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Area TEO and “Area ?”: Cytoarchitectonic confusion corrected by connectivity and cortical ablation

Kevin S. Weiner¹

¹Department of Psychology, University of California, Berkeley Berkeley, CA 94720

Abstract

Throughout history, researchers who examine the structure and function of the brain debate one another about how cortical areas are defined, as well as how these areas should be named. Different pieces of empirical evidence are used to define brain areas and it is important to preserve the accurate history of this evidence and the timeline of studies that lead to areal definitions that are either still used today or have been modified. As such, this paper traces the early history of a brain area located at the junction between the occipital and temporal lobes of the macaque known as TEO. This historical analysis leads to four main findings. First, even though Bonin and Bailey are credited with the definition of area TEO in 1947, they did not have the cytoarchitectonic evidence to support the distinction of TEO from adjacent areas. Second, the first evidence definitively separating area TEO from TE was actually based on connectivity as identified with strychnine neuronography by Petr and colleagues in 1949. Third, causal evidence from ablation studies conducted by Iwai and Mishkin (1969) supported this distinction by showing that TEO and TE were functionally distinct from one another. Fourth, researchers in the 1970s began referring to TEO as posterior inferotemporal (PIT) and TE as anterior inferotemporal (AIT), which is an important historical clarification as the PIT/AIT nomenclature is presently attributed to studies conducted more than a decade later. Altogether, this paper aims to preserve the historical origin of area TEO, as well as the empirical evidence that was used to originally differentiate this cortical expanse from surrounding areas.

Keywords

object recognition; inferior temporal cortex; ventral stream; occipito-temporal cortex

INTRODUCTION

These days, there are so many different acronyms for brain areas and brain structures across species that it is hard to keep up with the origins of those labels. Charlie Gross, a pioneering neuroscientist and lauded neuroscience historian, once referred to this variable combination of acronyms as an “alphabet soup” nearly a quarter century ago (Gross, 1994, pp. 463). This

Corresponding Author: Kevin S. Weiner, Department of Psychology, University of California, Berkeley Berkeley, CA 94720, kweiner@berkeley.edu.

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“alphabet soup” has only grown over the last few decades as the number of ways to functionally measure and map the brain has increased. Consequently, it is important to prevent confusion and misattribution by preserving the evidence supporting the parcellation of brain areas that produces these labels. As the young or experienced reader might imagine (or know), many brain areas have their own historical story and associated contention(s) among researchers. This paper focuses on the historical narrative of a brain area located at the junction between the occipital and temporal lobes of the macaque known as TEO. In particular, this paper discusses and clarifies how (a) strychnine neuronography evidence and (b) ablation and behavioral evidence supported the delineation of area TEO from neighboring areas while cytoarchitectonic evidence did not. This is an important clarification because Bonin and Bailey (1947) are credited with the TEO label, but their cytoarchitectonic monograph did not provide empirical evidence to differentiate this area from neighboring areas (Figure 1)¹.

This review is composed of seven sections. The first section discusses the namesake of TEO and what the acronym represents. The second section details the difficulty that Bonin and Bailey had in delineating a cytoarchitectonic area within the cortical expanse previously identified as area 37 by Brodmann (1907) and as area PH by Economo and Koskinas (1925). The third section provides evidence supporting that it was actually classic strychnine neuronography studies that differentiated TEO from TE based on the fact that the former had vertical connections that the latter did not have (Petr et al., 1949). The fourth section highlights cortical ablation studies by Iwai and Mishkin (1969) that provided causal behavioral evidence to functionally parcellate area TEO from area TE anteriorly and from area OA posteriorly, as well as determined the posterior boundary of TEO at the ascending limb of the inferior occipital sulcus. The fifth section provides evidence that a number of different research groups conducting cortical ablation studies referred to this cortical expanse as posterior inferotemporal, or PIT, in the 1970s. Further in this section, I also discuss how Iwai and colleagues provided evidence of a vertical anatomical tract connecting posterior inferotemporal cortex to intraparietal cortex (Umitsu and Iwai, 1980), which Iwai (1982) later proposed was likely a tract that served to enable different visual processing systems to interact with one another. The sixth section highlights the re-emergence of the PIT nomenclature in 1990 and discusses how this piece of cortex is referred to today. The seventh section briefly discusses modern understanding (and contention) regarding the functional heterogeneity of TEO, as well as Iwai’s approach to nomenclature (e.g. using separate acronyms to refer to anatomical and functional definitions of brain areas). Quoted passages from prior work are included within these sections in order to preserve the original words of the authors that are exceptionally relevant for this historical narrative.

¹During the time periods discussed in the present paper, pioneering brain research was being conducted with different types of methods. However, the focus of the present paper is on the studies of cortical ablation and strychnine neuronography as they are critical historically for the original distinction among areas TE, TEO, and OA. Pioneering neurophysiology studies of TE and TEO (Gross et al., 1969, 1972; Boussaoud et al., 1991; and many others) were also being conducted during the time periods discussed in the present paper, but discussion of these studies is beyond the scope of the present review. I should also clarify that particular attention is placed on studies conducted by Iwai and colleagues as many of them are conference proceedings that remain in the stacks of libraries. As such, they are largely excluded from the modern literature, but are integral for the historical origin of TEO.

1. What is the origin of the “TEO” label?

Because the focus of this paper is on area TEO, it is necessary first to discuss the origin of its namesake. Through my own personal discussions with many cognitive neuroscientists who study vision, an assumption is that TEO is an acronym that represents a combination of temporal (TE) and occipital (O). From my historical digging, it seems that (a) this assumption is only partly true and (b) there is not a single study that specified what TEO stands for². This is likely because, as discussed in the next section, Bonin and Bailey (1947) only labelled one plate as ‘TEO’ in their entire 1947 monograph, but do not otherwise discuss this area by name in the text or in schematics. Thus, to fill this gap in knowledge, in this section, I use a combination of evidence compiled across papers and atlases to postulate that the TEO label was generated because Bonin and Bailey emulated the cytoarchitectonic studies of Economo and Koskinas and as such, they also mirrored their strategy for labeling areas of the brain.

For instance, in the beginning of their monograph, Bonin and Bailey (1947) clearly state their preference for Economo and Koskinas’ brain map over Brodmann’s as well as other anatomists such as those of the Vogt school. This also includes a preference for Economo and Koskinas’ nomenclature over Brodmann’s numerical system. Specifically, Bonin and Bailey (1947) write:

“On looking over our own material from animals used for studies of physiological neuronography (see McCulloch, 1944) we became very much dissatisfied with existing maps of the macaque cortex and decided to undertake our own detailed study. This has led us, with considerable reluctance, to abandon Brodmann’s numerical system in favor of Economo’s (1929) symbols. We have done this because our ultimate goal is to understand the human brain, and Economo has published the only acceptable detailed description of human cortex. Brodmann (1907), it is true, prepared a map of the human brain which has been widely reproduced, but, unfortunately, the data on which it was based was never published. Economo, in collaboration with Koskinas (1925), on the other hand, has made available all the details necessary for purposes of comparison. The analyses of C. and O. Vogt (1919), of Beck (1934), and of Filimonoff (1932), all of which came out of Vogt’s laboratory, are so elaborate and based on such minute distinctions that we have been totally unable to follow them. Moreover, our physiological experiments have failed to convince us of their usefulness.” Bonin and Bailey, 1947, pgs. 1–2³

Of course, a preference for “Economo’s (1929) symbols” as quoted above does not explain what those symbols represent. Economo’s symbols - and nomenclature more generally – are perhaps best explained by Lazaros Triarhou, who has published several papers about

²If such a description does exist in the literature and I have missed it, I am hopeful that a reader would contact me or write a letter to the journal (or both) in order to assure that the history of TEO is preserved.

³Initially, it was unclear as to why Bonin and Bailey cited Economo (1929) consistently throughout their monograph instead of the original Economo and Koskinas (1925) atlas that was published four years prior. But, in a paper published by Peden and Bonin (1947) in the same year as the Bonin and Bailey monograph, a footnote revealed that the reason was because of availability. Peden and Bonin write: “We prefer to cite Economo’s English summary since it is more readily available than the costly cytoarchitectural atlas published with Koskinas in 1925.” Peden and Bonin (1947), pg. 40.

