The Journal of Neuroscience, February 1987, 7(2): 330–342

Functional Subdivisions of the Temporal Lobe Neocortex

Gordon C. Baylis, Edmund T. Rolls, and Christiana M. Leonard[a]

University of Oxford, Department of Experimental Psychology, Oxford OX1 3UD, England

In order to gather evidence on functional subdivisions of the temporal lobe neocortex of the primate, the activity of more than 2600 single neurons was recorded in 10 myelo- and cytoarchitecturally defined subdivisions of the cortex in the superior temporal sulcus (STS) and inferior temporal gyrus of the anterior part of the temporal lobe of 5 hemispheres of 3 macaque monkeys. First, convergence of different modalities into each area was investigated. Areas TS and TAa, in the upper part of this region, were found to receive visual as well as auditory inputs. Areas TPO, PGa, and IPa, in the depths of the STS, received visual, auditory, and somatosensory inputs. Areas TEa, TEm, TE3, TE2, and TE1, which extend from the ventral bank of the STS through the inferior temporal gyrus, were primarily unimodal visual areas. Second, of the cells with visual responses, it was found that some neurons in areas TS–IPa could be activated only by moving visual stimuli, whereas the great majority of neurons in areas TEa–TE1 could be activated by stationary visual stimuli. Third, it was found that there were few sharply discriminating visual neurons in areas TS and TAa; of the sharply discriminating visual neurons in other areas, however, neurons that responded primarily to faces were found predominantly in areas TPO, TEa, and TEm (in which they represented 20% of the neurons with visual responses); neurons that were tuned to relatively simple visual stimuli such as sine-wave gratings, color, or simple shapes were relatively common in areas TEa, TEm, and TE3; and neurons that responded only to complex visual stimuli were common in areas IPa, TEa, TEm, and TE3. These findings show *inter alia* that areas TPO, PGa, and IPa are multimodal, that the inferior temporal gyrus areas are primarily unimodal, that there are areas in the cortex in the anterior and dorsal part of the STS that are specialized for the analysis of moving visual stimuli, that neurons responsive primarily to faces are found predominantly in areas TPO, TEa, and TEm, and that architectural subdivisions of the temporal lobe cortex are related to neuronal response properties.

The temporal lobe neocortex of the primate is known to have a close association both with sensory systems such as vision and audition and with limbic structures. In particular the superior temporal gyrus is regarded as an auditory association area, the inferior temporal gyrus (ITG) as a visual one. Gross and his colleagues (Gross et al., 1969, 1972; Bruce et al., 1981) have shown that a large proportion of neurons are visually responsive throughout the inferior temporal cortex and cortex in the superior temporal sulcus (STS) of the anesthetized macaque. These neurons had very large, often bilateral receptive fields, and in some circumstances very specific stimulus requirements. Throughout this area of cortex as a whole, these workers could find no topography in terms of position of receptive fields in visual space, although particular topographically ordered subareas could not be ruled out.

Damage to the inferior temporal cortex can lead to deficits in visual discrimination tasks (Butter, 1972; Dean, 1976; Pribram et al., 1980; Laursen, 1982). These may be due to an inability to select relevant information (Bender and Gross, 1981), to cope with interfering information (Cowey and Gross, 1970), or to control gaze appropriately (Wilson et al., 1977).

The inferotemporal cortex has been implicated in short-term memory processes by the findings by Mikami and Kubota (1980), Fuster and Jervey (1981), and Baylis and Rolls (1986) that single neurons in this area code information useful in the performance of delayed match to sample (Konorski) tasks. For example, some neurons respond more to the first (sample) than to the second (match) stimulus. However, it has been shown that inferior temporal neurons did not respond differently to novel and familiar stimuli in a recognition memory task when more than 1 stimulus intervened between the first (novel) and second (familiar) presentations of a stimulus (Baylis and Rolls, 1986). Therefore, these neurons do not appear to be suitable for a longer term form of memory that must be held over a number of intervening stimuli. Gaffan and Weiskrantz (1980) have shown that it is the acquisition of serial recognition tasks (in which many stimuli intervene between the novel and familiar presentations of a given stimulus) that is retarded by inferotemporal lesions and that final performance level is not affected. These findings are consistent with the view that inferior temporal cortex neurons would be useful for a visual short-term memory with spans of 0–1 item but would not be useful for a longer term recency memory store (Baylis and Rolls, 1983, 1986).

Using association memory tasks, Rolls and his colleagues (1977) did not find any neurons in the inferotemporal cortex which discriminated between visual stimuli on the basis of reward value, although such neurons are found in the amygdala and lateral hypothalamus (Sanghera et al., 1979; Rolls et al., 1979; Rolls, 1981a, b, 1985). Thus, the inferotemporal cortex may be afferent to structures involved in association memory, but it does not appear to be itself implicated in association memory. Lesion studies are consistent with this, in that they demonstrate an association memory deficit after amygdala lesions (Speigler and Mishkin, 1981).

Received Dec. 4, 1985; revised May 27, 1986; accepted July 14, 1986.

This research work was supported by the Medical Research Council.

Correspondence should be addressed to Dr. Edmund T. Rolls, University of Oxford, Department of Experimental Psychology, South Parks Road, Oxford OX1 3UD, England.

[a] Present address: Department of Neuroscience, University of Florida College of Medicine, Gainesville, FL 32610.

Table 1. Microstructure

Cortical subarea	Myeloarchitecture			Cytoarchitecture				
	IB	EB	VM	IG	3P	45	56	6C
TS		X				X	X	
TAa					X	X	X	
TPO		X	X		X	X	X	
PGa								X
IPa								X
TEa	X	X			X	X	X	
TEm	X	X	X		X	X	X	
TE3	X	X				X	X	
TE2		X		X				
TE1				X				

Abbreviations: IB, presence of strong internal band of Baillarger; EB, presence of strong external band of Baillarger; VM, presence of strong vertical myelination of cortex; IG, infragranular layers thicker than supragranular; 3P, presence of many large pyramidal cells in layer 3c; 45, good demarcation between layers 4 and 5; 56, good demarcation between layers 5 and 6; and 6C, presence of clumps of cells in layer 6.

Table 2. Cortical inputs

Cortical subarea	SP	ST	AP	PP	OA	MT	TEO	TEa	TEm	TE3	TE2
TS		X	X								
TAa	X	X									
TPO		X		X	X	X	X				
PGa		X	X	X	X		X				
IPa		X	X	X			X	X			
TEa					X		X	X	X	X	
TEm					X		X	X	X	X	
TE3					X		X	X	X	X	
TE2									X	X	X
TE1											X

Abbreviations: SP, supratemporal plane; ST, superior temporal gyrus; AP, anterior parietal gyrus; PP, posterior parietal gyrus; OA and TEO, areas according to von Bonin and Bailey (1949); MT, see Van Essen et al. (1981); other areas, see Seltzer and Pandya (1978).

The extent to which the cortex within the STS and of the ITG can be divided into different functional subareas is not clear from the above studies. Desimone and Gross (1979), recording from single neurons in the anesthetized macaque, distinguished a polymodal but predominantly visual area in the depths and upper bank of the STS, which they designated STP (superior temporal polysensory), from auditory cortex dorsally and visual TE ventrally. One class of visually selective neurons, with responses selective for faces, has been found in a number of regions within the cortex in the STS (Gross et al., 1969; Bruce et al., 1981; Perrett et al., 1982; Desimone et al., 1984; Baylis et al., 1985). On the basis of microstructure, von Bonin and Bailey (1949) anatomically distinguished area TA, which included most of the superior temporal gyrus and extended into the dorsal bank of the STS, from area TE, which started here and extended through the ITG almost to the rhinal sulcus. However, more recently these regions have been divided into many smaller areas on the basis of cytoarchitecture and myeloarchitecture (see Pandya and Sanides, 1973; Jones and Burton, 1975; Seltzer and Pandya, 1978).

In the study described here we addressed the question of whether the response properties of neurons vary consistently with anatomical location within the cortex of the STS and ITG of the macaque. We combined anatomical methods of cyto- and myeloarchitectonics with recordings of the activity of single neurons in order to identify any heterogeneity in neuronal response properties throughout this region of the cortex.

Definition of anatomical subareas

Seltzer and Pandya (1978) proposed a large number of subdivisions of this area of cortex, according to cyto- and myeloarchitectonic criteria. When these workers investigated cortical connectivity between subareas, a high degree of correspondence was found between microarchitecture and connectivity. The myeloarchitectonic criteria used were the presence and strength of internal and external bands of Baillarger, and the presence of diffuse vertical myelination. Cytoarchitectonic criteria included the relative thickness of infra- and supragranular layers, presence of large numbers of large pyramidal cells in layer 3c, demarcation of layer 4/5 and 5/6 boundaries, and clumping of cells in layer 6.

The characteristics of the various subareas are shown in Table 1. The presence of a particular attribute in a given area is denoted by an X in that cell. A photomicrograph of coronal sections taken through 2 representative regions of the temporal lobe neocortex from our material is shown in Figure 1. The positions of boundaries between the subareas are indicated by arrows. Use of the classification system shown in Table 1 yields a large number of easily discriminable subareas with associated differences in connectivity, and it is adopted throughout this study.

The topology of these subareas can be appreciated most easily by performing an orthographic transform of the cortex. This transform turns the 3-dimensional (3D) surface of the temporal lobe cortex into a 2-dimensional (2D) plan that maintains first-order topology. The 2D plan was made directly from measurements of distances in the histological sections. Sheer distortion was minimized by separating the surface into 2 (overlapping) 2D plans, one showing the STS and the other showing the ITG. The results of this tranform are shown for the left temporal lobe of monkey R in Figures 2 (STS) and 3 (ITG).

