

Single neuron studies of inferior temporal cortex

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Abstract

This paper reviews our experiments on the response properties of single neurons in inferior temporal (IT) cortex in the monkey that were carried out starting in 1965. It describes situational factors that led us to find neurons sensitive to images of faces and hands and summarizes the basic sensory properties of IT neurons. Subsequent developments on the cognitive properties of IT neurons and on imaging the responses of human temporal cortex to facial images are outlined. Finally, this paper summarizes recent results on fMRI imaging of the responses of temporal cortex to facial images.

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I was one of Larry Weiskrantz's first two research (graduate) students. For my dissertation I worked on the effects of frontal cortical lesions on various learning and memory tasks in macaques. When I finished, in spite of eight papers on the subject and a fat thesis (reviewed in Gross & Weiskrantz, 1964), I had no idea what the frontal cortex might do. I then went to H.-L. Teuber's new department at MIT that was to become the first neuroscience department, bringing together neuroanatomy, neurophysiology, neuropsychology and what was later called cognitive psychology (Gross, 1994a). Since the frontal lobes seemed intractable to me, I turned to study inferior temporal cortex.

Larry, working with Mort Mishkin and others in Karl Pribram's lab at the Institute of Living in Hartford Connecticut, had made major advances in understanding the role of inferior temporal (IT) cortex in visual memory and learning in monkeys. They had shown that damage to this region, also known as cytoarchitectonic area TE, was responsible for the psychic blindness component of the Klüver-Bucy syndrome that followed temporal lobectomy. Inferior temporal lesions produced impairments in visual learning and memory whereas the other aspects of the syndrome such as docility, hypersexuality and strange eating habits followed only from damage to the amygdala. Furthermore, inferior temporal lesions did not alter learning and memory in other

modalities, nor did it seem to produce any losses in basic visual functions such as visual acuity, the integrity of the visual fields or various visual thresholds. Thus, damage to this part of the brain produced a **visual agnosia** (Freud's term), a visual recognition deficit in the absence of any sensory losses sufficient to explain the deficit (reviewed in Gross, 1973, 1994b).

At first, it was puzzling how an area so far from striate (or primary visual) cortex could be visual in function. By the time I began my work on IT cortex it was realized that the visual learning and memory functions of IT cortex depended on a multi-synaptic cortico-cortical input that it received from each striate cortex (Mishkin, 1966). Soon after it became clear that the monkey's cortical mantle between striate and IT cortex contained a multiplicity of visual areas now known as V4, TEO and others. My initial work at MIT as a post doc was studying the effect of IT lesions on perception and visual learning (reviewed in Gross, 1973). But then, as this was the time of the brilliant successes of Hubel and Wiesel (1965) and others in using single neuron recording to study cortical function, I decided to use this technique in addition to lesions in my studies of IT cortex. So I thought I should look around for another post doc position to learn the requisite skills, as I had never seen, for example, a microelectrode. However, Teuber urged me to stay in his department, offered to equip an electrophysiology lab for me and in order to learn how to use it, he suggested I collaborate with George Gerstein, a post doc then working on the auditory system in Walter Rosenblith's Communication Biophysics Laboratory at MIT.

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6 Basic Properties of IT neurons:

1. RFs not retinotopically organized, but included center of gaze (projection of fovea).
 - magnitude of response ↑ at fovea
 - important for object recognition
2. Large RFs relative to RFs in earlier visual areas w/ fovea.
 - affords opportunity for considerable generalization across retinal translation w/in a single RF
3. Almost 1/2 of IT RFs extend across midline into ipsilateral visual field
4. Responses of IT cells dependent on size & color (sometimes both)
 - Complicated responses & no clear "optimal stimulus"
5. Responses of IT cells to shape usually remained invariant over Δ's in stimulus size, color, contrast, & exact position w/in central portion of the RF
 - ↑ distance from fovea = ↓ response
 - Resembles Shape Constancy (perception)
6. Small proportion of IT cells responded best or only to images of faces & smaller proportion to hands

After Gerstein and I set up an electrophysiology lab, he left for the University of Pennsylvania but continued as a collaborator. We were soon joined by a newly arrived post doc, Peter Schiller. We showed that single neurons in inferior temporal cortex responded to visual stimuli and not auditory stimuli and the opposite was true in superior temporal cortex (cytoarchitectonic area TA) (Gross, Schiller, Wells, & Gerstein, 1967). In these experiments the animals were anesthetized.

We also recorded from single IT neurons in awake behaving animals during a visual delayed match from sample task and in a crude “attention” task, and found suggestions of attentional and mnemonic modulation of IT activity (described later in Gross, Bender, & Gerstein, 1979). It was difficult to dissociate a possible attention effect from the alternative possibility that the neurons had receptive fields that always included the fovea (both eventually turned out to be the case). So we returned to the use of immobilized preparations to plot visual receptive fields more carefully than we had tried before. By this point I had moved to the Harvard psychology department and had been joined by David Bender and Carlos Eduardo Rocha-Miranda. The three of us worked out most of the six basic properties

of IT neurons that are described below (Gross, Bender, & Mishkin, 1977; Gross, Bender, & Rocha-Miranda, 1969; Gross, Rocha-Miranda, & Bender, 1972; Rocha-Miranda, Bender, Gross, & Mishkin, 1975). Further exploration of the properties of IT cells was carried out later with Bob Desimone, Tom Albright, Charlie Bruce and others (e.g. Albright & Gross, 1990; Bruce, Desimone, & Gross, 1981; Bruce, Desimone, & Gross, 1986; Colombo, Eickhoff, & Gross, 1993; Desimone & Gross, 1979; Desimone, Albright, Gross, & Bruce, 1984; Gochin, Colombo, Dorfman, Gerstein, & Gross, 1994; Gochin, Miller, Gross, & Gerstein, 1991; Gross, Bruce, Desimone, Fleming, & Gattass, 1981; Gross, Desimone, Albright, & Schwartz, 1984; Gross, Desimone, Albright, & Schwartz, 1985; Gross, Rodman, Gochin, & Colombo, 1993; Miller, Gochin, & Gross, 1991; Miller, Gochin, & Gross, 1993; Rodman, Gross, & Scalaidhe, 1993; Rodman, Scalaidhe, & Gross, 1993; Rodman, Skelly, & Gross, 1991; Schwartz, Desimone, Albright, & Gross, 1983).

