## Charles G. Gross
### Award for Distinguished Scientific Contributions

### Citation

"For his outstanding discoveries on the role of the cerebral cortex in perception and behavior. Charles G. Gross has radically expanded our view of the workings of the primate visual system by finding that neurons in the inferior temporal cortex respond selectively to complex features of visual objects, including faces and hands. These remarkable findings have had a major influence in the field of neuroscience and have contributed greatly to our understanding of sensory processing and pattern recognition. His research has attracted many students to his laboratory, several of whom are now outstanding investigators in their own right. His collaborative work has contributed to a better understanding of 'blindsight' and sensorimotor integration."

### Biography

Charlie Gross was born in Brooklyn, New York, on a February 29th, of Communist intellectuals. His elementary school experience was a disaster, inducing hyperactivity and attention disorder. His frustrated academic drive was channeled into earning Boy Scout merit badges, making him the youngest Eagle Scout in Brooklyn. At Erasmus Hall High School, a large heterogeneous school, he fell in with a group of very smart students, which transformed him into a good student. Charlie edited the school math and science magazines and was an editor of the newspaper. He was a finalist in the Westinghouse Science Talent Search for a project in ecology—

plant succession—a natural choice of topic because he had spent every summer up to that point camping with his parents on an island in Lake George, New York.

At about the time that Charlie's father began to lose teaching jobs because of his politics, Charlie went off to Harvard. He would have liked to have majored in history but soon found that his politics were inconsistent with getting As, so he majored in biology. As a freshman, he took a graduate seminar in the history of biology with I. B. Cohen, and this subject has continued to be a major interest. He took physiological psychology with Phil Teitelbaum, history of psychology with E. G. Boring, and "Skinner" with B. F. Skinner, all of which had profound and permanent effects on him.

Charlie researched bird navigation and published his first scientific paper with Don Griffin, codiscoverer of bat echolocation and one of the great experimental naturalists of our time. One day Griffin said, "Gross, bring me the car battery from the next room," and Charlie replied, "What does a car battery look like?"—confirming that "you can take the boy out of Brooklyn but you can't take Brooklyn out of the boy." As a senior, Charlie was admitted to Harvard Medical School and was awarded graduate fellowships from the National Institutes of Health and the National Science Foundation in biology. To avoid choosing, he postponed them all and accepted a Fulbright scholarship to study ethology at Cambridge University (to England because he spoke no foreign languages, and in ethology because that was only done at that time at Cambridge and Oxford, and they seemed like fun places to go; they were).

At Cambridge, Charlie wandered around for about six months, rowing on the Jesus College crew (his first organized sports activity and the last until he ran the New York City marathon in 1990), luxuriating in the political freedom that was lacking in McCarthyite America. Eventually, he ended up as Larry Weiskrantz's graduate student in psychology. Life was fun: There were no classes or exams, only a thesis. He coauthored prethesis papers on such things as taste, peripheral vision, hippocampal and frontal cortex stimulation (the subject of his first paper for *Science*; Weiskrantz, Mihailovic, & Gross, 1960), tranquillizers, and the academic record of members of the Royal Society (his first paper for *Nature*), and he wrote pop science articles and film and book reviews for student and local publications. Weiskrantz was then and forever thereafter extraordinarily supportive of him. Charlie's thesis, "Some Alterations in Behavior Following Frontal Lesions in Monkeys," yielded a number of publications, none of which is ever cited now (except by his students). After six months of work on the historical introduction to his thesis, he had reached Galen in the second century, and Weiskrantz suggested that Charlie might "get on with" the more empirical material; thus the thesis never had a historical introduction, but the unused historical draft subsequently yielded a number of publications and became the core of his book *Brain,*

*Vision, Memory: Tales in the History of Neuroscience* (Gross, 1998).

Charlie was a postdoctoral fellow at the Massachusetts Institute of Technology (MIT) in 1961 under Hans-Lucas Teuber, who was organizing the first neuroscience department in the world. Charlie abandoned the study of the frontal lobe because he thought, incorrectly it turned out, that the frontal lobe was permanently relegated to some limbo outside of physiology and anatomy. He turned instead to inferior temporal cortex.