Cortical connectivity of subareas

The subareas described above have been shown to have different patterns of cortical connectivity. The afferents to each region are summarized in Table 2, based on the findings of Desimone et al. (1978, 1980), Herzog and Van Hoesen (1976), Seltzer and Pandya (1978), and L. Ungerleider (personal communication).

Materials and Methods

Recording techniques

The activity of single neurons was recorded with glass-insulated tungsten microelectrodes (after Merrill and Ainsworth, 1972, but without the platinum plating) in both hemispheres of 3 alert rhesus macaque monkeys (*Macaca mulatta*; weight, 3.0–6.5 kg) seated in a primate chair using techniques that have been described previously (Rolls et al., 1976). The action potentials of single cells were amplified using techniques described previously (Rolls et al., 1979), were converted into digital pulses using the trigger circuit of an oscilloscope, and were analyzed online using a PDP11 computer. The computer collected peristimulus rastergrams of neuronal activity for each trial and displayed, printed, and stored each trial, as well as computing the peristimulus time histograms by summing trials of a given type. The cumulative sum distribution was calculated from the sum peristimulus time histogram to provide a sensitive and accurate method for determining the neuronal response latency. For each trial the number of action potentials occurring in a 500 msec period starting 100 msec after the stimulus onset was printed. This period was chosen because the neurons studied responded

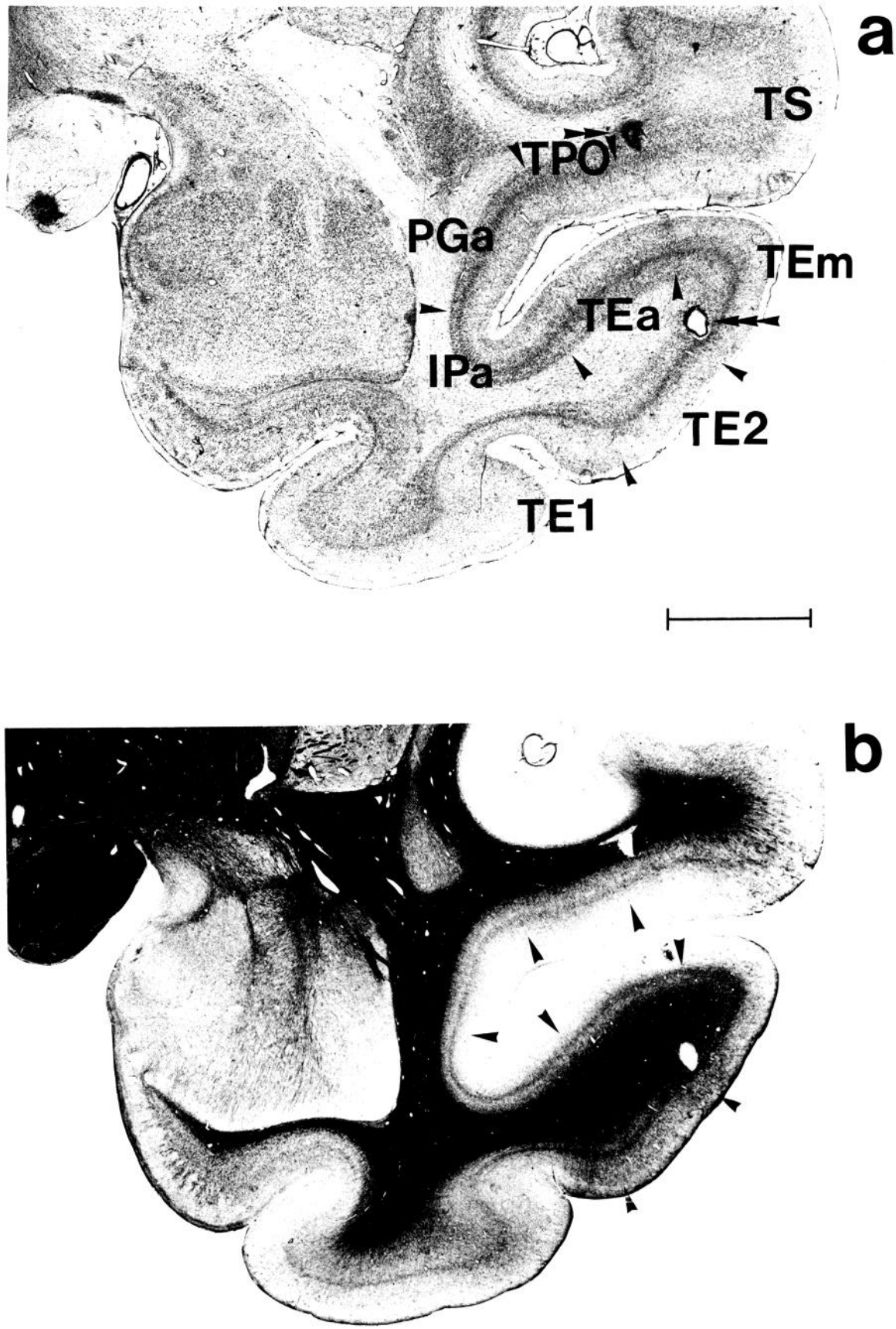
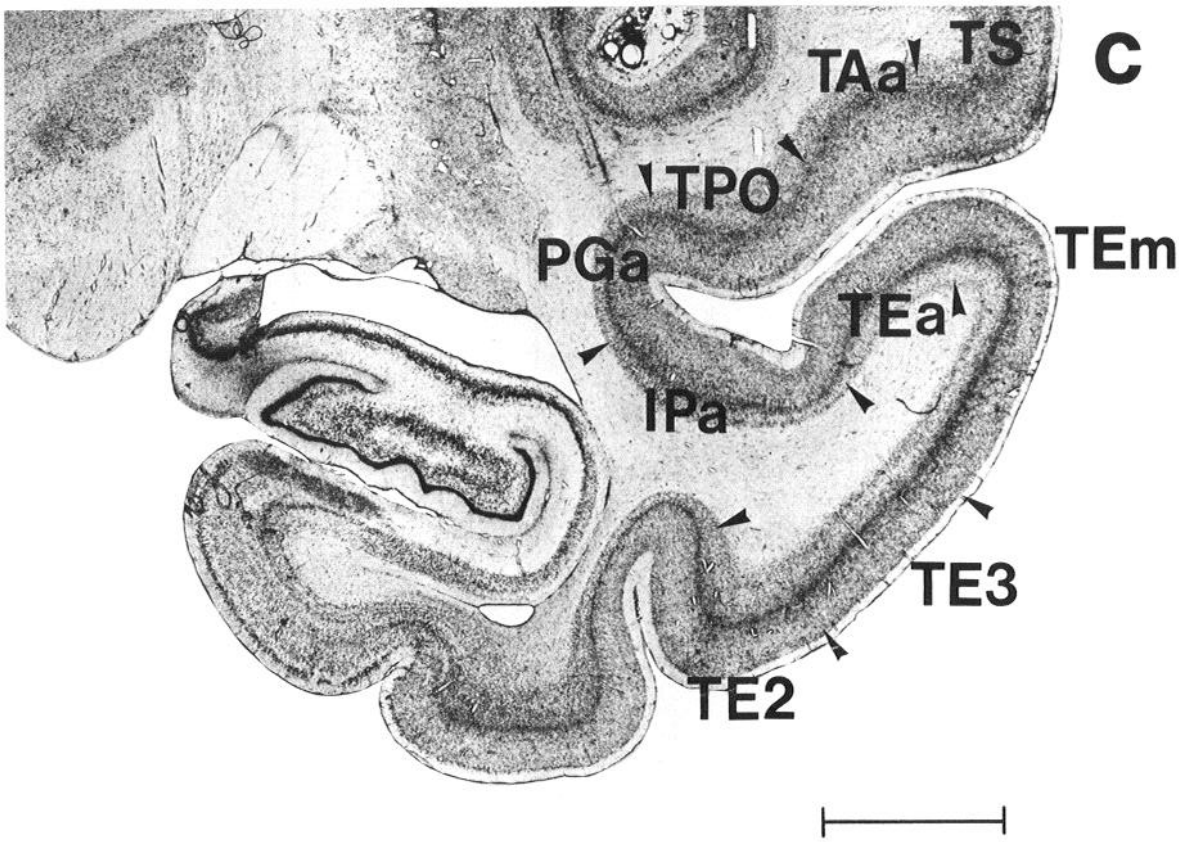
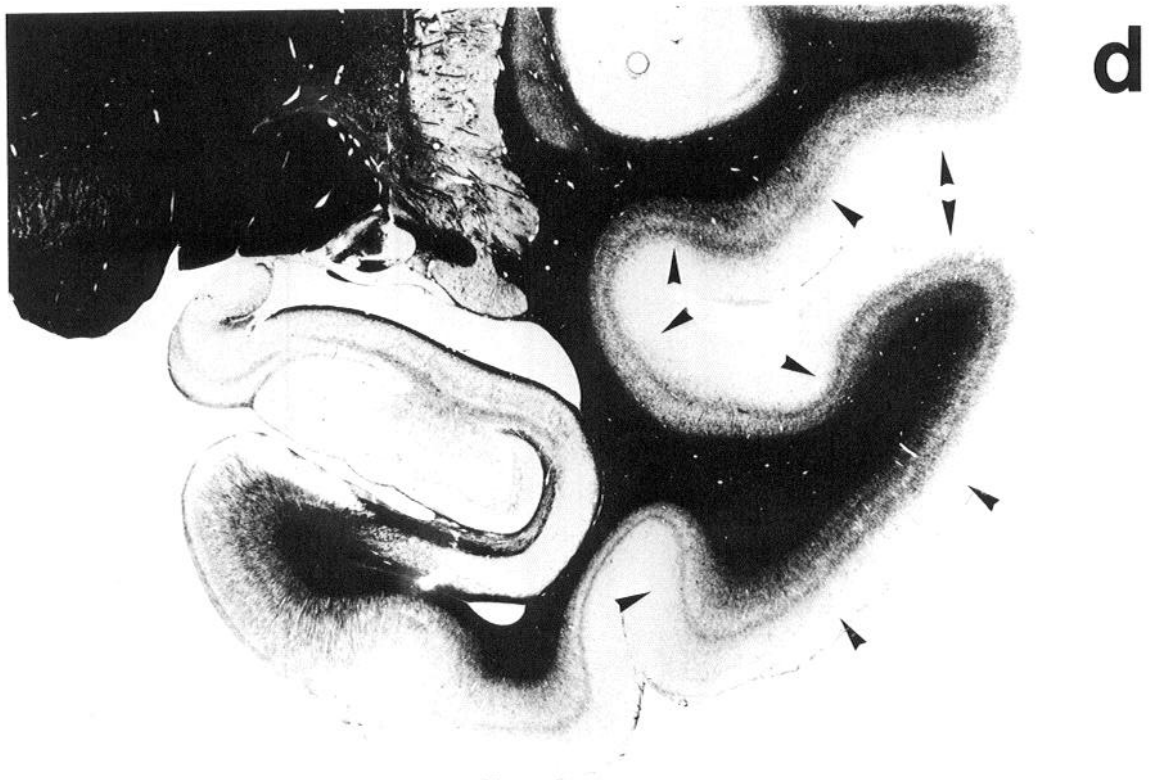


