Visual Neuroscience (2015), **32**, e020, 13 pages.

doi:10.1017/S0952523815000176

SPECIAL COLLECTION

Controversial Issues in Visual Cortex Mapping

REVIEW ARTICLE

Human V4 and ventral occipital retinotopic maps

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(RECEIVED February 3, 2015; ACCEPTED June 3, 2015)

Abstract

The ventral surface of the human occipital lobe contains multiple retinotopic maps. The most posterior of these maps is considered a potential homolog of macaque V4, and referred to as human V4 ("hV4"). The location of the hV4 map, its retinotopic organization, its role in visual encoding, and the cortical areas it borders have been the subject of considerable investigation and debate over the last 25 years. We review the history of this map and adjacent maps in ventral occipital cortex, and consider the different hypotheses for how these ventral occipital maps are organized. Advances in neuroimaging, computational modeling, and characterization of the nearby anatomical landmarks and functional brain areas have improved our understanding of where human V4 is and what kind of visual representations it contains.

Keywords: Retinotopy, HV4, Population Receptive Fields (PRF), Functional Magnetic Resonance Imaging (FMRI), Ventral Occipital Cortex, Visual Field Map, Human

Introduction

Since the 19th century, scientists have known that human visual cortex is located in the two occipital lobes (Henschen, 1893), and by the early 20th century they had determined that the primary visual cortex, or V1, contains a map of the contralateral visual field (Inouye, 1909; Lister & Holmes, 1916; Holmes, 1918). A major question, confronting neurologists, anatomists, and physiologists following the discovery of V1, was whether the human visual center was defined by this single large map only or whether it contained multiple representations of the visual field (Zeki, 1993). This question lays at the heart of a debate as to whether cortical damage could result in a deficit of a particular visual ability, like seeing words, color, or faces, while sparing other visual functions (Meadows, 1974*b*; Zeki, 1990).

The question of one visual area or multiple areas, once highly controversial, has been conclusively resolved. Numerous studies of both human and animal visual systems have shown that there are visual areas tiling much of the occipital lobe (reviewed in Felleman & Van Essen, 1991; Tootell et al., 1998; Wandell et al., 2007), and many more visual areas have been identified in human temporal, parietal, and frontal cortices (Malach et al., 1995; Silver et al., 2005; Swisher et al., 2007; Arcaro et al., 2009; Jerde & Curtis, 2013). Furthermore, visual deficits following brain injury, such as prosopagnosia and achromatopsia, are believed to arise from damage to separate regions important for processing faces and colors (Meadows, 1974*a*,*b*; Zeki, 1990; Bouvier & Engel, 2006), supporting the notion that there are multiple distinct visual areas. Many of these visual areas, like V1, are defined by retinotopic maps (Wandell & Winawer, 2011), while others are typically defined by their preference for certain classes of visual images, such as faces or scenes (Kanwisher, 2010).

Many neuroscientists seek to understand visual processing by characterizing and comparing the responses within different cortical visual areas. We believe that this endeavor is premised on the hypothesis that visual areas, either singly or in clusters, represent computational units (Wandell et al., 2005). Hence to understand vision, we must understand what computations and representations occur in the different visual areas. Clearly, this approach requires well-justified and reproducible methods for defining visual areas.

In this review, we focus on recent progress in characterizing one visual area, human V4. Study of the location and organization of the first three cortical retinotopic maps in human—V1, V2, V3—has been quite successful, with wide agreement between research groups on the general organization and properties of these maps.[1] The fourth visual area is less well understood with disagreements in the literature about nomenclature, location and organization of retinotopic maps (and even the number of maps), and visual response properties. Despite two decades of disagreements

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[1]Despite this wide agreement, there is some inconsistency in nomenclature. Most groups refer to the two quarterfield maps surrounding human V2 as ventral and dorsal V3 (V3v and V3d), implying that the two quarterfield representations comprise a single hemifield map; other groups refer to the two maps as VP (on the ventral side of V2v) and V3 (on the dorsal side of V2d) to be consistent with the macaque literature (Burkhalter et al., 1986). We use the V3d/V3v convention here, as it is more parsimonious to consider to the two quarterfield representations surrounding V2 to be a single map (Zeki, 2003). Nomenclature aside, to our knowledge there is little disagreement about the gross retinotopic organization of V1/V2/V3 in human occipital cortex.

