. The discovery of the neurophysiological mechanisms of motor control of the hand in the macaque could eventually help individual humans with brain damage recover at least some degree of hand function.

Through laborious experimentation, the Rizzolatti team had acquired an impressive understanding of the actions of these motor cells during various "grasping" exercises with the monkeys. (They are called motor cells because they are the first in the sequence that controls the muscles that move the body.) Then one day, about twenty years ago, the neurophysiologist Vittorio Gallese was moving around the lab during a lull in the day's experiment. A monkey was sitting quietly in the chair, waiting for her next assignment. Suddenly, just as Vittorio reached for something—he does not remember what—he heard a burst of activity from the computer that was connected to the electrodes that had been surgically implanted in the monkey's brain. To the inexperienced ear, this activity would have sounded like static; to the ear of an expert neuroscientist, it signaled a discharge from the pertinent cell in area F5. Vittorio immediately thought the reaction was strange. The monkey was just sitting quietly, not intending to grasp anything, yet this neuron affiliated with the grasping action had fired nevertheless.

Or so goes one story about the first recorded observation of a mirror neuron. Another involves one of Vittorio's colleagues, Leo Fogassi, who picked up a peanut and triggered an excited response in F5. Yet another credits Vittorio Gallese and some ice cream. There are others, all plausible, none confirmed. Years later, when the importance of mirror neurons was clearly understood, the Parma colleagues went back to their lab notes, hoping to put together a fairly accurate timeline of their earliest observations, but they simply couldn't do it. They found references in their lab notes to "complex visual responses" of the monkeys' motor cells in area F5. Such notes were unclear, because the scientists did not know what to make of their observations at the time. Neither they nor any neuroscientist in the world could have imagined that motor cells could fire merely at the perception of somebody else's actions, with no motor action involved at all. In light of both knowledge and theory at the time, this made absolutely no sense. Cells in the monkey brain that send signals to other cells that are anatomically connected to muscles have no business firing when the monkey is completely still, hands in lap, watching somebody else's actions. And yet they did.

In the end, it does not matter much that the "Eureka!" moment for mirror neurons stretched over a period of years. What matters is that the team did soon grapple with the odd goings-on in their laboratory. They had a hard time believing these phenomena themselves, but in time they also sensed that the discovery, if confirmed, could be potentially groundbreaking. They were right. Twenty years after that first recording in the laboratory, a cascade of well-controlled experiments with monkeys and later with humans (different kinds of experiments, for the most part; no needles inserted through skulls) have confirmed the remarkable phenomenon. The simple fact that a subset of the cells in our brains—the
mirror neurons—fire when an individual kicks a soccer ball, sees a ball being kicked, hears a ball being kicked, and even just says or hears the word “kick” leads to amazing consequences and new understandings.

THE FAB FOUR

We now know that about 20 percent of the cells in area F5 of the macaque brain are mirror neurons; 80 percent are not. Given those odds, the group in Parma was bound to come across mirror neurons sooner or later. When they did, the background assumptions not only of their lab but of neuroscientists around the globe were put to the test. In the 1980s, neuroscientists were deeply invested in the paradigm that held that the various functions implemented by the brain—macaque or human—were confined to separate boxes. Under this paradigm, perception (seeing objects, hearing sounds, and so on) and action (reaching for a piece of food, grasping it, putting it in the mouth) are entirely separate and independent of one another. A third function, cognition, is somehow “in between” perception and action and allows us to plan and select our motor behavior, to attend to specific things that are relevant to us, to disregard extraneous matters, to remember names and events, and so on. These three broadly construed functions were typically assumed to be separate in the brain. The paradigm reflected the justified bias in science for the most parsimonious explanation of phenomena. To dissect a complex phenomenon into simpler elements is a good principle for investigation. It is still the dominant approach in neurophysiology and neuroscience, and in many specialized areas of research it works well. For instance, researchers have identified neurons that respond only to horizontal lines in the visual field, while others code for vertical lines.

Many brain cells do seem to be highly and narrowly specialized. The neuroscientist who assumes that neurons can be so easily categorized, however—with no crossing over between perception, action, and cognition—may miss entirely (or dismiss as a fluke) neuronal activity that codes with much more complexity, that reflects a brain that is dealing with the world in a much more “holistic” fashion than previously understood. Such was the case with mirror neurons. The Parma investigators, each and every one of whom was a superb scientist, were nevertheless unprepared for a motor neuron that was also a perception neuron. An old quip makes this point in general terms: “Progress in science proceeds one funeral at a time.” That is rather morbid and also a great exaggeration, but we all know that it is hard to give up the old paradigm, to think outside the box, to change—and not just in science. Indeed, quite a few years were required for them (and, by then, other investigators around the world) to figure out the “complex visual responses” recorded in the lab. Initially, scientists were not mentally ready to challenge the assumptions inherited from generations of researchers; those assumptions had guided a lot of productive research. Moreover, no findings prior to that moment had contradicted the assumptions.\(^2\)

Now they did—and in more ways than one. During the years of early work with mirror neurons, the Rizzolatti team
was also uncovering a set of cells in area F5 with another feature for which they could not account. These were cells that fired during grasping behavior and also at the very sight of graspable objects. They were later called canonical neurons, a bit ironically. Both of these patterns of neural activity contradict the old idea that action and perception are completely independent processes confined to their separate boxes in the brain. In the real world, as it turns out, neither the monkey nor the human can observe someone else picking up an apple without also invoking in the brain the motor plans necessary to snatch that apple themselves (mirror neuron activation). Likewise, neither the monkey nor the human can even look at an apple without also invoking the motor plans necessary to grab it (canonical neuron activation). In short, the grasping actions and motor plans necessary to obtain and eat a piece of fruit are inherently linked to our very understanding of the fruit. The firing pattern of both mirror and canonical neurons in area F5 shows clearly that perception and action are not separated in the brain. They are simply two sides of the same coin, inextricably linked to each other.