Figure 1. Examples of coronal sections through the temporal lobe of monkey R showing architectonic subareas. *a,* Section 4.7 mm posterior to sphenoid (Aggleton and Passingham, 1981) stained for cytoarchitecture with cresyl violet; microlesions used in the reconstruction are also shown





(*double* and *triple arrows*). *b,* As in *a,* but stained for myeloarchitecture according to the method of Gallyas (1979). *c,* Section 10.0 mm posterior to sphenoid; cresyl violet. *d,* As in *c*; myelin stain. Scale bars, 5 mm.

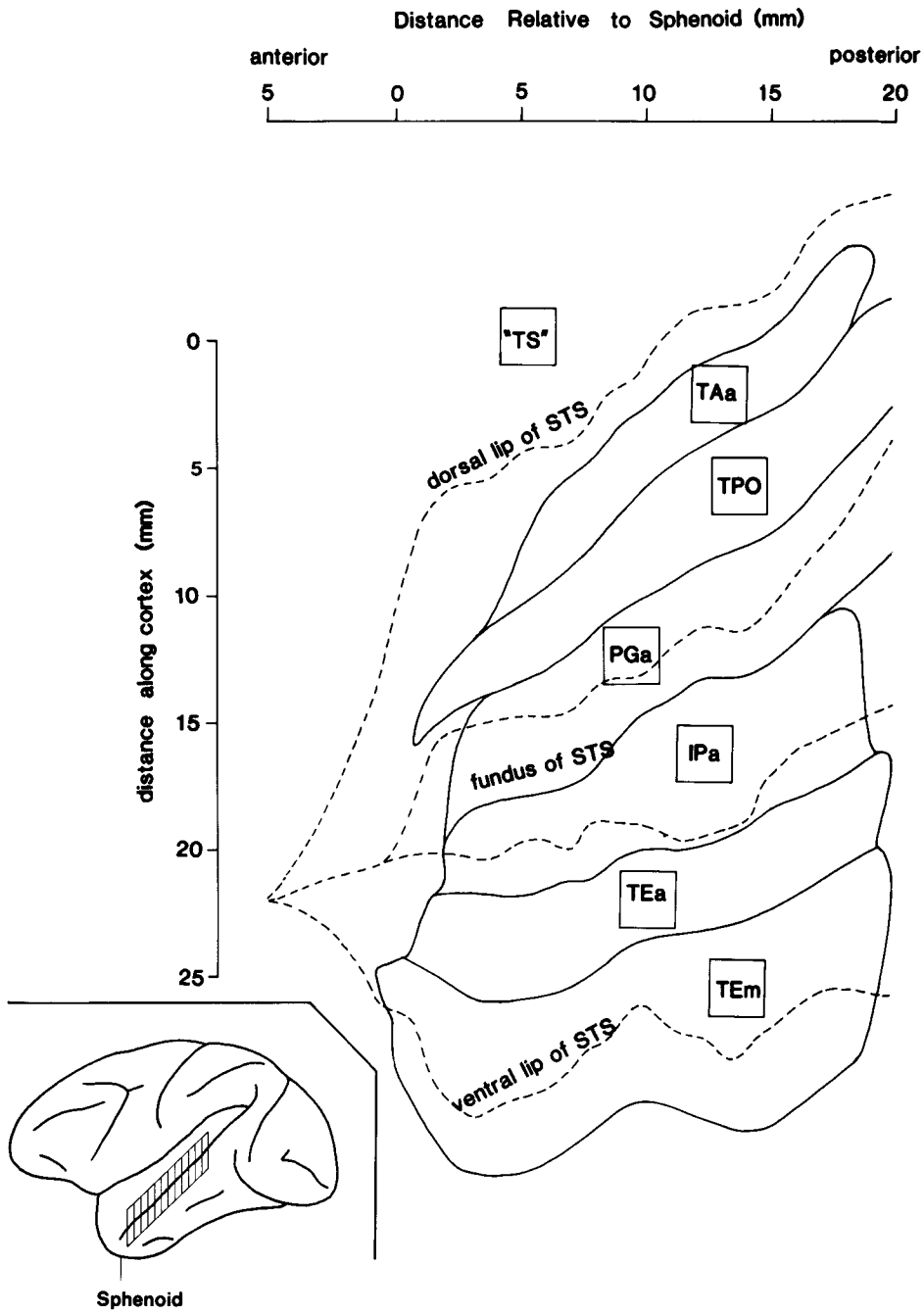


Figure 2. Plan view of the cortex in the STS opened into a 2-dimensional surface that preserves topology (see text).

to visual stimuli with latencies that were typically 100 msec or more, and the monkeys constantly fixated the stimuli for this period. Fixation of the stimuli was confirmed using permanently implanted silver/silver chloride electrodes for electro-oculogram (EOG) recording. The EOG recordings provided eye position with an accuracy of 1°–2° and were sampled by the computer every 10 msec and saved with the action potentials for each trial. Data from trials during which the monkey was not already fixating the screen when the stimulus was switched on or during which eye movements of more than 3° occurred in the first 600 msec (while the firing rate was being measured) were rejected.

The position of the microelectrode on each recording track was measured relative to permanently implanted reference electrodes and bony landmarks using accurate X-radiographs in the coronal and sagittal planes. The position of cells was reconstructed from the X-ray coordinates taken together with serial histological sections (50 μm stained with cresyl violet for cytoarchitecture, and 25 μm stained by the method of Gallyas (1979) for myeloarchitecture), which showed the reference electrodes and microlesions made at the end of some of the microelectrode tracks (see Fig. 1, *a, b*). A regression analysis between the microlesions and the corresponding X-ray coordinates was performed for each of the anteroposterior, lateral, and dorsoventral planes to determine the relation between the X-ray coordinates and the position in the histological section. From these regressions, the position of any cell could be determined from its X-ray coordinates. The accuracy of the method was approximately 0.2 mm, as shown by the SD of the intercepts of the regression analyses. The position of every cell recorded was then reconstructed for each monkey by making large-scale drawings of histological sections at 250 μm intervals throughout the temporal lobe. On these drawings the positions of all cyto- and myeloarchitectonic transitions as defined by Seltzer and Pandya (1978) were marked. Myeloarchitecture was identified with low-power microscopy, whereas higher power (60×) was generally used for cytoarchitectural analysis. In this way the architectonic subregion within which each neuron was located was determined.

