ELSEVIER

Neuropsychologia 46 (2008) 841–852

NEUROPSYCHOLOGIA

www.elsevier.com/locate/neuropsychologia

Single neuron studies of inferior temporal cortex

Charles G. Gross *

Department of Psychology, Green Hall, Princeton University, Princeton, NJ 08540, USA

Received 23 February 2007; received in revised form 27 September 2007; accepted 2 November 2007

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.

Keywords: Inferior temporal cortex; Inferotemporal cortex; Area TE; Faces; FMRI

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 multisynaptic 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 Water Rosenblith's Communication Biophysics Laboratory at MIT.

---

* Princeton University, Tel.: +1 609 258 4430; fax: +1 609 258 1113.
E-mail address: cggross@princeton.edu.

0028-3932/$ – see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2007.11.009

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-

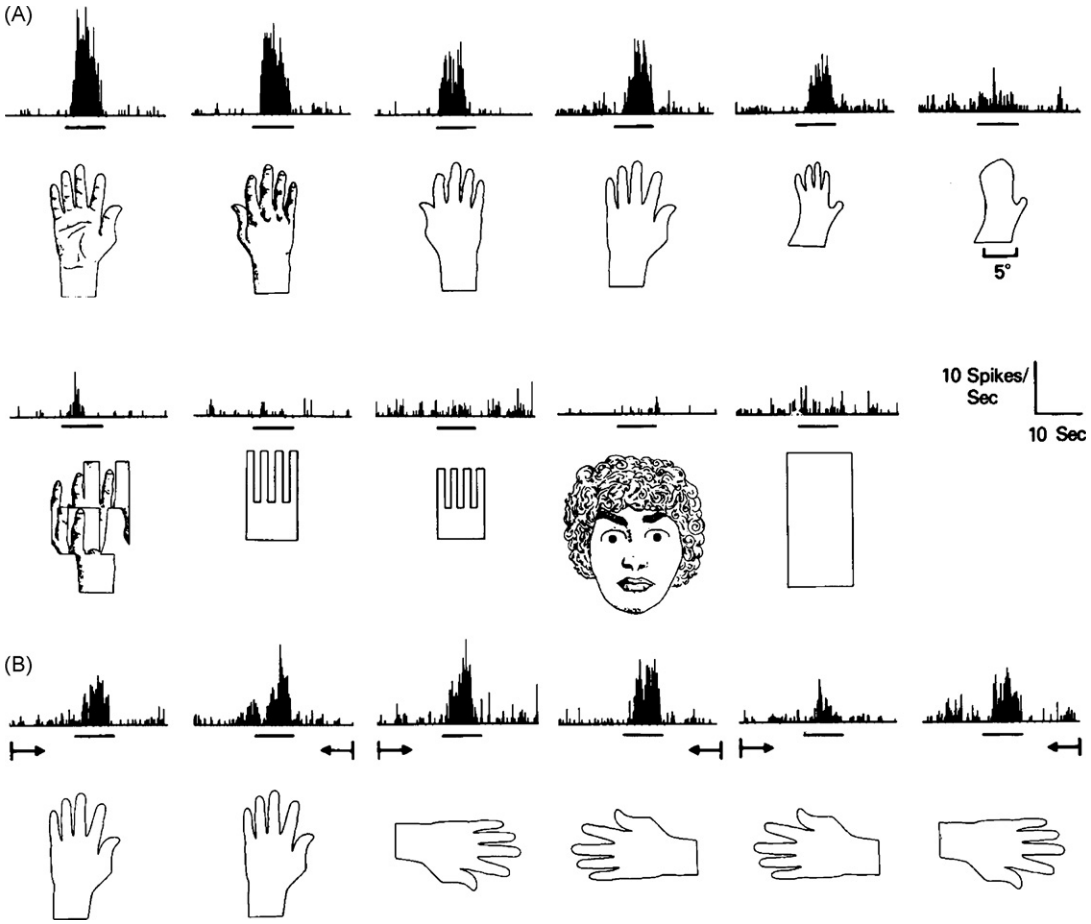

Fig. 1. Responses of an IT neuron that responded more strongly to hands than to any other stimulus tested. (A) Comparison of responses to hand-like and other patterns. Stimuli were a 3D model of a human hand, a cutout with the shape of the hand model, a cutout with the shape of a monkey hand, a cutout with the shape of a monkey hand with the inter-digit spaces removed ("mitten"), 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 $1.2^\circ\ \mathrm{s}^{-1}$ 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).