Some of the earliest macaque experiments in Parma—back in the 1980s, years before the puzzling episodes that turned out to mark the discovery of mirror neurons—supported these same conclusions about the tight link between perception and action. At that time, the team conducted a set of experiments focused not on area F5 in the motor cortex, but on the adjacent area F4. In area F5, as we have seen, the cells most readily fire while the monkey performs actions with the hands. Neurons in area F5 also fire when the monkey makes mouth actions such as biting, as well as facial communicative gestures such as lip smacking, which has a positive social meaning in primates. Indeed, some neurons in F5 fire for hand actions and for mouth actions. The firing pattern of these neurons is yet another feature that contradicts those models of the brain made of separate boxes, with one box for the hand and a separate one for the mouth. (This is how an engineer, I guess, would probably build a brain.) Neurons that code for both hand and mouth actions, however, make perfect sense to holistic interpretations of brain functions, in which motor cells are concerned with the goal of an action. Indeed, the hand brings the food to the mouth. In area F4, the cells fire mostly while the monkey moves the arm, the neck, and the face. That was the thinking, and those were the results of the experiments before the discovery that the cells also fire in response to sensory stimulation alone, with no movement from the monkey. Moreover, they respond to stimulation only from real objects. Simple lights or shapes projected on a screen do not trigger any discharge from these cells. Also, they fire only when the objects in question are quite close to the monkey's body, and they fire more strongly when the objects are rapidly approaching. Another peculiar feature of these cells: they respond to a simple touching of the face, neck, or arm of the monkey. Conclusion: the visual receptive field (that part of the surrounding space in which visual stimuli trigger the firing of the cell) and the tactile receptive field (that part of the body that, when touched, triggers the firing of the cell) are related in these neurons in area F4. Their amazing responses suggest that they are creating a map of the
space surrounding the body, what we call a peripersonal space map. And they also trigger the monkey's movement of the arm, say, in that space. Two very different functions are manifested in one group of cells. These physiological properties suggest that the space map surrounding the body is a map of potential actions performed by the body.\(^4\)

As it happens, the new paradigm inaugurated by the discovery of these F4 and F5 neurons—including mirror neurons, of course—was foreseen in a way by Maurice Merleau-Ponty, a French philosopher working in the early twentieth century. Merleau-Ponty was a member of a school of philosophy known in the decades around 1900 as phenomenology. Other members were Franz Brentano, Edmund Husserl, and the great Martin Heidegger. They criticized the classical philosophical approach as being seduced by the holy grail of discovering the very essence of phenomena and thus getting bogged down in musing about abstractions (the Platonic tradition), and they proposed instead to "go back to the things themselves" (the Aristotelian instinct, in effect). The phenomenologists proposed to pay close attention to the objects and phenomena of the world and to our own inner experience of these objects and phenomena. In the lab in Parma, Rizzolatti and his colleagues were very traditional in the techniques they used to study the cells in areas F4 and F5 in the frontal cortex of their macaque monkeys, but over time, they were able to overcome the traditional framework for interpreting their results: separate compartments for motor, perception, and cognition cells. They were able to wipe away the ruling paradigm and hypotheses. They didn't waste years trying to extract complex and abstract computational rules to explain the apparently bizarre observations that were piling up. Instead, they were able to employ a fresh, open-minded approach to the research, which I call neurophysiologic phenomenology. Their new attitude was the only means of realizing that perception and action are a unified process in the brain.

The head "philosopher" in Parma was the bearded and dark-eyed neurophysiologist Vittorio Gallese. Gallese was the one digging into Merleau-Ponty's work, finding the appropriate analogies between philosophy and neuroscience, explaining the group's discoveries in less scientific and more philosophical terms. Gallese was also more willing to speculate about the most profound implications of mirror neurons. Indeed, his presentation at a meeting titled "Toward a Science of Consciousness," in Tucson, Arizona, in 1998, was the catalyst for making mirror neurons well known in the scientific world for the first time. At that meeting Gallese met coincidentally Alvin Goldman, a philosopher interested in the problem of other minds. Goldman is a paladin of the simulation theory, which holds that in order to understand what another person feels when, say, she is in love, we must pretend to be in love ourselves. He immediately caught the implications of this new mirror neuron research for his own thinking, and he and Gallese worked together on a paper that proposed for the first time that mirror neurons may be the neural correlate of the simulation process necessary to understand other minds.\(^5\)

Gallese's passion for philosophy and science is surpassed
only by his love for the opera, which is not at all unusual in Parma. He is one of the twenty-seven members of the exclusive Club dei 27 (www.clubdei27.com), wherein each member personifies one of Giuseppe Verdi's twenty-seven operas. I do not use the term "exclusive" lightly. There will be no more operas from Verdi, may he rest in peace, so it will never be Club dei 28. The only way one can become a member is for another member to pass the torch (highly unlikely) or pass away. Gallese personifies a lesser-known opera of the Maestro, *I Lombardi alla prima crociata*, but of course he had no choice in this. He grabbed the only available opening! A highlight of Gallese's third career (neuroscience and philosophy are the first two) was the night that the Club dei 27 bestowed a medal on the peerless Spanish tenor Plácido Domingo. Gallese joined his twenty-six confreres in singing for the listening pleasure of one of the greatest of all Verdi interpreters.

Is that preceding paragraph a digression? I don't think so. With the rarest of exceptions, great science is about the combined, dogged legwork of at least several if not many individuals. It's all about teamwork. And what makes a great team of any sort? Nobody really knows, but when it happens, anyone can clearly see the results. In the lab in Parma directed by Giacomo Rizzolatti, a collection of neuroscientists contributed to the magic in many different ways. Vittorio Gallese's interest in philosophy and phenomenology was not incidental at all; in fact, it was probably critical. His philosophical tendency and his passion for the opera are markers of a personality with broad interests and an ability and willingness to think outside the box. In my experience, the best scientists are interesting people.