Inferior temporal (IT) cortex was known to be important for visual learning and memory, in part from the work of Mort Mishkin, one of Charlie's long-term friends and mentors. Thus, it was usually considered a "learning and memory" structure rather than a "visual structure." In addition to his lesion studies, Charlie wanted to begin parallel single neuron recording studies on IT cortex. However, there was no equipment or expertise in the department, and, indeed, he had never turned on an oscilloscope or seen a microelectrode. Teuber offered to buy whatever was needed, and more important, suggested a collaboration with George Gerstein, a postdoctoral fellow in the Communication Biophysics laboratory at MIT. Gerstein knew all about oscilloscopes and electrodes but left for the University of Pennsylvania before the first experiment was conducted.

Charlie was soon joined by Peter Schiller, another postdoctoral fellow. In order to teach themselves the myriad requisite but previously unfamiliar electronic, surgical, and physiological techniques, their experiment was embarrassingly simplistic but did manage to show that IT neurons were exclusively visual, whereas superior temporal ones seemed to be auditory. In most of these experiments, the animals were anesthetized, but some involved unanesthetized ones. The results from awake animals were puzzling, suggesting that perhaps the cells had foveal receptive fields and were modulated by attention and memory.

In 1965, Charlie moved to the Department of Psychology at Harvard and was joined by Carlos Eduardo Rocha-Miranda (a Brazilian aristocrat who subsequently was a leading figure in opossum neuroscience) and Dave Bender (who started as a Harvard undergraduate and left about 15 years later to a chair at the State University of New York at Buffalo). They discovered that IT cells had large receptive fields that included the fovea, were not retinotopically organized, and responded to complex stimuli much more than to spots, slits, or edges. A few responded best to faces, and a very few to hands.

There were several factors that probably sensitized Charlie and his colleagues to find IT cells with complex stimulus selectivities, including to faces. First, they had been studying the effects of IT lesions on visual discrimination and knew the more complex the discriminanda, the greater the effect of the lesions. Second, Charlie had visited the Polish neuroscientist Jerzy Konorski, who had pos-

tulated the existence of "gnostic neurons" such as ones selective for faces, facial expressions, body parts, simple objects, and scenes. Furthermore, he suggested they would be found in IT cortex. Third, Teuber was constantly telling stories about prosopagnosia after temporal lesions. Fourth, Charlie's lab was in the same building as that of Jerry Lettvin, who was studying bug detectors in the frog and who invented the term *grandmother cell*. Finally, they were working near Hubel and Wiesel, who had just published on hypercomplex cells and had suggested that cells with even more complex properties would be found in other areas.

Apparently, nobody much believed the IT neuron story until it was replicated starting 12 years later by an increasing number of groups in the United States and abroad. However, the prolonged disbelief seemed to have no deleterious effect on Charlie's getting grants or, in 1970, a job at Princeton.

Throughout his adult career, Charlie has been extraordinarily fortunate in three main ways. The most important was the truly great collection of graduate students, postdocs, and research technicians who found their way to his lab. They made research, teaching, writing, and, in the early days, staying up all night an unalloyed joy. They were, and still are, loyal, hardworking, and enthusiastic colleagues. Goat and pig roasts in Charlie's backyard, canoe trips, hikes, and stormy lab meetings tied their lives together. Charlie likes to boast that they went on (or will be going on) to well-rewarded careers, often receiving awards, memberships in honor societies like the National Academy of Sciences and the American Academy of Arts and Sciences (much earlier than he had achieved such distinctions), as well as professorial chairs and administrative and editorial positions that nobody ever offered him. This group includes Tom Albright, Dave Bender, Charlie Bruce, Chris Curcio, Bob Desimone, Charmaine Eastman, Laura Frishman, Maz Fallah, Ricardo Gattass, Michael Graziano, Rick Manning, Tirin Moore, Earl Miller, Martha Neuringer, Marlene Oscar-Berman, and Hillary Rodman.

Charlie has also been fortunate in his association with the enthusiastic MIT, Harvard, and Princeton undergraduates who have worked with him, many of whom have gone on to distinguished neuroscience careers. Finally, the institutions he has taught at and those that supported his research continue to give him the opportunity to travel, take photographs, and lecture all over the world.

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## Processing the Facial Image: A Brief History

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*The study of the neural basis of face perception is a major research interest today. This review traces its roots in monkey neuropsychology and neurophysiology beginning*

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*with the Klüver–Bucy syndrome and its fractionation and then continuing with lesion and single neuron recording studies of inferior temporal cortex. The context and consequence of the discovery of inferior temporal neurons selective for faces is described and current lines of research on inferior temporal cortex and face processing in both monkeys and humans are outlined.*

Today the study of the role of the brain in face perception is a large and active field. It has two principal roots: clinical neurology and studies of monkey cortex. Although Charcot (1883) and Wilbrand (1892) in the 19th century described difficulties in face perception after brain damage, a specific face agnosia was not described until 1947 by Bodamer, who coined the term *prosopagnosia* for it.

