Visual Topography of Area TEO in the Macaque

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ABSTRACT
Previous studies have mapped the visuotopic organization of visual areas from V1 through V4 in the occipital cortex and of area TE in the temporal cortex, but the cortex in between, at the occipito-temporal junction, has remained relatively unexplored. To determine the visuotopic organization of this region, receptive fields were mapped at 1,200 visually responsive sites on 370 penetrations in the ventral occipital and temporal cortex of five macaques. We identified a new visual area, roughly corresponding to cytoarchitectonic area TEO, located between the ventral portion of V4 and area TE. Receptive fields in TEO are intermediate in size between those in V4 and TE and have a coarse visuotopic organization. Collectively, receptive fields in TEO appear to cover nearly the entire contralateral visual field. The foveal and parafoveal representation of TEO is located laterally on the convexity of the inferior temporal gyrus, and the peripheral field is represented medially on the ventral surface of the hemisphere, within and medial to the occipitotemporal sulcus. Beyond the medial border of TEO, within cytoarchitectonic area TF, is another visually responsive region, which we have termed VTF; this region may also have some crude visual topography. Bands of constant eccentricity in TEO appear to be continuous with those in V2, V3v, and V4. The upper field representation in TEO is located adjacent to that in ventral V4, with a representation of the horizontal meridian forming the boundary between the two areas. The lower field representation in TEO is located just anterior to the upper field but is smaller. In contrast to the orderly representation of eccentricity in TEO, we found little consistent representation of polar angle, other than the separation of upper and lower fields. The results of injecting anatomical tracers in two animals suggest that TEO is an important link in the pathway that relays visual information from V1 to the inferior temporal cortex. TEO is thus likely to play an important role in pattern perception.

Key words: temporal lobe, visual cortex, extrastriate cortex, pattern vision, monkey

Cytoarchitectonic area TE (Bonin and Bailey, '47), located within the inferior temporal cortex, is known to play a crucial role in the ability to recognize and remember visual objects (for reviews, see Dean, '82; Gross, '73; Desimone and Ungerleider, '89). Neurophysiological studies have found that TE neurons have complex stimulus selectivities and large, nontopographically organized receptive fields, which almost always include the center of gaze and frequently extend into both visual hemifields (Gross et al., '72; Desimone and Gross, '79). One of the major inputs to TE is from area V4 in prestriate cortex (Kuypers et al., '65; Desimone et al., '80; Fenstermaker et al., '84; Weller and Kaas, '85; Felleman et al., '86; Ungerleider et al., '86), an area that has also been mapped physiologically and anatomically (Van Essen and Zeki, '78; Ungerleider et al., '83; Maguire and Baizer, '84; Gattass et al., '88). V4 neurons show less complex stimulus selectivities than do TE neurons (Desimone and Schein, '87) and have relatively restricted receptive fields that topographically represent the contralateral visual field.

Another region that provides a major input to TE is the cortex that lies between the ventral portion of V4 and area TE, at the occipito-temporal junction (Kuypers et al., '65; Desimone et al., '80; Weller and Kaas, '87). In terms of sulcal landmarks in macaques, this intermediate cortex typically lies between the ascending portion of the inferior occipital sulcus and the posterior middle temporal sulcus. In their study of the cytoarchitecture of macaque cortex, Bonin and Bailey ('47) labeled this region with a question mark on their section drawings but showed a photomicro-
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graph through the region that they labeled “TEO.” Iwai and Mishkin ('68, '69) later reconstructed on a lateral view of the macaque brain the zone labeled with question marks on the Bonin and Bailey section drawings. They discovered that the questionable zone corresponded well with a region that they had found plays an important role in pattern discrimination, based on lesion data, and termed the region TEO. This region has also been variously termed “posterior inferior temporal cortex” and “foveal prestriate cortex.” Terminology aside, subsequent studies have confirmed that lesions involving TEO cause a devastating impairment in the ability of monkeys to learn visual pattern discriminations, which may be even larger than the impairment caused by lesions of TE (Cowey and Gross, '70; Kikuchi and Iwai, '80).

To help understand the visuotopic organization of this cortex located between areas V4 and TE, we mapped it with microelectrode recordings. A brief report of the results has appeared previously (Boussaoud et al., '88).

METHODS

Physiological recording

Five Macaca mulatta weighing 3.5–6.4 kg were used. Most had previously served as normal controls in behavioral studies. Recordings of unit and/or multiunit activity were carried out over 6–10 sessions in each monkey. The physiological, anatomical, and histological procedures have been described in detail previously (Desimone and Gross, '79; Desimone and Ungerleider, '86). Rows of vertical microelectrode penetrations were made in the frontal plane (in one case) or in the parasagittal plane (in 4 cases). Rows were spaced 1.5–2.0 mm apart, and penetrations within a row were spaced 1.0–2.0 mm apart. Recording sites along each penetration were separated by a minimum of 500 μm. Recording sessions were limited to a 4-week period, since, in our experience, penetration tracks begin to fade after this amount of time.

Visual stimuli

Receptive fields were plotted with a hand-held projector on the translucent hemisphere located in front of the animal. Occasionally, three-dimensional objects, such as brushes, were also used as visual stimuli. The length, width, orientation, and eccentricity of the receptive fields were recorded and were subsequently entered into a computer, which graphically displayed the sequence of receptive fields along each row of penetrations. Receptive fields are shown with best-fitting rectangles in the figures.

