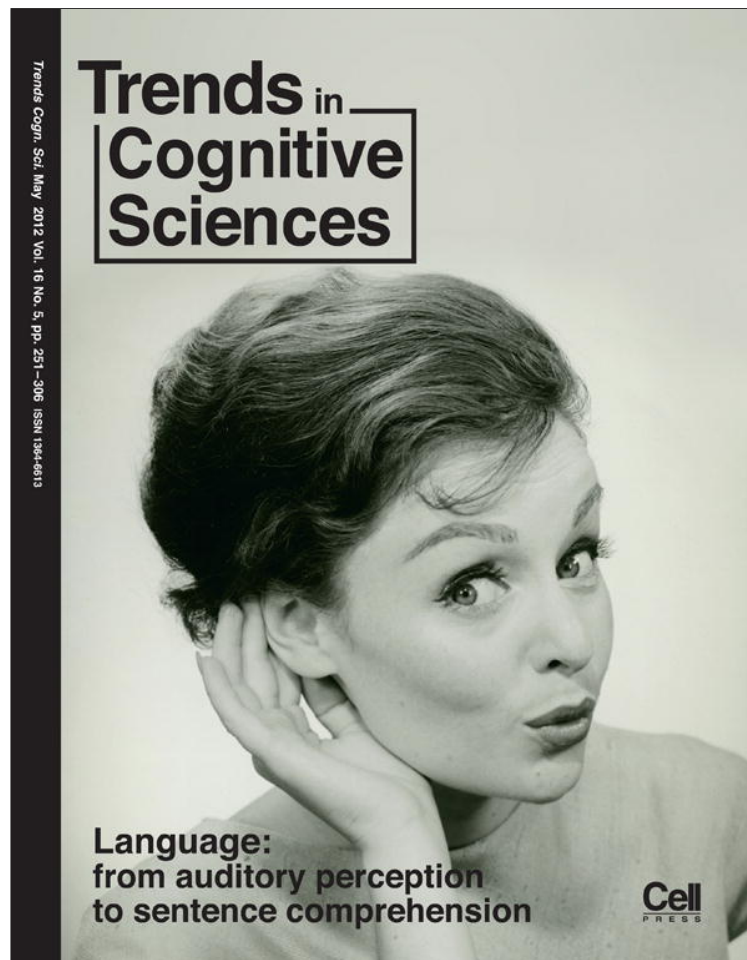


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The improbable simplicity of the fusiform face area

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The fusiform face area (FFA) is described as an easily identifiable module on the fusiform gyrus. However, the organization of face-selective regions in ventral temporal cortex (VTC) is more complex than this prevailing view. We highlight methodological factors contributing to these complexities and the extensive variability in how the FFA is identified. We suggest a series of constraints to aid researchers when defining any functionally specialized region with a pleasing realization: anatomy matters.

Introduction

Nearly a decade ago, Semir Zeki discussed improbable visual areas in the primate brain [1] (see also [2]). In his critique, Zeki questioned the accuracy and theoretical logic of defining extrastriate cortical areas based on partial retinotopic maps as well as the variable parcellation criteria used across research groups. However, his discussion stopped at human V4 and did not extend into VTC where high-level visual representations for faces, body parts, objects, and places are located (Figure 1a). We apply Zeki's concerns of accuracy and parcellation criteria to the FFA and ask: Does the FFA exist in the way it is depicted in journals, textbooks, and everyday media – as a 'blueberry-sized' module on the fusiform gyrus [3]? To address this question, we first discuss various depictions of the FFA and highlight factors contributing to this variability. We then summarize a recent organizational framework developed to reconcile the many faces of the FFA and to accommodate complexities of VTC organization more generally.

Functional localizer approach identifies the FFA but is it time for an update?