The other root of the contemporary study of neural mechanisms of face processing is single neuron recording from face-selective neurons in inferior temporal (IT) cortex in the monkey. My colleagues and I began our studies in this area in the early 1960s. Our investigations, their background, and their eventual extension by others to both monkeys and humans are the main subjects of this article.

First, I describe how IT cortex, so far away from primary visual cortex, became recognized as a visual area. Second, I summarize our early work on the properties of IT cortex. Third, I describe how and why we came across "face cells" and how the scientific community received those observations. Fourth, I briefly summarize how this work on monkeys was replicated and expanded by others. Finally, I describe how the findings on monkeys were extended to the human brain.

### The Klüver–Bucy Syndrome

The modern story of IT cortex begins with Heinrich Klüver, professor at the University of Chicago for many years and a pioneer in the development of methods for studying cognition in monkeys. Klüver was also quite interested in the effects of mescaline. He wrote a little book called *Mescal: The "Divine" Plant and Its Psychological Effects* (Klüver, 1928), based in part on his own experiences with mescaline. He thought the drug might act on the temporal lobes because mescaline hallucinations seemed to resemble the aura preceding temporal lobe seizures. Furthermore, both mescaline and temporal lobe epilepsy induced a similar pattern of lip smacking (Nahm, 1997). To test this idea, Klüver obtained the collaboration of Paul Bucy, a distinguished neurosurgeon at the University of Chicago. They removed the temporal lobes of several monkeys in order to see whether mescaline would still make the monkeys act as if they were on mescaline trips. The effects of mescaline, including lip smacking, seemed the same after the temporal lobectomies as before. Klüver stopped studying mescaline, at least in monkeys. However, the lobectomized monkeys showed a strange and intriguing set of behaviors, which Klüver turned to study in detail (Klüver & Bucy, 1937, 1938, 1939).

This constellation of dramatic behavioral changes after temporal lobectomy became known as the Klüver–Bucy syndrome. It had four salient characteristics. First, the animals showed "psychic blindness," or visual agnosia: They lost the ability to recognize the meaning of objects visually. They were deficient in learning and remembering visual discrimination habits, although they seemed to show no visuosensory deficits. Second, they tended to compulsively touch and mouth objects and to eat previously inedible material. Third, they no longer showed fear or anger. Fourth, they manifested markedly increased and indiscriminate sexual behavior.

Actually, Brown and Schäfer had published similar observations in 1888. However, that was a time of violent controversies on the location of the primary sensory areas such as visual and auditory cortex, and so their observations of these monkeys showing "generalized dementia" were lost.

The immediate question about the syndrome was whether its different aspects had a single underlying cause or whether they could be fractionated by smaller temporal lesions. This was taken up at the Yerkes Laboratory of Primate Biology in Orange Park, Florida, by the students and associates of Karl Lashley, particularly K.-L. Chow, Karl Pribram, and Mort Mishkin. They showed that smaller temporal lobe lesions could fractionate the components of the syndrome. The impairment in visual learning and memory only followed temporal cortical lesions, whereas the other three symptoms only followed amygdala lesions (Blum, Chow, & Pribram, 1950; Chow, 1951, 1952; Pribram & Bagshaw, 1953). Further work showed that only lesions of the cortex on the inferior convexity, IT cortex, corresponding to cytoarchitectonic area TE, produced the visual learning and memory deficits (Mishkin, 1954; Mishkin & Pribram, 1954).

There was now a period of intensive analysis of the behavioral effects of IT lesions. These studies showed that after IT lesions (a) there was a severe and permanent deficit in postoperative learning and retention of visual discrimination tasks; (b) there were no sensory threshold changes, such as in visual acuity, in the integrity of the visual fields or in other visual thresholds sufficient to account for the learning and memory deficits; (c) there were no impairments in learning and memory in modalities other than vision; and (d) the deficit occurred with visual discriminanda differing in a variety of single or multiple dimensions and tested in different ways provided the tasks were relatively difficult, as measured by the performance of matched control animals. Thus the deficit that followed IT lesions fit Freud's classic definition of a visual agnosia:

a deficit in recognition in the absence of any elementary sensory disturbances (Gross, 1973; Mishkin, 1966).