Economo and Koskinas, as well as their atlas (Triarhou, 2005, 2006, 2007a,b). In one such paper, Triarhou (2007a) breaks down the method of the meaning behind the nomenclature in which he writes:

“The monumental Atlas of Cytoarchitectonics of the Adult Human Cerebral Cortex of Economo and Koskinas represents a gigantic intellectual and technical effort, never sufficiently recognized. One reason might have been the limited number of copies produced; another, the complex (albeit logical and precise) symbol notation, which comprises a Roman capital (from the initial of the respective lobe), a calligraphic capital (the sequence of a gyrus within a lobe), and a Latin or Greek subscript (for microscopic features).” Triarhou, 2007a, Pg. 195

As such, each area of the brain would be represented with an acronym that consisted of at least two letters. For example, in the temporal lobe, Economo and Koskinas identified 10 main areas beginning with TA (Figure 1A), in which area TE was the 5th area due to the fact that E is the fifth letter in the alphabet. However, Economo and Koskinas (1925) did not define an area with the label of TEO. So where did this label come from in Plate L of Bonin and Bailey (Figure 2)? Well, in addition to a third symbol of a Latin or Greek subscript indicating microscopic features representative of the area in question, Economo and Koskinas (1925) also used a third capital letter to indicate the lobe in which the area was located if the area traversed multiple lobes. For example, as highlighted in Figure 1A (dotted red outline), the 8th area in the parietal lobe, area PH, extended into portions of the temporal and occipital lobe in which PHT represents the portion of PH within the temporal lobe and PHO represents the portion of PH within the occipital lobe⁴. Since Bonin and Bailey emulated Economo’s methods and nomenclature, it is most likely the case that the origin of the TEO label reflects similar logic in which TE is the 5th area within the temporal lobe and their definition of TEO reflects the portion of TE that extends into the occipital lobe.

In addition to TEO and PH, additional labels and combinations of acronyms were used to refer to this piece of cortex and will be referenced, as well as further explained, in subsequent sections. For example, ‘37’ was proposed by Brodmann (1907) as already mentioned. Additionally, PIT, which stands for posterior (P) inferotemporal cortex (IT) was introduced by ablation studies (Wilson et al., 1972; Iwai, 1978; Sahgal and Iversen, 1978; Bolster and Crowne, 1979) that examined how removing cortical tissue affected an animal’s behavior. Combinations of labels were also used. For example, in their monograph of the chimpanzee brain, Bailey, Bonin, and McCulloch (1950) adapted the TEO nomenclature to include reference to PH as TEO (PH).⁵ This strategy – including the reverse order of PH (TEO) – was later repeated by subsequent investigators such as Iwai (Table 1; Iwai, 1978). The relationship among the differences in nomenclature was formally discussed by scientists during this time period including Gross (1973) and Iwai (1978), which we will discuss in the fifth section. Nevertheless, as done here, it is necessary to introduce these labels in the first section of the manuscript as these labels will be referenced throughout the paper. Altogether,

⁴Consistent with this idea, Triarhou (2007b) refers to area PHP as the “Basal (temporooccipital) parietal area at parietal entrance,” area PHT as the “Basal (temporooccipital) parietal area at temporal entrance,” and PHO as the “Basal (temporooccipital) parietal area at occipital entrance” (Triarhou, 2007b, Table 2, pg. 208).

⁵Interestingly, while Bonin and Bailey did not include TEO in the frontispiece of their 1947 monograph of the macaque brain, they did include area PH on the frontispiece of their 1950 monograph (with McCulloch) of the chimpanzee brain.

while it does not often take more than 1,000 words to explain what an acronym stands for in the extended brain mapping field, as we will learn throughout this paper, it is not only the namesake of TEO that is complex, but also its history.

2. Area TEO and ‘Area ?’.

As discussed in the previous section, the first appearance of TEO in the neuroscience literature was in Bonin and Bailey’s 1947 monograph of the macaque brain. Using several previous atlases as a guide during their cytoarchitectonic examination – especially Brodmann (1907) and Economo and Koskinas (1925) – Bonin and Bailey had difficulty *seeing* the same cytoarchitectonic differences between neighboring pieces of cortex that these prior authors described. One such territory that they had difficulty identifying was a transitional area between the occipital and temporal cortices, which, as referenced in Section 1 above, Brodmann described as area ‘37’ and Economo and Koskinas referred to as ‘PH’. Indeed, while Bonin and Bailey are credited as identifying this piece of cortex as ‘TEO’ in their 1947 monograph, they did not find cytoarchitectonic evidence to do so. In fact, they did not include TEO in their frontispiece (Figure 1B). The description of their difficulty in cytoarchitectonically differentiating this piece of cortex from the surrounding areas TE (anteriorly) and OA (posteriorly) is included below in their own words:

“Situating in the ventral part of the human hemispheres, between the occipital and temporal lobes, is a zone which was considered as a part of the “parietal lobe “ by Economo and given therefore the symbol PH. He states that the chief characteristic of PH is the “fusion of V and VI into one single lamina.” Brodmann (1907) also distinguished an area in this region in the human brain which he called area 37. In the macaque we have been unable to find any zone between the occipital and temporal lobes which has parietal characteristics. Our Plate L taken from this intermediate region shows a very light fifth layer similar to OA.” Bonin and Bailey, 1947, pg. 41 (See Figure 2)

For reference, their Plate L is included in Figure 2 alongside plates illustrating the cytoarchitecture of area TE and OA. It appears that the only place that they include the label TEO is in the title of Plate L (Bottom of Figure 2, middle). They were so unsure that this truly was a distinct cytoarchitectonic area that they labeled this piece of cortex between OA and TE as ‘?’ in figures throughout their monograph (Figure 3A for one such example). Iwai and Mishkin would then recreate the location of this questioned piece of cortex, as well as use this uncertainty to motivate their 1969 ablation study (Figure 3B and further explained in Section 4 below).

Taken together, though Bonin and Bailey are credited with the TEO label, they doubted the little evidence they had to cytoarchitectonically differentiate it from adjacent pieces of cortex that they (1) excluded it from the frontispiece of their monograph, (2) only labeled it in the title of their Plate L, and (3) used a question mark to denote this piece of cortex in their figures throughout the monograph.

3. Evidence from strychnine neuronography is used to distinguish TEO as a separable area from TE.

Four years prior to their cytoarchitectonic monograph, Bonin, Bailey, and their collaborators used strychnine neuronography to examine the connectivity among cortical areas in macaque (Bailey et al., 1943; Bailey et al., 1942; McCulloch et al., 1944). Strychnine neuronography is a method that uses chemical stimulation to examine connections of cortical foci. Specifically, electrical activity is propagated between cortical foci through the application of strychnine, which allows the examination of cortical connections among areas. The findings from Bailey and colleagues provided evidence for vertical connections from the dorsal aspects of the occipital lobe to ventral aspects of occipito-temporal cortex, which the authors summarize as support for the vertical occipital fasciculus (Bailey et al., 1943; Bailey et al., 1942; McCulloch et al., 1944; Takemura et al., 2017; Takemura et al., *under review*). In 1949, Petr and colleagues built on the foundation of these prior studies and also used strychnine neuronography to examine the connections of the brain. In order to motivate their studies, Petr and colleagues particularly emphasized the fact that the cortical expanse corresponding to TEO could not be differentiated from TE based on prior evidence of cytoarchitecture (for a related discussion and images from Petr et al., 1949, please see Takemura et al., *under review*). Their results revealed that the cortical expanse corresponding to TEO actually had a different set of connections compared to neighboring regions. They interpreted these findings as evidence to distinguish TEO as a separable area from adjacent regions – particularly TE – based on ‘characteristic connections’. The authors write:

“Strychnine applied to the posterior part of the third temporal gyrus fired more posteriorly. This region is intermediate between the perioccipital cortex OA and the true temporal cortex TE. Although it could not be recognized by Bonin and Bailey, 1947 as a separate cytoarchitectonic area, it has such characteristic connections that there can be little doubt that this region is the precursor of the separable area called by Economo in man PH. When strychnized it fires the second temporal convolution, the fusiform gyrus, both fore and aft the lunate sulcus (OA and OB) and into the parietal lobe both above and below the intraparietal sulcus (PEp and PG). We could not find any firing along the sulcus principalis but we did find reverse firing into the intermediate region (TEO) from the sulcus principalis and also from the angular gyrus at the junction of the sulcus intraparietalis and the lunate sulcus (fig.1 TEO). “ Pg. 102–103

Thus, Petr and colleagues re-iterate that TEO could not be identified as a distinct cytoarchitectonic area by Bonin and Bailey (1947), as well as provide evidence differentiating this cortical expanse from the more anterior TE for the first time based on a difference in connectivity profiles between the two areas.