Injections of anatomical tracers

Following the final recording session in one animal (case 3), we injected the retrograde tracer bisbenzimide (Bi) into the splenium of the corpus callosum to help determine the location of the vertical meridian representations (Zeki, '70; Newsome and Allman, '80; Van Essen et al., '82; Kennedy et al., '86). These injections were made by directly visualizing the splenium. The animal was anesthetized with sodium pentobarbital and prepared for aseptic surgery. The scalp was incised, and a large bone flap was removed over the midline. The hemispheres were gently retracted, and, under an operating microscope, 25 injections of 0.2 μl each of Bi (10%) were made into the splenium. After the injections, the splenium was covered with gel-film, the bone flap was replaced, and the muscle, subcutaneous tissues, and scalp were closed in anatomical layers.

Following the last recording session in two other animals (cases 1 and 2), we injected anatomical tracers into cortical areas. In case 1, the retrograde tracer nuclear yellow (NY) was injected into area V4 on the prelunate gyrus. Under an operating microscope, six injections of 0.25 μl each of NY...
(10%) were made into the ventral two-thirds of the gyrus. In case 2, we injected tritiated amino acids (AA) into the physiologically identified upper field representation in TEO. In this case, at the end of the recording session, we advanced the guide tube to the injection site and lowered the injection needle through the tube. We injected 0.15 µl of AA (100 µCi/µl of an equal parts mixture of tritiated proline [New England Nuclear L-(2,3,4,5-H)4, specific activity 100–140 Ci/mmol] and tritiated leucine [New England Nuclear L-(3,4,5-H)4(N)], specific activity 100–140 Ci/mmol) at a rate of 0.02 µl/2 minutes. After the injection, the syringe was left in place for 20 minutes, before it was withdrawn into the guide tube, to help prevent leakage of tracer up the needle track.

**Histology**

During the recording sessions, small electrolytic lesions were made periodically along the penetrations by passing a low current (4 microamps for 20 seconds) through the electrode. After either the last recording session or after the survival period following the anatomical injections (6 days for case 2, and 2 days for cases 1 and 3), the animals were deeply anesthetized with pentobarbital and perfused transcardially with 0.9% saline (500 ml) followed by 4% paraformaldehyde (1,000 ml).

Frozen sections, 50-µm thick, were cut in either the coronal or parasagittal plane. For cases 1 and 3, every fifth section was mounted for fluorescent label analysis. The remaining sections were stained for either cell bodies, with thionin, or for myelin, with the method of Gallyas (‘79). For case 2, a series of sections for autoradiography were mounted, dipped in Kodak NTB2 emulsion, and exposed at 4°C for 20 weeks. After this period, the autoradiographs were developed in Kodak D19, fixed, and counterstained with thionin.

For purposes of analysis, the locations of retrogradely labeled cells, anterogradely labeled terminals, and architectural borders were charted onto enlarged photographs of thionin-stained sections. The locations of the recording sites were placed onto drawings of these sections. All of the data were then transferred onto two-dimensional “flattened” reconstructions of the cortex. The method of these reconstructions has been described previously (Desimone and Ungerleider, ‘86; Boussaoud et al., ‘90).

**RESULTS**

A total of 1,200 visually responsive sites were recorded on 370 penetrations. The recording sites extended from ventral V2, posteriorly, to area TE, anteriorly, and from the calcarine fissure, ventrally, to the middle temporal visual area (MT) and fundus of the superior temporal visual area (PST), dorsally within the superior temporal sulcus. As might be expected, we found the visual topography of the region between ventral V4 and TE to be coarser than that in V4 but not completely absent as in TE. Likewise, receptive fields were intermediate in size between those in V4 and those in TE. Because of both the coarseness and the variability in topography between animals, it was not possible to draw boundaries between visual areas that were either sharp or certain. Yet, there was convincing evidence for a new visual area lying immediately in front of the upper field representation of V4 and adjacent to TE, with a coarse representation of the upper and lower contralateral visual field. We term this area TEO because Iwai and Mishkin (‘69) had previously defined a visual area named TEO in this location, based on both the cytoarchitectonic descriptions of Bonin and Bailey (‘47) and lesion data.

Although TEO is the focus of the present report, we also found evidence for another visually responsive region medial to TEO, on the parahippocampal gyrus anterior to the upper peripheral field representations of V2 and V3v. This region also appears to have some visual topography. Although we do not yet know if this region contains more than one visual area, we have tentatively named it VTF because it lies within cytoarchitectonic area TF (Bonin and Bailey, ‘47) and is visually responsive, unlike more anterior portions of TF. Finally, we have distinguished area TEO from the visually responsive cortex adjacent to it within the superior temporal sulcus. In the remainder of the Results, we first summarize the location of area TEO in the five cases, then illustrate how we determined the borders between TEO and the surrounding areas, and finally present representative sequences of receptive fields. In a later section, we also present evidence for anatomical links between TEO and V4.

**Location of TEO**

Figure 1 shows the location of area TEO in the five cases on lateral and ventral views of the hemisphere, reconstructed from serial sections. Figure 3 shows the overall recording area on a two-dimensional flattened reconstruction of the cortex, and Figures 4–6 show the location of TEO and surrounding areas on flattened reconstructions in each of the five cases. In some of the cases, the recording sites did not reach all of the boundaries of TEO, and, consequently, its boundaries are incomplete in some of the illustrations.