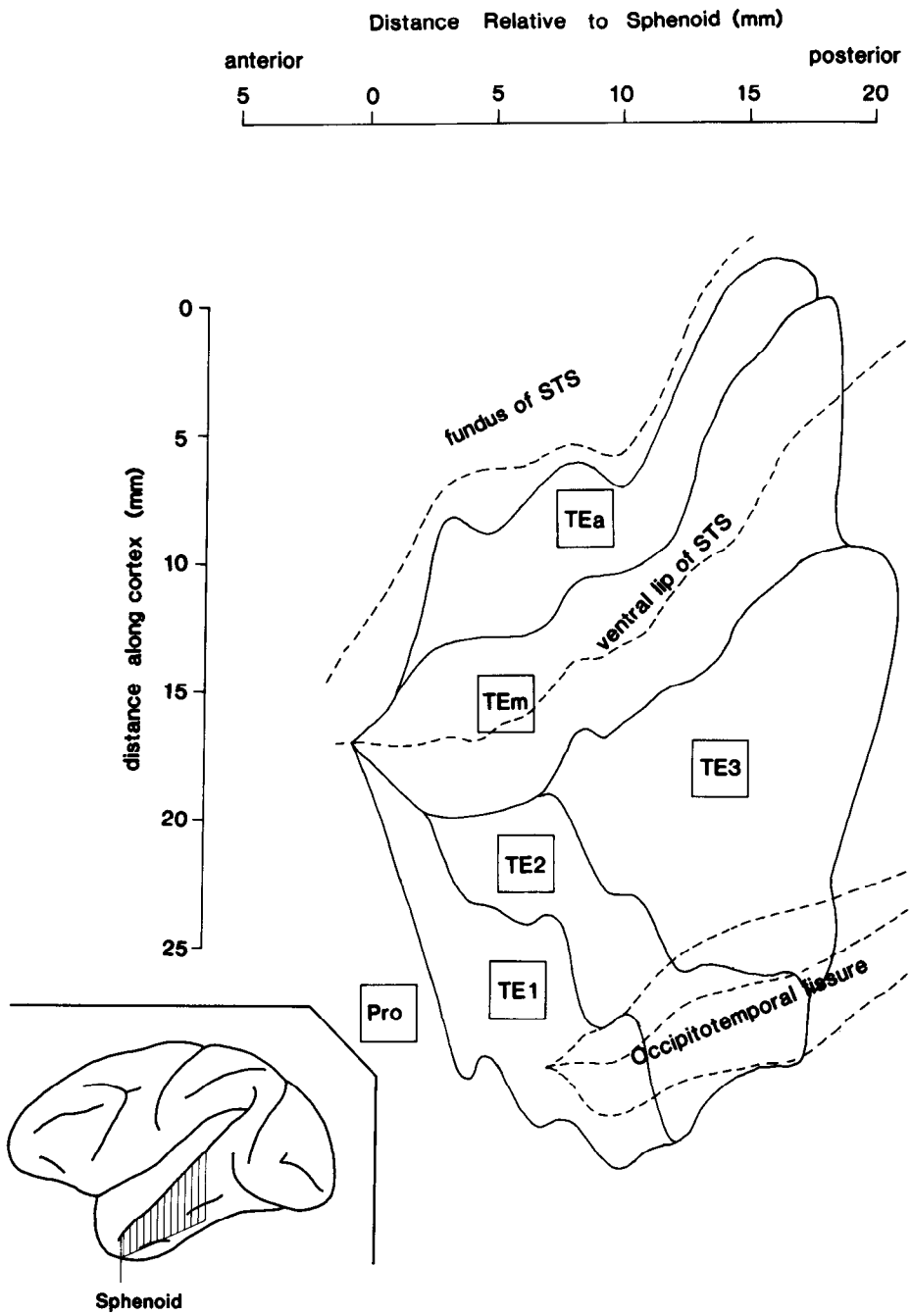


Figure 3. Plan view of the cortex on the ITG represented on a 2-dimensional surface that preserves topology (see text).

Assessing modality specificity

Visual responsiveness. This was assessed in 3 ways. First, stimuli were stored in digital form on a computer disk and displayed on a video monitor (Microvitec) using a video framestore (Matrox QRGB 256). The resolution of these images was 256 wide × 256 high with 256 gray levels. The monitor provided maximum and minimum luminances of 8.0 and 0.13 footlamberts, respectively, and was adjusted internally for linearity to within 3% using a photometer. The computer randomized the order of presentation of these stimuli, switched the stimuli on and off for each trial, and synchronized its data collection so that the stimulus was turned on at the start of the 21st bin of the peristimulus time histogram (which consisted of 100 bins each 10 msec long). This method allowed completely standardized and randomized presentation of quantitatively specified stimuli as diverse as sine-wave gratings and faces, and allowed image-processing techniques such as spatial frequency filtering and subregion extraction to be applied to the stimuli presented.

Second, stimuli were presented by the opening of a fast rise time (less than 15 msec), large-aperture shutter (Compur Electronic 5FM, 6.4 cm aperture) that opened for 1.0 sec after a 0.5 sec signal tone (400 Hz) provided to allow the monkey to fixate before the shutter opened. The stimuli were presented against a uniform background (a large white screen). This method allowed the presentation of 3D stimuli such as real faces and 3D objects that differed over a wide range of parameters such as size, shape, and color, and also allowed 2D stimuli such as photographs of a wide range of faces to be presented. The monkeys performed a visual discrimination task during the testing with these methods to ensure that they looked at the stimuli (see Baylis et al., 1985). Fruit juice could be obtained by licking a tube in front of the mouth for all stimuli except for a square, which indicated that the monkey had to refrain from licking in order to avoid saline (S-).

Third, "clinical" testing consisted of showing the monkey objects, food, photographs, and the experimenter himself in an interactive way, and without restricting the monkey's field of view. The stimuli were

either held stationary, moved, or swept across the visual field. The firing rate of the neuron was measured during the presentation of the stimuli. The criteria for classifying a neuron as visually responsive were the same as those previously used by Rolls et al. (1977) and Sanghera et al. (1979).

Having established a cell as visually responsive, large numbers of tests were applied to investigate the stimulus requirements for the response. These tests are described below.

Auditory responsiveness. Running counts of neuronal firing rate were taken in the quiet to estimate the baseline firing rate of the neuron, and then counts were taken during the production of a number of simple and complex sounds. The simple sounds consisted of tones of various frequencies and frequency-modulated tones. The complex sounds included normal human speech, imitations of monkey vocalizations, and a set of natural sounds that included scraping and tapping made in the laboratory. Any neuron showing a significantly increased firing rate (as tested by an analysis of variance) to one or more sounds was classified as having an auditory response.

Somesthetic responses. Tactile stimuli were applied by gentle pressure or stroking to the face, trunk, legs, or arms of the monkey. The neuronal responses were collected and assessed in a way analogous to that described for auditory stimulation.

Oral responses. Any cell showing a significant response while the monkey was licking, chewing, or drinking fruit juice from a syringe was placed in this category. Also any neuron showing a response to gentle touch in or around the mouth or during mouth movements was included.

Other responses. A few cells exhibited activity that was influenced by the state of interest or arousal of the monkey. Other cells showed an increase in firing rate during particular, or general, movements of the monkey.

Analysis of visual response properties

Having established that a cell was visually responsive, a number of tests were carried out as described next to further assess its response properties and stimulus requirements. The distribution of such properties across different areas was then compared.

Visual stimulus requirements. Neurons with visual responses were classified into 6 mutually exclusive categories (SB, SS, MB, MD, MS, and MX). The criteria for categorization were as follows. First, the neuron was categorized as responding best to stationary (S in the first character position) or to moving (M in the first character position) visual stimuli. If no response was found to any stationary visual stimulus, but a significant response occurred to one or more moving visual stimuli, then it was classified as requiring movement (M). Neurons with responses that were more than 2 SD larger to moving than to stationary stimuli were also placed in this M class. Second, neurons were categorized according to the type of selectivity they showed, indicated by the second character, as either broad (B) or selective (S). The criterion of broad versus selective responsiveness defined the degree of discriminability (d') of the neuronal responses to different visual stimuli. The discriminability (d') of 2 responses was measured by the number of (joint) SD separating those responses (see Egan, 1975; Rolls et al., 1984; Baylis et al., 1985). Any neuron for which the discriminability of the responses to the most effective and least effective stimuli was greater than 2.0 was classified as narrowly tuned or selective (S), and all others were classified as broadly tuned to different visual stimuli (B in the second character position). (Note that tuning in this context is used to refer to the change of responsiveness produced by different stimuli, which are not necessarily along a single physical dimension such as spatial frequency.) Cells in the M (movement) class were subclassified as being responsive to any moving stimulus (MB) or to the direction of motion (MD), the nature of the shape or object being moved (MS), or both (MX). This subclassification was determined by the results of a 2-way analysis of variance in which the factors were stimulus type and direction of motion, with significance level set at 0.05.

Stimulus requirements of cells showing visual selectivity. For all cells falling into the class of those responding to stationary stimuli, and having responses that were selective between the different stimuli (class SS), further testing and analysis were performed to establish the stimulus requirements.

When digitized visual stimuli were being presented on the video monitor, 1 set of 4–12 visual stimuli was used at a time. Each set of stimuli was designed to provide neuronal response data relevant to one or several hypotheses. For example, 1 set included 5 different faces, to test whether the neuron responded differently to different faces, and some non-face stimuli such as a sine-wave grating, a boundary curvature descriptor (see below), and a complex non-face visual image of the type described below (see Baylis et al., 1985, Fig. 1), to provide an indication of whether the neuron responded differently to face and to non-face stimuli. Another set consisted of a series of low- and high-pass spatial frequency filtered images of 1 face (see Rolls et al., 1985). Another series consisted of sine-wave gratings with different spatial frequencies and orientations, and another of boundary curvature descriptors (see Schwartz et al., 1983). The computer randomized the sequence in which the members of the set were presented, and after it had presented the sequence once, it restarted the set with another random sequence. The computer was allowed to repeat the set 4–10 times to provide sufficient data for an analysis of variance in order to determine whether the neuron responded significantly differently to the different stimuli within the set. After data had been collected on 1 set, the experimenter then started a different set. Within each set, S- trials appeared with a probability that was usually specified as 0.25 but could be reduced.

Face stimuli. Photographs were prepared of macaque monkey faces (looking directly at the camera) and of human faces. The photographic negatives were digitized using a Scandig 3 (Joyce-Loebl Ltd., Gateshead, U.K.) scanning digitizer of photographs, and stored in an image file with a resolution of 256 × 256 × 8 bits, ready for presentation on the Matrox QRGB 256 framestore.

Non-face stimuli. The responses of the cells were tested to a wide range of non-face stimuli, as follows.

Sine-wave gratings: A set of sine-wave gratings with spatial frequencies of 1–64 cycles/image and with orientations spaced $\pi/4$ radians apart was presented on the video monitor in random sequence. Each image subtended 12° at the retina.

Boundary curvature descriptors: A set of boundary curvature descriptors with frequencies of 0–15 cycles, with amplitudes ranging from 0.5–2.0 and with 4 different phases, was presented (see Schwartz et al., 1983).

3D objects: More than 1000 3D "junk" objects were collected, and 6–30 of these, chosen randomly, were used to test whether there was any indication that a neuron responded to a complex visual stimulus. If there was any indication of a response, much more extensive testing with non-face stimuli was performed. The objects were chosen for differences in size, shape, color, surface pattern, and texture, but for convenience of storage the objects were less than 20 cm long. Since these objects varied along different visual dimensions, testing neuronal responses to several of them could potentially reveal selectivity for particular visual characteristics. Objects were positioned between 2 cm and 1 m behind the shutter.