(or perhaps because of it), there has been considerable progress in recent years in understanding the fourth visual area. Progress has been made in defining its general anatomical location, its precise functional boundaries, its neighbors on the cortical surface, and its retinotopic organization and properties. This progress has brought the field closer to resolving some of the competing claims regarding this area. We begin with a brief history of the fourth visual area in human and macaque. Second, we review the different proposals for parcellating this region into retinotopic maps in the human brain. Third, we discuss advances in neuroimaging methods and how this furthers our knowledge of the map organization and the properties within the retinotopic maps in ventral occipital cortex. Finally, we discuss why this area is of wide interest to vision scientists, and what the limitations are in our current knowledge of this cortical area.

The discovery of the fourth visual area in monkey and human

In rhesus monkeys, an extrastriate visual area anterior to V3 was first identified by anatomical methods and labeled "Visual 4" or "V4" (Zeki, 1971). Soon thereafter, V4 was shown to contain many cells whose responses were selective to wavelength (Zeki, 1973). In the following two decades, positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) methods identified a visual area in humans in the vicinity of the lingual and fusiform gyri, and anterior to ventral V3 ("V3v"), with larger responses to chromatic spatial patterns than to luminance-matched achromatic patterns, a stimulus comparison called "color exchanges" (Lueck et al., 1989; McKeefry & Zeki, 1997). Given these apparent functional homologies to macaque V4, this region in humans was also initially called V4. In order to determine whether these color-responsive regions in human contained a map of the visual field, McKeefry and Zeki (1997) measured responses to color exchanges limited to either the upper or the lower visual field. The response to upper visual field color exchanges resulted in a locus of activation near but distinct from the response to lower field color exchanges, demonstrating both chromatic and retinotopic tuning in the same area (Fig. 1A). These results showed that V4 as defined by chromatic selectivity contained at least a crude retinotopic organization which appeared to span a hemifield.

From color exchanges to retinotopic maps: V4v/V8

The finding that color-selective responses on the ventral surface overlap with a representation of the contralateral hemifield was further investigated in a series of studies by Roger Tootell's lab, which first characterized the V4 retinotopic map (Sereno et al., 1995) and then examined the retinotopy and color responses in the same individual subjects (Hadjikhani et al., 1998; Hadjikhani & Tootell, 2000; Tootell & Hadjikhani, 2001). Hadjikhani et al. (1998) used a traveling wave experimental design, in which stimuli slowly and repeatedly sweep out a dimension of visual space (either eccentricity or angle) to probe retinotopic responses. This method, developed several years earlier (Engel et al., 1994; Sereno et al., 1995; Engel et al., 1997), allowed for a more precise quantification of the visual field preference of each voxel compared to the upper *versus* lower field color exchange methods. The data analysis also improved on the previous V4 work by visualizing maps on a representation of the unfolded cortical surface of individual hemispheres (Fig. 1B), a procedure that has become essential and routine in studies of visual cortex (Dale et al., 1999; Wandell et al., 2000).

At least two important advances came from this work. First, these authors reported a foveal representation in ventral occipital cortex,[2] distinct from the foveal representation in register across the V1, V2, and V3 maps at the occipital pole (Fig. 1B). Second, they showed clear images of the organization of polar angle preferences adjacent and anterior to V3v. However, their method for dividing the cortical surface beyond V3v into areas brought them into conflict with Zeki's previously proposed labeling of V4. The maps identified by Hadjikhani et al. (1998) were V4v, adjacent to V3v and containing a representation of only the upper contralateral quarterfield, and a new map they called V8, adjacent to V4v representing the entire contralateral hemifield. Unlike studies in macaque, these researchers did not identify a dorsal counterpoint to V4v, leaving the V4v upper quarterfield orphaned (Tootell & Hadjikhani, 2001). Moreover, the chromatic responses identified in these studies were now in the region identified as V8, and not the region identified as V4v, hence the conclusion that V8, and not V4, is color-selective and likely the substrate of cerebral achromatopsia. This claim does not necessarily conflict with other reports that the fourth visual area carries color-selective signals, as the V4v map proposed by Hadjikhani et al. is not identical to the V4 area described by McKeefry and Zeki (1997), nor the hV4 map discussed in the next section.

