

REVIEW ARTICLE

Topographic organization of areas V3 and V4 and its relation to supra-areal organization of the primate visual system

M.J. ARCARO^{1,2,*} AND S. KASTNER^{1,2}

¹Princeton Neuroscience Institute, Princeton University, Princeton, New Jersey 08544

²Department of Psychology, Princeton University, Princeton, New Jersey 08544

(RECEIVED January 20, 2015; ACCEPTED April 2, 2015)

Abstract

Areas V3 and V4 are commonly thought of as individual entities in the primate visual system, based on definition criteria such as their representation of visual space, connectivity, functional response properties, and relative anatomical location in cortex. Yet, large-scale functional and anatomical organization patterns not only emphasize distinctions within each area, but also links across visual cortex. Specifically, the visuotopic organization of V3 and V4 appears to be part of a larger, supra-areal organization, clustering these areas with early visual areas V1 and V2. In addition, connectivity patterns across visual cortex appear to vary within these areas as a function of their supra-areal eccentricity organization. This complicates the traditional view of these regions as individual functional “areas.” Here, we will review the criteria for defining areas V3 and V4 and will discuss functional and anatomical studies in humans and monkeys that emphasize the integration of individual visual areas into broad, supra-areal clusters that work in concert for a common computational goal. Specifically, we propose that the visuotopic organization of V3 and V4, which provides the criteria for differentiating these areas, also unifies these areas into the supra-areal organization of early visual cortex. We propose that V3 and V4 play a critical role in this supra-areal organization by filtering information about the visual environment along parallel pathways across higher-order cortex.

Keywords: Visual cortex, Topography, Eccentricity, Supra-areal, Primate

Introduction

A large portion of cortex, including auditory, motor, somatosensory, and visual cortex, consists of orderly representations of our environment along sensory surfaces. These topographic representations are commonly thought of as fundamental organizational principles for the processing of sensory information (Mountcastle, 1957; Kaas, 1997). Within the visual system, a prominent topographic representation is the visual field map, in which the receptive fields (RFs) of adjacent neurons along the cortical surface typically receive input from adjacent points on the surface of the retina. Individual visual field maps have been traditionally identified by cytoarchitecture, labeling anatomical connections with an area whose visual map is already known, and mapping the boundaries between areas and characterizing the response properties with electrophysiology. These invasive methods typically limit their applications to nonhumans. In the past two decades, functional neuroimaging methods have enabled the simultaneous exploration of visual field maps across visual cortex in humans noninvasively. Over two-dozen visual field maps have

been identified across primate visual cortex (Van Essen, 2004; Gattass et al., 2005; Wandell & Winawer, 2011; Wang et al., 2014).

Visual maps are thought of as functional units that exhibit some degree of specialization. Neurons within a map often share similar response selectivities (Zeki, 1993). For example, neurons in a retinotopic region of the middle temporal cortex (area MT) are tuned to speed and direction of visual motion (Maunsell & Van Essen, 1983b), and damage to this region impairs motion perception, but not contrast detection thresholds (Newsome & Pare, 1988). As such, the visual field map provides important information about the location of a particular perceptual process within the brain. Identifying individual areas and characterizing their functions have been a major focus of investigation in understanding the visual system. While there is a general consensus on the identification and organization of some areas such as primary and secondary visual areas, V1 and V2, and motion-sensitive middle temporal area, MT, there is still much debate over the organization and function of extrastriate areas such as V3 and V4. Key criteria for differentiating V3 and V4 from each other as well as from neighboring areas have been their visuotopic organization and relative anatomical location, though these areas have also been differentiated based on myeloarchitecture and anatomical projections (Van Essen et al., 1986; Gattass et al., 1988; Felleman et al., 1997; Pinon et al., 1998;

*Address correspondence to: Michael Arcaro, Princeton Neuroscience Institute, Princeton University, Princeton NJ 08544. E-mail: marcara@princeton.edu

Lyon and Kaas, 2002b; Rosa et al., 2005; Ungerleider et al., 2008; Jeffs et al., 2013). Across both V3 and V4, the response properties of neurons are heterogeneous, though functionally homogenous subdivisions for color (Conway & Tsao, 2009), orientation (Ghose & Ts'o, 1997), and shape contours (Tanigawa et al., 2010) have been found in V4. The functional response properties of these neurons and their anatomical connectivity suggest that V3 and V4 play a critical role in transmitting information from primary visual cortex to higher order areas in temporal and parietal cortices for further stages in visual processing.

At a broader scale, the topography of visual cortex and its anatomical connections not only emphasize distinctions within each area, but importantly also provide links across these areas as being part of structures that are defined by larger organization principles. Specifically, the eccentricity organization of V3 and V4 reveals a larger, supra-areal organization linking these areas with visual areas V1 and V2 (Rosa, 2002; Wandell et al., 2005; Buckner & Yeo 2014). Further, the functional organization and anatomical connectivity patterns appear to vary within these areas (Van Essen et al., 1986; Gattass et al., 2005; Rosa & Tweeddale, 2005; Ungerleider et al., 2008). This complicates the traditional view of these visual field maps as individual functional "areas."

Here, we review the functional and anatomical evidence for supra-areal organization across V3 and V4 in primates and discuss what such organization can inform us about the functional role of these areas in the visual system as well as how the visual system may utilize such large-scale organization to integrate information across areas. We will discuss recent functional imaging studies highlighting this organization in humans and present new data that extend prior concepts of supra-areal organization. We will discuss the computational benefits of such supra-areal organization, particularly, for intermediate areas such as V3 and V4 that bridge early visual cortex with temporal and parietal cortices, but also will discuss potential complications with such organization.

Identification of individual areas

Cortical areas are typically defined based on one or more criteria including visuotopic organization, chemoarchitecture, anatomical connectivity, and functional response properties (Van Essen, 1985). Since cortico-cortical connections link neural populations that represent the same region of visual space, the visuotopic organization of one area can be inferred by tracing connections to and from another area, whose visual field map is known. Cortico-cortical connections may also link partially matching representations of the visual field, which limits the precision of this method. Electrophysiological recordings in monkeys enable a systematic, precise mapping of the visuotopic organization of an area. However, detailed mapping often requires focusing on an individual area, limiting the extent of what can be mapped at one time in an individual. Further, areas with high cortical folding provide a challenge for accurate reconstruction of recording sites. Optical imaging in monkeys enables the mapping of an extended region at a high spatial resolution, but is limited to surface structures. Due to the invasive nature of these techniques, their application has been limited to nonhuman primates. Functional neuroimaging has proven useful for noninvasively probing the visuotopic organization of multiple areas that are distributed across the brain in both humans and monkeys. However, the spatial resolution of functional magnetic resonance imaging (fMRI) is much coarser than what can be revealed with invasive techniques such as single unit recordings or optical

imaging. Though any individual methodology is capable at revealing visuotopic organization, converging evidence across methodologies provides the strongest support for an area's organization. Despite decades of investigation, the organization of extrastriate cortex is still heavily debated. Here, we review the organization and function of two extrastriate areas V3 and V4.

Organization of area V3

In primates, occipital cortex, anterior and adjacent to visual area V2, contains representations of the contralateral visual field. The exact definition of this area in nonhuman primates is still under debate. There are two general models of the topographic organization anterior to V2 in nonhuman primates: the V3 model and the DM model (Fig. 1A and 1B). In the V3 model, cortex anterior and adjacent to ventral and dorsal V2 contains representations of the upper and lower contralateral visual fields, respectively (Fig. 1A, left). This model is based on electrophysiological recordings and anatomical studies in Old World monkeys (Zeki, 1978; Gattass et al., 1988; Kaas & Lyon, 2001; Lyon & Kaas, 2001), but also has been reported in New World monkeys (Lyon et al., 2002) and prosimians (Fan et al., 2012) using optical imaging. Similar to area V2, area V3 is proposed to form a "second-order" representation of visual space with a discontinuity in the representation of the horizontal meridian that anatomically separates upper and lower visual field representations in ventral and dorsal occipital cortex, respectively. Unlike V2, single unit studies in macaques suggest that the anterior border of dorsal V3 contains a second visual field discontinuity at the lower vertical meridian representation, which varies across individuals (Gattass et al., 1988; also see Fig. 2A, asterisks). Some mapping studies report that dorsal and ventral halves are anatomically separate (Gattass et al., 1988), while others suggest that they are continuous through the fovea (Pinon et al., 1998). Cortex medial and anterior to dorsal V3 contains representations of both upper and lower visual space and has been referred to as V3A in macaques (Van Essen & Zeki, 1978; Zeki, 1978) as well as DM in New World monkeys (Lyon & Kaas, 2002a). Several imaging studies in macaques have reported visuotopic organization comparable with the V3 model (Fig. 1B; Brewer et al., 2002; Fize et al., 2003; Kolster et al., 2009; Arcaro et al., 2011; Janssens et al., 2014; though see Rosa & Tweeddale, 2005 for alternative interpretation). Based on asymmetries in motion direction and color selectivity (Burkhalter & Van Essen, 1986; Felleman & Van Essen, 1987) as well as V1 connections (Burkhalter et al., 1986; Felleman et al., 1997), dorsal and ventral V3 (referred to as VP) have been proposed to be distinct areas instead of counterparts. Some degree of these asymmetries could be attributed to variance in recording location and sample size (Lyon & Kaas, 2002b). Subsequent anatomical studies have found connections between V1 and both dorsal and ventral halves of V3 (Lyon & Kaas, 2001; Lyon & Kaas, 2002a), which support, though do not prove, that dorsal and ventral halves are part of the same functional region. However, these anatomical data have been reinterpreted to be consistent with other models (see Rosa et al., 2013), and subsequent anatomical mapping that sampled dorsal cortex at a higher spatial resolution in New World monkeys supports the DM model (Jeffs et al., 2013). The DM model proposes that cortex anterior to dorsal V2 includes both upper and lower visual field representations of contralateral visual space (Fig. 1A, right). This cortical region has been referred to as DM as well as V6. The DM model is based on anatomical work and physiological recordings in New World monkeys (Allman &