## Single Neuron Recording From IT Cortex

In the early 1960s my colleagues and I began to study the properties of single neurons in IT cortex in the hope of understanding their critical role in visual learning and memory. No one had tried to do so before. Furthermore, at this time little was known of the connections of IT cortex with the visual system: The multiple extrastriate visual areas had not yet been described. Striate cortex (V1) and V2 were the only known retinotopically organized visual areas in the monkey. However, by 1966 Mishkin had shown that the role of IT cortex in visual learning was dependent on information it received from striate cortex over a cortico–cortical pathway that included the corpus callosum and at least one synaptic stage in "prestriate" cortex (Mishkin, 1966).

In the first single neuron recording study of IT cortex, carried out with Peter Schiller (still active at the Massachusetts Institute of Technology [MIT]) and George Gerstein (recently retired from the University of Pennsylvania), we established that IT neurons would respond to visual and not auditory stimuli and that the opposite was true for neurons in the superior temporal gyrus (Gross, Schiller, Wells, & Gerstein, 1967). These results were found in immobilized animals given local anesthesia, nitrous oxide anesthesia, or whose ocular motor nerves had been immobilized. We then began recording from IT cells in awake behaving monkeys but were rather puzzled by the results (Gross, Bender, & Gerstein, 1979). The cells fired vigorously only when the monkey fixated at something of great apparent interest, such as a human eye at a hole or a flaming Q-tip. We suggested that these neurons were modulated by attention, had foveal receptive fields, or both. "Both" eventually turned out to be the case.

In order to test the foveal receptive field possibility, we turned to studying immobilized animals under nitrous oxide anesthesia. "We" now included Carlos Eduardo Rocha-Miranda from Brazil and David Bender, then a Harvard undergraduate. Carlos Eduardo went on to become Brazil's leading neuroscientist, and David recently retired as professor of physiology at the University at Buffalo, State University of New York. We worked together for three years and uncovered basic sensory properties of IT neurons (Gross, Bender, & Rocha-Miranda, 1969; Gross, Rocha-Miranda, & Bender, 1972). Many of these properties were different from those found in previously studied cells. These novel properties began to indicate why this area is so crucial for normal visual perception and visual learning.

First, unlike in previously known cortical visual areas, the receptive fields were not retinotopically organized. Rather, they all included the fovea or center of gaze. This seems appropriate for an area specialized for object recog-

nition, which is normally done foveally. Subsequent work on the ventral processing stream from striate cortex to IT cortex showed that as one moves from striate cortex to V2, then to V4, and then either directly to IT cortex or by way of area TEO, there is a systematic decline in retinotopic organization until it is gone in IT cortex (reviewed in Gross, Rodman, Gochin, & Colombo, 1992).

A second major property of the receptive fields of IT cells was that they were relatively large, especially for fields including the fovea. The median size was about 25 degrees square, with some extending virtually throughout the visual field. This afforded the opportunity for considerable generalization within the receptive field of a single cell.

Third, whereas all striate receptive fields are confined to the contralateral half field, about 40% of the IT fields were bilateral, extending into the ipsilateral visual field. Subsequent work showed that increasing bilaterality was another systematic trend as one moves from striate cortex to IT cortex (reviewed in Gross et al., 1992). As we later showed, this ipsilateral extension of the receptive fields is dependent on both the corpus callosum and anterior commissure (Gross, Bender, & Mishkin, 1977; Rocha-Miranda, Bender, Gross, & Mishkin, 1975). Thus, the two halves of spaces are united for the first time in IT cortex.

A fourth property of IT cells and one particularly relevant for their role in object recognition was that their responses to visual stimuli were dependent on the shape or color of the stimulus and sometimes on both parameters. Furthermore, few cells responded to diffuse light or even to light or dark spots. Rather, most cells responded best to more complicated stimuli.

Fifth, the responses of IT cells to shape usually remained invariant over change in size, contrast, and location within their receptive fields (Desimone, Albright, Gross, & Bruce, 1984; Schwartz, Desimone, Albright, & Gross, 1983). That is, they showed shape constancy, a crucial element of object recognition.

Sixth, from rather preliminary experiments, we suggested that the magnitude of IT responses could be modulated by attention and by the animal's previous experience—that is, by memory (Gross et al., 1979).

Finally, we come to the cells that are the occasion for this article: the small proportion of cells that responded best or only to faces and the even smaller number that responded specifically to hands. We discovered a "hand" cell before the "face" cells. The first of these hand-selective cells were reported in 1969 (Gross et al., 1969). Here is the account of its discovery (Gross et al., 1972):

> One day . . . having failed to drive a unit with any light stimulus, we waved a hand at the stimulus screen and elicited a very vigorous response from the previously unresponsive neuron. We then spent the next 12 hr testing various paper cutouts in an attempt to find the trigger feature for this unit.