Area TEO is found in a band of cortex that runs ventrally from the lip of the superior temporal sulcus to about 2–8 mm medial to the occipitotemporal sulcus. It ranges from 10–15 mm wide (average 11 mm) at its most lateral position on the hemisphere, and from about 5–7 mm wide (average 6 mm) medially. The posterior border of TEO is roughly at the anterior lip of the ascending portion of the inferior occipital sulcus, but the exact location varied among the cases. In cases 1, 2, and 4, the posterior border was found just anterior to the lip, whereas in cases 3 and 5, it was within the anterior bank of the sulcus, close to the lip. Rostrally, TEO ended approximately at the anterior tip of the posterior middle temporal sulcus in cases 1, 2, and 4, whereas it extended to about 3.5 mm in front of this sulcus in case 3. In case 5, the recordings did not extend rostrally enough to allow the determination of the anterior border of TEO.

In area TEO, the foveal and paraffoveal visual field is represented laterally on the convexity of the inferior temporal gyrus, and the peripheral field is represented medially on the ventral surface of the hemisphere. We found an asymmetry in the size of the upper and lower field representations, in that the representation of the upper quadrant was much larger than that of the lower quadrant (see Figs. 1, 5). The upper field representation is adjacent to the upper field representation of area V4, whereas the lower field representation is farther anterior, adjacent to TE. The lower peripheral field representation was located in the cortex below the anterior tip of the posterior middle temporal sulcus in each of the four cases in which we had lower field data. Although the lower field representation...
Fig. 1. Location of area TEO and surrounding cortical areas shown on lateral and ventral views of the right hemisphere. The borders between cortical areas are represented by dashed lines, and the limit between upper and lower visual field representations within TEO is indicated by a dotted line. The plus (+) and minus (−) signs indicate upper and lower field representations, respectively, of TEO. The question marks (?) indicate indeterminate zones. The sulci are labeled on lateral and ventral views of a typical rhesus monkey brain (bottom right). For areal and sulcal abbreviations in this and subsequent figures, see list in text.
appears to end medially at the occipitotemporal sulcus (forming a wedge between the occipitotemporal and posterior middle temporal sulci), the upper field representation continues medially across the occipitotemporal sulcus, "hugging" the upper field representation of V4 in most cases.

**Architecture of TEO and surrounding areas**

Myeloarchitecture and, to a lesser extent, cytoarchitecture was an aid in identifying the boundaries of TEO and other visual areas within the recording region, especially in conjunction with physiological data in the same animals. Within the dorsal portion of the recording region, we were able to identify MT and FST in the superior temporal sulcus, using criteria defined in other studies (Allman and Kaas, '71; Spatz and Tigges, '72; Zeki, '74; Ungerleider and Mishkin, '79; Baker et al., '81; Gattass and Gross, '81; Van Essen et al., '81; Albright, '84; Felleman and Kaas, '84; Maunsell and Van Essen, '83a-c; Desimone and Ungerleider, '86; Ungerleider and Desimone, '86a). Ventrally, in the occipital and temporal cortex, we were able to make the following distinctions, which are illustrated in Figure 2.

V2. On sections stained for myelin with the Gallyas method, ventral V2 is usually distinguishable by its two dark bands of Baillarger, separated by a thin light band (see also Ungerleider and Desimone, '86b; Gattass et al., '81, '88).

V3v. The ventral portion of V3 (V3v) can often be distinguished from V2 but is not easily identifiable from more anterior areas on the basis of myeloarchitecture alone, as was noted previously (Burkhalter et al., '86; Ungerleider and Desimone, '86b; Gattass et al., '88).

V4. Although we could not reliably see the boundary between V3v and V4 in myelin sections, the inner and outer bands of Baillarger become more prominent as one moves anteriorly out of V3v and through V4 (see Gattass et al., '88). Anterior to V4 it is possible to see in most sections a transition to more lightly myelinated cortex, which corresponded to either TEO or TF, depending on location.

**TEO.** We could not always identify TEO on the basis of myeloarchitecture alone, but we typically found that it differed from V4 by its broader and paler bands of Baillarger. We used this myeloarchitectural difference whenever possible to confirm the physiological transition from V4 to TEO.

**TF.** Cytoarchitectonic area TF is easily distinguishable from surrounding regions not only on the basis of cytoarchitecture (Bonin and Bailey, '47), but also by its much paler myelin stain, with the inner band of Baillarger being almost absent. Within TF, we could not see subdivisions on the basis of myeloarchitecture. However, our physiological data showed a visually responsive zone (VTf), located in posterior TF, and a visually unresponsive zone in anterior TF.

**TE.** Although the cytoarchitecture of TE differs from posterior visual areas, the transition is too gradual to mark a boundary reliably, as has been noted previously (Desimone and Gross, '79). Likewise, the myeloarchitecture in TE is variable, and there does not seem to be one pattern whose description could apply to the whole of area TE. This
heterogeneous myeloarchitecture may reflect functional subdivisions within TE (see Seltzer and Pandya, '78; Weller and Kaas, '87). At a minimum, there are at least two different zones, one adjacent to TEO with myeloarchitecture that is even paler than this latter area's, and an anterior zone with darker myelination.

Visual topography in TEO and surrounding regions

We distinguished TEO from surrounding areas on the basis of visual topography, receptive field size, and myeloarchitecture. Although one could not be very confident of the boundaries of TEO based on any of these three properties taken alone, the boundaries could be estimated fairly reliably from their combination. The overall distribution of receptive field data from the five cases is shown on flattened reconstructions, or maps, of the cortex in Figures 4-6.

Eccentricity. Figure 4 shows the eccentricities of the receptive field centers recorded in TEO and surrounding areas in each of the five animals. The dashed lines on the maps represent the estimated boundaries of the areas. In some cases the boundaries are incomplete because of insufficient data. For clarity, each number on the map represents the average eccentricity for 2-3 nearby receptive fields. The shading on the maps represents isoeccentricity bands, ranging from central (0-7°, light shading) to far peripheral (>30°, dark shading). The representation of eccentricity in ventral V2, V3, and V4 is consistent with the results of previous studies (Ungerleider et al., '83; Newsome et al., '86; Gattass et al., '81, '88). In TEO and TE there are few receptive fields whose centers have very small eccentricities because the average receptive field size in these areas is so large.