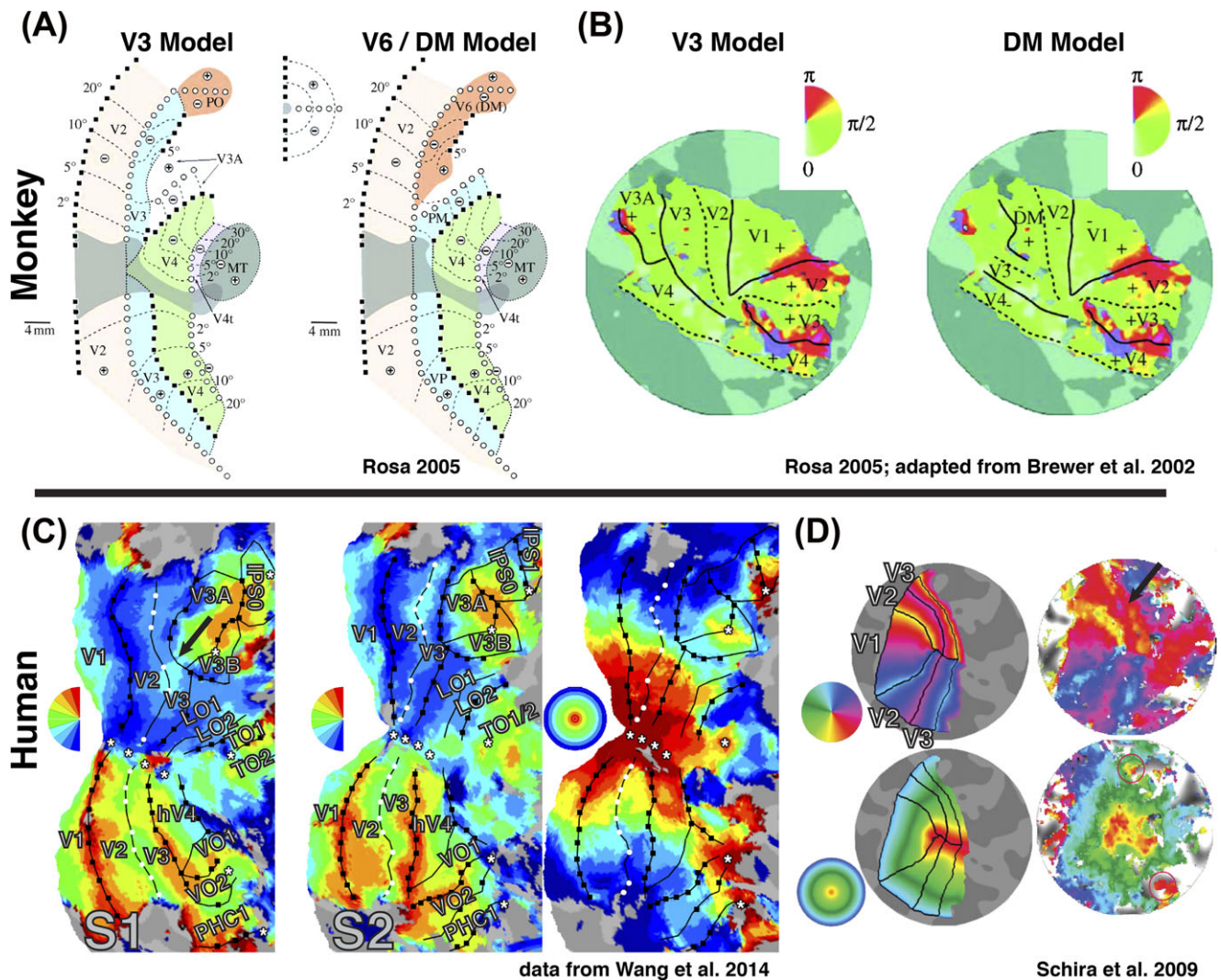


Fig. 1. Visuotopic organization of primate V3. (Top) V3 and DM visual field models applied to (A) physiology data and (B) fMRI data in nonhuman primates. (A & B, left side) In the V3 model, cortex anterior and adjacent to ventral and dorsal V2 contains representations of the upper (+) and lower (−) contralateral visual fields, respectively. An area medial and anterior to V3 (V3A) contains a complete representation of the contralateral hemifield. (A & B, right side) In the DM model, cortex anterior and adjacent to dorsal V2 contains a complete representation of the contralateral visual field (DM/V6). A lower visual field representation (PM/V3) is located anterior and laterally to DM/V6, and the upper visual field counterpart is located anterior and adjacent to ventral V2. This lower visual field representation only borders the foveal most region of dorsal V2. Even based on the same data, there is no consensus in interpreting the visuotopic organization of the “third tier” area in monkeys. (Bottom) The visuotopic organization of V3 as defined by fMRI in humans. (c) Polar angle and eccentricity mapping data for two subjects from our lab (see Wang et al., 2014 for details on mapping stimulus and analysis). Both subjects show a lower visual field representation anterior to dorsal V2 consistent with the V3 model. In subject S1, but not S2, there is a discontinuity in the anterior border of V3d (black arrow). This variability across individuals is similar to prior reports in the macaques (Gattass et al., 1988). (C) Black and white dots correspond to areal boundaries defined at vertical and horizontal meridian representations, respectively. Asterisks denote foveal regions. (D) Mapping data from a high spatial resolution fMRI study targeting occipital cortex (Schira et al., 2009). These data fit a retinotopic atlas that included the V3 model. A discontinuity in the lower vertical meridian of V3d is also apparent in the raw data (black arrow). (Fig. 1A and 1B are from Brain Maps, great and small: lessons from comparative studies of primitive visual cortical organization by Marcello G.P. Rosa and Rowan Tweeddale in Philosophical Transactions B Copyright © 2015, The Royal Society. Fig. 1B is modified from Fig. 8a from Visual Areas in Macaque Cortex Measured Using Functional Magnetic Resonance Imaging by A.A. Brewer, W.A. Press, N.K. Logothetis, and B.A. Wandell used with permission of the Journal of Neuroscience, December 1, 2002, 22(23):10,416–10,426. Fig. 1D is used with permission of The Journal of Neuroscience, 15 July 2009, 29(28):9050–9058 from Fig. 8 in The Foveal Confluence in Human Visual Cortex by Mark M. Schira, Christopher W. Tyler, Michael Breakspear, and Branka Spehar.).

Kaas, 1975; Krubitzer & Kaas, 1993; Rosa & Manger, 2005; Rosa et al., 2005; Jeffs et al., 2013). In this model, V3d is not located in-between V2d and DM. Instead, a lower visual field representation, which has been referred to as VLP, PM, and DLc, is located anterior and laterally to DM/V6, and the upper visual field counterpart is located anterior and adjacent to ventral V2. This lower

visual field representation only borders the foveal-most region of dorsal V2. Even though area DM in New World Monkeys shares some similarities to area V3A in the Old World monkeys (Krubitzer & Kaas, 1993), this region may better correspond to area V6 based on anatomical connectivity data with area DA in New World monkeys corresponding to area V3A in Old World monkeys (Rosa et al., 2013;

Solomon & Rosa, 2014). Differences between New and Old World monkeys could have influenced the initial identification of V3d and DM, respectively. However, both models have been argued for in both primate groups (Rosa & Tweedale, 2005; Lyon & Connolly, 2012). Differences across studies could be attributable to the noted variability in the visuotopic organization of cortex anterior to V2d across individuals (Gattass et al., 1988). However, both models have been argued for from the same data (e.g., Fig. 1A and 1B). Variance in anatomical localization, sparse sampling of tracers, and potential inaccuracies in electrode track reconstructions leave ambiguities in prior results that allow for differing interpretations (Lyon, 2013; Rosa et al., 2013). Future studies obtained with higher-resolution electrophysiology and anatomical mappings in New and Old World monkeys may help clarify these issues (e.g., Jeffs et al., 2013).