4. Cortical ablation studies functionally differentiate TEO from TE and solidify the posterior boundary of TEO at the ascending limb of the inferior occipital sulcus

Twenty years after the study by Petr and colleagues, Iwai and Mishkin (1969) provided behavioral evidence following cortical ablation to functionally parcellate TEO from TE. To

motivate their studies, they first accurately summarize the neuronography and cytoarchitectonic work in which they write:

“In a study of intercortical connections based on the method of strychnine neuronography, Petr, Holden, and Jirout (16) found that the cortex at the temporo-preoccipital junction in the monkey has characteristics which distinguish it from both OA and TE. Further on the basis of its interconnections, they suggested that it might be considered the precursor of area PH in higher primates. Bonin and Bailey later adopted their suggestion (4, pp. 384–386) and relabeled the transitional area “TEO (PH),” though they had not been able to establish this classification on cytoarchitectural grounds.” Iwai and Mishkin, 1969, Pg.592

Iwai and Mishkin (1969) also include a figure with an approximate location from which Plate L was taken in Bonin and Bailey (1947; Figure 3). Consistent with the discussion in the first section of the present paper, the authors further state confusion regarding Bonin and Bailey’s frontispiece in terms of misleading transitions of color and the absence of TEO, as well as the lack of cytoarchitectonical evidence delineating area TEO as a transitional area between OA and TE. The authors write:

“However, the diagram, which is based on their colored map, does not depict the gradual transition between OA and TE that is represented on the original charts by color-shading. In fact, on closer examination it turns out that the cytoarchitectural identity of the transitional cortex is still unsettled. Although Bonin and Bailey designated the posterior inferotemporal area as OA on their map, they often refrained from labelling it on the actual cross sections, stating (p. 75) that the general similarity of OA and TE rendered classification of the transitional zone extremely difficult.” Pg. 591

Iwai and Mishkin (1969) then conclude that the evidence from their ablation studies, in combination with the neuronography evidence, functionally distinguishes TE from TEO anteriorly and TEO from OA posteriorly. They write:

“The behavioral data presented here tend to support the neuronographic separation of TEO from the rest of OA. Although the cytoarchitectural identity of TEO is unclear, it seems from the foregoing evidence that this cortex is distinguishable from surrounding cortex on several other grounds. On this basis, the visual area defined in the present study consists of two neurally different subareas, TE and TEO. The possibility that the inferotemporal visual area is also divisible functionally offers a new approach to the problem of behavioral analysis.” Pgs. 592–594

Interestingly, because the cytoarchitectonic findings from Bonin and Bailey (1947) were unconvincing and the findings from Iwai and Mishkin (1969) were convincing, subsequent studies sometimes credited Iwai and Mishkin for labelling TEO. For example, Desimone and colleagues (1980) write:

“Although originally included within area OA by von Bonin and Bailey³⁸, Iwai and Mishkin have termed this area TEO¹⁹. Our physiological recordings in this region

have established that most of it is devoted to the foveal and parafoveal visual field 7,15. “ Pg. 46

Additionally, results from Iwai and Mishkin (1969) as well as subsequent ablation experiments (Iwai, 1980; Kikuchi and Iwai, 1980) found that inclusion of the ascending limb of the inferior occipital sulcus (AIOS) was critical to produce the resulting decrement on pattern discrimination behavior. In summary of these results, Iwai (1980) writes:

“Therefore, it is concluded that the posterior limit of the visual learning area is at the AIOS, and then the visual learning area comprises two anatomical areas TE (the AIT subdivision) and possible TEO (the PIT subdivision) and does not extend into areas OA and OB (the PS cortex).” (Iwai, 1980; Pg. 280)

Taken together, the fact that TEO was not differentiated based on cytoarchitectonic evidence was accurately relayed by studies in the 1960s and 1970s. The posterior boundary of TEO at the ascending limb of the inferior occipital sulcus was determined by cortical ablation studies (Iwai and Mishkin, 1969; Iwai, 1980; Kikuchi and Iwai, 1980). These studies also provided causal evidence that functionally differentiated area TEO from areas OA posteriorly and TE anteriorly. Interestingly, the passage from Iwai (1980) quoted above also used the PIT and AIT nomenclature, which is one of the topics discussed in the next section.

5. Structure (TEO and TE) vs. Function (PIT and AIT) and the role of vertical connections for the integration of form and visual space

As the focus of this paper is the complex history of area TEO, an important component of this history is the contention over its namesake – a contention that was introduced in Section 1 of the present manuscript. Specifically, in addition to other labels such as 37 or PH as referenced in previous sections, researchers during this time period who were examining the effects of cortical lesions on behavior referred to this piece of cortex as posterior inferotemporal (Iwai and Mishkin, 1969; Mishkin, 1972), which was later abbreviated to PIT (Wilson et al., 1972; Iwai, 1978; Sahgal and Iversen, 1978; Bolster and Crowne, 1979), PT (Iversen and Humphrey, 1970), or PIF (Iversen, 1973).

Still others (Covey and Gross, 1970; Gross, 1973) argued that “foveal prestriate” was more appropriate than “posterior inferotemporal.” For example, Gross (1973)⁶ relates foveal prestriate lesions to the lesions of Iwai and Mishkin (1969) in which he writes:

⁶Covey and Gross (1970) included a footnote in their paper with similar concerns. They write: “*The terminology for the subdivisions of the non-striate visual areas of the occipital and temporal lobes of the monkey is still rather confusing. This is hardly surprising, for the subdivision of these areas on cytoarchitectonic grounds by different authorities is contradictory and the study of the properties of single units in these areas has only begun. Although the recent demonstrations by Zeki (1969b) and Cragg and Ainsworth (1969) that lateral striate cortex has two topographic and a third non-topographic projection onto prestriate cortex is a major step forward, the exact boundaries of these projections and their detailed relations to the various cytoarchitectonic subdivisions and subdivisions based on electrophysiological data are not yet entirely clear. Since the terminology used in behavioural studies of lesions of the non-striate visual areas is also inconsistent, it may be helpful to explain the terminology we have used in this report. We have called our posterior lesions “foveal prestriate lesions” because they include the entire area of prestriate cortex to which foveal striate cortex selectively projects (Zeki, 1969b; Cragg and Ainsworth, 1969). Simply to call them prestriate cortex lesions or posterior inferotemporal cortex lesions is misleading because they include far less than the former and far more than the latter. Our inferotemporal lesions correspond closely to Von Bonin and Bailey’s “Area TE”. However, numerous publications on the behavioural effects of removing “inferotemporal” cortex illustrate lesions which often extend posterior to “Area TE” as far as the inferior occipital sulcus and thus may include part of foveal prestriate cortex. We therefore wish to stress that our inferotemporal lesions are restricted to area TE and may not be comparable to some “inferotemporal” lesions in other studies.*” Covey and Gross (1970), Pgs. 128–129

“ We have called these lesions “foveal prestriate lesions” because they include the entire area of prestriate cortex to which foveal striate cortex selectively projects [210, 45]. Simply to call them “prestriae cortex” lesions or “posterior inferotemporal cortex” lesions is misleading because they include far less than the former and far more than the latter. IWAI and MISHKIN [98, 130] have called essentially the same lesion one of “Area TEO”. Note that since the anterior border of foveal prestriate cortex is still unspecified, it is possible that the deleterious effects of “foveal prestriate lesions” could have been due, at least in part, to the removal of tissue between Area TE and the foveal projection onto prestriate cortex, rather than entirely to the ablation of the latter area. That is, a functionally and anatomically discrete area may exist between Area TE and the circumstriate belt.” Gross, 1973 Pg. 461