The most striking aspect of the maps is that whereas the ventral visual areas are organized as a series of strips running dorsal-to-ventral, the isoeccentricity bands appear to form rough arcs that cut across the areas nearly orthogonally, including area TEO. The most central visual fields are lateral, extending forward from the foveal representation of V2 into lateral TEO, and the most peripheral fields are medial, within or near the occipitotemporal sulcus and parahippocampal gyrus. We found a similar arrangement of "strips and arcs" in the maps of visual areas surrounding MT in the superior temporal sulcus (Desimone and Ungerleider, '86). Indeed, the isoeccentricity arcs in the temporal cortex may even be continuous with those in the caudal superior temporal sulcus. A possible exception to this scheme is the portion of the sulcus just above TEO, where we found considerable variability in eccentricity both within and between the five cases.

Within TE, we did not find distinguishable eccentricity bands, in that receptive field centers recorded at adjacent recording sites sometimes had very different eccentricities (reflecting differences in receptive field size and laterality). Upper and lower visual fields. Figure 5 shows the distribution of receptive fields centered in either the upper visual field (open circles) or lower visual field (filled circles), or centered on the horizontal meridian (squares) in each of the five cases. Consistent with previous findings (Gattass et al., '81, '88; Newsome et al., '86), the ventral portions of V2, V3, and V4 contained representations of the upper visual field. The few scattered receptive fields with centers in the lower visual field in the ventral portions of these areas were all in the foveal or parafoveal representations and had centers located very close to the horizontal meridian. Likewise, the few fields located dorsally in the hemisphere
Fig. 4. Visuotopic organization and distribution of receptive field (RF) properties of cells in TEO and surrounding areas shown on two-dimensional reconstructions of the cortex: Eccentricity of RF centers. A-E. Cases 1–5, respectively. Sults are indicated by heavy lines, and the estimated borders between areas are indicated by dashed lines. For clarity, each number on the reconstruction represents the average eccentricity of 2–3 receptive fields of cells at nearby locations. Note that the isoeccentricity bands, represented by shadings, run continuously across areal boundaries, intersecting them roughly perpendiculary.

with centers in the lower visual field had field centers located close to the horizontal meridian.

In TEO, the upper visual field was represented in a strip close to the upper field representation of V4. The lower visual field in TEO was found within and under the posterior middle temporal sulcus, adjacent to area TE, in each of the four cases with data in the anterior portion of TEO. (Since completing this study, we have confirmed a lower field representation in TEO at this same location in three additional animals.) It should be noted that, because of its compression relative to the upper visual field, the lower visual field representation in TEO is actually bordered by the upper field in TEO medially as well as posteriorly.

Dorsal to TEO, in the adjacent superior temporal sulcus, receptive fields centered in the upper and lower visual fields
Anterior to TEO, in TE, the receptive fields were generally parallel to the variability we found in field eccentricity. The animals. This variability in the location of field centers appeared to be mixed, with substantial variability among the animals. This variability in the location of field centers may be due to the TEO neurons' large receptive field size, which are so large that many fields touch both meridians. However, even in the central field representation, TEO could be distinguished from V4 on the basis of larger average receptive field size in TEO. In case 4, there were very few fields that included the horizontal meridian, but the recording sites in this case were not closely spaced and there were only a few fields directly on the presumed V4/TEO border. In case 5, the multicell receptive fields recorded in V4 were, in general, somewhat larger than in the other cases and thus often included (except in the far periphery) both meridians even when located near the V4/TEO border.

Anterior to the representation of the horizontal meridian at the V4/TEO border, we found little orderly representation of polar angle in TEO beyond that of the separation of upper and lower visual fields described earlier in the Results. This contrasts with the reasonably orderly representation of eccentricity in TEO. Although receptive fields did not bounce chaotically between the horizontal and vertical meridians on any given row of penetrations, neither did they present a consistent pattern across rows (see next section). In particular, there was no consistent tendency for receptive fields at the anterior border of TEO to represent the vertical meridian. Rather, in passing from TEO into TE, receptive fields increased substantially in size, typically included the fovea, and typically included portions of the ipsilateral as well as the contralateral visual field, consistent with previous studies (Gross et al., '72; Desimone and Gross, '79).

In part, the poor representation of polar angle in TEO may be due to the TEO neurons' large receptive field size, which are so large that many fields touch both meridians. Consistent with this, callosally projecting neurons were found throughout nearly the entire extent of TEO. Another possible reason for a problem in representing polar angle is that, on the one hand, the representation of the horizontal meridian forms one of the outer borders of TEO, which should force TEO to have a “second-order” transformation of the visual field (Allman and Kaas, '74), such as occurs in V2 and V3. On the other hand, the upper and lower peripheral visual fields are represented adjacent to each other in TEO, which should force TEO to have a “first-order” transformation of the visual field, such as in V1 and MT. There may be no graceful way to resolve these conflicting demands. We consider this issue and also other possible interpretations of TEO topography in the Discussion.