The classic work by Kanwisher and colleagues has been highly influential – ushering in nearly 2500 citations in the past 15 years – for introducing the elegant functional localizer method to the field of functional magnetic resonance imaging (fMRI) and for convincingly demonstrating the existence of face-selective regions in the human brain [4]. The localizer approach first identifies a region of interest in individual subjects with one set of data (e.g. comparing fMRI responses to images of faces with those of objects) and then examines its functional properties with independent experiments (e.g. images of faces with eyes removed, face profiles, etc.). Our critique does not question the logic of the methodology or the existence of face-selective regions

but, instead, the resulting localization accuracy. Recent results show that the FFA is one of the least consistently localized functional regions across subjects despite consistencies in macroscopic anatomical landmarks [5]. This inconsistency occurs because the application of the FFA localizer assumes a single face-selective module on the fusiform gyrus. In actuality, the clustering is more complex necessitating a reinterpretation of how face selectivity is organized in visual cortex [6–9].

FFA: multiple and discontinuous, smoothed and simplified, or hindered by artifacts

The complexity begins when experimenters run an FFA localizer only to find approximately eight face-selective clusters across ventral and lateral aspects of the temporal lobe depending on the scanning parameters used [4,6,7,10] (VTC shown in Figure 1b–d). Often, more than one face-selective region is detected on the fusiform gyrus (Figure 1b–d) [4,6–11]. Aligning with the influential theoretical model, researchers commonly combine all fusiform face-selective regions into the FFA (Figure 1b,c). We question this practice for two reasons. First, the fusiform is a large cortical extent. To give the reader a sense of scale, the average length of the fusiform gyrus is 50 mm, which is comparable to the cortical distance between human V1 and V5/MT [12]. Thus, the fusiform gyrus is large enough to contain several visual areas. Second, just because these regions are defined from the same measure of face selectivity does not mean they are neurally homogenous. For example, both V1 and V5/MT respond selectively to moving compared to static stimuli, however, researchers do not combine V1 and V5/MT into a single module for motion processing because they differ from each other structurally and functionally. By contrast, much less is known about the structure and function of VTC. Thus, the question then becomes how to deal with these multiple face-selective regions. It was recently suggested to separate the FFA into distinct components [6] (Figure 1c), but without formal parcellation criteria this division has not been widely adopted.

The complexity continues when the measurement of these regions is either altered by common methodological procedures such as spatial smoothing and group analyses, or hindered by artifacts of fMRI acquisition. Spatial smoothing, for example, can effectively create an FFA by merging anatomically distinct regions (Figures 1d and 2b). Group analyses can further blur the loci of multiple activations into one spatially contiguous region by fitting each brain to common anatomical templates that are typically insensitive to the structural nuances of each brain