Joining Gallese and the lab director, Rizzolatti, as key members of the team were Luciano Fadiga and Leo Fogassi. These four neuroscientists are all quite different from one another in personality and intellectual inclinations. Maybe this is one of the reasons things worked out so well. In any event, each made a unique contribution to the collective work, as would be the case in any world-class scientific enterprise. Fadiga, tall and slender, has a knack for developing new tools for the laboratory and possesses the social skills necessary for management and fund-raising. Modern science requires all three: technological innovation, management skills, and lots of money. (With machines that can easily cost hundreds of thousands of dollars or as much as two or three million, basic research in neuroscience is particularly expensive.) Typically, the scientists who are great with technical matters in the lab are not so good at the "people" end of the job. Fadiga is one of the exceptions to this rule. He was the team member who first applied the relatively new technique of transcranial magnetic stimulation (TMS) to the study of the mirror neuron system in humans (a subject for later discussion). He recently moved to the University of Ferrara, where his new lab is already an efficient and productive machine. No surprise there.

In contrast with Fadiga, Leo Fogassi is by far the least outspoken individual of the four Parma neuroscientists. In the years just after the discovery of mirror cells in the early 1990s, Fogassi was definitely less involved in communicating the ex-
peripheral findings to the scientific community. Communication is a fundamental aspect of science, of course, but it is just not Fogassi’s forte. He’s a great lab man, probably the one scientist who has directly performed or supervised the largest number of single-cell recordings in the mirror neuron system in the world. In the last few years he has taken the lead in a variety of important projects, most important of which is the series of experiments on the role of mirror neurons in understanding the intentions of others. I’ll discuss this vital work shortly.

This brings us to the leader of the group, Giacomo Rizzolatti, who should be considered as nothing less than a Renaissance man. In modern science, specialization is the order of the day, and then specialization within specialization. Most scientists focus on a single research issue, using just one modality of investigation. Rizzolatti’s research ranges far and wide, including visual neurophysiology in cats, behavioral neurology in brain-damaged patients, experimental psychology in healthy volunteers, anatomical and neurophysiological studies in primates, brain imaging in humans, and—in addition to all this—computational neuroscience! Rizzolatti’s ability to connect all these different lines of research in an integrated and coherent view of human brain function is almost uncanny and definitely unique in modern neuroscience. Above all, his intuitions about how the brain works are incomparable. (Maybe this talent for deep insight is why his somewhat ruffled white hair always reminds me of Albert Einstein.) The early work in Parma, which led to the discovery of mirror neurons, originated from Rizzolatti’s intuitions about the role of premotor areas in creating “space maps” surrounding the body. He called this theory the premotor theory of attention. Several years ago, by simply looking at the pattern of reaction-time data in healthy volunteers during a visuospatial task (certainly not the most self-explanatory piece of information with regard to brain function), Rizzolatti proposed a model of visuospatial attention—that is, how we pay attention to some object or movement on our left side and not on our right side—that was confirmed by brain imaging techniques many years later.6

Rizzolatti, Gallese, Fogassi, and Fadiga were the Fab Four; and together they changed everything. The discovery of mirror neurons and the development of their possible implications was primarily due to the collaborative chemistry of these four neuroscientists. In the years to come, even the educated layperson’s understanding of how we humans really see the world, and how we function as social animals within it, will never be the same.

MIRRORS IN THE BRAIN

Isn’t the devil in the details? In neuroscience, at least, this always seems to be the case, and it is definitely so with mirror neurons. It is the slight variations of the experimental setups in labs around the world that have revealed the subtlety of responses from these neurons, which in turn have opened the doors to our understanding. On the other hand, there was nothing unique about the investigative tools used in Parma.
Using the classic methodology of single-cell neurophysiology, Rizzolatti and his colleagues implanted electrodes in area F5 of the macaque subjects and recorded any electrical changes—"action potentials"—on the surface of individual neurons as the monkeys performed certain tasks in exchange for rewards of food. The electrical activity in the brain is what tells us that a particular neuron has been activated at a particular time. It has "fired," as we say, and it has done so in order to code either a sensory event (seeing some object or action), a motor act (grasping the apple), or a cognitive process (the memory of grasping the apple). (Under the old "separate boxes" paradigm, as we have seen, any given cell would code for one and only one of these three activities. Mirror neurons code for two of them, breaking down the barrier between perception and action.) These electrical discharges are also the way brain cells send signals to one another. Even cells that are far from each other in the brain can communicate through action potentials, as long as they are physically connected with axons, which are long extensions of the cell that serve as extension cords of a sort.

These classical experiments give us access to brain activity at its most exquisite, fine-grained level—the single cell—and provide exquisite spatial and temporal "resolution." We are working not only with the single cell, but instant by instant. This research provides incredibly important information. From our understanding of the brain mechanisms of our evolutionary predecessors we can infer neural mechanisms in the human brain. These experiments with the macaques are invasive, no doubt about it. Implanting the electrodes requires brain surgery. Although extreme care is taken to avoid discomfort in the implanted subjects, ethics preclude conducting such experiments on humans or the great apes (chimpanzees, gorillas, orangutans, and bonobos). The only exception to the rule is with certain neurological patients (most commonly epileptics) who have electrodes implanted for medical reasons. In such instances, single-cell research is perfectly ethical when permission is granted, as it almost always is. This limited research has yielded important results, as we will see later. And now, of course, the amazing new technology of noninvasive brain imaging (functional magnetic resonance imaging or fMRI, magnetoencephalography or MEG, and others that I will describe in later chapters) allows experimentation with human subjects that combines with the single-cell research on monkeys to yield the results and insights that are the subject of this book.