In contrast to the physiology and anatomical data in monkeys, there is a general consensus on the visuotopic organization of human V3 from functional imaging studies in support of the V3 model. Functional imaging studies demonstrate the existence of lower and upper visual fields within cortex adjacent to dorsal and ventral halves of area V2, respectively (Fig. 1C and 1D; Sereno et al., 1995; Deyoe et al., 1996; Press et al., 2001). A high-resolution fMRI study targeting the foveal representation of occipital cortex found that dorsal and ventral halves of V3 were continuous (Fig. 1D; Schira et al., 2009), consistent with some accounts in the monkey as discussed above. Though the second discontinuity in the lower visual field representation of dorsal V3 reported in macaque physiology studies (Fig. 2A, asterisks; Gattass et al., 1988) has not been documented in human imaging studies, such discontinuous representations of the anterior border are apparent in several of our data and in published maps from several different labs (Fig. 1C and 1D, black arrow). Despite this variability in the anterior border, the visuotopic organization of cortex anterior to V2 contains a representation of the lower visual field that is consistent with a V3d model across a large population of subjects ($N = 53$; Wang et al., 2014). In further support of the V3 model of organization in humans, imaging and electrophysiology studies have found comparable RF sizes (Smith et al., 2001), selectivity to second-order motion (Smith et al., 1998), and response latencies between dorsal and ventral portions (Hagler, 2014).

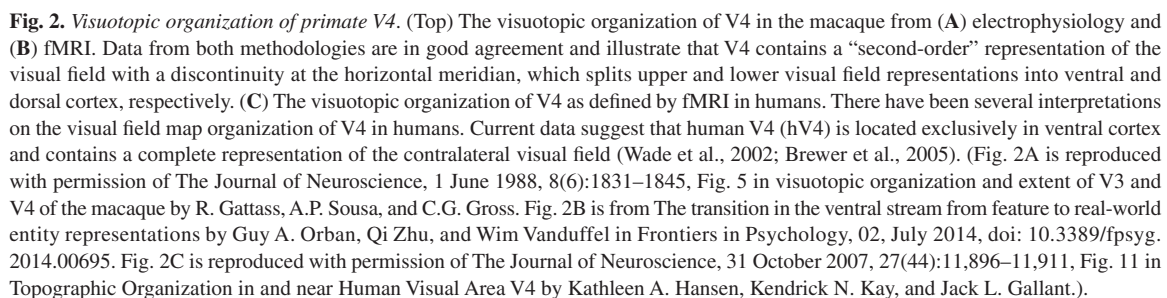
Traditionally, V3 has been associated with motion processing, though its anatomical connections and the functional response properties of neurons are heterogeneous. Anatomical studies in macaques have shown that V3 receives input from layer 4B in V1, which also projects to motion sensitive area MT (Felleman et al., 1997), and has direct projections to MT (Ungerleider & Desimone, 1986). A di-synaptic relay from the superior colliculus selectively targets areas V3 and MT (Lyon et al., 2010). V3 also projects to dorsal extrastriate and posterior parietal areas DM/V3A, DP, VIP, LIPv, as well as inferotemporal areas V4, VTF, and VOT (Felleman et al., 1997). Neurons in monkey V3 respond selectively to various aspects of stimulus motion such as direction, speed, as well as to plaid patterns (Felleman & Van Essen, 1987; Gegenfurtner et al., 1997; Adams & Zeki, 2001), but also to orientation, color, and binocular disparity (Felleman & Van Essen, 1987). Further, subpopulations of cells responsive to color and to motion overlap in macaques V3 (Gegenfurtner et al., 1997), and there is some evidence for a band-like modular organization (Lyon & Kaas, 2001). Thus, functional and anatomical studies in nonhuman primates suggest that area V3 not only plays an important role in the visual processing of motion, but also is involved in other aspects of visual processing, and could play a role in linking higher-level parietal and temporal processing streams.

Organization of area V4

In primates, area V4 is located anterior and adjacent to V3 (Fig. 2). In monkeys, V4 also forms a second-order representation of visual space that is split into dorsal and ventral halves. The exact boundaries of V4's map have undergone several revisions as subdivisions are broken off into separate, adjacent areas (Zeki, 1969a; Van Essen & Zeki, 1978; Maguire & Baizer, 1984). Consistent across all V4 models in monkeys, cortex anterior to dorsal and ventral portions of V3 contains representations of the lower and upper visual field, respectively (Fig. 2A and 2B). Similar to V2 and V3, V4 forms a "second-order" representation with a discontinuity near the horizontal meridian, though data from one electrophysiology mapping study suggest that the discontinuity is shifted within the lower visual field representation (Fig. 2A, bottom; Gattass et al., 1988). In some models of V4, the anterior border is adjacent to area MT or to an intermediate area referred to as V4t. Electrophysiological recording studies have found a separate representation of the visual field anterior to V4, leading to the proposal of an additional area adjacent to V4, referred to as V4A as well as D_{Lr} (Zeki, 1969a; Pigarev et al., 2002; Stepniewska et al., 2005). Recent imaging studies in macaques also support the existence of additional visual field maps anterior and adjacent to V4 (Fig. 2B; Janssens et al., 2014; Kolster et al., 2014).

The topographic organization of V4 appears to differ between humans and monkeys. An initial fMRI mapping study in humans reported an upper visual field representation adjacent to ventral V3 (Sereno et al., 1995), similar to monkey V4v, though no dorsal counterpart was identified. Another study reported a dorsal region of V4, though the visuotopic organization varied across individuals and differed from monkeys (Tootell & Hadjikhani, 2001). Subsequent fMRI mapping studies have proposed several different segmentations of V4 (Fig. 2C). Contrary to the monkey model, several groups identified a complete representation of the contralateral visual field anterior to ventral V3 with no counterpart in dorsal cortex (Wade et al., 2002; Brewer et al., 2005). This human first-order visual field map was labeled hV4 to indicate the species-specific difference in organization. Some imaging studies have reported an underrepresentation in the visual field of hV4 near the lower vertical meridian (Hansen et al., 2007; Arcaro et al., 2009). This underrepresentation, in combination with a representation of the lower visual field anterior to dorsal V3, was taken as evidence that human V4 is split into dorsal and ventral portions that contain a discontinuity within the lower visual field, not at the horizontal meridian (Hansen et al., 2007). These data are consistent with a macaque model of V4's topography where the discontinuity between dorsal and ventral components lies within the lower visual field representation (Fig. 2A, bottom; Gattass et al., 1988). However, the lack of a robust lower visual field representation in hV4 may be due to an imaging artifact from local vasculature (Winawer et al., 2010), and the lower visual field representation anterior to dorsal V3 has been attributed to another visual field map, LO1, that contains a complete representation of the contralateral hemifield (Larsson & Heeger, 2006). Despite the difference in topographic organization between species, several functional commonalities have been established between V4 in macaques and hV4 in humans such as color selectivity, modulation during directed attention, and shape selectivity (see Orban et al., 2004; Roe et al., 2012 for detailed review). The differences in organization and relative location of the V4 map across species may reflect developmental pressures particular to each species (Rosa, 2002).

Similar to area V3, V4's functional selectivity and anatomical connectivity are heterogeneous. Given its extensive connectivity with



The functional and anatomical organizations of areas V3 and V4 are complex. Visuotopic mapping provides important criteria for the segmentation of cortex into individual functional areas. However, despite decades of investigation, there is still much disagreement on the areal boundaries. Further, the profile of functional response properties of neurons within these two areas is diverse, complicating the interpretation of these areas as functional units. Below, we discuss the supra-areal organization of visual cortex that emphasizes common functional roles across areas and provides a complementary framework to probe visual function of areas V3 and V4.

Supra-areal organization

The organization of the visual system emphasizes a principle of functional continuity; similar functions are typically located in close spatial proximity. An advantage to such an organization is that the wiring length between interconnected neurons is minimized (Young, 1992; Kaas, 1997). For complex systems, such as cortex, the requirement that all neighboring points in a high-dimensional space map to neighboring parts of cortex cannot be achieved. Instead, an optimal solution requires minimizing connection distances across all dimensions while allowing for disruptions along any one dimension (Durbin & Mitchison, 1990). For example, the pin-wheel organization of orientation and ocular dominance columns within V1 is an optimal arrangement to maximize local continuity

(Durbin & Mitchison, 1990; Chklovskii, 2000). Visual field maps satisfy local continuity within an area and facilitate local processing. The principle of local continuity is not confined to cortex as several visual field maps have been identified in the primate thalamus (Kaas et al., 1972; Bender, 1981) with adjacent cortical visual areas projecting to neighboring parts of the thalamus (Dick et al., 1991; Shipp, 2003).