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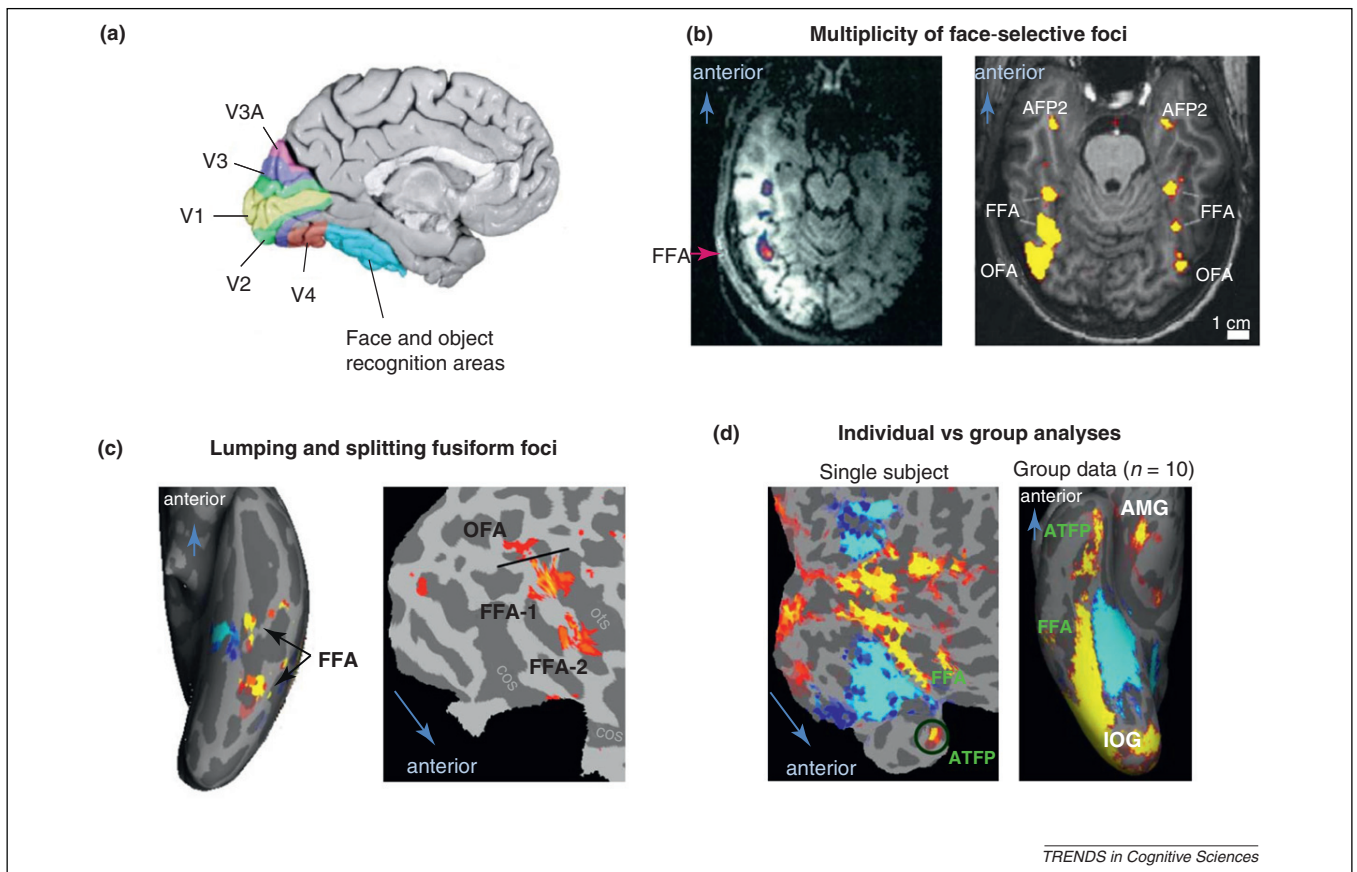


Figure 1. Face selectivity in visual cortex: more complex than simplistic. **(a)** Zeki's original critique stopped at human V4, a functional border to where our discussion begins [1]. **(b–d)** Images from groups examining the clustered organization of face selectivity (warm colors). **(b)** Ventral temporal cortex contains a multitude of face-selective clusters extending from the inferior occipital gyrus to the tip of the temporal lobe [3,7]. **(c)** Researchers commonly face the decision of whether to lump (left [11]; inflated cortical surface) or split (right [6]; flattened cortical surface) face-selective regions on the fusiform. **(d)** Relating face selectivity maps in individual subjects (left [10]) to resulting group maps (right [10]) creates additional complexities in interpreting the functional organization of what is described as an easily identifiable module. Differences in statistical thresholds and spatial smoothing used across groups generate further variability. We use the FFA as an example, but these issues are relevant when examining the clustered organization of any functionally specialized system with fMRI. *Abbreviations:* AFP2: anterior face patch 2; AMG: amygdala; ATFP: anterior temporal face patch; CoS: collateral sulcus; FFA: fusiform face area; IOG: inferior occipital gyrus; OFA: occipital face area; OTS: occipitotemporal sulcus. All images were adapted with permission from authors.

(Figure 1d). In addition, the ear canal and transverse sinus [13] produce fMRI artifacts that decrease the detectability of activations on the fusiform and inferior occipital gyri. The spatial extent of these artifacts and resulting fMRI signal dropouts vary with voxel size (decreases with smaller voxels [8]), slice orientation, and slice placement. Thus, localizing only one face-selective region on the fusiform may be a result of specific analysis methods or poor measurements rather than a feature of brain organization.