When the entire set of stimuli used were ranked according to the strength of the response that they produced, we could not find a simple physical dimension that correlated with this rank order. However, the rank order did correlate with similarity (for us) to the shadow of a monkey hand. (pp. 103–104)

We briefly reported temporal cortex neurons selective for faces in 1972, 1980, and in more detail in 1981 (Bruce, Desimone, & Gross, 1981; Gross et al., 1972; Gross, Bruce, Desimone, Fleming, & Gattass, 1981). In the Bruce et al. (1981) study, the face-selective cells were actually not in IT cortex proper but were in the dorsal bank of the superior temporal sulcus in an area we termed the *superior temporal polysensory area*, or STP. Although all STP cells were visually responsive, unlike IT neurons some were also responsive to auditory or somesthetic stimuli. In addition to the face-selective neurons in STP, we also found STP neurons that were sensitive to biological motion (Bruce et al., 1981).

Our first (relatively) quantitative account of inferior temporal neurons selective for faces was published in 1984 (Desimone et al., 1984). Some of the cells would respond only or best to faces in profile, whereas others preferred faces viewed from the front, and still others responded to all views. Some would continue to respond, although more weakly if aspects of the face were altered, whereas others would only respond to an intact face.

There were several factors that primed us to notice cells selective for such complex stimuli as hands and faces. First, a few years earlier I had spent several weeks visiting the Polish neuroscientist Jerzy Konorski, who had postulated the existence of "gnostic neurons" such as ones selective for faces, facial expressions, body parts, simple objects, and scenes. He had suggested that they would be found in IT cortex (Konorski, 1967). I had recently written a long review of his book in which he put forth these ideas (Gross, 1968). Second, we had begun these IT studies at MIT in the department of the neuropsychologist Hans-Lucas Teuber, who was constantly telling stories about prosopagnosia after temporal lesions. Third, our first lab at MIT was down the hall from that of Jerry Lettvin, who was working on bug detectors in the frog (Lettvin, Maturana, McCulloch, & Pitts, 1959) and who had invented the term *grandmother cell* (Gross, 2002). (It was Horace Barlow [1953] who first used the term *bug detectors*, and I had heard him lecture on the subject when I was a graduate student in England.) Finally, we were working across the river from Hubel and Wiesel, who had just published on hypercomplex cells in V2 of the cat and had suggested that cells with even more complex properties would be found beyond V2 (Hubel & Wiesel, 1965). No wonder we found face and hand cells in this environment!

For some time, our findings on the unusual sensory properties of IT cells and our finding of face- and hand-selective cells seemed to have little or no impact on the field. Although we published in such high-profile places as *Science* and the *Journal of Neurophysiology*, there were no attempts to replicate and extend (or deny or even comment on) our results until 12 years after our initial paper. At that point, Richmond and Wurtz (1982) confirmed our work on the basic receptive field properties of IT units, and Rolls (1981) and his colleagues (Perrett, Rolls, & Caan, 1982) confirmed our reports of IT face-selective cells. Soon after there was a dramatic expansion of research on the properties of IT and STP cells, particularly in the laboratories of Rolls (reviewed in Rolls, 1992), Perret (reviewed in Perrett, Hietanen, Oram, & Benson, 1992), Miyashita (reviewed in Miyashita, 1990), Tanaka (Tanaka, Saito, Fukada, & Moriya, 1990), and Yamane (reviewed in Yamane, Komatsu, Kaji, & Kawano, 1990). Among the early major advances beyond our work were the demonstration (a) of a higher concentration of face-selective cells (about 20%) in both banks of the superior temporal sulcus than elsewhere in IT cortex (Baylis, Rolls, & Leonard, 1987); (b) that face cells selective for direction of eye gaze and for emotional expression were more common in both banks of the superior temporal sulcus, whereas cells sensitive to identity tended to be located on the lateral surface (Hasselmo, Rolls, & Baylis, 1989; Perrett et al., 1985); and (c) of correlates of short- and long-term memory in the activity of IT cells (e.g., Fuster & Jervey, 1981; Miller, Li, & Desimone, 1991; Miyashita, 1988).

## Recent Developments

In the last decade, research on the activity of IT neurons has expanded in a variety of directions by an increasing host of investigators. There is only space in this account to briefly indicate these interrelated directions and a few examples of each.