In setting the stage for the discovery of mirror neurons, I stated that the Parma investigators had acquired a pretty good picture of the actions of these motor cells during various "grasping" exercises with the monkeys. Let's now consider those early results in more detail. They are indeed fascinating, beginning with the fact that the motor cells fire throughout the whole grasping action, and not in correspondence with the contractions of any specific muscles. Even more surprisingly, the same cell often fires for both right-hand and left-hand actions and also, as anticipated earlier, when the monkey is moving the mouth. The team expected more specificity in the firing pattern—right hand only, left hand only, mouth only. What they saw, however, was this kind of specificity with the type of
grasp the monkey was using. Some of these neurons fired only while the monkey was grasping small objects using two fingers, such as the handle of a cup using the thumb and the index finger. We call this type of grasp the precision grip. Other neurons in F5 fired only while the monkey was grasping large objects, such as a cup, using the whole hand—the wholehand grip. It is in some way irrelevant to the monkey whether she grabs the cup with the right hand or the left hand, but the manner in which she grabs it is relevant. This is strange to us. Equally strange to us is the fact that these “grasping” brain cells do not fire when the monkey is scratching her head or performing another hand action, even though the very same finger muscles are used. These peculiarities suggest the existence of a somewhat complex vocabulary, in neural terms, of simple object-oriented actions and—the key point—at the level of the single cell.7

Of course, some—just some—of these cells also respond to visual stimulation, the surprising capacity that makes them either canonical neurons or mirror neurons. As discussed, the canonical neurons fire at the sight of certain graspable objects, the mirror neurons at the sight of grasping actions. As we might guess by now, these responses also have their peculiarities. The canonical neurons are sensitive to the size of the graspable object. For instance, if a cell fires when the monkey grasps a small object, such as a piece of apple, using the precision grip of thumb and index finger, the same cell will fire only when the monkey sees a comparably small object. This cell will not fire when the monkey sees a whole apple, which can be grasped only with a whole-hand grip. Likewise, canonical neurons in area F5 that fire when the monkey grasps a whole apple with a whole-hand grip will also fire when the monkey sees a whole apple, but will not fire when the monkey sees a raisin, which would require a precision grip to grasp. The correlation between action and perception in canonical neurons is tight indeed.

What about mirror neurons? Some mirror neurons also show this tight correlation between action and perception. These cells are called strictly congruent mirror neurons because they fire for identical actions, either performed or observed. For instance, a strictly congruent mirror neuron fires when the monkey grasps with a precision grip and when the monkey sees somebody else grasping with a precision grip. Another strictly congruent mirror neuron would fire when the monkey grasps with a whole-hand grip and when the monkey sees somebody else grasping with a whole-hand grip. Other mirror neurons, however, show a less strict relationship between executed and observed actions. These are the broadly congruent mirror neurons. They fire at the sight of an action that is not necessarily identical to the executed action but achieves a similar goal. For instance, a broadly congruent mirror neuron may fire when the monkey is grasping food with the hand and when the monkey is seeing somebody else getting food with the mouth.

In no case so far observed has the discharge of mirror neurons during action observation been modulated by the identity of the object to be grasped. Apple or orange? Peanut or raisin? It doesn't matter. Only the size matters, which makes perfect sense for motor purposes. Larger objects require the
whole-hand grasp, smaller ones the precision grip. The discharge of mirror neurons during an observed action is also largely unaffected by the distance to the action. The scene can be close or far away. Mirror neurons also fire equivalently at the sight of a grasping human hand or a grasping monkey hand. They also fire similarly whether the experimenter grasping a piece of food eventually gives the food to a second monkey in the lab or to the subject monkey with the implanted electrodes. In short, the rewarding value of the grasping action does not affect the response of mirror neurons.8

A very interesting class of mirror neurons codes observed actions that are preparatory or logically related to the executed actions. A “logically related” mirror neuron is one that, for instance, fires at the sight of food being place on the table and also while the monkey grasps the piece of food and brings it to the mouth.9 This class of cells may be part of neuronal chains of mirror cells that are important for coding not simply the observed action but also the intention associated with it. This intention is achieved through a sequence of simpler actions: reaching for the cup, grasping it, bringing it to the mouth, and then drinking from it.

A really telltale feature of the macaques’ mirror neurons is that they do not fire at the sight of a pantomime. Performing a grasping action in the absence of an object does not trigger a discharge. This may seem odd to us, but it isn’t particularly so, because these monkeys do not typically pantomime. We humans, however, do pantomime, and indeed our mirror neuron areas are activated by more abstract actions than are those of the monkeys. The several evolutionary steps dividing monkeys from humans can easily account for such difference. A subject for future discussion here will be the theory by computational neuroscientist Michael Arbib that mirror neurons are key precursors of neural systems for language. He proposes that pantomime plays a critical role in the evolutionary progression from the relatively simple mirror neuron system in monkeys to the much more sophisticated neural system that supports the high level of abstraction in human language.10

As we have seen, mirror neurons in area F5 fire at the sight of mouth actions as well as hand actions. In this capacity, these cells belong to two main categories: those that code for ingestive movements—eating a banana, drinking juice—and others that code for communicative movements such as lip smacking, a slight protrusion of the lips.11 The existence of mirror neurons for communicative mouth movements suggested to Rizzolatti and his colleagues in Parma that these cells may have a profound role in the ability to communicate between individuals and in the understanding of other people’s behavior. Thus they devoted a whole series of experiments to deeper aspects of the role of mirror neurons in coding the actions of other individuals.