First, IT neurons had visual receptive fields but they were not organized retinotopically as was the case for previously described visual areas. Rather, virtually all the receptive fields included the center of gaze (the projection of the fovea). Fur-

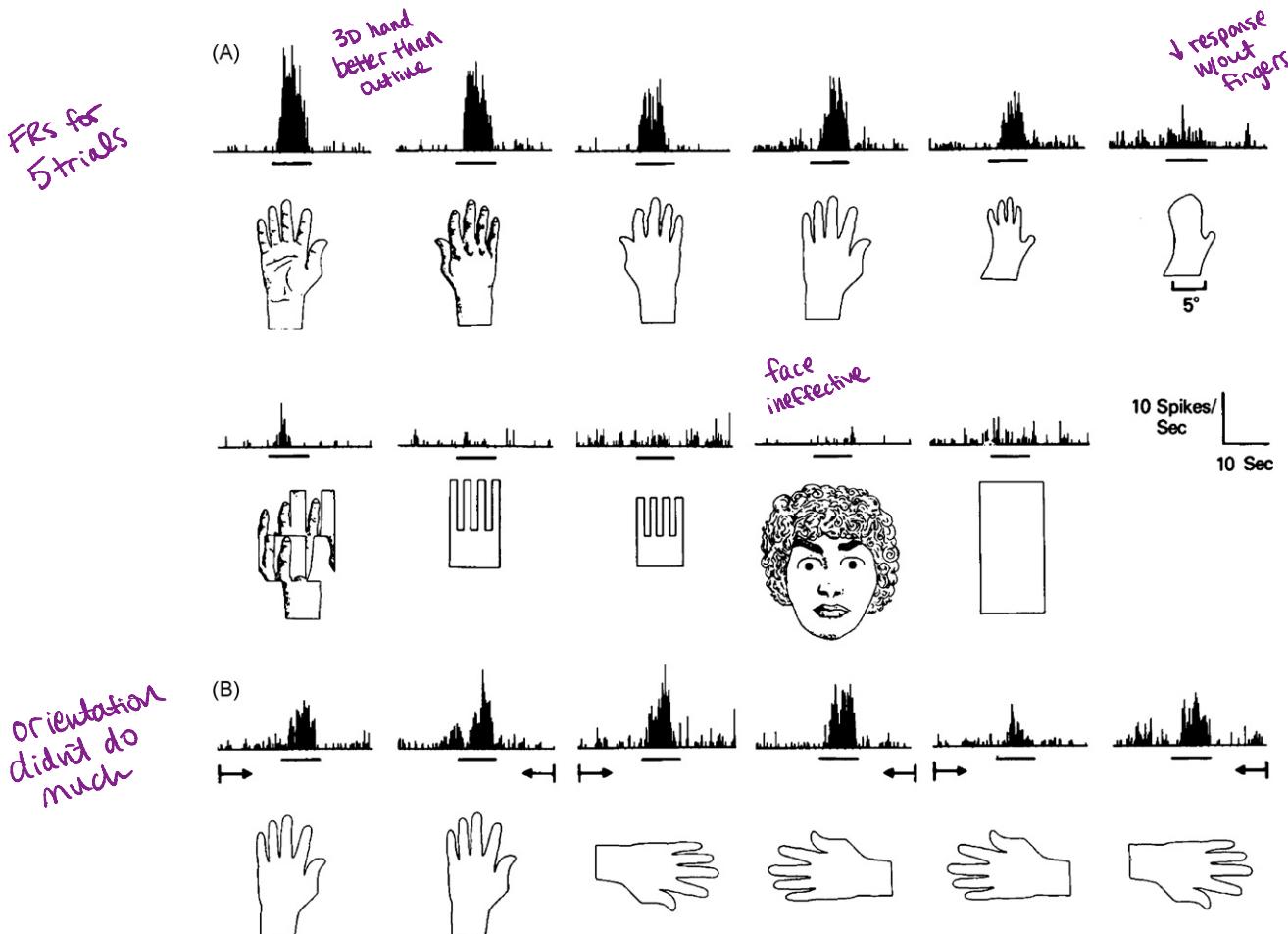


Fig. 1. Responses of an IT neuron that responded more strongly to hands than to any other stimulus tested. (A) Comparison of responses to hand-like and other patterns. Stimuli were a 3D model of a human hand, a cutout with the shape of the hand model, a cutout with the shape of a monkey hand, a cutout with the shape of a monkey hand with the inter-digit spaces removed (“mittens”), a partially scrambled photograph of the model of the back of the human hand, two “grating-like” hands, a 3D model of a human face and a rectangle. Stimuli were randomly interleaved and moved at 1.2° s^{-1} from contralateral to ipsilateral into a 15° window centered at the fovea as indicated by the horizontal lines. The histograms were based on five trials. (B) Responses to the hand cutouts in different orientations. The arrows show the direction of stimulus motion and of time in the histograms. Other parameters as in A (Desimone et al., 1984).

thermore, the magnitude of response was almost always greater to stimuli presented at the fovea. This emphasis on the fovea reflects its important role in object recognition.

Second, the receptive fields were very large relative to the receptive fields in earlier visual areas that included the fovea. The median size was about 25 square degrees and some extended throughout most of the visual field. This affords the opportunity for considerable generalization across retinal translation within a single receptive field (Gross & Mishkin, 1977).

Third, almost half of the IT receptive fields extended across the midline into the ipsilateral visual field unlike in earlier visual areas where the RF's are confined to the contralateral half field.