Non-face video images: More than 500 non-face video images of complex scenes were available on the system and were used in recognition memory tasks (Baylis and Rolls, 1983, 1986). Neurons that responded to these stimuli but not to faces or to simple visual stimuli were included in the complex (X) class.

Classes of visually responsive cells

Using the methods described above, visually responsive cells in each area with stimulus selectivity for stationary stimuli (SS) were placed into the following classes. The criteria for being included within 1 of the following classes were, first, that there was a significant effect of stimulus variation within that class (as indicated by $p < 0.01$ in an ANOVA) and, second, that the response to the optimal stimulus within that class was more than twice that to the least effective stimulus in that class, with this difference being significant at the $p < 0.05$ level.

Face selective. In addition to the criteria described above, further criteria used to define a face-selective neuron were that the neuron had to respond to the optimal face stimulus with a change of firing rate at least twice that to the optimal non-face stimulus and that this difference be significant ($p < 0.05$). The majority of the neurons classified as showing responses selective for faces responded much more specifically to faces than required by these criteria. For half these neurons, their response to the most effective face was more than 5 times as large as to the most effective non-face stimulus, and for 25% of these neurons, the ratio was greater than 10:1 (see Baylis et al., 1985, for further details).

Fourier boundary curvature descriptors. Selectivity in terms of frequency of modulation, phase, or both was determined according to the methods and criteria described above.

Spatial frequency selectivity. The number of cells showing selectivity

Table 3. The number of neurons sampled in the different regions, and the number found with visual responses

Area	Subarea	Number of neurons	
		Total	Visual
TA	TS	207	45
	TAa	98	38
	TPO	547	244
TE	PGa	144	52
	IPa	184	75
	TEa	411	250
	TEm	379	232
	TE3	152	88
	TE2	152	51
TG	TE1	58	33

for particular sinusoidal gratings, in terms of orientation, frequency, or both was determined using the methods and criteria described above.

Shape and color selectivity. Cells showing selectivity in terms of either shape or color were so classed, using the criteria described above.

Idiosyncratic selectivity. Any cell showing a significantly different response ($p < 0.01$) to different stimuli, but where no understanding of the dimension of selectivity was possible, was included in this category. Also cells showing selectivity for more than 1 of the above dimensions were included in this category.

Procedure

More than 2600 neurons were isolated and studied in the cortex in the inferior part of the temporal lobe of 6 hemispheres of 3 rhesus monkeys in 160 tracks. Similar numbers of neurons were analyzed in the left and right hemispheres, and no differences were observed. A very large number of tests could be applied to any neuron. Every test was not applied to every neuron, partly because in many cases it was of little value to perform some tests after null results to certain others had been obtained (e.g., to test for visual selectivity if the cell did not have visual responses) and partly because of limitations of time for which cells could be held. However, it is unlikely that there was any bias to the number and type of tests applied to a given neuron with respect to the area in which the neuron was located, in that at the time of testing the experimenter did not know what subregion was being sampled.

After the neurons had been categorized as described above, the proportion of neurons of each type in each of the areas as determined by cyto- and myeloarchitectonics was determined. To obtain the proportion for each area the number of cells in each category was divided by the number of visual cells tested for that form of selectivity.

The numbers of neurons sampled in each area and the numbers of neurons with visual responses in each area, and which therefore form the sample size for subsequent analyses of visual responsiveness within that area, are summarized in Table 3.

Results

Response properties

Modality

First, it was clear that these areas were influenced differently by inputs from the different modalities (Fig. 4). In particular, it was of interest that areas TS and TAa were influenced by visual and auditory inputs; that areas TPO, PGa and IPa were influenced by somatosensory, visual, and auditory inputs; and that areas TEa, TEm, TE3, TE2, and TE1 were influenced primarily by visual inputs (Fig. 4).

Visual stimulus requirements

Second, it was clear that within the visual modality, the types of response found were different across these different areas (Fig. 5). For example, in areas TS and TAa, most of the visual responses to stationary stimuli were broadly tuned (SB), and some neurons responded only to moving stimuli; in areas TPO, PGa, and IPa, neurons that responded to stationary stimuli were often selective (SS), and relatively many neurons responded to moving visual stimuli, sometimes with movement, direction, and stimulus selectivity combined (MX); and in areas TEa–TE1 (i.e., TEa, TEm, TE3, TE2, and TE1), relatively many neurons responded to stationary stimuli with stimulus selectivity (SS), and few neurons responded to moving visual stimuli (Fig. 5).

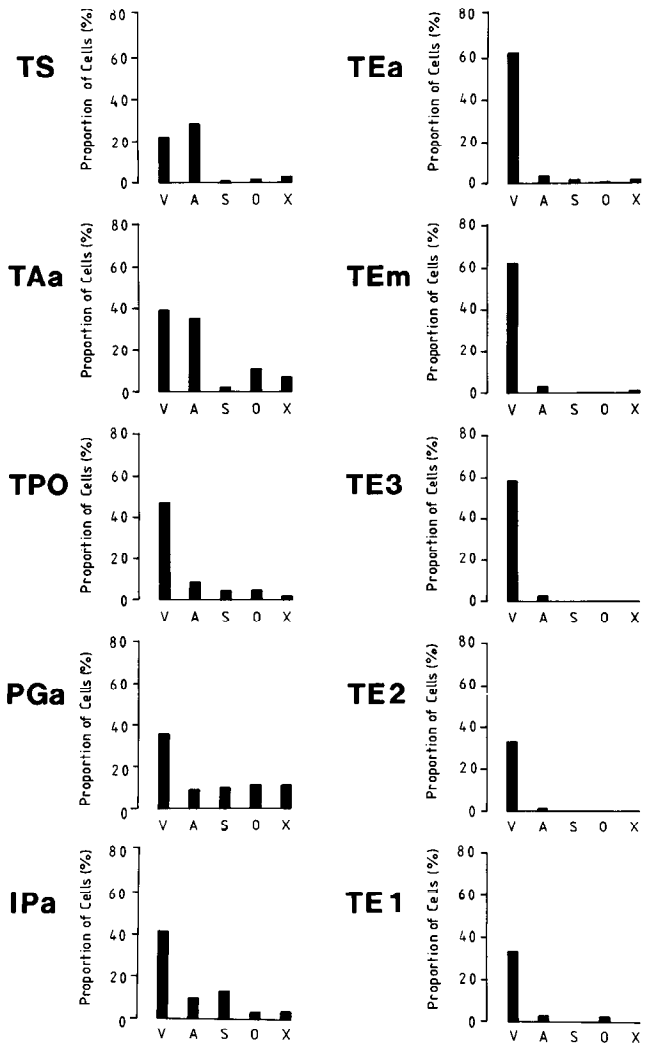


Figure 4. Proportions of neurons in different areas of the cortex within and close to the STS with responses to stimuli in different modalities. Abbreviations: *V*, visual; *A*, auditory; *S*, somatosensory (for example, touch to the leg or body); *O*, oral, including mouth movements or touch; *X*, other responses, including body movement. The numbers of neurons sampled in each area are given in Table 3.

Optimal stimulus for visually selective neurons

Third, it was clear that the neurons that responded with stimulus selectivity were localized, with different types of selectivity predominating in different architectonic areas (Fig. 6). For example, neurons that responded primarily to faces were found predominantly in areas TPO, TEa, and TEm: In these areas 18, 21, and 22%, respectively, of visual cells showed selectivity for faces. A few such cells were found in areas IPa, PGa, and TE3. Neurons

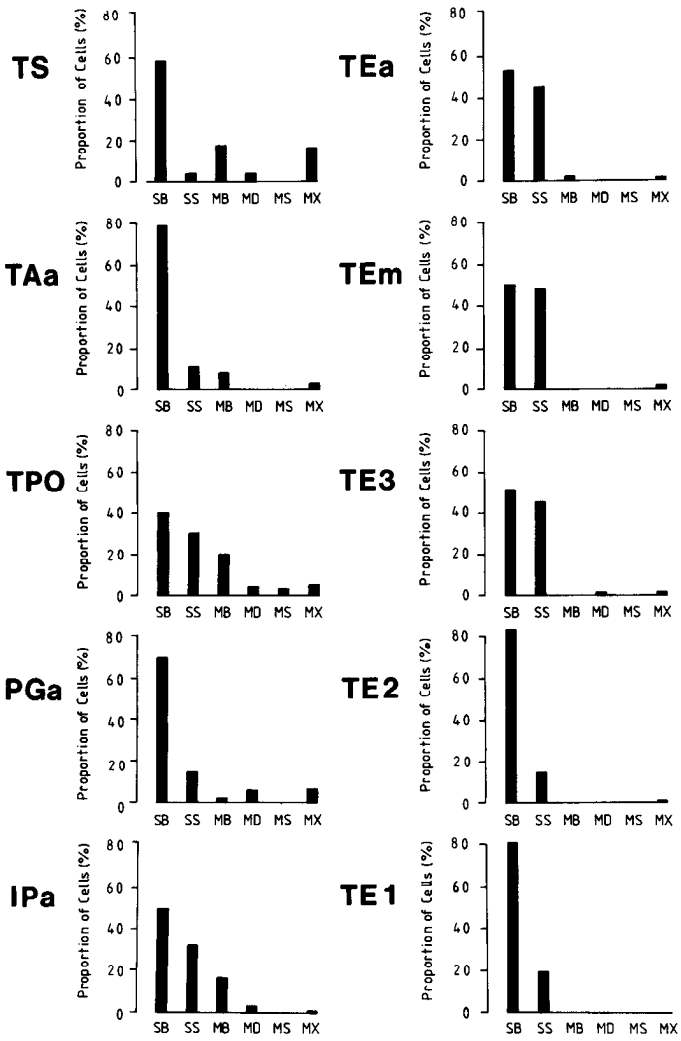


Figure 5. Proportions of neurons in different areas of the cortex within and close to the STS with responses to different types of visual stimuli. Abbreviations: *SB,* cells responding to stationary stimuli with broad tuning; *SS,* cells responding to stationary stimuli with selective responses to only some stimuli; *MB,* cells responding only to moving visual stimuli, with broad tuning; *MD,* cells responding only to moving visual stimuli, with direction tuning; *MS,* cells responding only to moving visual stimuli, with stimulus selectivity; *MX,* cells responding only to moving visual stimuli, with both directional and stimulus selectivity. The numbers of visual neurons sampled in each area are given in Table 3.