HV4 and the VO maps

Many of the core findings of Hadjikhani et al. (1998) have been widely replicated across labs, including the second foveal representation in ventral occipital cortex, the presence of at least two retinotopic maps anterior to V3v on the ventral occipital surface, and the fact that at least one of these maps contains a representation of both the upper and lower contralateral quarterfields (Wade et al., 2002; Brewer et al., 2005; Arcaro et al., 2009). However, while there is broad agreement about much of the retinotopic data, more recent work has argued for an alternative organization of the maps anterior to V3v which we will call the hV4/VO model.

This hV4/VO organization differs from the V4v/V8 model in several ways. The fourth visual area (hV4) is still adjacent to V3v, but is much shorter than V3v, and so does not share the entire upper vertical meridian with V3v (Fig. 2B). This fact has important implications for how much of the visual field hV4 represents, which we return to in sections "Population Receptive Fields" and "Visual Field Coverage". Further, hV4 responds to stimuli in both the upper visual field and the lower visual field (Wade et al., 2002; Brewer et al., 2005), unlike V4v which only contains a representation of the upper contralateral quarterfield. Anterior to the hV4 hemifield map, Brewer et al. (2005) described two additional hemifield maps around the ventral occipital fovea, called VO-1 and VO-2 ("ventral occipital" 1 and 2) (Fig. 2).

The hV4/VO proposal from the Wandell lab preserves several aspects of the V4v/V8 proposal, in particular the ventral occipital fovea and the multiple retinotopic maps (Fig. 2A and 2B), but it also resolves an important issue with the V4v/V8 proposal. By positing that hV4 is a hemifield map rather than a quarterfield map, it resolves the question of the missing lower quadrant representation of V4 (Tootell & Hadjikhani, 2001). According to Wade et al. (2002)

[2]The location of this displaced foveal representation might be considered temporal rather than occipital, because it is on the fusiform gyrus and on the lateral side of the occipital branch of the collateral sulcus. For consistency with other literature, we refer to it as ventral occipital.