The two halves of space were represented in single cells for the first time in visual cortex. Later work showed that the visual responsiveness of IT cells in the ipsilateral half of space is dependent on the corpus callosum and the anterior commissure.

Fourth, the responses of IT cells were dependent on the shape or color of the stimuli and sometimes on both properties. Very few IT cells responded well to spots or slits or other simple stimuli. Rather, most cells responded to more complicated stimuli although it was often (or always) impossible to be sure of the "optimal stimulus". In general the cells did not act like narrow filters for a specific shape but tended to respond at different rates to a variety of different stimuli.

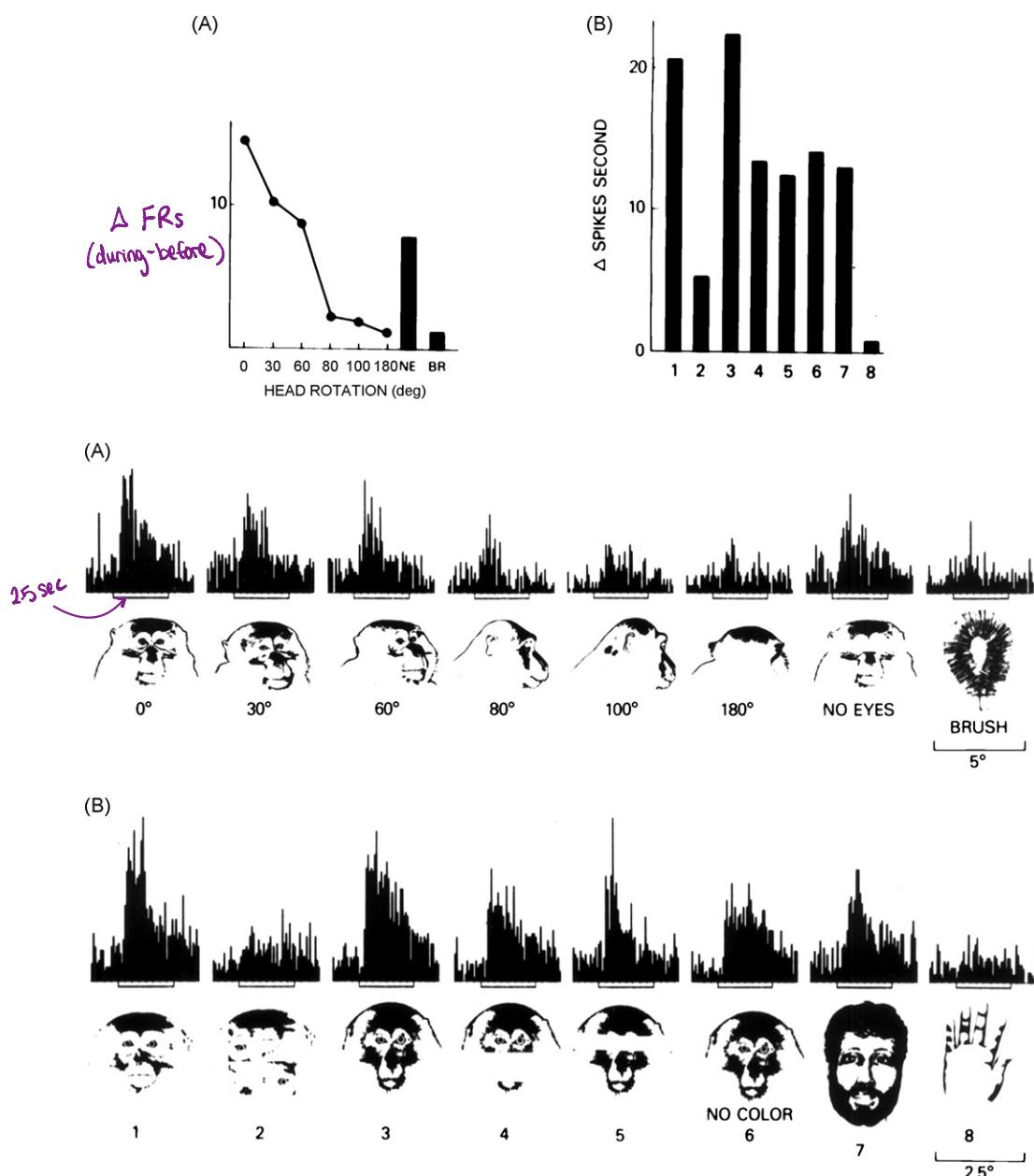


Fig. 2. Responses of an IT neuron that responded more strongly to the front view of faces than to any other stimulus tested. The stimuli were interleaved colored slides projected centered on the fovea for 2.5 s indicated by the horizontal lines under each histogram. (A) Responses to a monkey face in different degrees of rotation. (B) Comparison of responses to faces, to faces with components removed and to a hand. The line and bar graphs (above) indicate the response rate during stimulus presentations minus the rate in the preceding period (after Desimone et al., 1984).

Fifth, the responses of IT cells to shape usually remained relatively invariant over changes in stimulus size, contrast, color and exact position within the central portion of the receptive fields. The magnitude of the response usually was reduced as the stimuli were placed further from the fovea but the pattern of relative selectivity remained the same. This invariant response to shape resembled shape constancy, a central characteristic of perception.

The sixth property of IT cells initially elicited the greatest skepticism and eventually considerable interest, namely that a small proportion of IT cells responded best or only to images of faces and a even smaller proportion specifically to hands. A “hand” cell was found before the first “face cell”. Here is the original description of that finding (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 h 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.”