Representative sequences of receptive fields

Figures 7–11 show representative sequences of receptive fields recorded on rows of penetrations through TEO and surrounding areas. Because of the coarse topography, we frequently found it difficult to assign the borders of TEO based solely on visual topography in a single row of penetrations. Likewise, differences in receptive field size alone were not always sufficient to confidently localize the borders of TEO on a single row of penetrations because of
Fig. 5. Visuotopic organization of TEO and surrounding areas shown on two-dimensional reconstructions of the cortex. Distribution of cells with receptive fields centered in the upper visual field, the lower visual field, or on the horizontal meridian. A–E, Cases 1–5, respectively. For other conventions, see Figure 4.

overlap in the distributions of TEO and V4 receptive field size and, to a lesser extent, of TEO and TE field size, even though the average size field in TEO clearly differed from that in both V4 and TE (see below). Thus whenever possible we tried to assign borders based on a conjunction of topography, field size, and myeloarchitecture, preferably across more than one row of penetrations.

Figure 7 shows a typical row of penetrations made in the parasagittal plane through a lateral portion of TEO. The most posterior recording sites (1–3) were in the anterior bank of the inferior occipital sulcus from which small receptive fields were recorded in the upper foveal and parafoveal representation of V4. Farther anterior and medial in V4 (sites 4–8, triangles), receptive fields were located at an eccentricity of 10–15° in the upper visual field and progressed to the horizontal meridian at the V4/TEO border, between sites 8 and 9. Moving into TEO, receptive fields increased in size and remained within the upper field
for approximately 2 mm (sites 9–12, open circles) before abruptly shifting across the horizontal meridian into the lower visual field (sites 13–18, filled circles). The most anterior receptive field recorded in TEO (site 18) had an eccentricity of about 60" within the middle of the lower visual field. At more anterior sites (19–21, asterisks), in TE, receptive fields jumped abruptly to the fovea and were large, bilateral, and included the fovea, as in the previous case. Receptive fields were found at a greater eccentricity than in the parahippocampal gyrus (case 2). The first site was in V3v and the next was just beyond it at the V3v/V4 border, with a receptive field on the vertical meridian in the upper field. Moving anteriorly through V4 to its anterior border (sites 2–7, filled triangles), receptive fields progressed from the vertical to the horizontal meridian. Moving out of V4 into the visually responsive region we have termed VTF, receptive fields (sites 8–9, squares) jumped abruptly back to the fovea. Further anteriorly in TF, we were unable to obtain any visual responses (sites marked “U” on the section and the flattened map). The VTF sites were clearly in Bonin and Bailey’s (’47) area TF, based on both cytoarchitecture and myeloarchitecture (see Fig. 2). The fields at these sites were foveal and thus could not be considered to be within TEO because the foveal representation of TEO was located far lateral on the inferior convexity of the hemisphere.

Figure 8 shows a row of penetrations at a similar lateral level in another case, along with corresponding anatomical data from an injection of tritiated amino acids into the upper field representation of TEO. The most posterior recording sites (1–4, triangles) were in the upper field representation of V4, and, consistent with the upper field location of the injection site, labeled terminals were also found in this region. The terminals were concentrated in the supragranular and infragranular layers, avoiding layer IV. Moving anterior and medial through V4 to the V4/TEO border, the receptive fields moved from the vertical meridian in the upper visual field to the horizontal meridian, at an eccentricity of about 15°. Moving through TEO, receptive fields were located first in the upper visual field (sites 5–9, open circles) and then in the lower visual field (sites 10–13, filled circles), just as in the previous case. Receptive field size was so large that nearly the entire central 20° of both the upper and lower visual field was encompassed by the fields recorded over just a few millimeters. Again, consistent with the upper field location of the injection site, intrinsic label in TEO appeared largely to avoid the lower field representation of TEO in this and other sections. Passing into TE, receptive fields jumped abruptly from the lower periphery to the fovea. The TE fields (sites 14–18, asterisks) were large, bilateral, and included the fovea, as in the corresponding row of the previous case. Labeled terminals resulting from the TEO injection were found in TE, concentrated in layer IV, in a zone in which large receptive fields encompassed much of the upper visual field.

Figure 9 shows a typical row of penetrations made at a more medial portion of TEO in case 1, at the level of the occipitotemporal sulcus. Because the row was more medial, receptive fields were found at a greater eccentricity than in the row illustrated in Figure 7. The most posterior sites (1–4, triangles) were in V4, at an eccentricity of between 30–60° in the upper visual field. Moving anteriorly through V4, the fields progressed towards the horizontal meridian at the V4/TEO border, between sites 4 and 5. Moving through TEO (sites 5–10, open circles), receptive fields in this row progressed smoothly from the horizontal to the vertical meridian, at an eccentricity of about 50–60°. Because this row was medial to the representation of the lower visual field in TEO, receptive fields in TEO remained within the upper visual field. Finally, crossing into TE (sites 11–13, asterisks), receptive fields jumped abruptly to the fovea, and, as described for the previous two rows through TE (Figs. 7, 8), were large and bilateral.

Figure 10 shows a typical row of penetrations made at an even more medial level, beyond the medial edge of TEO in the parahippocampal gyrus (case 2). The first site was in V3v and the next was just beyond it at the V3v/V4 border, with a receptive field on the vertical meridian in the upper field. Moving anteriorly through V4 to its anterior border (sites 2–7, filled triangles), receptive fields progressed from the vertical to the horizontal meridian. Moving out of V4 into the visually responsive region we have termed VTF, receptive fields (sites 8–9, squares) jumped abruptly back to the fovea. Further anteriorly in TF, we were unable to obtain any visual responses (sites marked “U” on the section and the flattened map). The VTF sites were clearly in Bonin and Bailey’s (’47) area TF, based on both cytoarchitecture and myeloarchitecture (see Fig. 2). The fields at these sites were foveal and thus could not be considered to be within TEO because the foveal representation of TEO was located far lateral on the inferior convexity of the hemisphere.