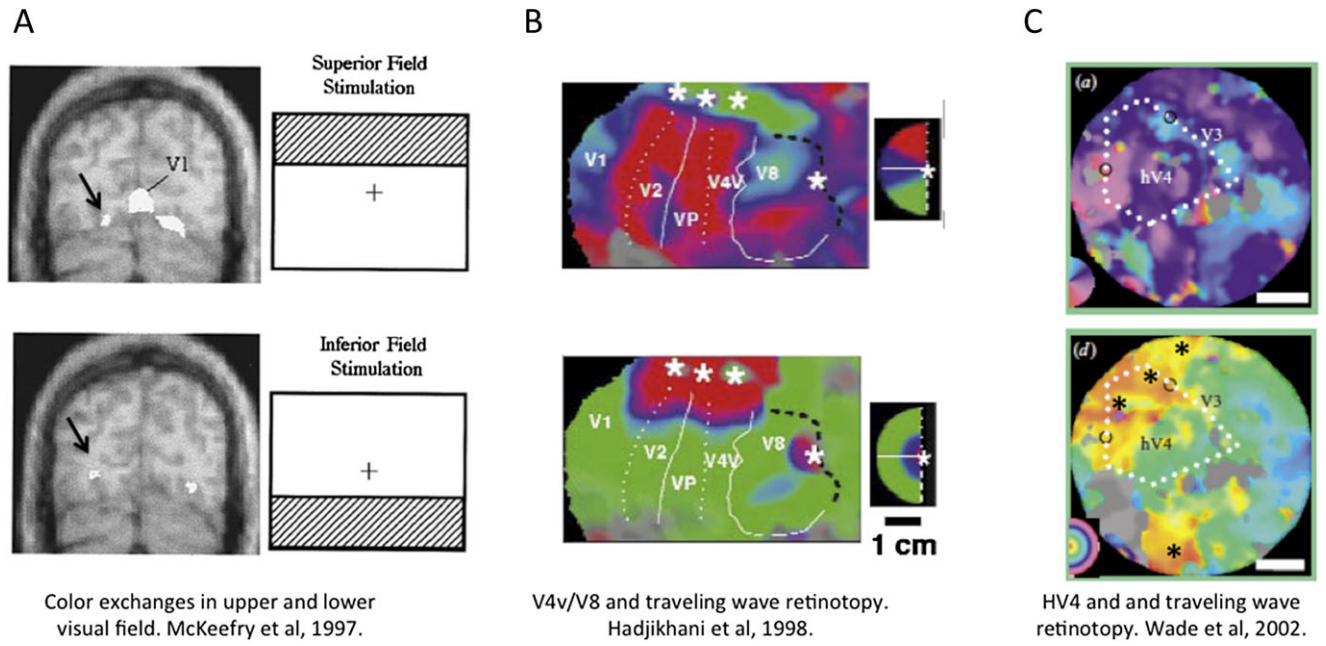

Fig. 1. Retinotopic responses in and around human V4. (**A**) Color exchanges in the upper and lower visual field, measured with fMRI, shown on a coronal anatomical image. The activations (white regions) indicate a greater response to chromatic contrast patterns than to achromatic patterns in an individual observer. The black arrows point to the ventral occipital responses in one hemisphere. The response to the upper field color exchange is more medial and inferior than the response to the lower field stimulation. (From Figure 7 in McKeefry & Zeki, 1997, by permission of Oxford University Press). (**B**) V4v/V8: Retinotopic data shown on renderings of right ventral occipital cortex, computationally flattened, and cut at the fundus of the calcarine sulcus (V1). The color maps show retinotopic angle data (upper panel) and eccentricity data (lower panel). In both panels, asterisks denote foveal representations and white lines mark boundaries between visual field maps. The three upper asterisks are the confluent fovea of V1–V3 near the occipital pole. The single asterisk is a displaced foveal representation in ventral occipital cortex. The organization of ventral occipital cortex proposed here is a quarterfield map, "V4v" adjacent to "VP" (also called V3v), and a hemifield map called "V8". V4v contains red and blue but not green colors in the upper plot, indicating responses to the upper left quarterfield. V8 contains the full range of angles from red to green [adapted by permission from Macmillan Publishers Ltd: Nature Neuroscience (Hadjikhani et al., 1998), copyright 1998]. (**C**) HV4 hemifield: Further retinotopic measurements are shown in a flattened region of ventral occipital cortex. The color maps show the retinotopic angle data (upper plot) and eccentricity data (lower plot). The region marked V3 corresponds to the region marked "VP" in panel B. These authors identified a retinotopic map with a representation of the contralateral hemifield next to V3v, called hV4, differing from the quarterfield V4v in panel B. The lower plot shows a large foveal representation (three asterisks) and a displaced fovea that is more anterior (single asterisk), similar to panel B (adapted from Figure 6 in Wade et al., 2002, by permission of the Royal Society).

and Brewer et al. (2005), the lower quarterfield representation is in fact within the hemifield map hV4. Brewer et al. (2005) showed that color exchange experiments elicit response modulations in both hV4 and VO-1, as well as VO-2.

There is not a simple correspondence between the V4v/V8 and hV4/VO proposals. V8 is not the same VO-1, and V4v is not the same as hV4. For example, V8 contains part of what Brewer et al. (2005) called hV4, and part of what they called VO-1 and possibly VO-2 (Fig. 3).

V4v/V4d

Neither the V4v/V8 model nor the hV4/VO model was accepted by all groups. An alternative proposal from the Gallant lab is more consistent with visual field map organization in macaque (Hansen et al., 2007). These authors made detailed and careful measurements of retinotopic maps in ventral occipital cortex, and noticed that the representation of the lower vertical meridian in the V4 maps on the ventral surface was variable across subjects. According to this proposal, the map anterior to V3v, which they call V4v (like Hadjikhani et al., 1998) is missing a representation of the lower vertical meridian. This conflicts with the hV4/VO model, in which hV4 responds to both upper and lower visual field stimuli, including those along the lower vertical meridian. Further, Hansen et al. argue that the portion of the visual field not represented in hV4 is found in a map adjacent to dorsal V3. They refer to this map as V4d, consistent with the topology and nomenclature in macaque V4, which is split into a ventral and dorsal arm. By positing a V4v and V4d map, the Hansen et al. map descriptions differ from V4v/V8 and hV4/VO. Their dorsal V4 map also conflicts with the dorsal topography described by Larsson and Heeger (2006), in which two representations of the contralateral hemifield lie between dorsal V3 and hMT, maps called LO-1 and LO-2.