The visuotopic organization across cortex also illustrates a large-scale coherence that emphasizes local continuity across individual visual field maps (Fig. 3). This supra-areal organization was first noted based on electrophysiological mapping studies across occipital cortical areas V1–V4 as well as for the region surrounding MT in monkeys (Rosa, 2002). RF position typically does not

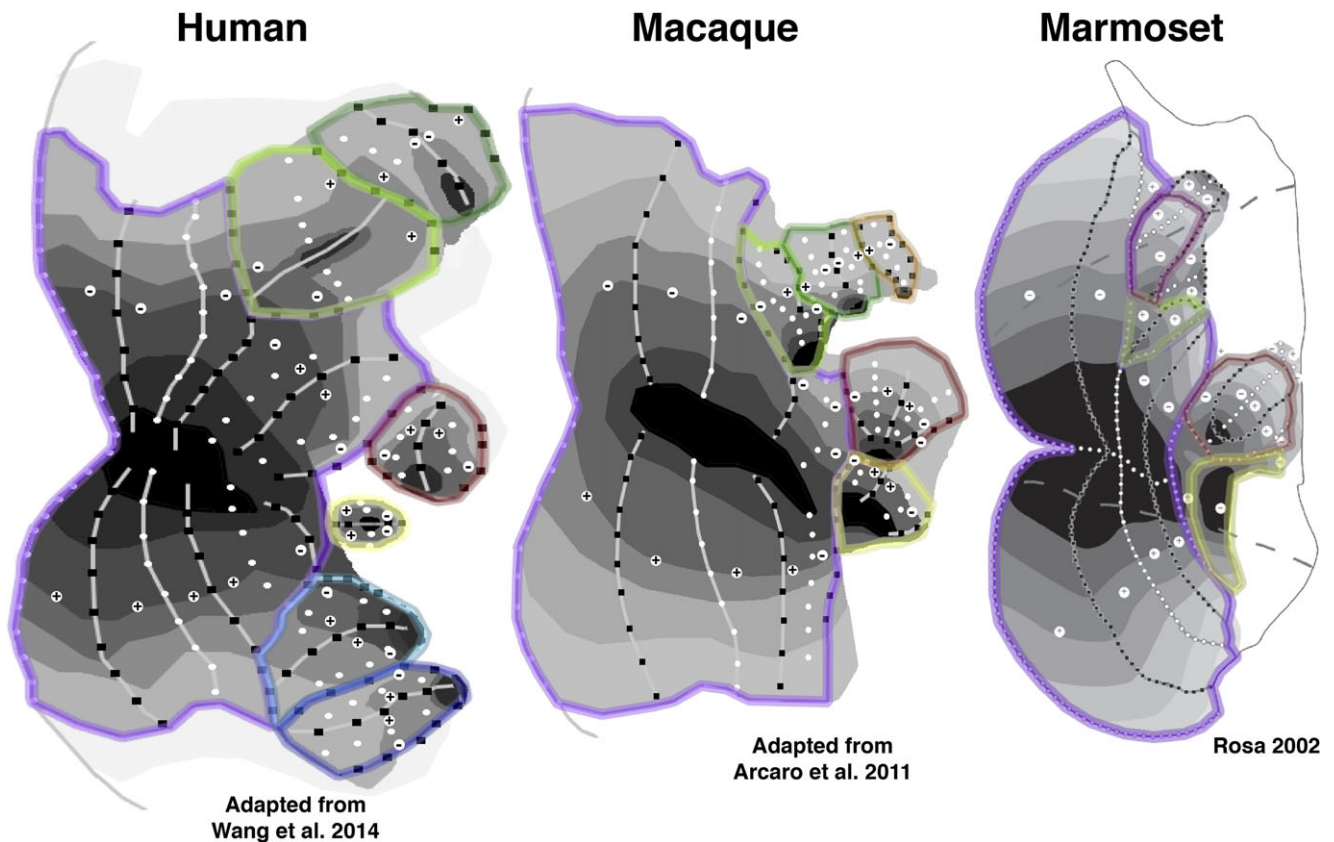


Fig. 3. Supra-areal organization of primate visual cortex. Illustration of the supra-areal organization of visual cortex in three primate species: humans (left), macaques (middle), and marmosets (right). Human and macaque illustrations were adapted from previously published data from our lab (Arcaro et al. 2011; Wang et al. 2014) as well as from other labs (Kolster et al., 2009; Kolster et al., 2010; Wandell & Winawer, 2011; Janssens et al., 2014; Kolster et al., 2014). The marmoset illustration is a reproduction from Rosa (2002). Surfaces are presented in flattened views, where a cut has been made within the calcarine sulcus (left side) in each species, artificially separating upper and lower visual field representations of V1 anatomically into dorsal and ventral halves. Across all species, eccentricity is a prominent component of the supra-areal organization. Several areas converge around a distinct foveal representation (black). Increasingly peripheral representations encircle foveal representations from parafoveal (dark gray bands) to far periphery (light gray bands) space, and span across areal borders. The extents of eccentricity maps that encircle distinct foveal representations are color-coded based on proposed homologues between species. For example, the occipital eccentricity map that contains areas V1–V4 in all primate species is outlined in purple. In some cases, such as VO (light blue) and PHC (dark blue) in human ventral temporal cortex, no clear correspondence has been established in other primate species. The supra-areal organization of cortex likely extends beyond the boundaries in this illustration as additional visual field maps and distinct foveal representations have been reported in regions of temporal, parietal, and frontal cortex. Future mapping studies targeting these regions may resolve the relation of these additional maps to the supra-areal organization of cortex. Future studies also may resolve discrepancies between prior reports on the organization of some clusters, e.g., the human MT cluster (Amano et al. 2009; Kolster et al. 2010), and on their relation to surrounding topographic areas. Black squares and white circles denote vertical and horizontal meridian representations, respectively. Upper (+) and lower (–) visual field representations are illustrated. (Rightmost image used with permission of M.G.P. Rosa, Visual maps in the adult primate cerebral cortex: some implications for brain development and evolution, Brazilian Journal of Medical and Biological Research, vol. 35, no. 12, December 2002.)

change suddenly at the boundary between areas. Instead, polar angle representations progress toward a vertical meridian representation at the border, then gradually revert in such a way that adjacent maps are mirror-symmetrical. By construction, eccentricity representations are aligned across areas. Foveal representations (Fig. 3, black) of V1–V4 are contiguous with each other, forming an elongated strip that does not respect areal boundaries. Encircling this inter-areal foveal representation, increasingly peripheral representations of the visual field form continuous bands (Fig. 3, increasingly lighter grayscale bands) that span across areal boundaries. Several eccentricity maps, each spanning multiple visual field representations, have been identified across primate visual cortex (Fig. 3, colored outlines). For occipital cortex in both humans and monkeys (Fig. 3, purple outline), an eccentricity map encompasses V1 as well as dorsal and ventral portions of V2, V3, and V4. A separate eccentricity map (Fig. 3, brown outline) encompasses middle temporal areas MT (TO1 in humans), MST (TO2 in humans), and FST. Additional eccentricity maps have been identified in parietal and temporal cortices in both humans and monkeys. Through this organization, local continuity is also preserved between areas.

Clusters

This supra-areal organization binds groups of visual field maps into clusters (Wandell et al., 2005). Approximately seven visual field map clusters have been proposed across occipital, temporal, and parietal cortices in both humans and macaques (Fig. 4; Wandell et al., 2007; Wandell & Winawer, 2011; Orban et al., 2014). Though the number of visual field maps varies across clusters, the organization of each cluster and the visual field maps contained within are consistent across individuals. For example, the occipital cluster encompasses the occipital pole (Fig. 3, purple outline) and contains visual field maps V1, V2, V3, and V4 (Fig. 4, purple outline). The organization of several clusters, such as the occipital cluster, is similar across species (Fig. 4, color-matched outlines). Neuroimaging studies suggest that the occipital cluster has expanded in humans to include two additional areas, LO1 and LO2, located adjacent and anterior to dorsal V3 (Fig. 4; Wandell et al., 2007). It is noteworthy that these regions are in the relative topographic location of dorsal V4 in the macaque (Fig. 4), suggesting that the organization of individual visual field maps may vary across species even when the large-scale cluster organization is preserved. Additional clusters likely exist as several visual field maps have been identified that have yet to be attributed to a cluster (Fig. 4, empty circles). Further, the organization of many visual field maps is still debated, and future studies could affect the proposed organization for several of these clusters. It is likely that any visual field map will be attributable to some cluster eventually.

Clusters typically border each other and can be differentiated based on the organization of the visual field. In some cases, clusters are differentiated based on reversals in the eccentricity organization at locally, peripheral-most representations. For example, the occipital and VO (Fig. 4, light blue outline) clusters contain distinct foveal representations in humans, and border each other at peripheral-most representations of hV4 and VO1 (Brewer et al., 2005; Arcaro et al., 2009). As such, hV4 and VO1 are attributed to different clusters even though they are anatomically adjacent and preserve local continuity. In other cases, clusters are differentiated based on discontinuities in visual field representations. For example, the fovea shared by V3A and area DP (Fig. 4, light green) borders mid-eccentricity representations of area V3 and peripheral representations of area V4 in the macaque. A similar discontinuity is apparent in dorsal extrastriate cortex of the marmoset.