Indeed, many ablation studies examined the effects of *foveal prestriate* lesions on various types of behavior (Manning et al., 1971; Manning, 1971, 1972; Bender, 1973; Bender and Gross, 1981; Christensen and Pribram, 1979; and others, see Mishkin (1972), Gross (1973), and Dean (1976) for comprehensive reviews of this work). On the other hand, Iwai (1978) believed that foveal prestriate seemed to be “at least inadequate” and instead preferred posterior inferotemporal and the acronym PIT. Iwai (1978) writes:

“Finally, we will consider the nomenclature for these subareas of the visual learning area (see Table 1)⁷. The above findings indicate that neither the OA nor the OB area is a part of the visual learning area. Generally speaking, the prestriate cortex consists of two anatomically distinguishable areas of the OA or prestriate and the OB or parastriate cortices. The visual learning area here defined is located within the IT. On this basis, I believe, the term foveal prestriate for the posterior subarea of the IT visual learning area seems to be at least inadequate. The term inferotemporal for the anterior subarea may also be unsuitable, since the anterior subarea occupies a rostral part of the IT and does not represent the whole IT. We therefore [sic] tentatively propose calling these two subareas of the visual learning area the anterior and posterior inferotemporal subareas (AIT and PIT), respectively, and using the term (total) inferotemporal visual learning area (TIT) for the combination of these subareas.” Pgs. 425–426

Consistent with Iwai’s description, additional research groups referred to this cortical expanse as PIT (and AIT for the cortical expanse immediately anterior to PIT) in ablation studies in the late 1970s (Sahgal and Iversen, 1978; Bolster and Crowne, 1979). The use of PIT and AIT in ablation studies reflects the fact that the exact macroanatomical landmarks delineating the limits for each cytoarchitectonic area were unknown. Thus, PIT and AIT served as labels reflecting the locus of cortical ablation that resulted in subsequent decrements in behavior and thus, were independent of the exact cytoarchitectonic boundary between areas.

To relate the different labeling schemes of the cytoarchitectonic and lesion methodologies to one another, Iwai often included both sets of labels in the figures of his papers starting in

⁷Table 1 included in the present manuscript is reproduced from Table 1 from Iwai (1978).

1978. For example, Iwai (1978) included TE and PH on the brain itself, while placing AIT and PIT in parentheses outside the image of the brain (Figure 4, top). Additionally, Iwai (1980) included TE and TEO on the schematic brain, while again placing AIT and PIT in parentheses outside the brain. This likely reflected the fact that Iwai believed inferotemporal cortex to contain at least two separate anatomical (TE and TEO (PH)) and functional (AIT and PIT) subdivisions. This idea is clearly conveyed in the following excerpt from Iwai (1980) in which he writes:

“Now, it is definitively concluded that the visual learning area comprises two anatomically and functionally different areas: Anatomically, it consists of areas TE and TEO; and functionally, the TE area or the AIT subdivision is closely concerned with visual memory or stimulus-reward (or – reinforcer) association, while the TEO area or the PIT subdivision is pre-dominantly involved in perception of, or selective attention to, visual stimuli. These findings give some support to the idea that an anatomically distinguishable area is predominantly concerned with a behaviorally distinguishable function.” Iwai, 1980, Pg. 283

In support of this idea, Iwai and colleagues not only showed that PIT and AIT were functionally separable based on distinct behavioral deficits following separate lesions to each area, but also showed that these areas were anatomically distinct. Specifically, in a 1980 conference proceeding, Umitsu and Iwai (1980) used horseradish peroxidase to examine anatomical connectivity among cortical areas and found that posterior inferotemporal cortex was anatomically distinguishable from anterior inferotemporal and prefrontal cortices (Figure 5A). Interestingly, and to link to the strychnine neuronography findings discussed in Section 3, Umitsu and Iwai (1980) showed that posterior inferotemporal cortex was vertically connected to the intraparietal sulcus (IPS), consistent with the findings from Petr and colleagues (1949)E. Two years later, Iwai (1982) would use these connections as evidence to propose four fundamental systems or constructs in which the “form vision system” and “spatial vision system” could “reciprocally interact” through these vertical connections (Figure 5B). In the section “A possible interaction mechanism between form vision system and spatial vision system,” Iwai writes:

“Our recent HRP studies indicated that the IT cortex receives projection from the ventral bank of the intraparietal (ip) sulcus in the parietal lobe (Fig. 3), while the IP cortex is projected from the ventral bank of the superior temporal (st) sulcus (6)...We are assuming, therefore, that the form and spatial visions reciprocally interact in the indirect or relay ways through the banks of the st and ip sulci. Presumably, the information of spatial cue-in-object perceived in the PIP allocentric spatial vision area is sent to the IT form vision area where the information of spatial cue-in-object is incorporated into the frame of form information to perceive fully the object as the unified gestalt-form. And, then, the information perceived as the gestalt-form in the IT form vision area is sent back to the spatial vision areas to perceive the object as an occupied position in the spatial world in relation to the spatial location information transmitted from the SC and Pul nuclei in the old visual sensory system (Sec. III-24). Of course, the question of whether or not the above speculation is the case is open for future studies.” Iwai, 1982, Pgs. 55–56

As is likely obvious to the reader, Iwai's proposal was during the same time period that Ungerleider and Mishkin (1982; Mishkin et al., 1983) proposed the two cortical visual systems hypothesis. A major unanswered question was the independence or interdependence between the two visual streams. To my knowledge, the role of vertical connections for cross-talk between the two streams was not proposed until much later (see Takemura et al., 2016, 2017; Takemura et al., *under review*). Thus, Iwai's proposal that the direct connections between posterior inferotemporal cortex and the parietal lobe may serve to support reciprocal interactions between the dorsal and ventral visual streams seems to be pre-emptive of what was to come later on in the field.

6. PIT and AIT re-emerge in 1990

Despite the fact that several research groups used PIT and AIT to refer to separable areas in cortical ablation studies in the 1970s (Wilson et al., 1972; Iwai, 1978; Sahgal and Iversen, 1978; Bolster and Crowne, 1979), the PIT/AIT nomenclature is often credited to Van Essen and colleagues over a decade later (Van Essen et al., 1990 - credited by Felleman and Van Essen, 1991, as well as Zeki, 1996). Interestingly, despite Iwai's clear proposal to use PIT to refer to the portion of extrastriate cortex commonly referred to as TEO quoted in the previous section, other researchers would credit him for supporting the TEO nomenclature from his work that was published in more visible journals. For example, Van Essen and colleagues (1990) would later cite Iwai as using the TEO nomenclature. Specifically, they write:

“Foci 1–4 include segregated patches of bilaminar label situated in posterior portions of IT, in the vicinity of what has been called TEO by other investigators (Fenstermaker 1986; Iwai and Yukie 1987).” (Pg. 688)

The discrepancy is likely because Iwai often referred to areas with anatomical labels (TEO and TE) during anatomical studies and functional labels (PIT and AIT) during cortical ablation studies. The study to which Van Essen and colleagues (1990) referred was anatomical in nature, which fit Iwai's criteria for using the TEO/TE nomenclature. In fact, the same year Van Essen and colleagues re-proposed the PIT nomenclature, Iwai and colleagues (1990) conducted a structural-functional study in which the structural portion contained an anatomical examination of connections between the amygdala and inferior temporal cortex (among other areas), while the functional portion of the study examined the effect of lesions on behavioral performance. When describing the anatomical portion of the study, the authors used the TEO and TE nomenclature. However, when describing the functional significance, the authors once again used the PIT and AIT labels (Figure 6).