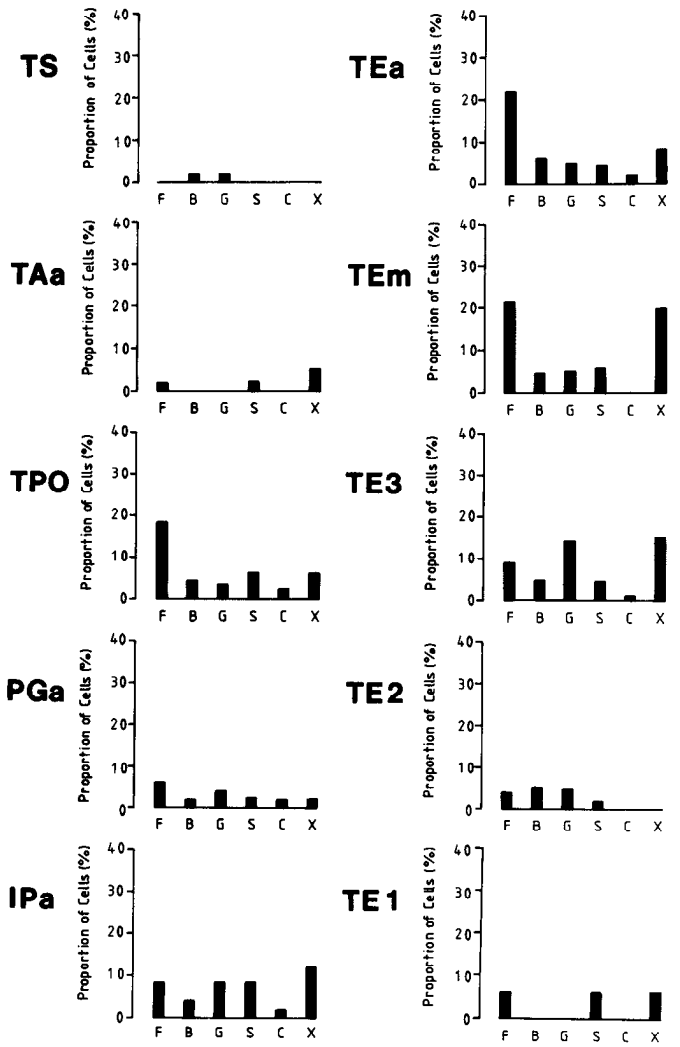


Figure 6. Proportions of neurons in different areas of the cortex within and close to the STS with responses to different patterns of visual stimuli. Abbreviations: *F,* selective response to faces; *B,* major response and tuned to boundary curvature descriptors; *G,* major response and tuned to sine-wave grating; *S,* shape selectivity; *C,* color selectivity; *X,* response only to complex stimulus. The numbers of visual neurons sampled in each area are given in Table 3.

that responded to simple visual stimuli such as sine-wave gratings (G) were relatively more common in areas TE3 and IPa. For example, cells tuned to the spatial frequency or orientation of sine-wave gratings comprised 14% of the cells analyzed in TE3. Neurons that responded only to complex visual stimuli were relatively common in areas TE1, TE3, and TEm (Fig. 6).

Visual response latency

The latencies of the visual responses of the cells recorded in each area are shown in Figure 7. It can be seen that the shortest response latencies were found in areas TPO, TEa, TEm, and TE3; that the latencies in areas TE2, PGa, and IPa were somewhat longer; and that the longest response latencies were in areas TS, TAa, and TE1. It is shown below that these latencies are related to connectional proximity to the prestriate cortex. It was noted that although a few cells shown in Figure 7 had latencies shorter than those typically reported for neurons in the temporal lobe visual cortical areas, in some cases the relatively short latency response at, for example, 70–80 msec did not differ between stimuli, and the responses only became differential at more typical response latencies of 90–100 msec.

Similarity of subareas based on response properties

In order to investigate statistically whether these architectonic areas contained different types of neurons, a separate χ^2 test was applied to the data shown in Figures 4–6. In all 3 cases the result was highly significant, indicating that different neuron types were found in the different architectonic areas.

In order to investigate statistically whether there were similarities between any of the areas, cluster analyses (Wishart, 1969) were performed on the data shown in Figures 4–7. For each cluster analysis, 18 parameters were used for each area. These parameters were the proportions of neurons in each of the groups

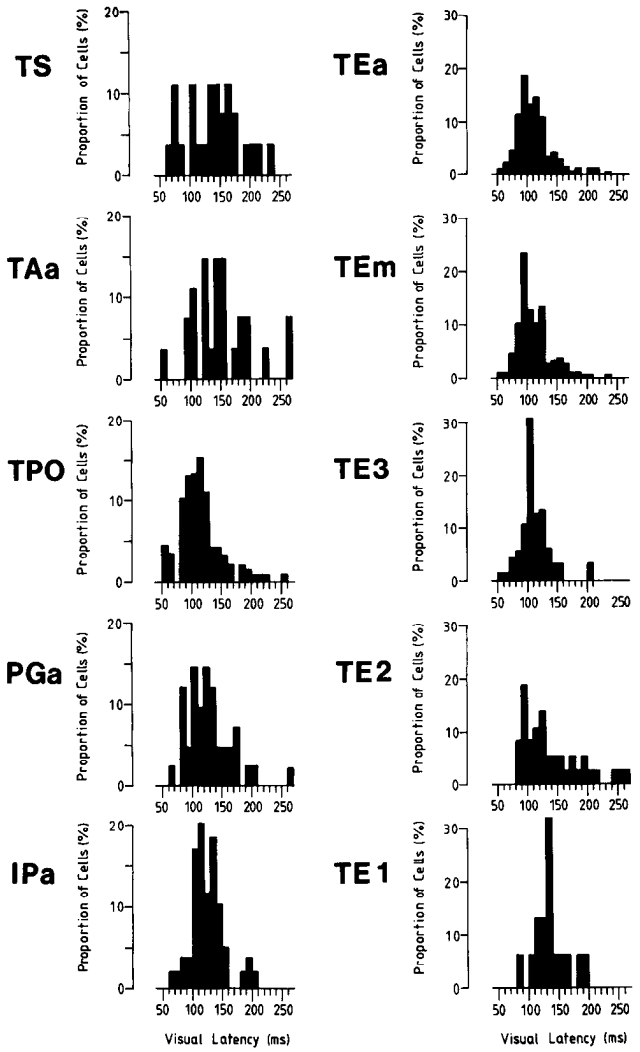


Figure 7. Latencies (in msec) of the visual responses of neurons recorded in different cortical areas. The numbers of visual neurons sampled in each area are given in Table 3.

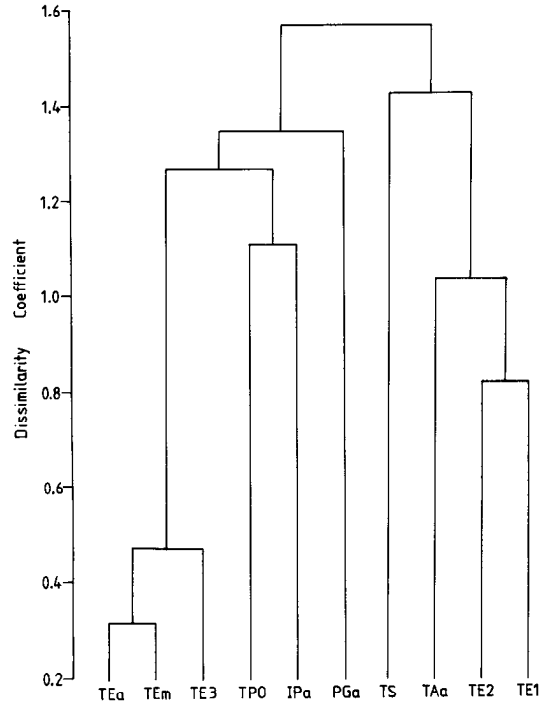


Figure 8. Hierarchical cluster analysis based on the response properties of neurons recorded in different cortical areas in the temporal lobe.

shown in Figures 4–6 and the median latency from Figure 7. The results of a hierarchical cluster analysis (using the average linkage method of Sokal and Michener, 1958) are shown in dendrogram form in Figure 8. This method groups members on the basis of low dissimilarity coefficients between them. Once groups are formed, they are represented as a single point, which may then form links with other elements or groups. Thus this method takes into account group structure in a way that many clustering techniques do not. It was felt important that group structure be respected because doing so will not beg the question of whether the cortical subareas truly represent functional units.

It is shown in Figure 8 that, first, areas TEa, TEm, and TE3 cluster together closely; next, areas TE1, TE2, and TAa cluster together. (In these 3 areas the visual tuning of the neurons was often relatively broad, as seen in Fig. 5.) Area TS, which also had many broadly tuned neurons, clustered towards this group. A third cluster was formed by TPO and IPa, which are both polysensory areas. Area PGa had similarities both with the third cluster (TPO and IPa) and with the first cluster (TEa, TEm, and Te3).