Figure 11 shows a typical row of penetrations through TEO made in the coronal plane (case 5). The most lateral penetrations passed through the upper parafoveal field representation in TEO (sites 1–3, open circles). Moving medially through TEO, across the occipitotemporal sulcus, receptive fields moved out into the upper periphery along the vertical meridian (sites 4–6). Further medially on the parahippocampal gyrus, in VTF, receptive fields jumped abruptly back to the central field (sites 7–8, squares). Finally, the last recording sites in this row of penetrations were visually unresponsive (marked as “U” on the section and the flattened map). As was the case in the sequence shown in Figure 10, both VTF and the adjacent unresponsive cortex were within the limits of cytoarchitectonic area TF.

Extent of visual field represented in area TEO

Figure 12 shows the extent of the visual field representation found in TEO across the five cases. The outer boundary on the visual field map shows the envelope of all recorded...
receptive fields, and the dots indicate the field centers. TEO appears to contain a representation of nearly the entire contralateral visual field.

**Receptive field size**

As noted by Gattass et al. ('88), multiunit receptive field size varies with electrode impedance; consequently, we found considerable variation in field size across the five cases. Figure 13 shows the relationship between multiunit receptive field size (square root of length times width) and eccentricity in ventral V4, TEO, and TE in one case (case 1) in which nearly all receptive fields were mapped with a single electrode. Receptive fields in TEO were intermediate in size between those in V4 and TE, on the average, but there was clearly overlap in the size of individual receptive fields in V4 and TEO, especially at small eccentricities. In this case, the regression equation relating receptive field size \( s \) and eccentricity \( e \) in TEO was 

\[
    s = 0.76e + 4.8^7
\]
RFs include:

- Vertical Meridian
- Horizontal Meridian
- Both
- Neither

(r = .95). There was no significant difference in either the slope (t = .42; p > .5; df = 120) or intercept (t = 1.23; p > 0.2; df = 120) for the regression equations computed separately for the upper and lower visual fields in TEO. For comparison, in ventral V4 the regression equation for receptive field size was $s = 0.46e + 3.4^\circ$ (r = .94), and in TE the equation was $s = 0.29e + 34.5^\circ$ (r = .18). The slope of the equation in TE was not significantly different from zero (p > .4), which is due to the fact that the TE fields generally were very large in size but had relatively small eccentricities as they were bilateral. Across all cases, the regression equation in TEO was $s = 0.70e + 7.0^\circ$ (r = .84), in V4 was $s = 0.47e + 6.5^\circ$ (r = .77), and in TE was $s = 0.64e + 22^\circ$ (r = .45).

Anatomical connections with dorsal V4

As described above, TEO appears to have connections with ventral (i.e., upper field) V4 (see Fig. 8, case 2). However, our own previous anatomical study (Ungerleider et al., '86) reported connections with the TEO region following tracer injections in dorsal (i.e., lower field) V4. That study was carried out before we had obtained a physiological map of TEO. Therefore, in one of the cases of the present study, we asked whether our physiologically defined TEO had connections with dorsal V4. In case 1, we made large injections of the fluorescent dye nuclear yellow into the middle and dorsal portions of the prelunate gyrus. The injection sites were entirely confined to the surface of the gyrus (avoiding area V3A in the adjacent lunate sulcus). This portion of the gyrus contains the representation of V4's parafoveal and peripheral lower visual field (Maguire and Baizer, '84; Gattass et al., '88).

Figure 14 shows the distribution of labeled cells following the injection. We will focus only on the data in the ventral occipital and temporal cortex. In spite of the fact that the injections were within the lower field representation of V4, labeled cells filled much of ventral V4, which represents the upper visual field. Thus V4 appears to have extensive intrinsic connections. There was also a heavy concentration of labeled cells within the boundaries of physiologically defined TEO. Interestingly, the cells were most extensive in the lower field representation of TEO (compare to Fig. 5A), although there were also patches of cells in the upper field representation, mainly in the periphery. Thus together with the anatomical data in case 2, the results indicate that TEO has connections with both upper and lower field representations of V4. In addition to TEO in the temporal cortex, dorsal V4 also appears to have connections with the cortex within the superior temporal sulcus just above TEO, with area TE, and with TF, which is consistent with previous anatomical findings (Kuypers et al., '65; Fehsenfelder et al., '84; Weller and Kaas, '85; Felleman et al., '86; Ungerleider et al., '86).

DISCUSSION

Relationship to other studies

There appears to be an overall, or "supra-areal," visual topography to the entire ventral occipito-temporal cortex, such that the central visual field is represented laterally and
Fig. 7. Case 1: Receptive fields of cells recorded on a row of electrode penetrations through the lateral portion of TEO and surrounding areas. The receptive fields, which are drawn as best fitting rectangles, are representative of a larger number of fields of cells recorded on the penetrations. The locations of the recording sites are shown on both a parasagittal section and a flattened reconstruction of the cortex; the ventral view of the hemisphere indicates the level of the parasagittal section (heavy line). Areal boundaries are indicated by arrows on the parasagittal section and by dashed lines on both the flattened reconstruction and the ventral view of the hemisphere. HM, horizontal meridian; VM, vertical meridian.
Fig. 8. Case 2: Receptive fields of cells recorded on a row of electrode penetrations through the lateral portion of TEO and surrounding areas. Drawings of two adjacent parasagittal sections (top right) show the location of the recording sites and the distribution of labeled terminals (fine dots) following an injection of tritiated amino acids into TEO (in black). Note that the injection site was restricted to the upper visual field representation, and that the label avoided the adjacent lower visual fields. For other conventions, see Figure 7.
Case 1