Fig. 1 shows some responses of a later studied hand cell. Note that the response to the realistic 3D model of the hand was greater than to the hand outline. A real hand gave an even stronger response. Eliminating the fingers or rearranging them reduced the response. The orientation and direction of movement of the hand had no effect except perhaps in the case where a severed wrist was the leading edge. The cell was not simply interested in body parts as a face was ineffective. The “grating-

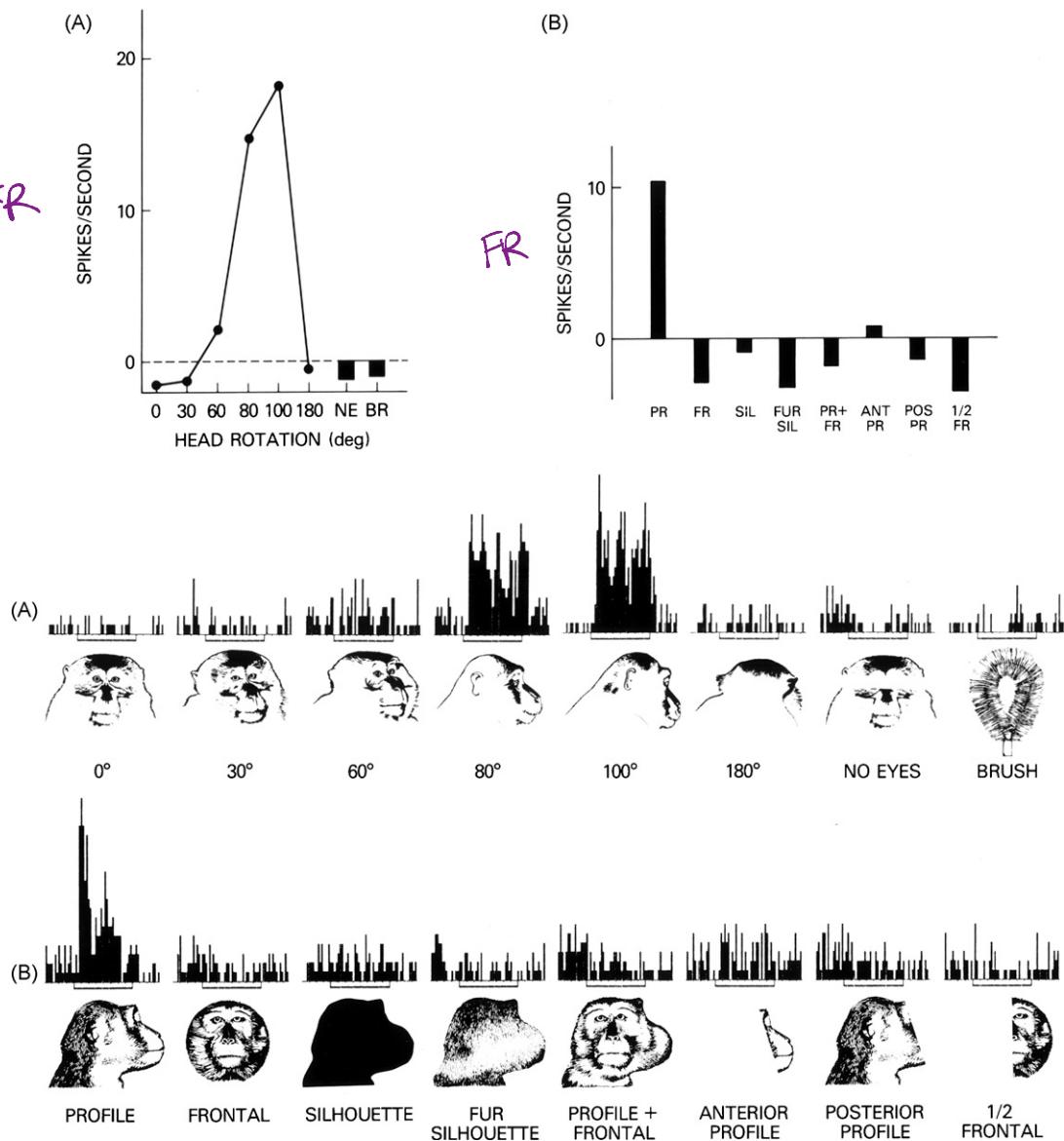


Fig. 3. Responses of an IT neuron that responded more strongly to profiles of faces than to any other stimulus tested. See also legend of Fig. 2 (after Desimone et al., 1984).

“like” hand stimulus was used because this was a time when the use of gratings was very fashionable in visual studies and it was suggested that our so-called hand cells might just reflect responsiveness to a grating of a particular spatial frequency. [A suggestion actually made by the original sponsor and paymaster of our IT research (Teuber, 1978).]

Some results from two of our early face cells are shown in Figs. 2 and 3. The response of both cells depended on the orientation of the face.

In the first cell, the response could be reduced by modifying the face, as by removing the eyes or the mouth. It was as if this cell was summing information about face parts that it received. The second cell, although also orientation selective would only respond to the entire face and not to any of its components. We saw a third class of cells that unlike the first two would respond to a face in any orientation but required, like the second type, the entire face not just some components.



Fig. 4. Responses of a neuron in the **superior temporal polysensory area** (i.e. in the dorsal bank of the anterior superior temporal sulcus) that responded better to faces than to other stimuli. Removing the eyes from the face or presenting a caricature elicited a reduced response. Cutting the face photograph into segments and rearranging the segments eliminated the response. The receptive field is shown on the lower right, C, contralateral, I, ipsilateral (Bruce et al., 1981).

The first two cells might be called **viewer-centered** and the third, **object-centered**.

We also found face units in an area immediately dorsal to IT cortex in the upper bank of the superior temporal sulcus, 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). The face units in STP seemed to have the same basic properties as those in IT as shown in Fig. 4. Both human and monkey faces elicited similar responses and size had no effect, but removal of the eyes reduced the response. Even a crude cartoon elicited a response greater than random lines or a hand. Later work by Perrett et al. (1985) showed that **face cells in STP are especially sensitive to direction of gaze suggesting that they play an important role in regulating social behavior.**

One of the reasons for the skepticism or sheer disbelief in our results may have been because our sparse use of quantitative methods and of mechanical stimulus presentation. Another reason may have been our use of even more unconventional stimuli than hands and faces, such as a toilet brush (Fig. 5). One of the very first groups to finally test and replicate some of our basic findings actually successfully used a toilet brush too (Richmond & Wurtz, 1982).