I KNOW WHAT YOU ARE DOING

I am cooking dinner, and my daughter, Caterina, a sixth grader, is doing her homework on the table in the kitchen nook. I can watch her while I cook. The table is covered with books, notebooks, pencils, erasers, and so on. (I often feel that
sixth graders these days have more homework than I had in high school.) As I cook dinner, I can't fully see what Caterina is doing. Her study materials are blocking my view. Still, I never feel I have to go on an elaborate inferential process to discern what she is doing. How is it possible? How can I have an immediate understanding of her movements even though I can't see them fully? Do my mirror neurons assist me in knowing and understanding what I cannot see? Alessandra Umiltà, now on the faculty at the University of Parma, was a graduate student in Giacomo Rizzolatti’s lab when she led an experiment that tested this exact hypothesis.

The first two conditions of her experiment had been previously tested. In one, a monkey observed a human experimenter grasping an object. As expected, mirror neurons did fire at the sight of this grasping action. In the other condition, the monkey observed a human experimenter pantomiming a grasping action, in the absence of a real object to be grasped. As expected, the pantomime did not trigger a discharge in the neurons. With these standard but necessary results in hand, Alessandra added two new conditions to test whether mirror neurons would fire during an action the monkey cannot really see. In one, a three-dimensional object, for instance an orange, was positioned on the table. Subsequently, a screen was placed in front of the orange (other kinds of objects were also used, as these experiments typically involve several trials for each condition). With this screen occluding the monkey's sight of the orange, a human experimenter reached with her right hand behind the screen. The monkey saw the reaching but not the actual grasping of the orange. The question is: Did mirror neurons fire when the grasping action itself was hidden? The answer was yes (and no). Approximately 50 percent of the mirror neurons recorded in that experiment did fire; half did not.

In the other new condition, the table was bare. The screen was moved into position blocking the monkey’s view of the bare table. Again, a human experimenter reached behind the screen with her right hand. Note that from the monkey’s visual standpoint the experimental condition at this moment was identical to the previous one: the monkey was seeing a hand reach behind a screen. The only difference between the two conditions is the animal’s prior knowledge concerning the presence of an object on the table. The question is: Did the monkey understand that this was a pantomime? If so, mirror neurons should not fire—and indeed they did not. The prior knowledge that there was no object on the table was sufficient for the mirror cells to now consider the hidden grasping action simply a pantomime, and thus not worth firing for.¹²

These experiments clearly show that mirror neurons do not simply form a neural system matching performed actions and observed ones. Even in the monkey, they provide a more nuanced coding of the actions of others, using prior information to differentiate the meaning of partially blocked actions that are visually identical. Is this sufficient evidence for us to conclude that mirror neurons code the intentions of the person grasping the object? Probably not, since the basic issue in the experiment was whether the hand grasped or not, as determined by the presence or absence of the object (the or-
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ange, in the example above). This experiment does not fully address the fundamental question of whether mirror neurons can differentiate between, say, grasping the orange in order to eat it versus grasping the orange in order to place it in the refrigerator. This is why Leo Fogassi, some years after Alessandra Umiltà’s experiment, led another experiment that more explicitly investigated the role of mirror neurons in understanding intentions.

I KNOW WHAT YOU ARE THINKING

I am having a row with my wife over some family plans. We are in the kitchen, and she reaches for a glass. Does she want to drink or put it in the dishwasher—or maybe throw it at me? It is very useful to be able to predict what other people are going to do next.

The most basic property of mirror neurons—that is, firing for both the action of grasping a cup and the equivalent grasping action I only observe—suggests that they are helpful for recognizing the actions of other people. They also suggest that the action recognition process thereby implemented is some sort of simulation or internal imitation of the observed actions. Given that our own actions are almost invariably associated with specific intentions, the activation in my brain of the same neurons I use to perform my own actions when I see other people performing these actions may also allow me to understand the intentions of the other people. However, it can’t be this simple. There’s a problem, and it’s the one I am

facing when I see my wife grasping the glass during our row: the same action can be associated with different intentions. In fact, there is rarely, if ever, a one-to-one correlation: this action, this necessary intention. Just as I may have different intentions when I grasp a glass, so may others. Do mirror neurons differentiate between the same action associated with different intentions?

Leo Fogassi’s recent experiment addressed this question directly by assessing the monkeys’ neural activity during a variety of conditions of grasping execution and grasping observation. An explanation of the experiment requires a good deal of detail, but it is important for understanding these neurons. In one of the execution conditions, the monkey, starting from a fixed position, reached for and grasped a piece of food, then brought the food to the mouth to eat it. In a subsequent condition, the monkey reached for an inedible object in the same location as the food in the previous experimental condition. The monkey placed this object in a container. In this condition, several trials were performed while the container was located close to the mouth of the animal, such that the arm and hand movements of the grasping-to-eat and grasping-to-place conditions were closely matched. The main question was whether mirror neurons fire differently when the same grasping action leads to eating food as opposed to placing an object in a container. Does the intention matter to these neurons? (Note also that after completing the placing-in-the-container trials, the monkeys were rewarded, so the amount of reward for grasping-to-eat and grasping-to-place was identical.)

Between a third and a fourth of the recorded neurons fired
equivalently during grasping-to-eat and grasping-to-place. The majority of the neurons, however, fired differently, with about 75 percent discharging more vigorously during the grasping actions that brought food to the mouth, about 25 percent more vigorously during the actions to place objects in containers. What are we to make of these numbers? Maybe the differential discharging—the preference for eating over placing—was due to the fact that in one condition the monkey was grasping food, whereas in the other condition the animal was grasping a less interesting and useful object for placement. To test for this possibility, the monkeys were tested under the condition of placing food. The results were the same as in the previous experiment. The majority of cells discharged preferentially during grasping for eating, a minority preferred grasping for placing, and the minority of cells that had shown no preference for eating or placing still showed no preference. Conclusion: the type of object grasped was irrelevant. The important issue for mirror neurons was eating versus placing. Most “preferred” eating.