The differences between the V4v/V4d model on the one hand, and the hV4/VO and LO-1/2 models on the other hand, are not just differences in naming conventions; rather, they are different claims about the data. For example, the V4v/V4d model posits that the lower vertical meridian representation is absent in the map adjacent to V3v, whereas the hV4 model is that it is present. Moreover, Hansen and colleagues claim that except for a narrow representation of the upper vertical meridian (V4d) right next to V3d, the cortical region between V3d and MT does not contain retinotopic organization, but rather is a nonretinotopic, object-selective region.

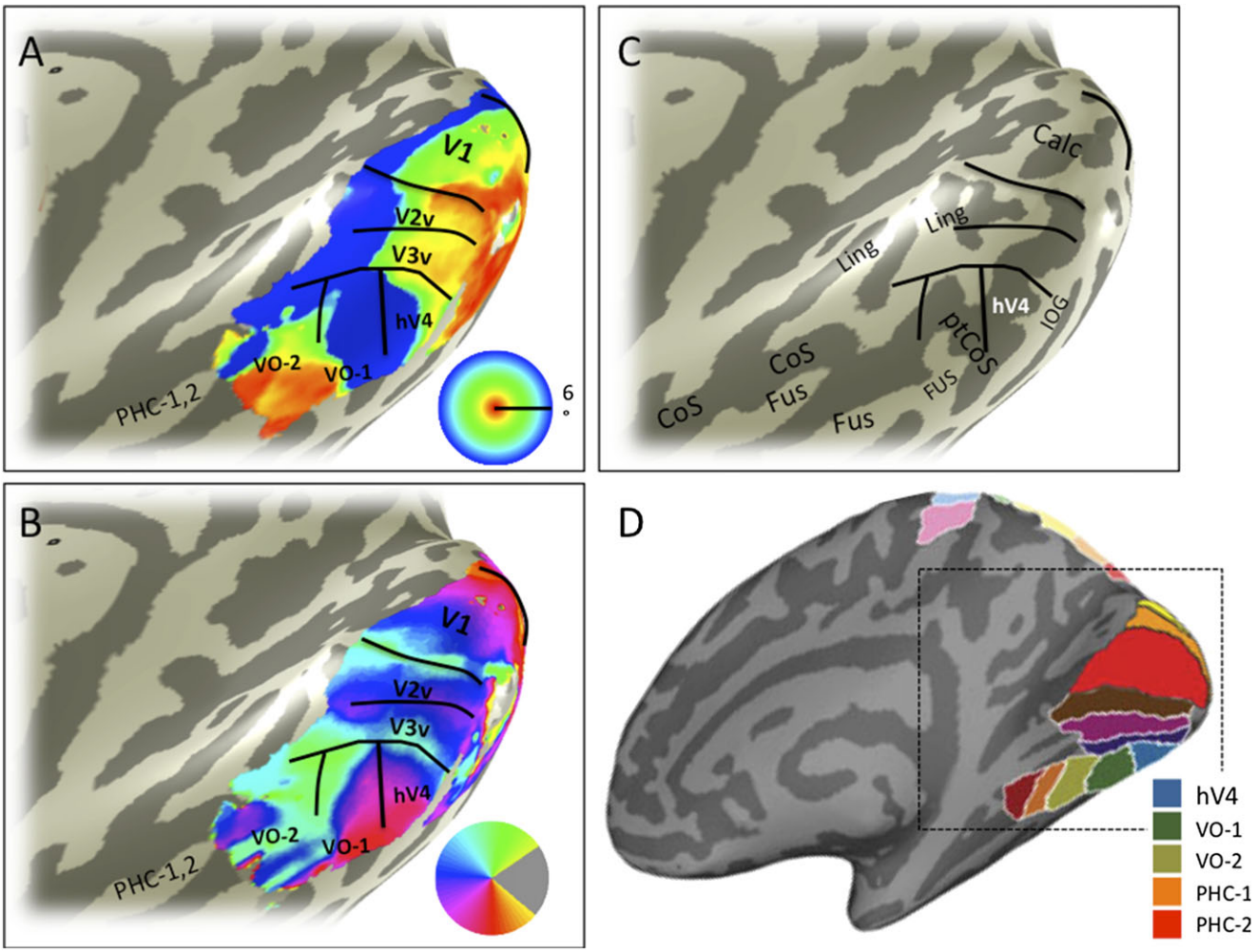

Fig. 2. HV4 and the VO maps in human visual cortex. Panels A, B, and C show renderings of the smoothed cortical mesh rendered from an individual subject's right hemisphere. The view is from the ventral medial surface of the posterior occipital and temporal lobes, similar to the region in the dashed box in panel D. Retinotopic data, from an experiment with a contrast pattern shown in a moving bar aperture, were analyzed using population receptive field mapping following the work of Dumoulin and Wandell (2008). (**A**) Eccentricity data up to 6 deg. There is a large foveal representation at the occipital pole (orange and red), and a second, displaced fovea near VO-1/2. The boundary between hV4 and VO-1 is an eccentricity reversal (blue). Anterior to VO-2, two additional maps called PHC-1 and 2 have been described (Arcaro et al., 2009) but were not measured in this data set. (**B**) Angle data from the same experiment. The boundary between V3v and hV4 is indicated by an upper vertical meridian angle reversal (green), as is the boundary between VO-1 and VO-2. (**C**) Major sulcal and gyral features of the ventral occipital cortex. These include calcarine sulcus, lingual gyrus, inferior occipital gyrus, collateral sulcus, and