Despite the same labels of PIT and AIT, it should also be stated that Van Essen and colleagues (1990) proposed a different parcellation scheme in this cortical expanse than that proposed by Iwai and colleagues, as well as the other groups referencing PIT and AIT within ablation studies during the 1970s (Wilson et al., 1972; Iwai, 1978; Sahgal and Iversen, 1978; Bolster and Crowne, 1979). Specifically, instead of two areas (PIT and AIT), Van Essen and colleagues (1990) suggested six areas: PIT, central IT (CIT), and AIT, each of which contain dorsal and ventral subdivisions. A year later, like Iwai (1978) and Gross (1973) quoted previously in Section 5, Felleman and Van Essen (1991) discussed the issue

of nomenclature. Specifically, they used PIT and TEO as an example of how brain areas typically have many names. They write:

“Most regions of the visual cortex have more than 1 name that is in common use. Table 1 provides a partial listing of these alternative terminologies. In dealing with the nomenclature issue, we have drawn a distinction between (1) names that are simply different descriptors for what is clearly the same underlying visual area (e.g., areas 17 vs. VI, V3 vs. VP, and MT vs. V5; column 7), and (2) names that reflect substantially different schemes for partitioning the cortex (column 9). In some cases, the alternative scheme is a more coarse partitioning than the one we prefer (e.g., TEO vs. PITd and PITv). In other cases, the alternative scheme is even more fine grained (e.g., POa-i and POa-e vs. LIP). In still other cases, most notably in the inferotemporal cortex (IT), the relationship between different schemes is more complex and irregular.” Felleman and Van Essen, 1991, Pg. 5

Furthermore, and to repeat a phrase used in the Introduction of this paper, this “alphabet soup” continued as Zeki (1971, 1977) previously referred to this cortical expanse as V4A during the same decade that PIT appeared in the literature. This plethora of labels for what could be the same brain area caused Zeki (1996) to write a paper titled, “*Are areas TEO and PIT of monkey visual cortex wholly distinct from the fourth visual complex (V4A)?*” In that paper, Zeki (1996) cites Van Essen and colleagues in reference to PIT. Specifically, he writes:

“Another name that has been used to describe this region of cortex is PIT or the Posterior Infero-Temporal area (Felleman & Van Essen, 1991⁸). PIT has been very inadequately and briefly described, but from its position and from such brief descriptions that we have, it is almost certain that a substantial part of PIT overlaps V4A and therefore also TEO.” Pg. 1544

In Zeki’s paper and the papers by Van Essen and colleagues (Van Essen et al., 1990; Felleman and Van Essen, 1991), the contributions of the cortical ablation studies referencing PIT (Wilson et al., 1972; Iwai, 1978, 1980, 1982; Iwai et al., 1990 Sahgal and Iversen, 1978; Bolster and Crowne, 1979) were not mentioned. It is worth highlighting that Iwai’s approach of using different labels depending on the methodology did not offer a solution to the fact that there were many labels used to refer to the same piece of cortex. However, Iwai’s approach did provide an explanation for when to use the TEO/TE nomenclature compared to the PIT/AIT nomenclature (though he was not always consistent). Thus, the present paper is not meant to claim that Iwai’s contribution solves the conundrum regarding which nomenclature to use and which parcellation is “correct.” Instead, it aims to preserve that Iwai’s studies, as well as the additional cortical ablation studies using the PIT and AIT nomenclature (Wilson et al., 1972; Sahgal and Iversen, 1978; Bolster and Crowne, 1979), should also be included in this conversation and the lengthy, historical story of TEO more generally.

⁸Though Zeki (1996) cites Felleman and Van Essen, 1991 for the definition of PIT, Van Essen and colleagues re-proposed the definition and name of PITd and PITv in a different paper the year prior (Van Essen et al., 1990) in which they write: “The fact that there are two pairs of topographically organized foci suggests that they form two distinct areas, which we have termed PITd and PITv (dorsal and ventral subdivisions of the posterior inferotemporal area).” Van Essen et al., 1990, Pg. 688

7. A brief note on the functional heterogeneity of TEO, as well as Iwai's approach to nomenclature

As stated throughout the present manuscript, the main goal of this paper is to preserve the historical origin of TEO. In addition to this goal, a logical question is: What is the present evidence supporting the functional and behavioral role of TEO, as well as TE? While this question is beyond the scope of the present paper, it is worth briefly elaborating on three methodological approaches that are aimed toward tackling this question.

First, modern ablation studies using classic approaches have shown that removing the cortical expanse that includes TEO induces deficits in selective attention (De Weerd et al., 2003a) and spatial generalization (De Weerd et al., 2003b), as well as affects neural responses in more anterior regions such as TE (Bertini et al., 2004; Buffalo et al., 2005). Second, modern mapping studies implementing functional magnetic resonance imaging (fMRI) differentiate representations of the visual field within the cortical expanse of TEO and TE with continued disagreements (as well as similarities) regarding nomenclature and areal definitions (Brewer et al., 2002; Fize et al., 2003; Kolster et al., 2014; Janssens et al., 2014; Arcaro and Livingstone, 2017). Interestingly, additional studies also show functional clusters, or patches, overlapping this cortical expanse that selectively process colors (Wade et al., 2008; Lafer-Sousa and Conway, 2013), curvature (Yue et al., 2014), objects (Tsao et al., 2003; Fize et al., 2003), faces (Tsao et al., 2006; Janssens et al., 2014), scenes (Kornblith et al., 2013; Arcaro and Livingstone, 2017), or bodies (Fisher and Freiwald, 2015; Pinsk et al., 2009). Third, modern causal manipulations using optogenetics, pharmacological suppression, and microstimulation show that focally inactivating these functional clusters, such as those selective for images of faces, induce perceptual deficits (Sagapopan et al., 2017; Afraz et al., 2015; Moeller et al., 2017). Consequently, while classic understanding ascribed broad functional distinctions between TEO and TE in which the former was involved in pattern perception or selective attention in visual discrimination learning and the latter in visual memory or associative learning, the cortical expanses within the boundaries of classically defined TEO and TE seem to be functionally heterogenous, which will be further clarified in future research.

Finally, in terms of nomenclature, interestingly, Iwai's approach of referring to the same piece of cortex with a different label depending on its anatomical or functional definition is also implemented today – especially for association cortices in both monkeys (Van Essen et al., 2012a,b; Van Essen, 2003; Tootell et al., 2003; Arcaro and Livingstone, 2017) and humans (Amunts and Zilles, 2015; Grill-Spector and Weiner, 2014). For example, in macaque, a face-selective region known as PL is described as being located within anatomically-defined TEO (Moeller et al., 2008) or PITd (Janssens et al., 2014). Likewise, in human, a face-selective region (pFus-faces/FFA-1) and a word-selective region (pOTS-words/VWFA-1) are both located within cytoarchitecturally-defined FG2 in the posterior fusiform gyrus (Weiner et al., 2017). Of course, this is just one example in monkey and human describing the location of a functional region relative to a cytoarchitectonic area across species, but these examples reflect a general trend across species in which researchers often use separate anatomical and functional labels depending on the methodology used to parcellate cortex into areas, which is consistent with Iwai's approach.

CONCLUSION

The historical analyses conducted in this paper produced four main findings. First, though the label TEO was first used by Bonin and Bailey (1947) (and they are accurately credited in the present literature with the label of TEO from the title of their Plate L as illustrated in Figure 2), they did not have the cytoarchitectonic evidence to support the distinction of TEO from adjacent areas OA and TE. Second, the first evidence used to support the separation between areas TE and TEO was based on the fact that TE and TEO had different connections as revealed by strychnine neuronography (Petr et al., 1949; Takemura et al., 2017; Takemura et al., *submitted*). Third, later ablation studies by Iwai and Mishkin (1969) provided causal evidence supporting that TEO was a functionally distinct area separate from OA and TE. Fourth, researchers in the 1970s began referring to TEO as posterior inferotemporal (PIT) and TE as anterior inferotemporal (AIT), which is an important historical clarification as the PIT/AIT nomenclature is commonly attributed to studies conducted more than a decade later. Additionally, in a series of conference proceedings and journal articles, Iwai proposed the use of the TEO and TE nomenclature for anatomical studies, as well as the PIT and AIT nomenclature for ablation and functional studies. While the definition and nomenclature for brain areas is still contentious using modern brain mapping methods in macaque and human, researchers commonly use separate labels to refer to the same piece of cortex depending on whether anatomical or functional methods were used for parcellation, which is consistent with Iwai's proposal. Altogether, these findings contribute to the preservation of the historical origin of area TEO and the empirical evidence that was used to originally differentiate this cortical expanse from surrounding areas.