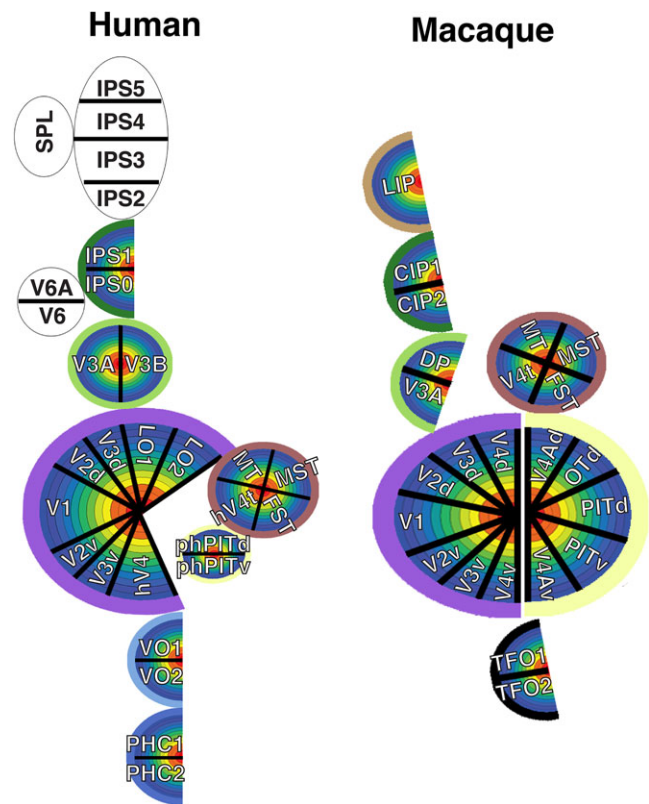


Fig. 4. Visual field map clusters in primates. Schematics of currently proposed visual field map clusters and their general location relative to one another for (left) human (adapted from Wandell et al., 2007) and (right) macaque cortex. Cluster data were assembled from mapping studies across several different labs (Amano et al., 2009; Arcaro et al., 2009; Kolster et al., 2009; Kolster et al., 2010; Arcaro et al., 2011; Wandell & Winawer, 2011; Janssens et al., 2014; Kolster et al., 2014; Orban et al., 2014; Wang et al., 2014). By default, clusters are illustrated as ovals and outlined in accordance with Fig. 3. Each oval contains an illustration of eccentricity coverage. For several clusters, studies have consistently reported that the coverage of visual field maps does not span a full 360° around the fovea. For example, the occipital cluster (purple outline) in humans expands from V1 dorsally to LO2 and ventrally to hV4, though LO2 and hV4 do not border each other. In these cases, the relative portion of the cluster oval between nonbordering maps is excluded. Several other clusters such as VO (light blue outline) and PHC (dark blue outline) in humans appear to be comprised of two visual field maps that are consistently lateralized with respect to the fovea (represented as a half circle) and are illustrated as half ovals. The topographic organization, if any, on the other side of these foveal representations has yet to be resolved. Additional visual field maps eventually may be identified within each of these clusters. In macaques, the occipital and occipital-temporal (yellow outline) clusters border each other, but have been differentiated based on separate foveal representations. Additional visual field maps such as V6/V6A and IPS2–5 have been reported, though their relation to visual clusters has yet to be established (illustrated as unfilled circles). The topographic organization of many regions, such as V3A/B in humans (Abdollahi et al., 2014), is still debated. The TFO cluster (black outline, also see Fig. 2B) in macaques may correspond to the VO or PHC (dark blue outline) clusters in the humans. As such, these cluster schematics may change as future studies resolve discrepancies between mapping studies.

As such, the visuotopic organization of individual areas appears directly related to the supra-areal organization of clusters across cortex.

At an even broader scale, the location of clusters relative to each other is consistent across individuals, suggesting multiple scales to the supra-areal organization of visual cortex. For example,

the V3A/B cluster (V3A/DP in macaques) is always anchored dorsally to the occipital cluster at the anterior border of dorsal V3, and the VO cluster is always anchored ventrally to the occipital cluster at the peripheral-most representation of hV4 across individuals (Fig. 4). The PHC cluster is always anchored anterior and medially to the VO cluster, and by extension of VO's relation to hV4, is also anchored to hV4 and the occipital cluster. The consistent spatial relationship between individual clusters may reflect a principle of optimal cortical organization whereby distances between functionally similar clusters are minimized (Aflalo & Graziano, 2011). As such clusters that are anchored together may reflect separate functional processing streams (Ungerleider & Mishkin, 1982; Cavina-Pratesi et al., 2010). This broad organization across cortex appears to be tied to the topography of individual visual field maps. Likewise, the organization of individual visual field maps may reflect constraints from this broad cluster topography. Thus, we propose that the organization of visual cortex reflects the optimization of functional continuity at multiple spatial scales. Below, we discuss potential developmental constraints and functional implications of the supra-areal organization across visual cortex.

Potential developmental constraints

The supra-areal organization of visual cortex may reflect key anchors that constrain the topographic organization of individual areas early in development (Rosa, 2002). Visual field map clusters may form from a single area that seeds the organization of adjacent maps. The most direct support for such a role comes from studies on the development of areas in the occipital and middle temporal clusters, which are anchored to the development of V1 and MT, respectively (Conde et al., 1996; Rosa & Tweeddale, 2005). V1 and MT both receive retinal projections *via* the thalamus and develop earlier than extrastriate areas that lack retinal projections (Bourne & Rosa, 2006; Warner et al., 2012). During early development, molecular distribution from V1 to subsequent visual maps could be guided by a foveal-peripheral gradient, though the constraints on establishing meridian boundaries are still unclear (Rosa, 2002). Consistent with this hypothesis, areas V2, V3, V4, and inferior temporal cortex in marmosets appear to develop in sequence (Bourne & Rosa, 2006). As such, the organization of V3 and V4 appears to be intrinsically tied to the development and organization of V1's visual field maps. These developmental constraints may manifest visual field map clusters that possess radiations of similarly responding columns spanning areal boundaries (Buckner & Yeo 2014). The development of clusters that lack retinal projections likely results from the seeding of visual field maps within the occipital or MT clusters, which could explain the consistency in the location of clusters relative to each other across individuals and similarities across species. For example, the development of the VO cluster could be dependent on the development and organization of the adjacent hV4 visual field map. Though this remains to be explicitly tested, the consistent relationship between particular clusters suggests that their development is inter-related.

Supra-areal functional specialization

The supra-areal organization of visual cortex may also reflect regional functional specializations. It has been proposed that maps within a cluster share resources such as circuitry that serve similar computational goals (Kaas & Catania, 2002; Wandell et al., 2005). As such, signals within clusters should be more thoroughly integrated than signals communicated between clusters and possibly

exhibit common functional response properties. Individual areas within a cluster may still serve specific functions, but these functions would presumably contribute toward the broader, common computational goal of a cluster. Given the commonalities in cluster organization across species, it might be expected that homologous clusters perform similar computations, though this need not be the case just as homologous individual areas may diverge in structure, function, and anatomical location (Orban et al., 2004). Consistent with the cluster specialization hypothesis, the MT cluster contains visual field maps that are all sensitive to stimulus motion (*vs.* static images) and direction in both species (Amano et al., 2009; Kolster et al., 2009; Kolster et al., 2010), though there also appears to be differences between species with the MT cluster showing selectivity to form stimuli in humans, but not monkeys (Konen & Kastner, 2008). In humans, the VO cluster contains two visual maps, VO1 and VO2, which are sensitive to color (Brewer et al., 2005), and the PHC cluster contains two maps, PHC1 and PHC2, which are both sensitive to scene images (Arcaro et al., 2009). These data provide support that visual clusters share similar computational functions. Admittedly, several accounts of functional variability within a cluster and shared functional properties across clusters challenge this hypothesis. For example, VO2, but not VO1, is selective for images of scenes (Arcaro et al., 2009). Foveal representations of VO are color-selective while peripheral representations are sensitive to object stimuli (Brewer et al., 2005). Given the heterogeneity in response selectivity of neurons in individual maps, such as discussed for V3 and V4, variability across maps within a cluster is not surprising. As such, it is also likely that these properties are not the relevant dimensions to characterize the functional specialization of individual clusters and to distinguish between clusters. Further, common functional properties could also be expected between bordering maps in different clusters that are developmentally related as discussed above.