Similarity of areas based on anatomy

As the areas grouped according to physiological properties, further cluster analyses were performed to determine whether the areas grouped on the basis of their anatomy, and if so whether similar groupings to those found physiologically were present. The anatomical data used were the architectonic features and the connections of each of the different areas. These data have been shown in Tables 1 and 2, and provided 19 binary parameters for the cluster analyses. The cluster method used was the average linkage hierarchical method of Sokal and Michener (1958). The result of this is shown in dendrogram form in Figure 9. The tightest clusters are formed by adjacent subareas, namely TS and TAa; PGa and IPa; TEa, TEm and TE3; and TE1 and TE2. Beyond this lowest level of clustering, no clusters are formed until very large dissimilarity coefficients are tolerated. Thus anatomically there is the suggestion of five main areas, i.e. the four noted above, and region TPO.

Discussion

The response properties of neurons will be discussed under the 5 main anatomical groupings identified above. All the between-group comparisons discussed next are based on data that show a χ^2 effect of group at $p < 0.01$. When comparisons are made of neuron types between areas within a group, the levels of significance of the χ^2 values are given. (It may be noted that the percentages of neurons responding in a particular way after the grouping will be similiar to, but not identical with, the percentages shown separately for each area in Figs. 4–7.)

TS + TAa

Although primarily an auditory region, as one might expect, a surprisingly high proportion (27%) of visual responses was found. It is interesting that these had rather long (median = 140 msec)

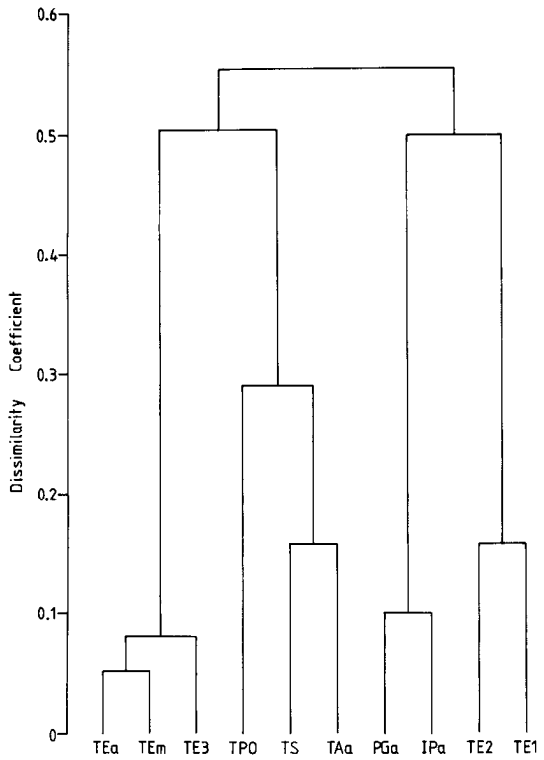


Figure 9. Hierarchical cluster analysis based on the architectonics and connections of the different cortical areas in the temporal lobe.

latencies, suggesting a somewhat indirect route. The visual cells were mainly nonselective (68%), but those showing selectivity were generally selective for moving stimuli (25% of the visual cells). The poor functional clustering between TS and TAa reflects the larger number of neurons excited by modalities other than auditory in TAa (52 vs 28%, confirmed as different at $p < 0.001$ using a χ^2 test). This suggests a more obviously auditory role for TS, with more cross-modal involvement of TAa.

TPO

This region is highly multimodal, with a moderate proportion of visually responsive neurons (45%), some auditory responses (8%), and other responses (10%). Those cells showing selective visual responses (60% of the visual cells) had a variety of preferred stimuli. Thus, 30% were tuned to moving stimuli, 18% to faces, 6% to other complex stimuli, and 14% to relatively simple stimuli. Area TPO had rather short visual latencies (median = 100 msec), consistent with the fact that area TPO has a strong input from prestriate cortex (Seltzer and Pandya, 1978).

PGa + IPa

Again, inputs from many different modalities elicit responses from neurons in this region. A large proportion (39%) of visually responsive neurons was found, and many (12%) neurons could be driven by somesthetic stimulation, presumably reflecting input from the parietal cortex. A smaller number of auditory (10%) and other (7%) responses was also found. The visual neurons had an intermediate latency (median = 120 msec), and only a small proportion (7%) showed selectivity for faces.

Although anatomically similar, these 2 areas exhibited many differences in response properties. For example, area IPa had a higher proportion of visual cells selective for particular static stimuli (32 vs 15%, $p < 0.01$).

TEa + TEm + TE3

This region is unequivocally a visual region, with 60% of cells showing visual responses, and only 6% showing any other type of responsiveness. The functional differences between the 3 subareas were small. The response latencies are short (median = 90 msec), as might be expected considering the inputs from TEO and OA. Half (49%) of the cells with visual responses showed marked stimulus selectivity, which was almost always to stationary visual stimuli. A relatively high proportion (19%, see Fig. 6) of the cells with visual responses in areas TEa and TEm was selective for faces, whereas the proportion was much smaller (9%, $p < 0.005$) in area TE3.

TE2 + TE1

Cells in these regions were similar to each other, and were the most difficult to excite of any of the regions studied. The proportion of neurons responsive to any part of the total battery of stimulation was only 36%. This compares to 67, 63, 74, and 64% for the other 4 main regions described above. This is despite the wide range of stimuli used in this study. Of those cells that did respond, almost all were visual (34% of all cells). This might be expected, as this region receives almost exclusively from TE3, which itself showed only visual responses. Although quite a high proportion (83%) of the visual cells appeared to be broadly tuned (Fig. 4), it must be remembered that they represent only 24% (83 × 34/100) of the cells recorded in this region. It may be that the other cells in this region have very specific stimulus requirements that were not often met even by the large array of visual stimuli available or that responses to one or another class of stimuli in the set were conditional on some concurrent process (such as learning). The sample size of cells in this region was the smallest ($n = 210$) of the 4 regions, and clearly further work is needed to characterize cell responses in this region better.

Face processing in the neocortex in the temporal lobe

The finding that the neurons with responses selective for faces are located primarily in architectonic areas TPO, TEa, and TEm, and are not simply the most complex cells found throughout the inferior temporal visual cortex, provides further evidence that they are a specialized population of neurons. The responses of these neurons to faces are selective in that they are 2–10 times as large to faces as to gratings, simple geometrical stimuli, or complex 3D objects (Perrett et al., 1982; Baylis et al., 1985). The cells are typically unresponsive to auditory or tactile stimuli and to the sight of arousing or aversive stimuli. The magnitude of the responses of the cells is relatively constant despite transformations such as rotation, so that the face is inverted or horizontal, and alterations of color, size, distance, and contrast (Perrett et al., 1982; Rolls and Baylis, 1986). Thus, these neurons at this high level of visual information processing have some properties of perceptual invariance that relate them closely to perception (Rolls and Baylis, 1986). Masking or presenting parts of the face (e.g., eyes, mouth, or hair) in isolation reveals that different cells respond to different features or subsets of features. For some cells, responses to the normal organization of cutout or line-drawn facial features are significantly larger than to jumbled controls (Perrett et al., 1982). These findings indicate that explanations in terms of arousal, emotional, or motor reactions, and simple visual feature sensitivity or receptive fields are insufficient to account for the selective responses to faces and face features observed in this population of neurons in the cortex in the STS (Perrett et al., 1982; Baylis et al., 1985; Rolls and Baylis,

1986). Observations consistent with these findings have recently been published by Desimone et al., (1984), who described a similar population of neurons located primarily in the cortex in the STS that responded to faces but not to simpler stimuli such as edges and bars or to complex non-face stimuli.

A population of neurons with responses selective for faces has been described in the basal accessory nucleus of the amygdala (Leonard et al., 1985). It will be of interest to determine how information about faces reaches these neurons. There is a projection from the cortex in the lower bank of the STS to the temporal pole (Seltzer and Pandya, 1978), which in turn projects into the basal accessory nucleus of the amygdala (Herzog and Van Hoesen, 1976; Aggleton et al., 1980). In addition, there is a projection from area TPO to a part of the entorhinal cortex that is reciprocally connected with the amygdala (Amaral et al., 1983). The relative functional significance of these 2 output pathways of areas of the cortex with neurons that respond selectively to faces remains to be investigated. It is also possible that the 2 anatomically distinct regions where cells with responses selective for faces are found (TPO and TEa-TEm) are directly connected anatomically. Further work is necessary to address this question and other possible output pathways from these regions.

Multimodal processing

A large part of the cortex in the banks of the STS has been shown to receive information from different modalities (see introduction, Table 2, and below). This region extends from the cortex in the fundus across the upper bank of the STS up to the external surface of the superior temporal gyrus, including areas IPa, PGa, TPO, and TAa. Desimone and Gross (1979) and Bruce et al. (1981) described multimodal regions in the temporal cortex of the anesthetized macaque. Although precise architectonic determinations were not carried out, it appears that the "superior temporal polysensory area" (STP) corresponds to the multimodal area analyzed here (R. Desimone and C. Gross, personal communication, 1985).

Within this region a high proportion of visually influenced cells show selectivity for moving visual stimuli. Many such cells show a complex specificity for the stimulus and for the direction of movement. [Such neurons have also been described in this region by Perrett et al. (1983).] This may partially support the contention of Desimone and Gross (1979) that this region has a role in visuospatial processing. However, a large number of neurons showing a high degree of stimulus selectivity are also found within this region of cortex. In particular, 1 subregion of this area, TPO, contains a large number of cells with responses selective for faces. The existence of large numbers of highly selective, visually responsive neurons here, together with neurons selective in other modalities, and neurons responsive to visual movement suggests that this region should be able to integrate or combine information both within and across modalities that has already been processed in different specialized subsystems. On the other hand, the more ventral areas, such as TEa and TEm, appear to be more concerned with highly specialized processing in the visual modality primarily.

References

Aggleton, J. P., and R. E. Passingham (1981) Stereotaxic surgery under X-ray guidance in the rhesus monkey, with special reference to the amygdala. Exp. Brain Res. *44:* 271–276.