With these results in hand, the experimenters then proceeded to test the monkeys as they merely observed the same experimental setups, with an experimenter seated in front of the monkey performing the same grasping actions as the monkey had previously performed—some for eating, some for placing. With a container present and visible to the monkey, the experimenter grasped the food and placed it in the container. With no container present, the experimenter grasped the food, brought it to the mouth, and ate it. Thus the presence of the container acted as a visual clue, allowing the monkey to predict the next movement of the experimenter. The empirical question was whether mirror neurons would register a distinction when the monkey was observing grasping-to-eat versus grasping-to-place. The results demonstrated that the intention of the experimenter did make a difference, and the pattern of neuronal firing during observation of this grasping closely mirrored the pattern of neuronal firing as the monkey executed the grasping actions. If a cell discharged more vigorously while the monkey was grasping the food in order to eat, that same cell discharged more vigorously while the monkey was observing the human experimenter grasping the food in order to eat. If a cell discharged more vigorously while the monkey was grasping the food in order to place it in the container, that same cell discharged more vigorously while the monkey was observing the human experimenter grasping the food in order to place it in the container. If a cell discharged equally while the monkey was grasping-to-eat and grasping-to-place, that same cell discharged equally also while observing the human experimenter.13

The results of Leo Fogassi’s experiment demonstrate that the coding of the actions of other people provided by mirror neurons is much more sophisticated than initially thought. Although Vittorio Gallese and Alvin Goldman had speculated soon after the discovery of mirror neurons that these cells may provide a key neural mechanism for understanding the mental states of others, they were in the minority at the time. Before Fogassi’s experiment, there was much more sup-
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Port in the scientific community for a more parsimonious account of the functions of mirror neurons, with the cells simply providing a form of action recognition. Fogassi’s experiment clearly supports the initial intuition of Gallese and Goldman. Mirror neurons let us understand the intentions of other people.

As I have stated, intention had always been considered off-limits for empirical study, too “mental.” Not anymore. Fogassi’s study and a soon-to-be-discussed imaging experiment with humans performed in my lab at UCLA strongly support the hypothesis that we understand the mental states of others by simulating them in our brain, and we achieve this end by way of mirror neurons. As I stated earlier, the fact that mirror neurons code differently the same grasping action associated with different intentions—not only when we perform the action, but also when we observe it in others—suggests that our brains are capable of mirroring the deepest aspects of the minds of others, even at the fine-grained level of a single cell.

I CAN HEAR WHAT YOU ARE DOING

I am working in my studio when I hear a distinctive noise from the living room. My daughter Caterina studies ballet, and she is at the age and proficiency level in which ballerinas start working en pointe. She is very excited and brings her new pointe shoes home for extra practice. Her steps with the pointe shoes make a distinctive sound on the hardwood floors.

MONKEY SEE, MONKEY DO

By simply listening, I know what she is doing. I know a lot of things by simply listening. Clapping, tearing paper, typing, breaking peanuts—these are all actions that produce sounds and can be easily recognized by all of us. We don’t give this ability a second thought. Most people think “we do it, that’s all,” but neuroscientists always ask how. And of course neuroscientists familiar with mirror neurons wonder whether these neurons might play a role in helping us recognize actions simply from hearing them. Evelyne Kohler and Christian Keysers are two such investigators. They performed their experiments on this subject in Giacomo Rizzolatti’s lab.

Following the usual procedures, Kohler and Keysers identified mirror neurons in area F5 by measuring the responses of the cells while the monkeys were performing goal-oriented actions and then simply watching experimenters perform the same actions. The key, clearly, was that these actions—breaking a peanut, ripping a sheet of paper, and so on—produce sound. (As a control, the monkeys were also tested for white noise and other sounds unrelated to the actions. The control sounds were used to rule out the possibility that mirror neuron responses to action sounds were simply due to the arousing, nonspecific effect of any sound.) With all the necessary groundwork in place, Kohler and Keysers then recorded mirror neuron responses under three different experimental conditions: vision and sound, vision only, and sound only. For the “vision only” condition, objects were prepared so that they could be manipulated to perform an action visually similar to the naturally occurring action but without produc-
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ing the sound. For instance, the peanuts were already broken in two parts and merely held in the initial position as if they were intact. The paper that was ripped was wet, so it produced no sound. In the “sound only” condition, digitized action sounds were used. There was no visual stimulation at all.

The results were clear and definitive: the mirror neurons discharged to all three experimental conditions. Some did seem to respond slightly more vigorously for the “vision and sound” condition, but the “vision only” and “sound only” conditions also yielded robust mirror neuron responses. These results are very important because they demonstrate that mirror neurons code the actions of other people in a fairly complex, multimodal, and rather abstract way. Those cells that fire when the monkey herself is performing the sound-producing action also discharge at the mere sound resulting from somebody else’s actions. That is, when we perceive the sound of a peanut being broken, we also activate in our brain the motor plan necessary to break the peanut ourselves, as if the only way we can actually recognize that sound is by simulating or internally imitating in our own brain the action that produces that sound.

Furthermore, the response of mirror neurons to auditory input is critical evidence in support of the hypothesized evolutionary link between these brain cells and language, the hypothesis proposed shortly after the discovery of mirror neurons by Giacomo Rizzolatti and Michael Arbib in a paper titled “Language Within Our Grasp.” The argument that mirror neurons are the evolutionary precursors of neural elements that enable human language was based first of all on an anatomical observation: area F5 of the monkey brain, where mirror neurons were recorded for the first time, is a homologue (that is, it corresponds anatomically) to an area of the human brain called Broca’s area. Broca’s area is an important brain center for language, named after the nineteenth-century French neurologist who discovered that a lesion here is typically associated with a disorder (Broca’s aphasia) that affects mostly language production.