Under this hypothesis, there should be a common computational goal shared between areas V3 and V4 as well as across the occipital cluster. V3 and V4 share many functional commonalities, notably; neurons in these areas are tuned for a wide array of stimulus properties including color, orientation, curvature, motion direction, and disparity (Burkhalter & Van Essen, 1986; Desimone & Schein, 1987; Felleman & Van Essen, 1987; Gegenfurtner et al., 1997; Ghose & Ts'o, 1997; Adams & Zeki, 2001; Tanigawa et al., 2010). However, these areas are differentiable based on their functional response profiles. Two prominent differences are that RF sizes at matched eccentricity representations are larger in V4 as compared with V3 and other occipital areas (Gattass et al., 1988), and attention effects are more robust (Luck et al., 1997). The functional organization within these individual areas also differs. For example, electrophysiological recordings in monkeys have shown that V1 neurons are arranged into mosaics with separable orientation and color selective zones (Lu & Roe, 2008). V3 lacks any apparent mosaic organization and many neurons are tuned for multiple properties such as color and orientation (Felleman & Van Essen, 1987; Gegenfurtner et al., 1997). Imaging and electrophysiology in macaques have revealed a mosaic organization of response properties in V4, but it differs in several ways from the organization in V1 (see Roe et al., 2012 for discussion). Overall, there is also a large degree of functional heterogeneity within each area. The diversity across areas does not necessarily refute the functional specialization hypothesis, though it does suggest that the common computational goal is not tied to any one of these individual functions. This diversity also highlights the heterogeneity of response properties within individual maps, which also challenges the common conception of individual

maps as functional units. While more work is needed to test the functional specialization of individual clusters, it is likely that any shared function across the occipital cluster is broader and more integrative than any one of these functional dimensions. In line with this assumption, it was recently proposed that the diversity of functions attributed to V4 neurons enables the “selective extraction of specific functional domain-based networks” (Roe et al., 2012). Such a unified function could easily be attributed to the occipital cluster as a whole with neurons across individual maps working in concert for the selective extraction of information that is filtered *via* specific sub-domains within the occipital cluster to later, specialized processing stages in temporal and parietal cortices. As such, emphasis shifts from understanding the functional role of individual areas (e.g., V3 or V4) to understanding how specialized sub-regions work in concert within a cluster to achieve a common computational goal.

Eccentricity as a supra-areal organizing principle

The organization of eccentricity is not only fundamental to the supra-areal formation of functional clusters; eccentricity also provides a fundamental dimension in linking individual areas and clusters across cortex. Below, we discuss the relation of eccentricity to connectivity within the occipital cluster and between the occipital cluster and higher-order visual areas in temporal and parietal cortices.

Connectivity within occipital cortex

The visuotopic organization of individual areas is preserved in their anatomical connections. Anatomical studies in primates have demonstrated that neurons with overlapping RFs are interconnected within and between areas (Cragg, 1969; Zeki, 1969b; Van Essen & Zeki, 1978; Maunsell & Van Essen, 1983a). Direct intra-areal anatomical connections between dorsal and ventral visual cortex have been identified at the horizontal meridians (Jeffs et al., 2009), as well as connections between both hemispheres at the vertical meridians (Hubel & Wiesel, 1967; Van Essen & Zeki, 1978; Newsome & Allman, 1980; Cusick et al., 1984; Kennedy et al., 1986). While labeled cells of lateral connections in macaque striate and extrastriate cortex exhibit some anisotropy with respect to the cortical surface, this is thought to reflect cortical magnification factor and yield isotropic visual field coverage (Angelucci et al., 2002). Such wiring is necessary for the integration of information within focal points of our visual environment.

Consistent with the well-established anatomical connections shown in monkeys between visual areas based on overlapping RFs (Cragg, 1969; Zeki, 1969b; Van Essen & Zeki, 1978; Maunsell & Van Essen, 1983a; Angelucci et al., 2002; Rosa et al., 2009), the BOLD signal between regions with overlapping RFs is correlated even in the absence of visual input within human visual cortex (Heinzle et al., 2011; Haak et al., 2012; Butt et al., 2013). At a coarse scale, imaging studies have identified a general foveal-peripheral functional distinction across much of occipital cortex in humans (Smith et al., 2012; Raemaekers et al., 2014) and in monkeys (Vincent et al., 2007; Nallasamy and Tsao, 2011). Recent imaging studies in humans using sophisticated spatial clustering techniques that extract the global similarity structure of correlated signals have identified a finer-scale organization across V1, V2, V3, and hV4 similar to the eccentricity map (Fig. 5A, black outlines; Yeo et al., 2011; Jbabdi et al., 2013; Baldassano et al., 2014). These clusters form elongated bands encircling the foveal representation

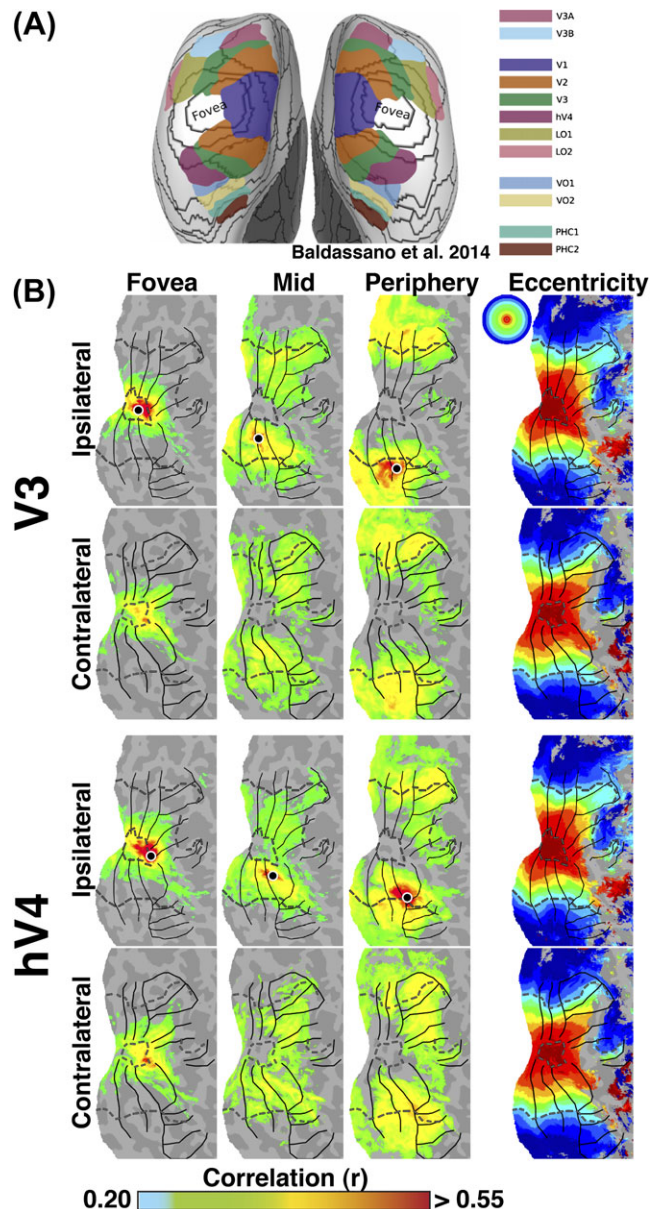


Fig. 5. Eccentricity-based functional connectivity in humans. (A) Segmentation of visual cortex based on patterns of correlated BOLD signal (Baldassano et al., 2014). The locations of 12 visual field maps are overlaid on the connectivity-based segmentation of visual cortex (black lines). The functional segments in occipital cortex generally corresponded to eccentricity bands. (B) Correlation maps in both hemispheres of group average data ($n = 14$) for resting state at three seed locations ($<1.0^\circ$, $\sim 5.5^\circ$, $\sim 11.5^\circ$; left to right) in ventral V3 and hV4. Correlations were computed between the mean signal in each seed location (black dot) and every voxel within visual cortex. Correlations were then averaged across subjects to derive group average maps. For each seed, the strongest correlations (red/yellow) span several visuotopic areas within an eccentricity range roughly corresponding to that of the seed area in both the ipsilateral and contralateral hemispheres. The correlations have a similar organization to eccentricity maps (far right). For visual comparison to the underlying visuotopic organization of occipital cortex, group average eccentricity maps are shown on the flattened surfaces for reference for the same group of subjects. Iso-eccentricity lines (gray, dashed) are drawn for foveal ($<1.0^\circ$) and peripheral space ($>10.0^\circ$). Data analyzed from Arcaro et al., 2015a. (Figure 5A is reproduced from Parcellating connectivity in spatial maps by Christopher Baldassano, Diane M. Beck, and Li Fei-Fei in PeerJ Computer Science, 19 February, 2015.)

of V1-hV4. This structure appears to be driven by the fact that BOLD signals in iso-eccentricity regions of V1-hV4 are more correlated than the intra-areal signals at distal eccentricities, as illustrated by correlation maps for foveal, mid-field, and peripheral seed locations of ventral V3 and hV4 in the right hemisphere (Fig. 5B). For both areas, peak correlations (red) were evident in parts of the visual field around each seed location with strong correlations (red/yellow) also extending across the visual field along an eccentricity ring corresponding to that of the seed location. Comparable correlation patterns were observed in the left hemisphere that represents the hemifield contralateral to that of the seed. Notably, this eccentricity-based connectivity pattern is dissociable from connectivity patterns based on overlapping RFs and is similar in the presence and absence of strong visual input (Arcaro et al., 2015a), suggesting that this structure reflects part of the intrinsic functional architecture of the visual system. Thus, the spatial organization of the correlated BOLD signal within and across V3 and hV4 reflects the visuotopic organization of individual maps as well as the supra-areal organization of the occipital cluster.