Many of the RF properties of IT cells were discovered by using, however crudely, standard visual neurophysiology methods of the time (e.g. those used by Hubel & Weisel, 1965). Faces, hands, brushes and other objects, however, were not standard visual stimuli at the time. Why did we use them and more importantly why were we primed to notice responses to such stimuli? There were several factors that probably lowered our threshold to seek and notice cells selective for such complex stimuli as hands and faces.

First, a few years earlier I had spent several weeks in Warsaw visiting the Polish neuroscientist Jerzy Konorski. He had postulated the existence of “**gnostic neurons**” such as ones selective for faces, facial expressions, body parts, simple objects and scenes (Fig. 6). He had suggested they would be found in inferior temporal cortex (Konorski, 1967). I had recently written a long review of his book which expounded these ideas (Gross, 1968).

Second, we had begun these IT studies at M.I.T. in the department of the neuropsychologist Hans-Lucas Teuber and he was constantly telling stories about **prosopagnosia** after temporal lesions.

Third, our first lab at MIT was down the hall from Jerry Lettvin's where he was working on bug detectors in the frog (Lettvin, Maturana, McCulloch, & Pitts, 1959). He had invented the term “**grandmother cell**” (Gross, 2002). [It was Horace Bar-

Responses to a toilet brush

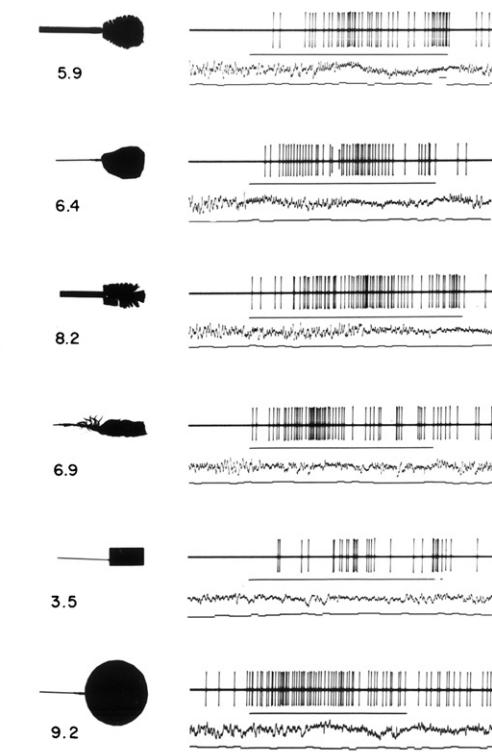
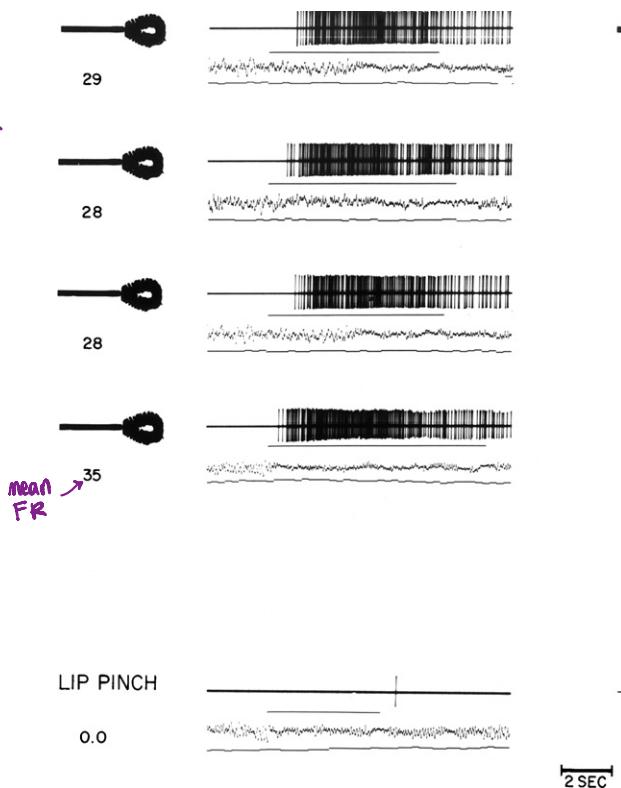


Fig. 5. Responses of an IT neuron that responded strongly to an oval brush. Shadows of the brush shown on the left also elicited strong responses. Presence of the handle, direction of movement and location within the receptive field (which extended 30° in all directions from the center of gaze) appeared irrelevant. Other shadows such as those shown on the right elicited weaker responses. The horizontal line indicates when the stimulus was moving through the receptive field at 8° s⁻¹ and the numbers are the mean rate of firing during that period. The scale indicates 2 s for the traces and 14° for the stimuli. This animal had received a section of the splenium but similar stimulus preferences were common in intact animals (after Gross et al., 1977). This figure may have not contributed to the credibility of our early reports on IT cortex.