Aggleton, J. P., M. J. Burton, and R. E. Passingham (1980) Cortical and subcortical afferents to the amygdala in the rhesus monkey (*Macaca mulatta*). Brain Res. *190:* 347–368.

Amaral, D. G., R. Insausti, and W. M. Cowan (1983) Evidence for a direct projection from the superior temporal sulcus to the entorhinal cortex in the monkey, *Macaca fascicularis.* Brain Res. *275:* 263–278.

Baylis, G. C., and E. T. Rolls (1983) Responses of neurons in the inferior temporal visual cortex in long and short term memory tasks. Soc. Neurosci. Abstr. *9:* 21.

Baylis, G. C., and E. T. Rolls (1986) Responses of neurons in the inferior temporal cortex in short term and serial recognition memory tasks. Exp. Brain Res. (in press).

Baylis, G. C., E. T. Rolls, and C. M. Leonard (1985) Selectivity between faces in the responses of a population of neurons in the cortex in the superior temporal sulcus of the monkey. Brain Res. *342:* 91–102.

Bender, D. B., and C. G. Gross (1981) Backward masking in monkeys after foveal prestriate and inferior temporal cortex lesions. Physiol. Psychol. *9:* 257–259.

Bruce, C., R. Desimone, and C. G. Gross (1981) Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. J. Neurophysiol. *46:* 369–384.

Bruning, J. L., and B. L. Kintz (1977) *Computational Handbook of Statistics,* 2nd ed., Scott Foresman, Glenview, Illinois.

Butter, C. M. (1972) Detection of masked patterns in monkeys with inferotemporal, striate or dorsolateral frontal lesions. Neuropsychologia *10:* 241–243.

Cowey, A., and C. G. Gross (1970) Effects of foveal prestriate and inferotemporal lesions on visual discrimination by rhesus monkeys. Exp. Brain Res. *11:* 128–144.

Dean, P. (1976) Effects of inferotemporal lesions on the behavior of monkeys. Psychol. Bull. *83:* 41–71.

Desimone, R., and C. G. Gross (1979) Visual areas in the temporal cortex of the macaque. Brain Res. *178:* 363–380.

Desimone, R., J. Fleming, and C. G. Gross (1978) Cortical afferents to inferior temporal cortex in the macaque. Invest. Ophthalmol Vis. Sci. (Suppl.) *282.*

Desimone, R., J. Fleming, and C. G. Gross (1980) Prestriate afferents to inferior temporal cortex. A horseradish peroxidase study. Brain Res. *184:* 41–56.

Desimone, R., T. D. Albright, C. G. Gross, and C. Bruce (1984) Stimulus-selective responses of inferior temporal neurons in the macaque. J. Neurosci. *4:* 2051–2062.

Egan, J. P. (1975) *Signal Detection Theory and ROC Analysis,* Academic, New York.

Fuster, J. M., and J. P. Jervey (1981) Inferotemporal neurons distinguish and retain behaviorally relevant features of visual stimuli. Science *212:* 852–955.

Gaffan, D., and L. Weiskrantz (1980) Recency effects and lesion effects in delayed nonmatching to randomly baited samples by monkeys *Macaca mulatta.* Brain Res. *196:* 373–386.

Gallyas, F. (1979) Silver staining of myelin by means of physical development. Neurol. Res. *1:* 203–209.

Gross, C. G., D. G. Bender, and C. E. Rocha-Miranda (1969) Visual receptive fields of neurons in inferotemporal cortex of the monkey. Science *166:* 1303–1306.

Gross, C. G., C. E. Rocha-Miranda, and D. B. Bender (1972) Visual properties of neurons in inferotemporal cortex of the macaque. J. Neurophysiol. *35:* 96–111.

Herzog, A. G, and G. W. Van Hoesen (1976) Temporal neocortical afferent connections to the amygdala in the rhesus monkey. Brain Res. *115:* 57–69.

Jones, E. G,. and H. Burton (1975) Areal differences in the laminar distribution of thalamic afferents in cortical fields of the insular, parietal and temporal regions of primates. J. Comp. Neurol. *168:* 197–248.

Laursen, A. M. (1982) A lasting impairment in circle ellipse discrimination after inferotemporal lesions in monkeys. Behav. Brain Res. *6:* 210–212.

Leonard, C. M., E. T. Rolls, F. A. W. Wilson, and Baylis, G. C. (1985) Neurons in the amygdala of the monkey with responses selective for faces. Behav. Brain Res. *15:* 150–176.

Manning, F. J. (1972) Serial reversal learning by monkeys with inferotemporal or foveal prestriate lesions. Physiol. Behav. *8:* 177–181.

Merrill, E. G., and A. Ainsworth (1972) Glass-coated platinum-plated tungsten microelectrodes. Med. Biol. Eng. *10:* 662–672.

Mikami, A., and K. Kubota (1980) Inferotemporal neuron activities and color discrimination with delay. Brain Res. *182:* 65–78.

Pandya, D. N., and F. Sanides (1973) Architectonic parcellation of the temporal operculum in the rhesus monkey and its projection pattern. Z. Anat. Entwicklungsgesch. *139:* 127–161.

Perrett, D., E. T. Rolls, and W. Caan (1982) Visual neurons responsive to faces in the monkey temporal cortex. Exp. Brain Res. *47:* 329–342.

Perrett, E. I., P. A. J. Smith, D. Milner, and M. A. Jeeves (1983) Visual cells selective for type of movement and stimulus form in the temporal cortex of the macaque monkey. Perception *12:* A35.

Pribram, K. H., A. Spevack, D. Blower, and D. McGuinness (1980) A decisional analysis of the effects of inferotemporal lesions in the rhesus monkey. J. Comp. Physiol. Psychol. *94:* 675–690.

Rolls, E. T. (1981a) Processing beyond the inferior temporal visual cortex related to feeding, learning, and striatal function. In *Brain Mechanisms of Sensation,* Y. Katsuki, R. Norgren, and M. Sato, eds., pp. 241–269, Wiley, New York.

Rolls, E. T. (1981b) Responses of amygdaloid neurons in the primate. In *The Amygdaloid Complex,* Y. Ben-Ari, ed., pp. 383–393, Elsevier, Amsterdam.

Rolls, E. T. (1984) Neurons in the cortex of the temporal lobe and in the amygdala of the monkey with responses selective for faces. Hum. Neurobiol. *3:* 209–222.

Rolls, E. T. (1985) Connections, functions and dysfunctions of limbic structures, the prefrontal cortex, and hypothalamus. In *The Scientific Basis of Clinical Neurology,* M. Swash and C. Kennard, eds., pp. 201–213, Churchill Livingstone, London, U.K.

Rolls, E. T., and G. C. Baylis (1986) Size and contrast have only small effects on the responses to faces of neurons in the cortex in the superior temporal sulcus of the monkey. Exp. Brain Res. (in press).

Rolls, E. T., M. J. Burton, and F. Mora (1976) Hypothalamic neuronal responses associated with the sight of food. Brain Res. *111:* 53–66.

Rolls, E. T., S. J. Judge, and M. K. Sanghera (1977) Activity of neurones in the inferotemporal cortex of the alert monkey. Brain Res. *130:* 229–238.

Rolls, E. T., M. K. Sanghera, and A. Roper-Hall (1979) The latency of activation of neurons in the lateral hypothalamus and substantia innominata during feeding in the monkey. Brain Res. *164:* 121–135.

Rolls, E. T., S. J. Thorpe, M. Boytim, I. Szabo, and D. I. Perrett (1984) Responses of striatal neurons in the behaving monkey. 3. Effects of iontophoretically applied dopamine on normal responsiveness. Neuroscience *12:* 1201–1212.

Rolls, E. T., G. C. Baylis, and C. M. Leonard (1985) Role of low and high spatial frequencies in the face-selective responses of neurons in the cortex in the superior temporal sulcus. Vision Res. *25:* 1021–1035.

Sahgal, A., and S. D. Iversen (1978) Categorization and retrieval after selective inferotemporal lesions in monkeys. Brain Res. *146:* 341–350.

Sanghera, M. K., E. T. Rolls, and A. Roper-Hall (1979) Visual responses of neurons in the dorsolateral amygdala of the alert monkey. Exp. Neurol. *63:* 610–626.

Saxton, W. O., and T. L. Koch (1982) Interactive image processing with an off-line minicomputer: Organization, performance and applications. J. Microsc. *127:* 69–83.

Schwartz, E. L., R. Desimone, T. D. Albright, and C. G. Gross (1983) Shape recognition and inferior temporal neurons. Proc. Natl. Acad. Sci. USA *80:* 5776–5778.

Seltzer, B., and D. N. Pandya (1978) Afferent cortical connections and architectonics of the superior temporal sulcus and surrounding cortex in the rhesus monkey. Brain Res. *149:* 1–24.

Sokal, R. R., and C. D. Michener (1958) A statistical method for evaluating systematic relationships. Kansas Univ. Sci. Bull. *38:* 1409.

Spiegler, B. J., and M. Mishkin (1981) Evidence for the sequential participation of inferior temporal cortex and amygdala in the acquisition of stimulus-reward associations. Behav. Brain Res. *3:* 303–317.

Van Essen, D. C., J. H. R. Maunsell, and J. L. Bixby (1981) The middle temporal area in the macaque: Myeloarchitecture, connections, functional properties and topographic organization. J. Comp. Neurol. *199:* 293–326.

von Bonin, G., and J. Bailey (1949) *The Cortex of Macaca Mulatta,* University of Illinois Press, Urbana, IL.

Wilson, M., W. A. Wilson, Jr., and R. Remez (1977) Effects of prestriate inferotemporal and superior temporal sulcus lesions on attention and gaze shifts in rhesus monkeys. J. Comp. Physiol. Psychol. *91:* 1261–1271.

Wishart, D. (1969) *Numerical Taxonomy,* Academic, New York.