Solution: anatomy matters

Improved scanning methods enable consistent localization of several face-selective regions in VTC when considering their spatial organization relative to surrounding regions and neuroanatomical landmarks [8,9] (Figure 2a). Such an approach reveals that face-selective regions are discontinuous and organized within and across subjects as opposed to discontinuous and variable as commonly reported. Specifically, face-selective regions have a periodic nature where each region is approximately 10 mm in diameter and separated by 10–15 mm of cortex. Further, the cortical expanse separating face-selective regions is typically filled with functional regions selective for stimuli other than faces. This alternating and adjacent nature of

VTC organization resembles the alternating and adjacent nature of visual field maps. Thus, similar to the way researchers delineate boundaries between visual field maps, it is possible to parcellate face-selective regions by placing boundaries where there is a change in selectivity [8,9] (e.g. from faces to limbs). Importantly, with every boundary there is a change in anatomical location, indicating a correspondence between gross anatomical landmarks and functional regions.

By implementing these well-known criteria used to parcellate early visual areas [14] – precise anatomical location and preserved spatial relationship among regions – distinct posterior-fusiform (pFus-faces) and mid-fusiform (mFus-faces) face-selective regions are reliably defined. Each region has a distinct set of anatomical and functional boundaries (Figure 2a): mFus-faces overlaps the mid-fusiform sulcus and is anterior and medial to a limb-selective region on the occipitotemporal sulcus (OTS-limbs), whereas pFus-faces overlaps the posterior fusiform gyrus, is posterior and medial to OTS-limbs, and directly lateral to ventral occipital (VO) visual field maps. Such criteria are useful because the spatial relationship between regions will always be preserved due to the coupling between functional regions and gross anatomical landmarks that