Connectivity between occipital and higher-order cortex

This supra-areal eccentricity structure may reflect a broader-scale anatomical organization of direct (and indirect) connections, facilitated *via* differences in intra-areal projections between occipital sites representing central and peripheral space across temporal and parietal cortices. As revealed in monkey tracer studies, the fovea of V1, but not periphery, projects directly to V4 (Zeki, 1969a; Nakamura et al., 1993). Peripheral representations of areas V1, V2, V3, and V4 project to area PO (Colby et al., 1988). Peripheral representations of V2 project to areas MST, VIP, and VTF. As illustrated in Fig. 6, the foveal region of V4 in monkeys mainly projects to temporal areas TEO and TE while peripheral V4 mainly projects to parietal areas such as V3A, DP, LIP, and MST, but also to medial temporal area VTF (Baizer et al., 1991; Ungerleider et al., 2008). Taken together, these prior studies illustrate broad differences in connectivity patterns between foveal and peripheral portions of occipital cortex and regions within parietal and temporal cortex. It is worth noting that alternative proposals exist for many of these areas (e.g., PO and TEO), which can affect the interpretation of whether connectivity exists (or lacks) between any two areas. Still, these prior studies highlight a broad distinction in connectivity patterns between cortex representing foveal and peripheral space. This distinction is preserved in pulvinocortical connectivity (Gattass et al., 2014; Ungerleider et al., 2014), suggesting that a distinction of foveal and peripheral space is a fundamental property of the visual system as a whole. Though we are not aware of studies directly investigating comparable distinctions in connectivity between V3 and higher-order cortical areas, it seems reasonable to assume that a similar pattern would be observed since these patterns are also observed in V2 (Gattass et al., 1997; Gattass et al., 2005). It is not known whether these anatomical connectivity patterns are “bi-modal,” only distinguishing central and peripheral space, or reflect a finer-scale organization where connectivity patterns with intermediate eccentricity representations are distinguishable from central and peripheral connectivity profiles. Given recent evidence from functional imaging studies in humans discussed above, we predict that these anatomical connections reflect a gradient, though this remains to be explored.

A similar differentiation in foveal-peripheral anatomical connectivity patterns has been recently revealed in humans. Using diffusion tensor imaging, the anatomical connectivity of category-selective

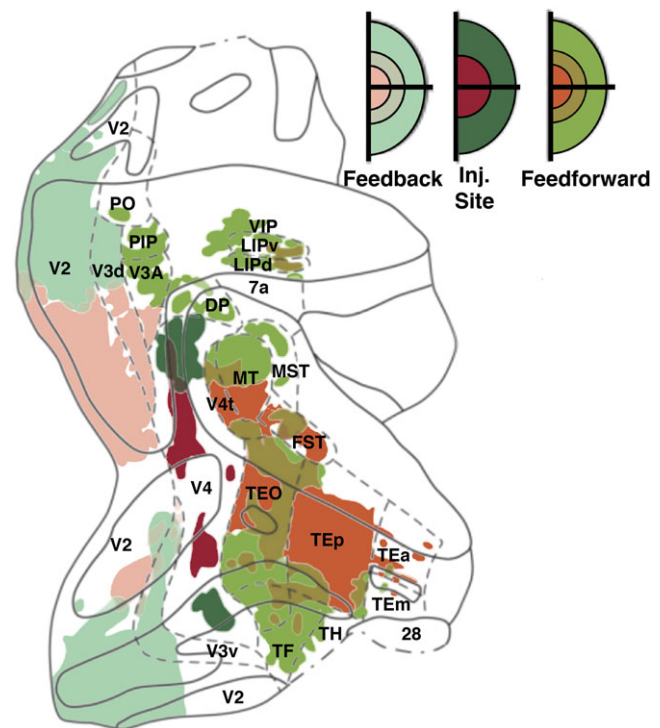


Fig. 6. Central-peripheral distinction of anatomical connections in macaque V4. Distribution of feedback, feedforward, and intermediate V4 connections with extrastriate cortex based on foveal (central 5°) and peripheral injections (>5°). See visual field schematic for color-coding of feedback and feedforward connections from foveal and peripheral V4 injections as well as their overlap. Feedforward connections (orange) with foveal V4 (red) were mainly found within temporal cortex, though projections were also found in parietal cortex (area LIP). Feedforward connections (light green) with peripheral V4 (dark green) were mainly found in dorsal extrastriate and parietal cortex, though projections were also found in ventral temporal cortex (areas TF). (Figure adapted from Fig. 3 of Leslie G. Ungerleider, Thelma W. Galkin, Robert Desimone, and Ricardo Gattass. Cortical connections of area V4 in the macaque cerebral Cortex (2008) 18 (3): 477–499, by permission of Oxford University Press.).

areas in temporal cortex varies as a function of eccentricity representation in human occipital cortex (Kim et al., 2005). Here, we illustrate the most probable connections (across subjects) with regions selective for views of face and scene pictures in lateral and medial temporal cortex, respectively (Fig. 7A). Face-selective regions are most connected (red) with foveal portions of hV4 while scene-selective regions are most connected (blue) with peripheral portions of hV4. These patterns are consistent with the divergence of anatomical projections in V4 in monkeys. Foveal regions of macaque V4 project to portions of TE (Ungerleider et al., 2008), where neurons selective for pictures of faces and body parts have been reported previously (Tsao et al., 2006; Pinsk et al., 2009; Bell et al., 2011). In contrast, peripheral regions of macaque V4 project to area TF in the occipito-temporal sulcus (Ungerleider et al., 2008), where neurons responding selectively to visual scenes have been reported (Kornblith et al., 2013). These connectivity patterns are also qualitatively apparent when evaluating the spatial pattern of correlated signal with face- and scene-selective regions in humans (Fig. 7B; also see Baldassano et al., 2012). The BOLD signal of face-selective regions is most strongly correlated with foveal regions in occipital cortex (Fig. 7B, red/yellow). The BOLD signal of scene-selective regions is most strongly correlated with