posterior transverse collateral sulcus (ptCoS). The boundary between hV4 and VO-1 lies with the ptCoS (Witthoft et al., 2013). (**D**) Location of a number of visual field maps in an individual subject from a study which computed probabilistic locations of visual field maps across observers (after Wang, L., Mruczek, R.E., Arcaro, M.J., Kastner, S. *Probabilistic maps of visual topography in human cortex*. Cerebral Cortex, 2015, Epub ahead of print, by permission of Oxford University Press). The ventral occipital maps identified in this study, including hV4 and VO-1/2, are situated similarly to the model proposed by Brewer et al. (2005), and depicted in panels A–C.

Larson and Heeger claim that this region in fact contains two maps. These LO-1/2 maps have been identified in several subsequent reports (Amano et al., 2009; Kolster et al., 2010), including two reports with probabilistic atlases (Abdollahi et al., 2014; Wang et al., 2014), lending support to the claim that this region in fact contains multiple retinotopic maps.

Ventral occipital map disagreements

Why is it that several groups, using similar equipment and similar (though not identical) experimental designs and analysis methods, arrived at different models of the visual field maps in ventral occipital cortex? This disagreement can be contrasted with the V1 to V3 maps, for which agreement is high and detailed, and for which automated tools for map identification have recently been developed (Benson et al., 2012; Benson et al., 2014). The fact that the organization of the V1–V3 maps appears to be broadly similar across many species (Sereno et al., 1995) likely helps research groups arrive at similar conclusions about these maps in human. By contrast, the V4v quarterfield map in two of the proposals (Hadjikhani et al., 1998; Hansen et al., 2007) preserves homology with macaque, whereas the hV4 hemifield model does not. How far along the