Fig. 9. Case 1: Receptive fields of cells recorded on a row of electrode penetrations through the medial portion of TEO and surrounding areas. Note that at this medial level, the row of penetrations did not pass through the lower visual field of TEO. Same conventions as in Figure 7.
Case 2

Fig. 10. Case 2: Receptive fields of cells recorded on a row of electrode penetrations through cortex medial to area TEO. Note that anterior to V4, within cytoarchitectonic area TF, there was a region of visually responsive cells (termed "VTF") and a more rostral region of unresponsive cells. Same conventions as in Figure 7.

the peripheral field medially, with bands of constant eccentricity spanning the region (see Fig. 15). Superimposed on this overall topography are separate visual areas that appear to be organized as strips that intersect the isoeccentricity bands. As described previously by others (Gattass et al., '81, '88; Newsome et al., '86), posterior to TEO these strips all contain representations of the upper visual field exclusively. Closest to the V1 border is area V2 (Gattass et al., '81), followed by area V3v (Gattass et al., '88; Newsome et al., '86), and area V4 (Gattass et al., '88). Each of these
areas has corresponding representations of the lower visual field located dorsally in the hemisphere (Zeki and Sandeman, '76; Van Essen and Zeki, '78; Maguire and Baizer, '84; Gattass et al., '88), with the possible exception of area V3v. Van Essen and his colleagues (Burkhalter and Van Essen, '86; Burkhalter et al., '86; Newsome et al., '86; Van Essen et al., '86) prefer to consider the dorsal and ventral portions of "V3" as two different visual areas, which they term V3 dorsally and VP ventrally, whereas we (Ungerleider et al., '83; Ungerleider and Desimone, '86b) and others (Gattass et al., '88) prefer to consider V3 a single area, whose upper and lower field representations (termed V3v and V3d, respectively) have somewhat different anatomical and physiological properties. Irrespective of any minor differences in
VISUAL AREA TEO

Fig. 12. Extent of the visual field covered by receptive fields and receptive field centers (dots) of cells in area TEO across the five cases. Same conventions as in Figure 7.

Fig. 13. Receptive field (RF) size (square root of RF area) as a function of eccentricity of cells in V4, TEO, and TE in case 1. The lines that describe the relationship between size and eccentricity in each graph were calculated by linear regression. See text for the equations of the regression lines. No regression line is shown for TE, since the slope of the equation in TE was not significantly different from zero.
Fig. 14. Distribution of retrogradely labeled cells following injections of nuclear yellow on the prelunate gyrus into dorsal V4, shown on lateral and ventral views of the hemisphere and on a two-dimensional reconstruction of the cortex. The injection sites are shown in black, and the dots indicate the relative density of labeled cells.

report by Felleman et al. ('85) that the anterior boundary of the upper field representation in TEO is formed by the representation of the vertical meridian. Although we found a vertical meridian representation at the boundary of the upper field representation of TEO on some rows of penetrations (e.g., the row shown in Fig. 9), this was not a consistent finding throughout TEO or across animals (e.g., the rows shown in Figs. 7, 8). In fact, given the large receptive field size and scatter, it may not be possible to establish whether the meridians of the visual field are discretely represented at all in TEO, except at the V4/TEO border.

Anterior to TEO, in TE, we found that receptive fields were extremely large, usually extending into both visual hemifields and including the center of gaze within or on their boundaries, consistent with previous studies (Gross et al., '72; Desimone and Gross, '79). Likewise, Desimone and Gross ('79) reported that the posterior boundary of TE, defined on the basis of receptive field size and laterality, was commonly located at the posterior middle temporal sulcus, which is just where we found the TEO/TE boundary in the present study.

Medial to TEO, in VTF, we found visually responsive cells with some evidence of visual topography. These cells were clearly located in the posterior portion of cytoarchitectonic area TF. Foveal fields were found close to the TEO border and more peripheral fields were found medially. Gattas et al. ('88) also reported preliminary physiological evidence for one or more visual areas in this vicinity, and we and others have found projections from V4 into posterior TF (Weller and Kaas, '85; Felleman et al., '86; Ungerleider et al., '86). Anterior to the visually responsive zone in TF, we were not able to activate cells. The border between responsive and unresponsive zones appears to correspond to the visual-nonvisual border described in TF by Maek and Mishkin ('85) based on metabolic mapping with 2-deoxyglucose.

Dorsal to TEO, in the superior temporal sulcus, we found receptive fields located in both the upper and lower visual fields, but we were not able to discern a clear visuotopic organization. Felleman et al. ('86) have described segregated projections to this region from the upper and lower field representations of V4, but did not report a consistent visuotopic organization. Finer mapping studies may reveal more than one visual area in this cortex.

Relative representations of the upper and lower visual fields in TEO

The representation of the upper visual field in TEO appears to be considerably larger than that of the lower field. Whereas this asymmetry is surprising, it appears to affect primarily the representation of the peripheral visual field. Within the foveal and parafoveal visual field, average receptive fields in TEO are 5–10° in linear dimension (see Fig. 13), and frequently extend across the horizontal meridian into both upper and lower visual fields. Furthermore, it is not the case that information from the lower visual field is not well represented in the temporal cortex. The center of receptive fields in TE are located, on the average, below the horizontal meridian (Desimone, unpublished data) and the
lower field representation of V4 projects extensively to TE (Ungerleider et al., '86 and in preparation). Thus it is possible that the lower peripheral field is not as well represented as the upper peripheral field in TEO because the converse is true in TE, which redresses the imbalance.