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A *Economo & Koskinas, 1925*

PH, PHP, PHT, and PHO are located on the lateral surface



PH extends medially into ventral temporal cortex

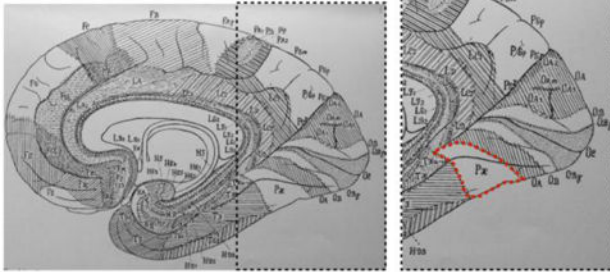


Plate LII: TE, Section 870

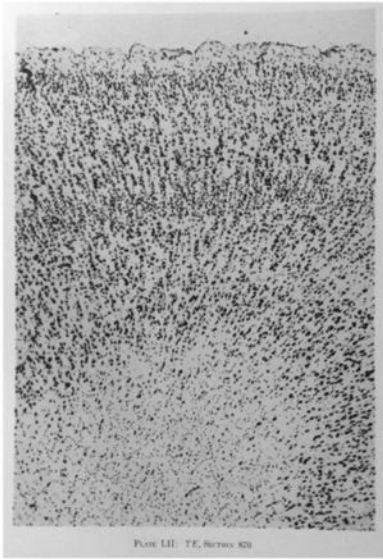
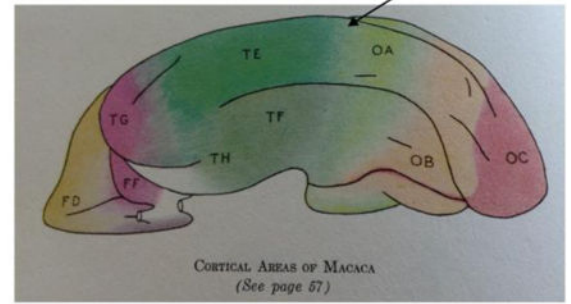
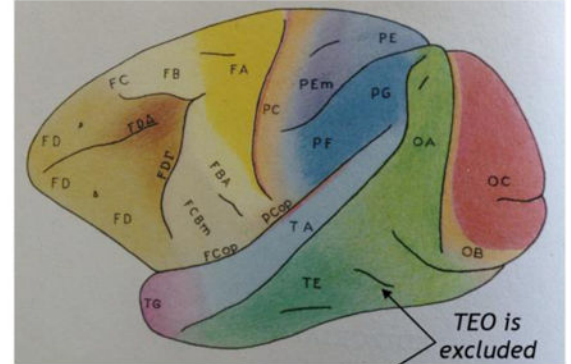


Plate LII: TE, Section 870

B *Bonin & Bailey, 1947*



CORTICAL AREAS OF MACACA
(See page 57)

Plate L: TEO, Section 890



Plate L: TEO, Section 890

Plate XLVI: OA, Section 840



Plate XLVI: OA, Section 840

Figure 1. The origin of the “TEO” label.

As specified in Section 1 of the main text, Bonin and Bailey admired the work of Economo and Koskinas and preferred their nomenclature over Brodmann’s nomenclature.

Nevertheless, Economo and Koskinas (1925) identified a transitional area (“PH”) between areas OA and TE in human (A, left) that Bonin and Bailey (1947) could not identify in macaque (B, right). As Economo and Koskinas also identified a portion of PH extending into the occipital lobe, which they labeled PHO (Figure 1A, top), it is likely that Bonin and Bailey mirrored the logic of Economo and Koskinas to generate the “TEO” label to

represent the portion of area TE extending into the occipital lobe. However, note that TEO is excluded from the frontispiece of their monograph. In fact, the only reference to “TEO” in the entire 1947 monograph is within their Plate L (Figure 2). **(A)** The brain map of Economo and Koskinas (1925). Top left: Lateral surface of the brain map. Top right: Zoomed portion (represented by the dotted black outline at left) indicates areas PH, PHT, PHP, and PHO in dotted red outline. Bottom left: Medial surface of the brain map. Bottom Right: Zoomed portion (represented by the dotted black outline at left) indicates that area PH (dotted red outline) extends medially into ventral temporal cortex. **(B)** Brain map of Bonin and Bailey (1947). Top: Lateral surface. Bottom: Ventral surface. Note that area TEO is not labeled between areas OA and TE.

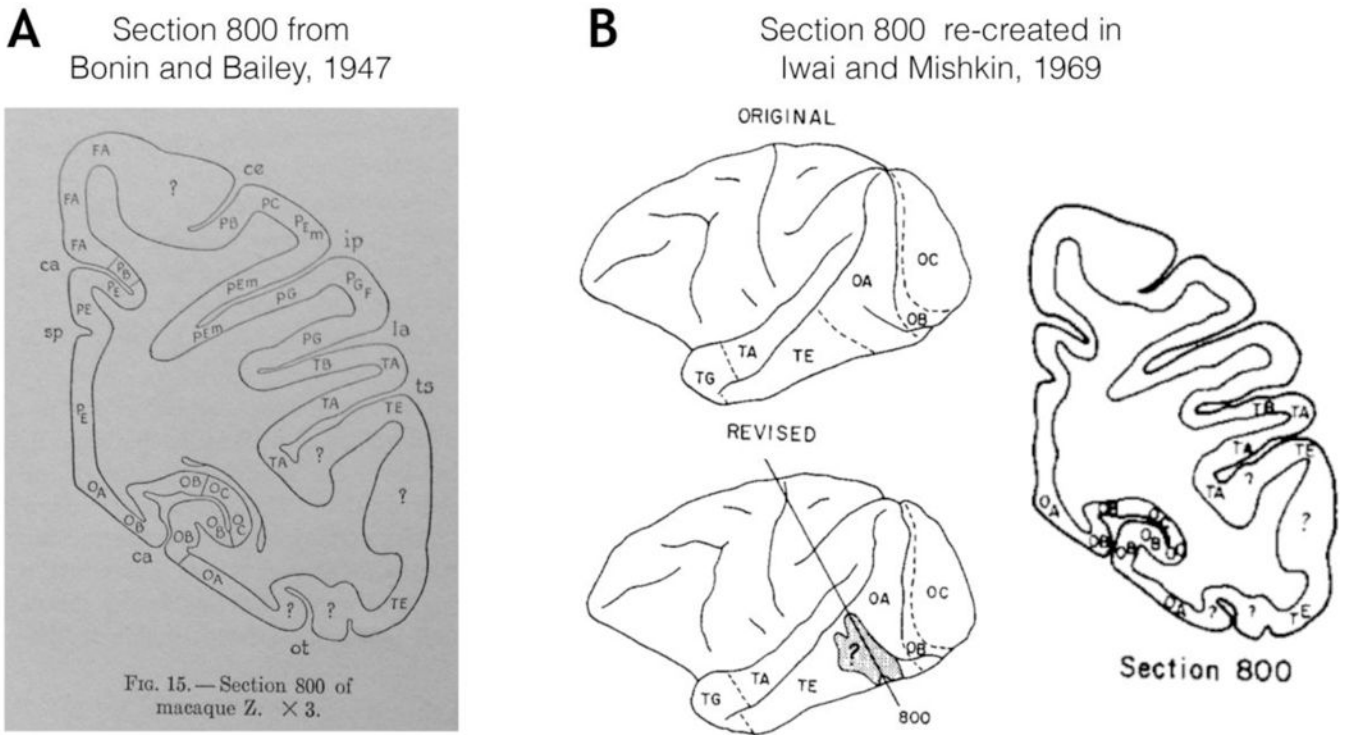


Figure 2. Bonin and Bailey (1947) had difficulty differentiating area TEO from neighboring areas TE and OA based on cytoarchitecture.

Bonin and Bailey (1947) Plates from Bonin and Bailey (1947) illustrating the cytoarchitecture of TE, TEO, and OA between sections 840 and 890. While TEO was not included in their frontispiece as depicted in Figure 1B, Bonin and Bailey included TEO in their plates to show the cytoarchitectonic similarity with areas OA and TE (a direct account of their description is included within Section 2 of the main text).

