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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

Editor's Note

Charles G. Gross received the Award for Distinguished Scientific Contributions. Award winners are invited to deliver an award address at the APA's annual convention. A version of this award address was delivered at the 113th annual meeting, held August 18–21, 2005, in Washington, DC. Articles based on award addresses are reviewed, but they differ from unsolicited articles in that they are expressions of the winners' reflections on their work and their views of the field.

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 cut-outs 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; Gauthier, 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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