The argument for mirror neurons as language precursors also stems from the subtle consideration that these cells, by coding both for your action and your observance of that action in others, seem to create a sort of common code—and therefore a sort of “parity”—between you and the other individual. Several years before mirror neurons were discovered, Alvin Liberman had proposed that, since sending and receiving a message require, respectively, production and perception, the two processes of production and perception must somehow be linked and have, at some point, the same format. Mirror neurons seem to provide precisely this common format.

However, the hypothesis that mirror neurons are precursors of neural systems dedicated to language had to face a problem. After all, language was initially spoken, occurring only through the auditory modality, whereas the sensory responses of mirror neurons had been initially investigated only in the visual domain. The discovery by Evelyne Kohler and Christian Keysers that mirror neurons also respond to action
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sounds provides strong support to the hypothesized links between mirror neurons and language. We will explore the language questions in much more detail in chapter 3.

MIRRORING TOOL USE

Until quite recently it was believed that only we humans use tools. We now know this is not true. Chimpanzees show some ability in using tools—nothing like ours, of course, but real nevertheless, and sufficient for scientists to study the evolutionary progression of tool use. In different locations in Africa, chimpanzees use the same tool, a stick, to achieve the same goal—eating ants—but they use this stick in fundamentally different ways from area to area. In the absence of any apparent difference in the environments of the different populations, the cultural difference suggests that the way tool use is learned and transmitted between chimpanzees is mostly through observation and then imitation.\(^7\) Is it possible that mirror neurons are the brain cells that allow such learning via imitation?

In macaque monkeys, as we have seen, mirror neurons do not respond to the sight of a pantomime of an action. This makes sense because mirror neurons seem to code only for those actions that the monkey can perform—that are in its motor repertoire, as we say—and monkeys do not pantomime. By extension, mirror neurons in monkeys should have only a limited role in observational learning in general and in tool-use learning in particular, because monkeys are not so skilled at using tools. Take the Japanese monkeys who “wash potatoes,” a behavior that apparently spread from one precocious individual to the whole community. This famous case has spawned a significant debate in animal behavior literature. Initially, the behavior was taken as evidence that monkeys can imitate novel actions, but it was then argued that this may not fit a stringent definition of imitative learning. According to the tougher standard, imitative learning requires learning a novel movement for your motor repertoire by watching somebody else performing the movement. A possible explanation of the monkeys’ behavior is that while the first monkey washes the potatoes, the attention of the observing monkeys is directed to the water (this is called stimulus enhancement). The next time the observing monkey is close to the water with a potato in her hand, a simple trial-and-error mechanism during the manipulation of the potato in the water may have helped the animal to learn how to wash the potato. This would not constitute imitative learning, which is of a higher order. One fact in favor of this more conservative explanation is that the practice of washing potatoes did not spread as rapidly as one would have expected. This case and similar ones have provoked a variety of opinions within the community of scientists studying animal behavior, but it is fair to say that the majority of scientists do not consider washing potatoes as strong evidence in favor of imitative learning in Japanese monkeys.

If the washing-potatoes behavior did spread mostly through stimulus enhancement rather than imitative learning, then it is very unlikely that mirror neurons played a crit-
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ical role, since these cells respond to the observation of action. Attending to inanimate things such as water is not within their purview. Yes, mirror neurons must have been involved in the recognition of manipulating and holding the potato, but their role in spreading this behavior would be limited to this initial form of action recognition. If, on the other hand, the spread of the behavior is attributed to some form of imitative learning, then one might consider a more direct involvement of mirror neurons. This hypothesis also requires some evidence that mirror neurons may actually respond to the observation of some actions that are not yet in the motor repertoire of the monkeys. This evidence has been provided by Pier Francesco Ferrari, an ethologist who had studied animal behavior (especially forms of social contagion in monkeys) for years before training as a neurophysiologist in the lab of Giacomo Rizzolatti. Here is what he found.

Rizzolatti's previous finding was that mirror neurons that fire at the sight of a human experimenter grasping a raisin with a precision grip (thumb and the index finger) do not fire when the experimenter grasps the raisin with a tool, pliers for instance. This might seem odd on first consideration, but recall the hypothesis that mirror neurons do not fire at the sight of actions that are not part of the monkey's motor repertoire (thus the disinterest of these cells in pantomime, because monkeys don't pantomime). Likewise, monkeys do not naturally use tools, so the monkey's mirror neurons draw a critical difference between the precision grip and holding a pair of pliers.

Ferrari and his colleagues were recording neurons mostly from the lateral part of area F5, a sector previously investigated only with regard to its motor properties, with the majority of cells coding for mouth actions. Ferrari's work came up with much more specific data. Almost all of these lateral F5 cells had motor properties, but there was a strong division of labor. Approximately one-fourth discharged during hand movements only, one-fourth during mouth movements only, and one-half during hand and mouth movements. Approximately two-thirds of the cells responded to visual stimuli; the majority were mirror neurons responding to the observation of actions of the experimenters. The novel finding, however, was that a robust contingent (approximately 20 percent of all recorded cells) responded to the observation of actions performed with tools (a pair of pliers and a stick with a metal tip). These mirror neurons responding to tool use also responded to actions performed with the hands and the mouth, but much more weakly. The main interest of this 20 percent minority was tool use.18

This discovery of a contingent of mirror neurons responding to the observation of "tool-use" actions is theoretically very important. These monkeys tested by Ferrari did not use tools themselves, so this is the first evidence of mirror neurons that prefer actions that are not in the motor repertoire of the observing animal. How should we interpret these findings? The first concept that comes to mind is that mirror neurons are concerned with goals more than with the specific actions to achieve those goals—a point demonstrated in the previously discussed data on the role of mirror neurons in distinguishing between intentions. The goal is the same whether...
the peanut is broken with the hand or with pliers. The goal is the same whether the food is grasped with the hand and eaten or speared with a stick and eaten.