Iwai, 1978

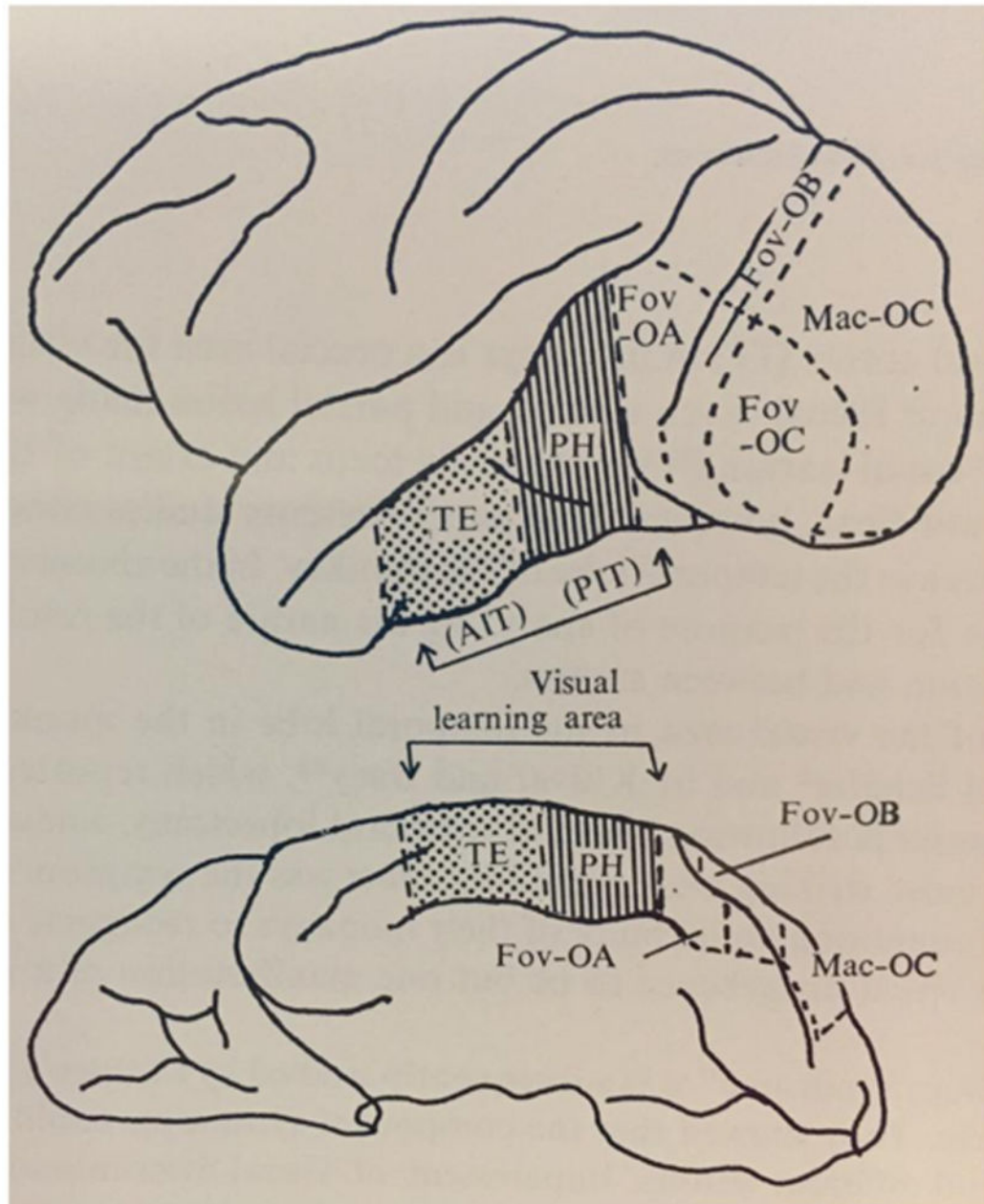


Figure 3. Area “?” in 1947 and re-created over two decades later.

(A) Fig. 15 from Bonin and Bailey (1947) depicting a schematic illustration of Section 800. Note that the piece of cortex between OA and TE is labeled with “?” and not “TEO.” This is because they were unsure that the piece of cortex between OA and TE was different from either area based on cytoarchitecture. (B) Iwai and Mishkin (1969) re-created the location of slice 800 to relate Bonin and Bailey’s cytoarchitectonic confusion to the location of their ablation studies. They concluded that while TEO is hard to cytoarchitectonically differentiate from TE, behavioral evidence after cortical ablation indicates that these are

indeed separable areas (details of which are included in Section 4 of the main text). The original caption from Figure 4 of Iwai and Mishkin (1969) reads: “Cytoarchitectural division of the occipitotemporal region after Bonin and Bailey (3). Top, line drawing based on original colored map. Middle, section No. 800 showing unidentified (“?”) area. Bottom, approximate reconstruction of unidentified area.” (Iwai and Mishkin, 1969, pg. 592; note that the original images were re-organized to accommodate the organization of the present figure).

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Iwai, 1980

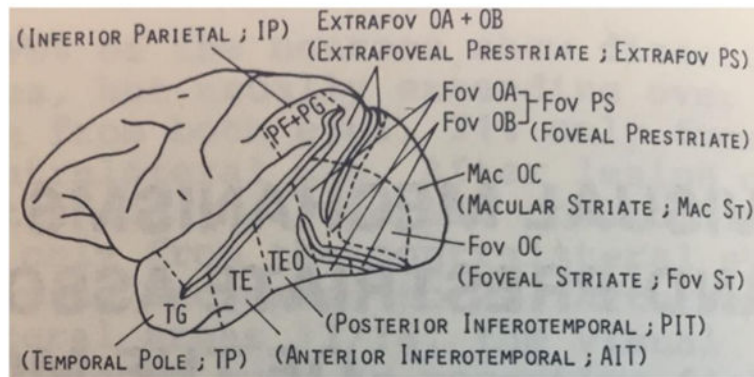


Figure 4. PIT, PH, and TEO in macaque by Iwai (1978, 1980).

Top: Fig. 1 from Iwai, 1978 in which he used PIT and AIT to refer to areas TEO (or PH) and TE, respectively. As described in the main text, Iwai used the TEO and TE nomenclature to refer to areas defined anatomically and used the PIT and AIT nomenclature when referring to areas defined functionally in his ablation studies with Mishkin and others. This is why there are two labels in each image. The original caption reads: “*Two visual learning foci in the temporal association cortex of monkeys, and diagrammatical representations of various cortical areas.*”

The visual learning area consists of two anatomically and functionally distinguishable sub-areas. The anterior inferotemporal subarea (AIT) or Area TE (dotted area) is concerned with visual memory or associative learning, and the posterior inferotemporal subarea (PIT) or Area PH (or TEO) (hatched area) is involved in pattern perception or selective attention in visual discrimination learning^{30,39}. The foveal prestriate cortex (Fov-Prest) is shown here outside of the visual learning area, and consists of Fov-OA and Fov-OB as indicated in the figure. “ (Iwai, 1978, pg. 420)

Bottom: Fig. 1 from Iwai (1980). The text from the original caption that describes this image reads: “In upper right, lateral view of monkey brain is shown, diagrammatically illustrating locus and extent of each visual area, where lesion or HRP injection was intended to make.” (Iwai, 1980, pg. 280)