Categories of visual stimulus objects probably represented in Gnostic fields in IT cortex

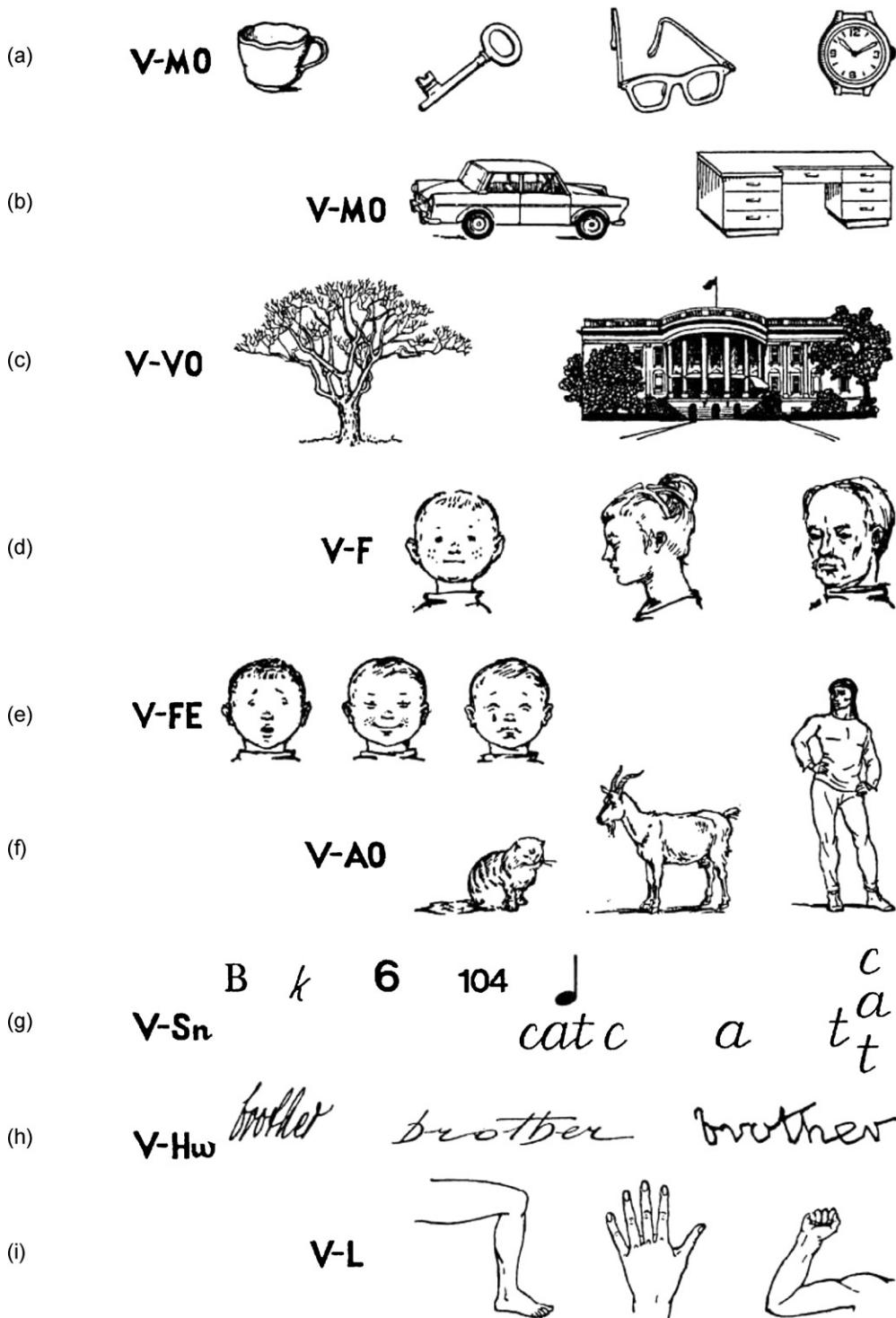


Fig. 6. Konorski's (1967) illustrations of "particular categories of visual stimulus objects probably represented in different Gnostic fields" in inferior temporal cortex.

low (Barlow, 1953) who first used the term bug detectors and I had heard him lecture on the subject when I was a 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). Thus it is not surprising we found face and hand cells in this

environment! What is surprising is that for some time, both our findings on the unusual receptive field properties of IT cells and our finding of face- and hand-selective cells seemed to have little or no impact on the field. Although our first reports were in high profile places, namely *Science* (1969) and the *Journal of Neurophysiology* (1972) there were few attempts to replicate and extend (or deny or even comment in print on) our basic results on IT neuronal properties for some time. There were several

abstracts and brief reports that some IT neurons were responsive to visual stimuli (Jarvis & Mishkin, 1977; Judge, Rolls, & Senghiera, 1976; Ridley & Ettlinger, 1973; Ridley, Hester, & Ettlinger, 1977; Rolls, Judge, & Senghiera, 1977). Then about 12 years after our first paper, Rolls, Perrett and their colleagues began reporting face selective cells in IT and in 1982 Richmond and Wurtz replicated the basic receptive field characteristic of IT cells, particularly their large size and inclusion of the center of gaze (Perrett, Rolls, & Caan, 1982; Richmond & Wurtz, 1981; Richmond, Wurtz, & Sato, 1983; Rolls, 1981a, 1981b). By contrast, our brief and rather too causal description of STP cells sensitive to biological motion (Bruce et al., 1981) was quickly taken up and very much extended by Perrett and his associates starting in 1984 (Perrett et al., 1984, 1985).

Are the face and hand cells found in IT cortex examples of the “grandmother cells” of Lettvin (in Barlow, 1995), cells that only respond to a specific visual concept, such as your own grandmother “however displayed, whether animate or stuffed, seen from behind, upside down, or on a diagonal, or offered by caricature, photograph or abstraction”? Are they examples of the earlier described “gnostic” cells of Konorski (1967), neurons that represent “unitary perceptions”? The available evidence provides an overwhelming “no”. There is no one-to-one relationship between a specific face (or any other object) and a specific IT cell. Rather IT face cells respond to varying degrees to a set of faces and never solely to one. Different IT cells show a different pattern of responses to a set of faces (see Fig. 7). Thus the coding of faces (and presumably other objects) appears to be done by the pattern of firing over a set of cells, that is, by what has been termed: “coarse coding”, “ensemble coding”, “population coding”, or “cross-fiber pattern coding”. This absence of one cell-one visual concept is true for both natural stimuli such as faces and arbitrary stimuli that evoke responses of IT cells after explicit training. I have discussed the origin of the term “grandmother cell” and its relation to IT cells in