This interpretation is plausible, but it does not explain why it took investigators so long to find neurons responding to tool use—approximately ten years from the first observation on mirror neurons. The Parma group had repeatedly attempted to measure such response but without success. I therefore think it is likely that these 20 percent of the mirror neurons in lateral F5 are the result of the repeated exposure of the animals to the sight of human experimenters using tools. This explanation of Ferrari's findings suggests that mirror neurons can acquire new properties, a key feature to support imitative learning. The formation of mirror neurons responding to tool use may be the first neural step in the monkey's brain to subsequently acquiring the motor skill to use those very same tools. Mirror neurons that respond to tool use are enticing evidence linking mirror neurons to imitative behavior, a powerful mechanism for learning.

**I KNOW THAT YOU ARE COPYING ME**

The case of the Japanese monkeys who wash their potatoes is just one example of an interest in imitation among animals that dates back at least to Darwin, who left detailed descriptions of various forms of mimicry in honeybees. There is ongoing heated debate on the question, as the old paradigm has been called into question. Among the naturalists of the nineteenth century there was a general consensus that imitation was quite widespread. For instance, George Romanes's book on animal intelligence, one of the most famous ethology treatises of the latter nineteenth century, describes monkeys as constant imitators: "they carry on this principle to ludicrous length." At the time, imitation was not considered the expression of a particularly high form of intelligence. Now it is. Indeed, a recent collection of essays describes imitation as "a rare ability that is fundamentally linked to characteristically human forms of intelligence, in particular to language, culture, and the ability to understand other minds." What a sea change since Romanes's times! And with this sea change comes another: the caution of researchers to acknowledge imitation as such. Behavior previously considered imitative in monkeys is now typically explained with some other, "simpler" cognitive mechanisms (such as the supposed stimulus-enhancement mechanism that might explain the spreading of potato washing in Japanese monkeys). This is now the dominant view among experts, but they must still deal with hard-to-refute evidence for imitative behavior in monkeys. Even neonates of rhesus monkeys are able to imitate some facial and hand gestures, such as lip smacking, tongue protrusion, mouth and hand opening, and opening and closing of the eyes. Still, most scholars consider true imitation—that is, the ability to learn simply from observation—limited to humans and maybe the great apes.

This debate goes to the heart of the essential question underlying all research on macaque monkeys: Why do they have mirror neurons? The replies vary. Some researchers say that
the real role of mirror neurons in monkeys is for action recognition, not action imitation. By activating mirror neurons in their own brains, observing monkeys recognize the actions of other individuals and apparently, to judge by the data from Leo Fogassi’s experiments on intention, the goal of those actions as well. This is obviously a very important mechanism that facilitates social behavior in monkeys. However, other scientists—and I am definitely one of them—point out that there is some evidence, albeit not overwhelming, for true imitation in monkeys. And even if one wants to discard such evidence, mirror neurons may also be involved in various forms of “contagion” (a technical term that does not imply disease). For instance, even assuming that the true mechanism of the spreading of potato washing among Japanese monkeys is stimulus enhancement, mirror neurons may be critical in the process by helping the recognition of the manipulative hand actions of the observed monkey. As it happens, Giacomo Rizzolatti, whose intuitions are to my mind without parallel in this field, has been quite conservative on these questions, emphasizing the role for these neurons in action recognition only. In recent years, however, he has been considering broader roles, and he is convinced of the role of mirror neurons in coding intentions. (As I’ve noted, his colleague Leo Fogassi’s grasping-to-eat versus grasping-to-place experiments have had a powerful impact on the entire neuroscience community.) I believe that Giacomo is now more receptive to the idea that monkeys do imitate and that mirror neurons would be critical for such imitation.

Of course, imitation can work both ways, and a recent behavioral study in monkeys has provided inferential evidence that mirror neurons play an important role in the ability to figure out if another somebody is imitating you. Here, the experimenters adapted a paradigm devised by the developmental psychologist Andrew Meltzoff, an expert in imitation and social cognition in babies and young children. During the initial experimental phase, called the baseline period, the monkeys observed two experimenters, each manipulating a wooden cube with a hole in each side. The experimenters were mimicking typical actions the monkey would direct at the cube, such as biting, poking at the holes, and so on. Then a third cube was placed within reach of the monkey. When the monkey started manipulating the cube, one of the two experimenters imitated accurately the monkey’s actions directed at the cube. The second experimenter, in contrast, performed different actions. For instance, if the monkey was poking at a hole, the imitator would also poke, while the non-imitator would bite. The monkey’s behavior was taped and analyzed with intriguing results. Initially, the monkey did not show any visual preference between experimenters, but then the monkey clearly looked much longer at the imitating experimenter. Clearly, the monkey—with what researchers call an “implicit” level of understanding—was able to recognize that one of the two humans was imitating her. An animal with an “explicit” understanding that she is being imitated will typically demonstrate behavioral strategies to test the imitator, such as sudden changes in behavior while looking directly at the imitator to gauge the response. The monkeys involved in the Ferrari study did not show this behavior. Their recog-
nition that they were being imitated was understood only implicitly, but even this more limited understanding has an important social value.

The classic single-cell experiments on mirror neurons that might corroborate these behavioral results have not yet been conducted. They will be, and it is very likely that they will corroborate the behavioral study. And with that not-so-bold prediction, I close this chapter on the experimentation on mirror neurons of the macaque monkeys at the level of the single cell—vitally important work, not only because of its inferential value for thinking about our own brains (which we generally cannot access at that level, for ethical reasons), but also because it tells us where to aim the new, noninvasive technology with which we can study the mirror neuron system in humans. I now turn to these machines and this fascinating research, which confirms in every way the importance of mirror neurons for our experience as complex social creatures.