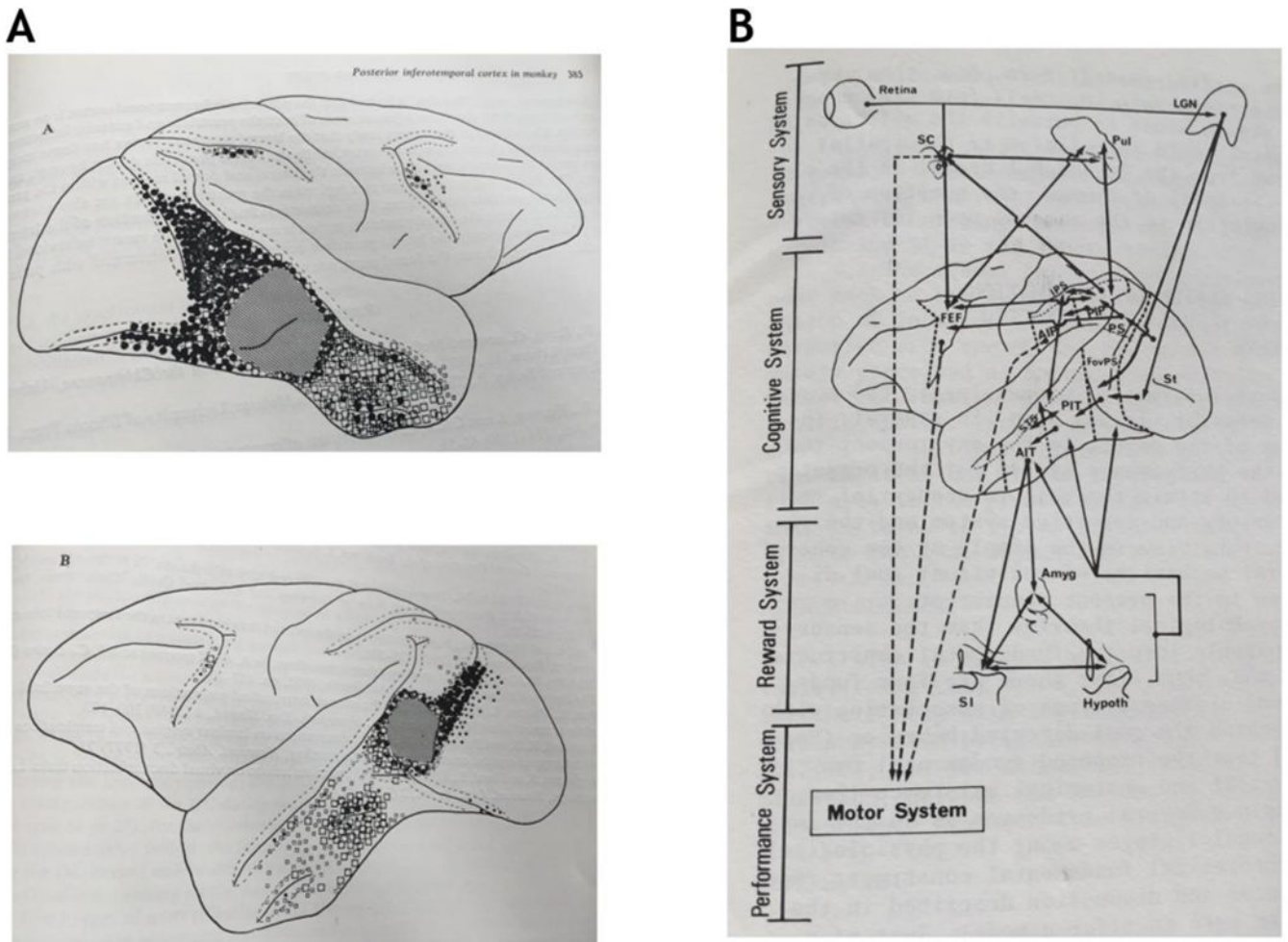


Fig. 5. Anatomical connectivity of TEO: Vertical connections may allow integration between “form vision system” and “spatial vision system.”

Umitsu and Iwai (1980) used horseradish peroxidase (HRP) to examine if the posterior inferotemporal cortex was distinguishable from adjacent pieces of cortex based on anatomical connections. (A) Original caption reads: “Two *representative cases in which multiple HRP injections were made into the posterior inferotemporal cortex (area TEO, Fig. 1-A) and into the lateral prestriate cortex (Fig 1-B). Hatched areas: HRP injection sites. Filled circles: HRP- labeled cells in the supgranular layers. Open squares: HRP-labeled cells in the infragranular layers. Each of the large circles and squares represents 100 labeled cells and each of small symbols represents 10 labeled cells.*” (Umitsu and Iwai, 1980, pg. 385) (B) As an extension of the findings in (A), Iwai (1982) proposed four fundamental systems or constructs in which the “form vision system” and “spatial vision system” could reciprocally interact through vertical connections (vertical arrow extending from IPS). Original caption reads: “*A model regarding central mechanisms of visual information processing in evocation of goal-directed behavior. Abbreviations, refer to charts in Fig. 2-B.*” (Iwai, 1982, pg. 55)

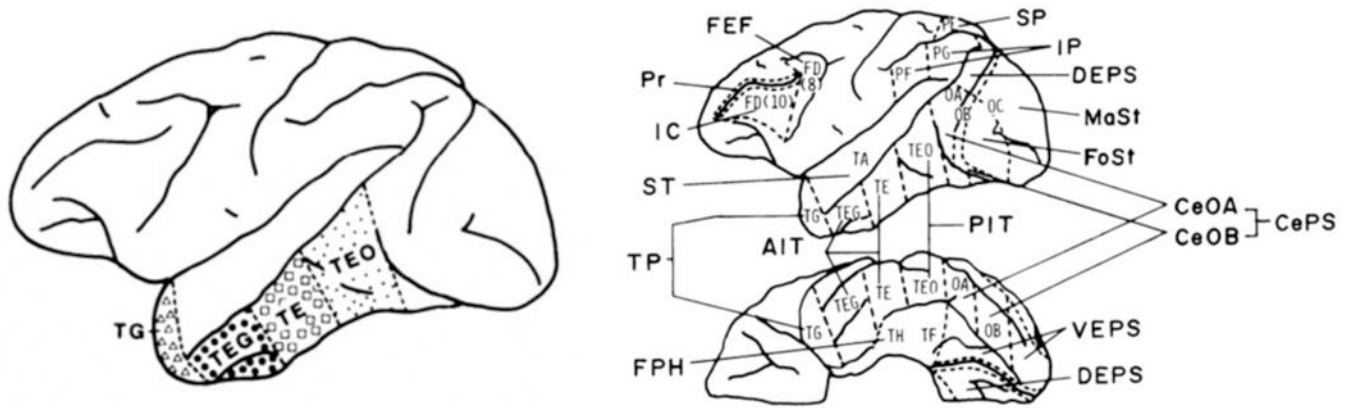


Figure 6. TEO and PIT: Multiple labels to refer to the same piece of cortex depending on the methodology even in the same study.

The same year that Van Essen and colleagues (1990) re-proposed the PIT nomenclature, Iwai et al. (1990) used both the TEO and PIT nomenclature in the same paper in which TEO was used during the first anatomical portion of the study (left) and PIT was used during the later behavioral and ablation portion of the study (right). The fact that Iwai used multiple labels to refer to the same piece of cortex depending on the methodology is an approach that is still used today - for example, using separate labels to refer to cortical areas if they are either defined based on cytoarchitectonic staining or functional magnetic resonance imaging (see Sections 6 and 7 of the main text for further discussion). Excerpts from the original captions (Iwai et al., 1990) that coincide with the images included here are as follows. Left: *“Diagrammatical delineation for areas TG, TEG, TE and TEO, which are denoted by open triangles, large filled dots, open squares and small dots, respectively.”* (Iwai et al., 1990, pg. 99) Right: *“Abbreviation: AIT; anterior inferotemporal, CeOA; central OA, CeOB; central OB, CePS; central prestriate, DEPS; dorsal extracentral pres-triate, FEF; frontal eye field; FoSt; foveal striate, FPH; fusiform-parahippocampal-lingual, IC; inferior convexity, IP; inferior parietal, MaSt; macular striate, PIT; posterior inferotemporal, Pr; principal, SP; superior parietal, ST; Superior temporal, TP; temporal pole, VEPS; ventral extracentral prestriate.”* (Iwai et al., 1990, pg. 99)

Table 1.
Loci and extents of visual learning subareas and their nomenclature according to various investigators (Reproduced from Iwai 1978)

Cytoarchitectural areas ^{29,48,49}	Area TE	Area PH	Area OA	Area OB
Investigators	(Foveal representation only [†])			
Iwai <i>et al.</i> ^{22,29}	Anterior Inferotemporal (or Area TE)	Posterior Inferotemporal (or Area PH, or TEO)	Foveal OA	Foveal OB
			Foveal Prestriate	
Iversen ²¹	Anterior Inferotemporal	Posterior Inferotemporal (including a part of ventral OA)	—	
Gross <i>et al.</i> ¹⁸	Inferotemporal	Foveal Prestriate		—
Pribram ¹²	Inferotemporal (corresponding to classical Inferotemporal)	Foveal Prestriate (sometimes including Macular Prestriate [†])		
Keating ³¹	Inferotemporal (corresponding to classical Inferotemporal)	Prestriate (corresponding to subtotal OA and OB areas in color map by von Bonin and Bailey)		

[†]Refer to Fig. 1.