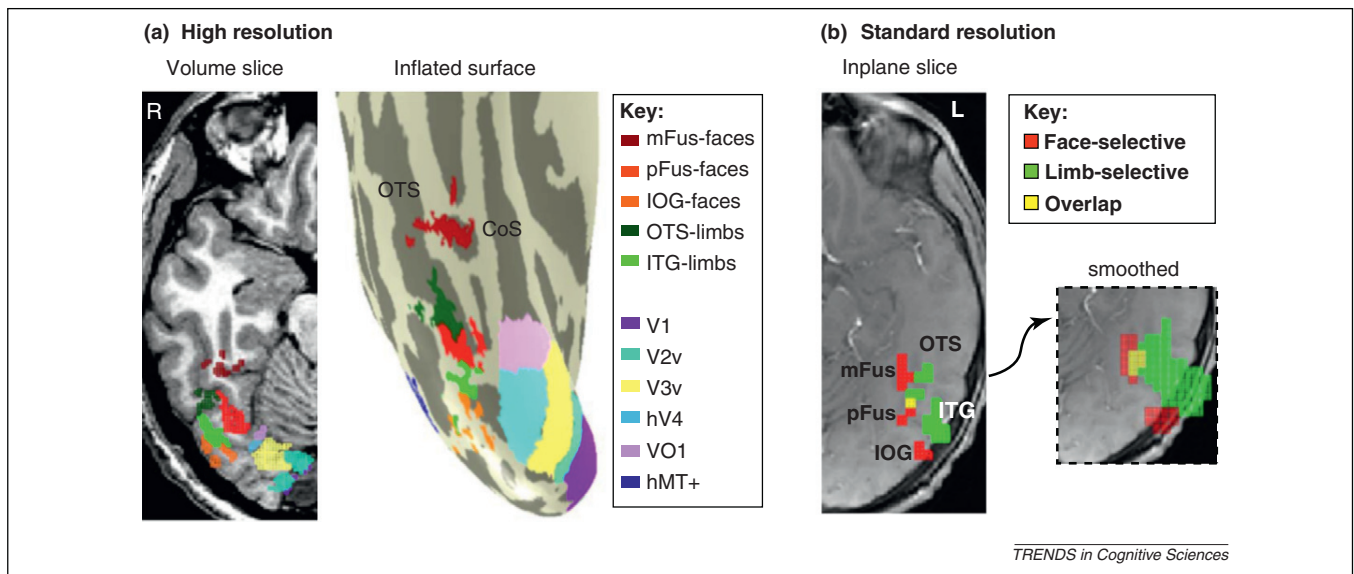


Figure 2. Anatomical and functional boundaries constrain the complexity of functional organization and generalize across methodological choices such as visualization and resolution. (a) High-resolution fMRI (1.5 mm voxels), inflated cortical surfaces, and multiple measurements in individual brains create a clearer visualization of the global structure of visual cortex enabling increased precision in the anatomical and functional boundaries of each region. Face-selective regions on the fusiform (mFus-faces and pFus-faces) are consistently dissociable across subjects, where each region has reliable boundaries relative to macroscopic anatomical landmarks, as well as neighboring functional regions and retinotopic visual areas [8,9]. These organizational features further reflect a topography of face and limb selectivity throughout visual cortex as opposed to isolated modules [8,15]. (b) Left: this framework is generalizable across scanning resolutions and visualizations [8] (inplane view is shown with voxels nearly eight times as large as those in our high-resolution studies). Right: spatial smoothing (8 mm kernel) transforms the data by joining separate face-selective regions (mFus- and pFus-faces; red) and increasing their overlap (yellow) with nearby limb-selective regions (green); for details, see ref [8]. *Abbreviations:* CoS: collateral sulcus; hMT+: human motion-selective complex; IOG: inferior occipital sulcus; ITG: inferior temporal gyrus; mFus: mid-fusiform; pFus: posterior fusiform; OTS: occipitotemporal sulcus; VO: ventral occipital.

has gone unreported until recently [8,9]. For example, anatomically, the occipitotemporal sulcus is always lateral to the fusiform gyrus. Functionally, then, OTS-limbs will always be lateral to mFus- and pFus-faces. Using these criteria, the parcellation of these face-selective regions is reliable across resolutions, varying statistical contrasts, and time (from 6 weeks to 3 years) but obscured by spatial smoothing (Figure 2b) [8]. These findings clarify the methodologically induced variability of the FFA and allow accurate parcellation of multiple face-selective regions within and across subjects, both of which have immediate implications for developmental, clinical, and empirical research.

Because clustering is a commonly implemented organizational strategy of the brain, understanding the intricacies of this organization is crucial for determining the computational and informational transformations across cortical clusters within the visual system. To do so, multiple measurements are needed to contextualize the anatomical and topological placement of a given cluster. For instance, when measuring face selectivity alone, each cluster appears as a discrete module (Figure 1). However, when measuring face and body part selectivity together, it is evident that each cluster is actually a component of a larger topographic map of alternating face and body part selectivity extending from VTC throughout lateral occipitotemporal cortex [8,9,15]. Such regularity in the anatomical and spatial positioning of these clusters across subjects suggests a functional purpose for their co-occurrence. For example, anatomically adjacent regions with differing selectivity may be more functionally similar than cortically separable regions with the same selectivity (e.g. mFus-faces and pFus-faces). Future research examining fine-scale anatomical, functional, and connectivity properties

of high-level visual cortex will further elucidate the organizing features of this cortical expanse and their influence on different aspects of perception and cognition.

Concluding remarks

It is not improbable that neural responses specific to faces cluster in the human brain. However, it is unlikely that face-selective responses cluster in a fashion consistent with the present description of the FFA. Instead, methodological factors such as spatial smoothing and fMRI artifacts contribute to the complexity and changing presence of face-selective responses. Zeki [1] concluded his paper with the notion that traditional and even conservative criteria have considerable merit when defining a visual area. We echo Zeki's stance and particularly stress the importance of neuroanatomical location and preserved spatial relationship for the consistent definition of functional clusters before determining what constitutes a visual area in high-level visual cortex.

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