The first class of major developments concerned the further study of IT neurons in monkeys. One such direction was the specification of the responses of IT neurons to faces and other shapes and patterns (e.g., Baylis & Driver, 2001; Janssen, Vogels, Liu, & Orban, 2001; Sigala & Logothetis, 2002). A related direction was the use of IT neuron properties to develop models for object recognition (e.g., Gochin, 1994; Gochin, Colombo, Dorfman, Gerstein, & Gross, 1994; Logothetis, Pauls, & Poggio, 1995; Riesenhuber & Poggio, 2002; Vogels, Biederman, Bar, & Lorincz, 2001). A third development was the detailed study of the color properties of IT neurons and the concomitant realization that IT cortex may play a special role in color perception (e.g., Cowey, Heywood, & Irving-Bell, 2001; Komatsu, Ideura, Kaji, & Yamane, 1992). A fourth development was the demonstration of a columnar organization in IT cortex by both single neuron and optical imaging techniques (Fujita, 2002; Tanaka, 1996). A fifth direction was the study of the modulation of IT responses by attention (e.g., Chelazzi, Duncan, Miller, & Desimone, 1998;

De Weerd, Desimone, & Ungerleider, 2003). A sixth direction concerned how the activity of IT neurons may underlie short- and long-term visual memory (e.g., Colombo & Gross, 1994; Desimone, 1996; Higuchi & Miyashita, 1996; Messinger, Squire, Zola, & Albright, 2001; Miller & Desimone, 1994; Miyashita, 1993). A seventh direction was the functional subdivision of IT cortex (e.g., Murray, 2000; Murray & Bussey, 1999; Tamura & Tanaka, 2001). An eighth was the application of techniques of molecular biology to understanding IT function (e.g., Okuno & Miyashita, 1996; Tokuyama, Okuno, Hashimoto, Li, & Miyashita, 2002; Wang, Fujita, Tamura, & Murayama, 2002).

The second class of major developments was the extension to humans. This began with the demonstration with positron-emission tomography of activation of ventral temporal cortex by faces (Haxby, Grady, Ungerleider, & Horwitz, 1991; Sergent & Signoret, 1992), which was followed by the recording of single neurons and electrographic responses to faces in ventral temporal cortex (Ojemann, Ojemann, & Lettich, 1992; Puce, Allison, Gore, & McCarthy, 1995). Then fMRI studies reported a highly localized face-processing module in IT cortex (Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996), now termed the *fusiform face area* (FFA). Soon after, a specific IT module for processing places and then one for body parts were reported (Downing, Liu, & Kanwisher, 2001; Epstein & Kanwisher, 1998). The latter would appear to be homologous to the IT neurons selective for body parts, but the former appears to have no known parallel in the properties of IT neurons in monkeys. A current issue in this imaging field is whether face processing (and by extension, the processing of other visual categories) is carried out in localized modules like the FFA or is widely distributed in IT cortex (Haxby et al., 2001; Haxby, Gobbini, & Montgomery, 2004; Spiridon & Kanwisher, 2002). Another issue that has been raised is whether the "face module" is actually specialized for faces or for "expertise" (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauther, Tarr, et al., 2000). Research on the properties of IT neurons has also influenced studies of computational and computer vision (e.g., Cottrell, Dailey, Padgett, & Adolphs, 2001; O'Toole, Wenger, & Townsend, 2001).

Recently, the monkey and human classes of research have converged in the use of fMRI imaging to study processing of faces and other visual categories in monkeys. Facial images were found to produce discrete activation of localized areas in IT cortex (Logothetis, Guggenberger, Peled, & Pauls, 1999; Pinsk, DeSimone, Moore, Gross, & Kastner, 2005; Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003). These results were surprisingly consistent with the early IT single-unit results in monkeys in two ways. First, the greatest activation occurred in STS as it does in the monkey. Second, specific areas were also activated by body parts just as specific neurons are.

## Summary

Contemporary research on functional imaging of visual categories in the human brain derives, at least in part, from neuropsychological and then neurophysiological studies on the temporal lobe of macaques. This began with the Klüver–Bucy syndrome and the realization that its visual components were due to damage to IT cortex. My colleagues and I recorded from single neurons in IT cortex and found a small number of neurons that responded selectively to images of faces and hands. The intellectual context in which we worked primed us for this discovery, yet it was ignored for about a dozen years, at which time there was a flowering of replications and extensions of this work. One of these developments was imaging of responses to faces in the human brain.

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