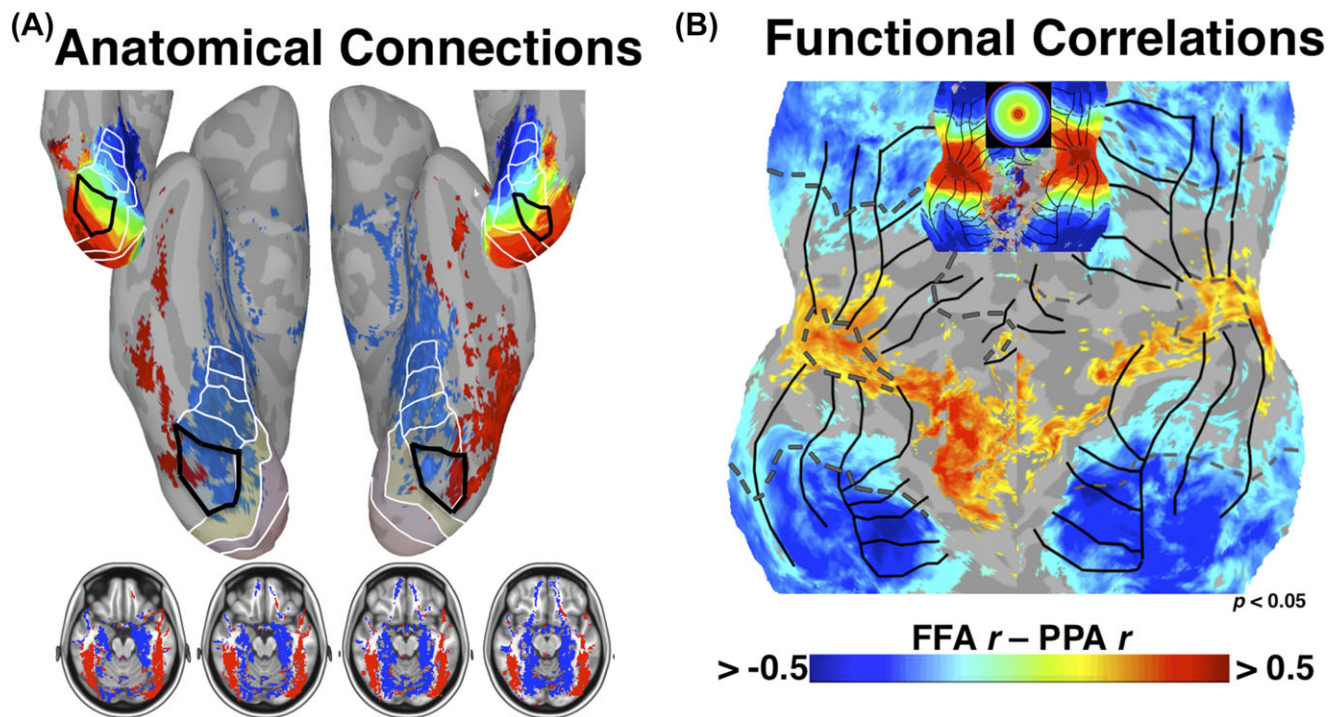


Fig. 7. Central-peripheral distinction of anatomical and functional connections in human temporal cortex. **(A)** Distinct anatomical connections with face- and scene-selective regions in ventral temporal cortex of both hemispheres. Probabilistic analyses on diffusion tensor imaging data identified white matter tracts (bottom, volume images) and gray matter connections (top, inflated surface images) from face- and scene-selective regions. All tracking was restricted to the ipsilateral hemisphere. Data were threshold to the top 10% of connections for each subject, binarized, then averaged ($n = 15$) to reveal gray matter voxels that were consistently identified as being connected with either face- or scene-selective regions across subjects. Tracking from face-selective regions (red) extended along the lateral fusiform, and posteriorly within foveal regions of hV4 and adjacent, lateral cortex representing foveal space. Tracking from scene-selective regions (blue) extended along the collateral sulcus and medial fusiform, and posteriorly within peripheral representations of hV4 (outlined in black). Group average eccentricity maps are shown on the inflated surface for each hemisphere. Data analyzed from Arcaro et al., 2015b. **(B)** Correlation maps in both hemispheres of group average data ($n = 14$) for resting state between face- and scene-selective regions in ventral temporal cortex and occipital cortex. Data are presented on flattened surfaces. Correlations were computed between face- and scene-selective regions and all voxels in visual cortex. Scene-selective correlation maps were subtracted from face-selective maps in each subject, and then averaged to derive group average maps. Difference maps revealed a central-peripheral distinction with face-selective regions more strongly correlated with foveal regions of V1-hV4 (yellow/red) and scene-selective regions more strongly correlated with peripheral regions of V1-hV4 (blue). Data are threshold at $ps < 0.05$ (voxelwise one-sample t -test on Fisher-transformed individual subject difference correlations). Group average eccentricity maps are shown on the flattened surfaces for reference. Iso-eccentricity lines (gray, dashed) are drawn for foveal ($<1.0^\circ$) and peripheral space ($>10.0^\circ$). Data analyzed from Arcaro et al., 2015a.

peripheral regions (Fig. 7B, blue). Taken together, these imaging data converge with the anatomical literature to provide additional support for a foveal/peripheral distinction in the connectivity patterns between occipital visual areas and higher-order cortex.

Eccentricity biases in higher order cortex

The apparent central-peripheral dichotomy in connectivity could reflect the topographic organization of higher-order cortex. Parietal and temporal areas contain neurons with large RFs that cover large swaths of the visual field (Desimone & Gross, 1979; Blatt et al., 1990). Feedback projections from these regions to early and intermediate visual areas could facilitate such widespread, eccentricity-dependent correlation patterns. Recent imaging studies have revealed the existence of several visual field maps within regions of parietal and temporal cortex in monkeys (Brewer et al. 2002; Kolster et al. 2009; Arcaro et al. 2011; Janssens et al. 2014; Kolster et al. 2014) and in humans (Brewer et al. 2005; Konen and Kastner 2008;

Arcaro et al. 2009; Amano et al. 2009; Kolster et al. 2010). It is interesting to note that when comparing the profile of anatomical connectivity between occipital areas and higher order cortex in monkeys (Fig. 6) with the eccentricity representations of these higher order regions (Figs. 2 and 3), it is clear that higher order areas mainly connected with peripheral parts of V4 (e.g., PO, PIP, LIP, DP, and TF) have a large peripheral representation, and areas mainly connected with foveal parts of V4 (e.g., TEO and TE) have a prominent foveal representation. It is unclear if any of these higher order maps only represent a constrained part of visual space. Functional imaging studies investigating the topographic organization of these higher order maps find complete representations of visual space, but a disproportionate amount of their cortical space represents a particular region of visual space (e.g., Hansen et al. 2007; Arcaro et al. 2009; Kolster et al. 2010; Wang et al. 2014). Such biases could explain why this apparent dichotomy is not absolute and why some projections exist from foveal regions in occipital cortex to regions with peripheral biases in higher-order cortex (and *vice versa*).

Previous imaging studies in humans have proposed eccentricity as a large-scale organizing principle for higher order visual cortex (Levy et al., 2001; Hasson et al., 2002; Malach et al., 2002). According to this model, higher order cortex lacks orderly representations of visual space and instead contains broad eccentricity biases that coincide with regions that are selective for particular categorical images (e.g., faces). Though visual field maps have since been reported in these higher order cortical regions (Brewer et al., 2005; Arcaro et al., 2009; Kolster et al., 2009; Kolster et al., 2010; Janssens et al., 2014), individual maps tend to contain a disproportionate (biased) representation of visual space with respect to eccentricity. Interestingly, these biases correspond to particular recognition processes. Higher order areas that predominantly contain foveal representations tend to be specialized in face and object recognition, whereas areas that predominantly contain peripheral representations tend to be involved in scene analysis (Levy et al., 2001; Hasson et al., 2002; Malach et al., 2002; Arcaro et al., 2009). This divergence in computational processes necessary for foveal and peripheral recognition is already evident in occipital areas such as V3 and V4 (Fig. 5) and in the connectivity patterns between temporal and occipital cortices (Figs. 6 & 7). Given the timeline of cortical development (Bourne & Rosa, 2006), the eccentricity biases in higher order cortex may be shaped by the organization of occipital areas such as V3 and V4 as well as the broader cluster organization.

Conclusion

The representation of visual space is a fundamental organizing principle for primate visual cortex at multiple spatial scales. The visuotopic organization of cortex provides criteria for the identification of individual areas, such as V3 and V4, as well as the grouping of these areas into map clusters, which appears to be part of a large-scale organization. In primates, areas V3 and V4 are part of the occipital cluster. While the identification of these visual field maps has promoted investigation on the functional roles of these areas as individual entities, the supra-areal organization of visual cortex provides a complementary framework to probe visual cortical function that emphasizes common functional roles across areas and a prominent role of eccentricity in the function and development of cortex.

The importance of eccentricity in supra-areal organization is emphasized in the inter-areal connectivity across the occipital cluster and with higher order cortex. Within the human occipital cluster, the BOLD signal in regions with shared eccentricity representations is correlated, regardless of polar angle representation. Anatomical projections with temporal, parietal, and frontal cortices differentiate central and peripheral occipital cortex in monkeys and may reflect the topographic organization and functional specialization within these higher order regions. Anatomical connections within human ventral temporal cortex also reflect this distinction. Regions selective for face images are connected with foveal portions of hV4. In contrast, regions selective for scene images are connected with mid-field and peripheral portions of hV4. Further, the spatial pattern of the correlated BOLD signal between these ventral temporal regions and occipital cortex also differentiated foveal from peripheral representations. Thus, this supra-areal eccentricity organization appears to be part of an intrinsic functional architecture that could support the integration of information across functionally specialized visual areas.

Through the supra-areal organization of visual cortex, areas V3 and V4 are linked with early visual areas V1 and V2. The clustering of V3 and V4 with V1 may reflect the organization of intrinsic anchors

that guide the development of these maps, but also implies shared resources and a common computational goal. The common juxtaposition of the V3A/B (V3A/DP) cluster to dorsal V3 and the VO cluster to hV4 (in humans) implies that developmental constraints and shared resources extend across cluster boundaries. However, further investigation is needed to explore this issue more thoroughly.

The functional roles of V3 and V4 are likely tied to the broader computational goals of the occipital cluster. Occipital cortex represents the primary cortical stage for visual processing. The diversity of response selectivities within each area and the multitude of connections between occipital areas support the extraction of basic visual features along functionally specific channels. V3 and V4 likely plays a critical role in additional filtering of information from V1 and V2, and the subsequent routing of information to higher order areas for further, functionally specific processing. V3 is interconnected with area MT *via* multiple routes and contains neurons that are selectively tuned for various aspects of stimulus motion that are commonly associated with the dorsal stream. V4 is interconnected with multiple areas in inferior temporal cortex and contains neurons that are selectively tuned for aspects of object processing that are commonly associated with the ventral stream. Through these connections, V3 and V4 support functionally specific channels for the filtering of information to higher order cortex. However, both areas are anatomically connected with areas spanning both the dorsal and ventral streams, and the profile of these higher order cortical connections appears to reflect the supra-areal eccentricity organization. As such, the supra-areal organization of V3 and V4 compliments their internal organization and provides important criteria for probing their functional roles in the visual system.

Acknowledgment

This work was supported by National Science Foundation grant BCS-1328270 and National Eye Institute grant R01EY017699.

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