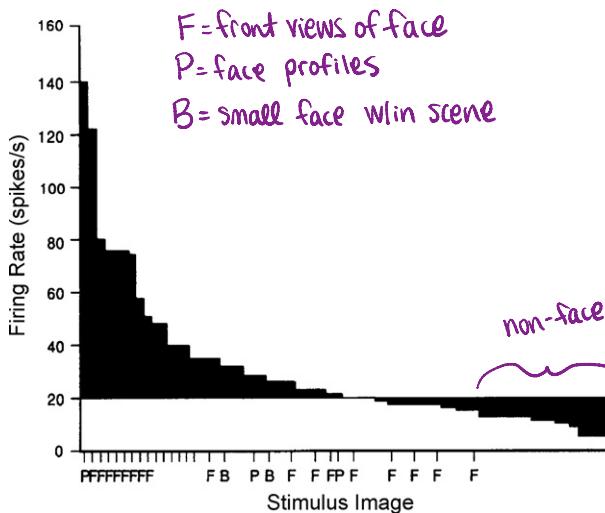


Fig. 7. Distribution of different strengths of response of one IT neuron to 68 faces and other images. F, stimuli that are front views of a face; P, face profiles; B, images that included a small face within a scene, sometimes including a whole person or other body parts. The non-face images are not labeled. The spontaneous rate of this neuron was 20 s^{-1} (Rolls & Tovee, 1995).

detail elsewhere (Gross, 1992, 2002) as have others (e.g. Barlow, 1972; Desimone, 1991; Perrett, Mistlin, & Chitty, 1987; Rolls, 2004).

However, the possibility of a true grandmother cell is not as dead as their apparent absence in IT cortex of the monkey might imply. Quiroga, Reddy, Kreiman, Koch, and Fried (2005) have reported cells in the medial temporal cortex of human patients that certainly seem to fit the criterion for a grandmother cell. For example, one such cell in the hippocampus fired only to a variety of images of one individual (known to the patient) including in various costumes and views and even to her name in letters and not at all to images or names of a number of other individuals also known to the patient (see Fig. 8).

The usual assumption has been that face IT cells are specifically involved in the perception of faces and there is some indirect support for this view (e.g. Perrett et al., 1984). However, until recently, there has been no direct evidence. IT lesions do impair face discrimination but they also impair many other types of visual discrimination tasks, the relative impairment depending on the difficulty of the discrimination as measured by the performance of control animals. Direct support for a role of face units came from a recent report of Afraz, Kiani, and Esteky (2006) in Teheran. They trained monkeys to look right if a face was presented and left for a non-face stimulus and then made the task harder by degrading both stimuli. When they electrically microstimulated in a cluster of face neurons the monkeys were more likely to report a face even if only visual noise was present. These effects were both spatially and temporal specific: they only occurred in an area of a cluster of face neurons and they occurred only in the brief interval in which IT neurons respond to a face.

In our early, preliminary studies we noted that the responses of IT neurons apparently could be modified by experience and attention and we began to systematically study the effect of previous experience on the responses of IT cells (Gross et al., 1979; Miller, Gochin, et al., 1991). Since then, the plasticity of IT cells has been studied in detail by a number of investigators. First, the repeated presentation of a stimulus with a short inter-trial interval usually leads to a decline in response magnitude (e.g. Li, Miller, & Desimone, 1993; Miller, Gochin, et al., 1991; Miller, Li, & Desimone, 1991; Wilson, Riches, & Brown, 1990). Second, extensive training on paired associates results in neurons responsive to both members of the pair whereas they were originally responsive to only one (e.g. Messinger, Squire, Zola, & Albright, 2005; Sakai & Miyashita, 1991; Takeda, Naya, Fujimichi, Takeuchi, & Miyashita, 2005). Third, extensive training to discriminate visual stimuli usually increases the strength and selectivity of IT responses to these stimuli (e.g. Erickson, Jagadeesh, & Desimone, 2000; Kobatake, Wang, & Tanaka, 1998; Logothetis, Pauls, & Poggio, 1995). Attention can also markedly modulate the responses of IT neurons, sometimes gating them to zero. Attention can affect both the size of the IT neuron's effective receptive field and its stimulus selectivity (Moran & Desimone, 1985; Fuster, 1990). Thus, cells in IT cortex have perceptual, attentional and short and long-term mnemonic functions. To what extent these functions are subsumed by the same individual neuron is not clear.