Alternatively, it is possible that our interpretation of the visual topography of TEO is not entirely correct. For example, we considered the possibility that a portion of the cortex we have included within TEO actually belongs to a different visual area. One candidate for an alternate visual area that would "mate" with a portion of TEO is area V4t. V4t is located in the caudal superior temporal sulcus and forms a narrow (approximately 2 mm wide) transition region between the representation of the horizontal meridian at the anterior boundary of dorsal V4, on the one side, and vertical meridian of MT on the other side (Maguire and Baizer, '84; Desimone and Ungerleider, '86;Gattass et al., '88; Fiorani et al., '89). Within this narrow strip, V4t contains a coarse representation of nearly the entire lower visual field but has no representation of the upper field. Is it possible that a similarly narrow strip of cortex adjacent to ventral V4 (i.e., the most posterior portion of our TEO) is the missing upper field representation of V4t? Although it seems very unlikely that the entire upper field representation of TEO actually belongs to V4t (leaving TEO without an upper field representation), it is possible that just a portion of it does. Given the coarse topography and large receptive field size in TEO, it is theoretically possible that the upper field is represented twice, once posteriorly in TEO in a narrow strip adjacent to V4 and again in the remainder of TEO. If so, then excluding the narrow strip from TEO might leave the remaining upper and lower field representations in TEO more comparable in size. If this strip were only 2 mm wide, like V4t, it would be difficult to rule out this alternative scheme based on our data, considering that our penetrations were normally spaced 1.5 mm apart. However, we examined all TEO receptive fields mapped within 2 mm of the V4/TEO border and found that in four of our five cases the fields were confined to the vicinity of the horizontal meridian, which is not consistent with the idea that this strip contains a complete representation of the upper visual field. Furthermore, the myeloarchitecture of V4t is distinctive, yet we did not see reliable myeloarchitectural divisions within TEO. Likewise, we did not find a reliable visuotopic boundary or transition inside of TEO. Much finer mapping studies, possibly coupled with studies of physiological properties and anatomical connections, will be needed to resolve this difficult question.
Functions of TEO

Anatomical, physiological, and behavioral studies suggest that TEO is an important link in the occipitotemporal pathway, the pathway known to underlie object recognition in primates (Mishkin, '82; Ungerleider and Mishkin, '82; Mishkin et al., '83). As we and others have shown, TEO receives “forward”-directed inputs from area V4 (Fenstermaker et al., '84; Weller and Kaas, '85; Follem et al., '86; Ungerleider et al., '86) and projects in turn to area TE (Kuypers et al., '65; Desimone et al., '80; Weller and Kaas, '87). Neurons in both V4 and TE are sensitive to many visual features relevant to object recognition, such as color, orientation, and spatial frequency in V4 (e.g., Zeki, '73, '78, '83; Desimone et al., '85; Desimone and Schein, '87), and color, shape, and texture in TE (Gross et al., '72; Schwartz et al., '83; Desimone et al., '84; Tanaka et al., '87). Preliminary studies indicate that neuronal properties in TEO are intermediate in complexity between V4, on the one hand, and TE, on the other (Fenstermaker et al., '85; Tanaka et al., '87). Likewise, our present results indicate that TEO receptive fields are intermediate in size between those in V4 and TE, suggesting that the neural coding of visual objects in TEO is based on object features that are more global than those in V4, but not quite as global as those in TE.

Although lesion studies involving the TEO region were necessarily conducted before the boundaries of TEO were established physiologically, in some early studies the location of the lesion was remarkably similar to the location of TEO described in the present study, and the behavioral results suggest an important role of TEO in pattern recognition. The first such study was one comparing the relative effects of several different “strip lesions” in temporal cortex on pattern recognition learning (Iwai and Mishkin, '68, '69). The strips were narrow zones oriented roughly parallel to the ascending portion of the inferior occipital sulcus, which, as it turns out, is the orientation of TEO. Strips I and II in that study were confined to TEO, and strips III through V were confined to TE. Strip lesions I and II, either alone or in combination, had a devastating effect on discrimination learning of simple two-dimensional patterns, which, in some cases, was even more severe than the effects of lesions of TE. By contrast, the strip lesions in TE caused a greater impairment than the TEO lesions on concurrent discrimination learning of multiple object pairs. In concurrent object discrimination, the objects can easily be distinguished from one another on the basis of multiple cues; the task is difficult to learn because of the high memory load caused by proactive and retroactive interference. Thus TEO appears to be particularly important in tasks emphasizing fine discrimination rather than memory. The large effect of TEO lesions on tasks taxing visual discrimination abilities has subsequently been confirmed by Kikuchi and Iwai ('80), using two-dimensional pattern discrimination. Conversely, the relative sparing of function (relative to TE lesions) on tasks taxing visual memory has been confirmed by Kikuchi and Iwai ('80), using concurrent and serial object discrimination, by Spiegler and Mishkin ('81), using one-trial object-reward association learning, and by Mishkin ('82), using a delayed nonmatching-to-sample task with trial-unique objects.

If TEO provides input to TE, why do TEO lesions not produce as severe an impairment on mnemonic tasks as TE lesions? As pointed out by Spiegler and Mishkin ('81), TE also receives input from V4 directly, bypassing TEO. The information provided by this direct pathway to TE is apparently sufficient for animals to make gross discriminations among three-dimensional objects differing along numerous dimensions, such as overall size, luminance, color, texture, etc., and to store coarse representations of these objects in memory. However, when tasks require fine or subtle judgments of shape, the essential contribution of TEO is revealed.

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LITERATURE CITED