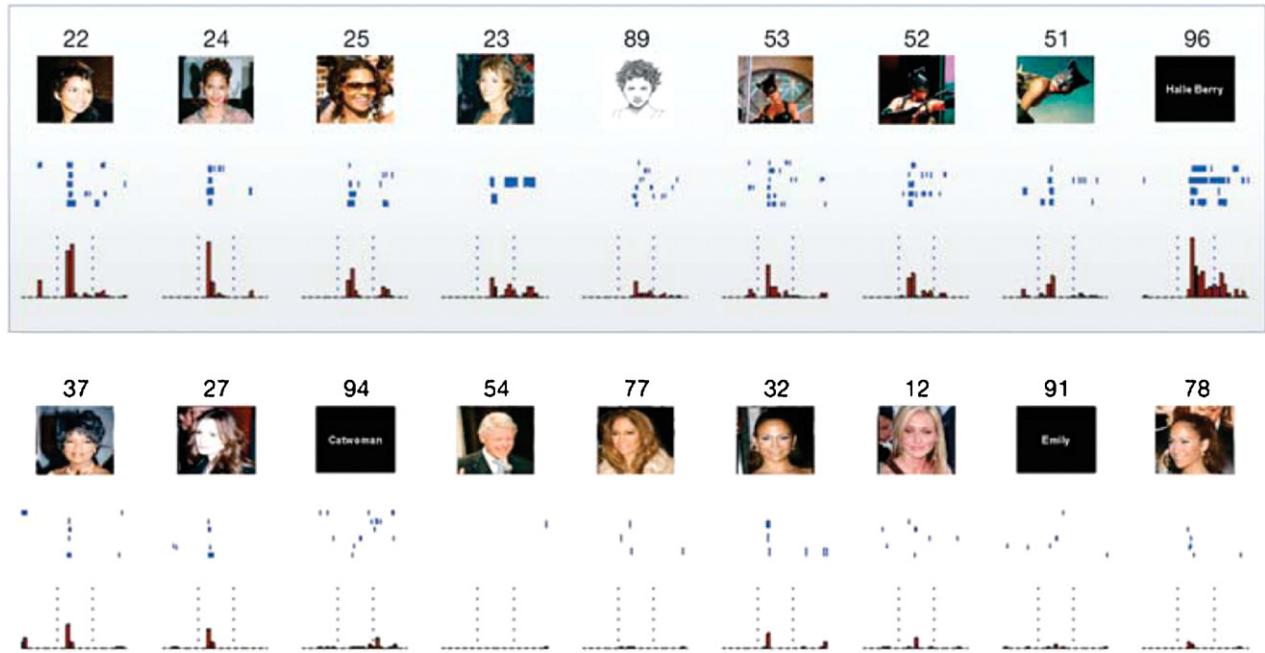


Fig. 8. A single unit in the human right anterior hippocampus that responds to different pictures of the actress Halle Berry including in costume and to the letter string of her name but not to other facial images or letter strings (Quiroga et al., 2005).

Whereas it took about 12 years for anyone to try and replicate our basic findings on IT neurons in monkeys, it took about 19 years for the search for specific responses to faces in the temporal cortex of humans to begin. Selective responses of faces were shown in human ventral temporal cortex, especially the fusiform gyrus, by PET scanning (Haxby, Grady, Ungerleider, & Horwitz, 1991; Sergent & Signoret, 1992), by single unit recording (Ojemann, Ojemann, & Lettich, 1992), by field potentials (Allison et al., 1994), by fMRI (Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996). Since then there has been a flood of imaging papers on face processing in the human temporal lobe.

More recently, in an attempt to bridge single unit studies in monkeys and imaging studies in humans, there have been several fMRI studies in monkeys of specific temporal cortex activation by faces (Logothetis, Guggenberger, Peled, & Pauls, 1999; Pinsky, Desimone, Moore, Gross, & Kastner, 2005;

Pinsky, Moore, Richter, Gross, & Kastner, 2005; Tsao, Freiwald, Knutson, Mandeville, & Tootell, 2003; Tsao, Freiwald, Tootell, & Livingstone, 2006). In these studies faces activated small and discrete portions of IT cortex in the region of the superior temporal sulcus (see Fig. 9). This fits nicely with the finding from single neuron studies in the monkey that there is a much higher concentration of face cells in the vicinity of the superior temporal sulcus (20–30%) than elsewhere in IT cortex (about 5%) and the finding of patches 3–4 mm wide, with a high incidence of face cells in this sulcus (Bayliss, Rolls, & Leonard, 1987; Harries & Perrett, 1991). Tsao et al. (2006) recorded from single neurons in one of these fMRI face hot spots near the superior temporal sulcus located by fMRI and found that virtually all of the visually responsive cells were face selective. Furthermore, the response properties of these neurons were similar to those reflected by the hemodynamic responses of the area. This area appears to be similar to the fusiform face area (Kanwisher et

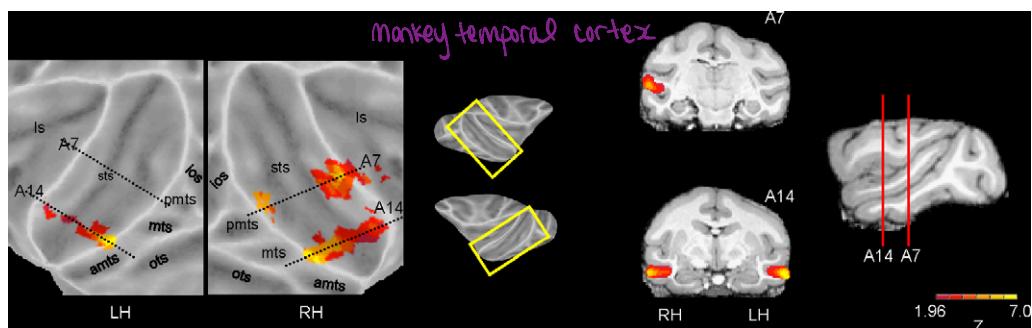


Fig. 9. Face-selective representations in monkey temporal cortex. (Left) Flattened cortical surfaces and coronal slices in monkey M1 depicting voxels activated significantly more by faces as compared to objects. (Right) Approximate locations of the coronal slices are indicated on a sagittal slice with distances from the interaural line (mm) noted. Scale indicates Z-score values of functional activity in colored regions. RH, right hemisphere; LH, left hemisphere; ls, lateral sulcus; sts, superior temporal sulcus; ios, inferior occipital sulcus; pmts, posterior middle temporal sulcus; mts, middle temporal sulcus; amts, anterior middle temporal sulcus; ots, occipital temporal sulcus.

al., 1997). The fact that virtually all the cells were face selective supports the idea that such areas may be exclusively devoted to face processing.

There are still many unanswered questions about face cells. Among them are: What are the different roles of and functional connections among the face cells located in different areas both within the temporal lobe (IT, STP and the amygdala) and outside it? What are the different roles of face cells in high concentrations and those more distributed? What is the afferent anatomy underlying the complex response properties of face cells? What is the basis of plasticity of face (and other IT) cells? What are the relations of the different complexes of face cells to such disorders as prosopagnosia and autism? Clearly, the continually increasing number of investigators working on the physiology of face mechanisms in humans and monkeys have many interesting questions before them.

Acknowledgments

I wish to express my deep appreciation to my co-workers on inferior temporal cortex. Their names appear as coauthors with me in the list of references. Previous attempts to put our work in its historical context include Chapter 5 in Gross (1998) and Gross (2005).

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