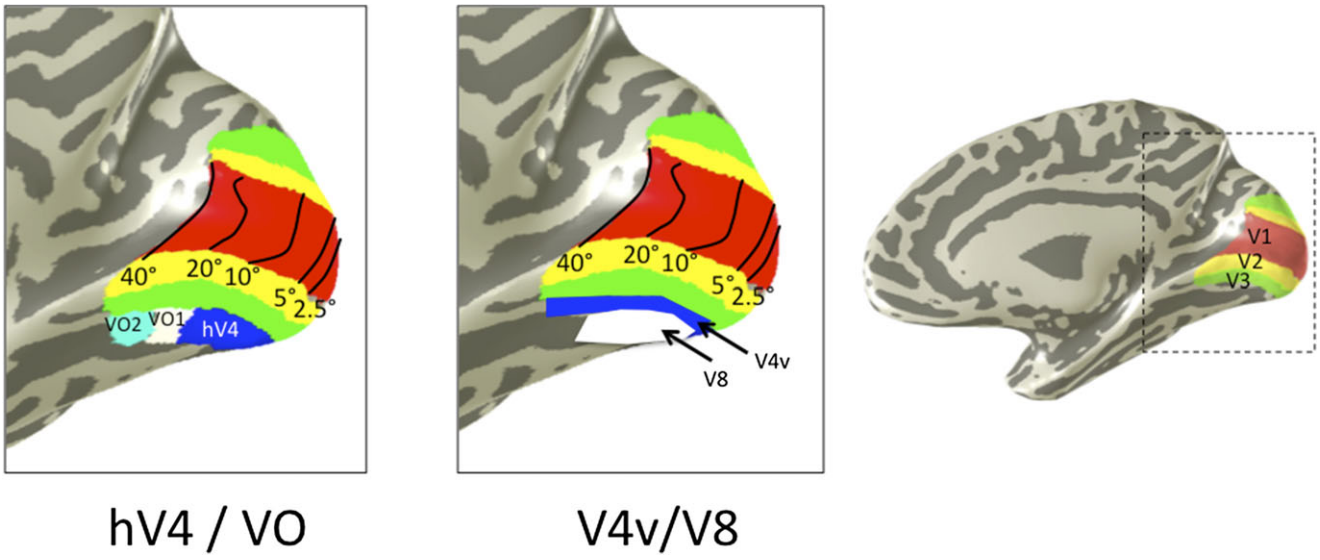

Fig. 3. Two proposals for ventral occipital maps. The inset on the right shows a medial view of an inflated right hemisphere, with V1, V2, and V3 shaded red, yellow, and green, respectively. Two magnified views of the posterior region are shown on the left, one indicating the hV4/VO maps (left), and one with the approximate positions of V4v and V8. The eccentricity lines in V1 were drawn based on retinotopic mapping (adapted from Figure 3 in Wandell & Winawer, 2011, with permission from Elsevier). The hV4 map extends in the anterior direction only about as far as the 10 deg representation in V1. The region labeled V8 is not identical to any single map in the hV4/VO organization.

visual hierarchy should we expect close homology between human and monkey in the organization and existence of visual areas?

Perhaps, differences in visual organization are not too surprising given the relatively large differences in size and folding between the human and macaque brain. In fact, closer inspection of V3 reveals significant species differences, including size (Lyon & Connolly, 2012) and stimulus selectivity (Tootell et al., 1997; Vanduffel et al., 2001). A similar divergence in organization is seen with face selective patches. In macaque, these line the lateral surface of the temporal lobe extending posteriorly nearly to V4d, while the corresponding regions in humans are found on the ventral surface in the fusiform and inferior occipital gyri, with the posterior patches in the close vicinity of hV4 (Tsao et al., 2008; Weiner & Grill-Spector, 2010; Grill-Spector & Weiner, 2014; Janssens et al., 2014). A further important consideration in comparing species is methodology. Conclusions about retinotopic maps in human derived from fMRI may differ from conclusions about maps in animal models based on electrophysiology. For example, while fMRI samples at a much coarser scale than single unit recording, it does allow for measurement over as much cortex as desired. Recent macaque studies using fMRI have provided detailed descriptions of several maps in the vicinity of V4, including a newly proposed area "OTd" (Janssens et al., 2014; Kolster et al., 2014). The fact that there is not yet complete consensus about the organization of visual field maps in macaque despite many decades of measurements should caution one against treating the macaque model as the gold standard in guiding understanding of the human maps (see also section 7b in Wandell et al., 2005). The degree of homology between the ventral occipital maps in the two species cannot be assumed, but rather remains an area of active research (Vanduffel et al., 2014).

Other reasons for the lower agreement concerning the ventral occipital maps compared to the V1–V3 maps lie in the data themselves. For example, the ventral occipital maps are smaller, with fewer sample points on the cortex with which to identify the maps. Moreover, the stimulus driven, retinotopic signals in the hV4 and VO maps are less robust than the V1–V3 maps. For example, in an fMRI study which used a pyramid of Gabor's model of visual encoding to decode which of a large number of natural images a subject viewed while being scanned, the V1–V3 models were highly accurate, but the V4 and other extrastriate models were much less accurate (Kay et al., 2008). Together this means the quality of the retinotopic data is likely to be less robust in the maps beyond V1–V3, leading to more intersubject differences in measurement. As a result, none of the templates will fit perfectly across every data set.

Measurement limitations: HV4 and the transverse sinus

Despite these limitations, recent observations of the ventral occipital anatomy have improved the precision and consistency with which the maps can be measured. Some failures of the hV4 template arise due to distortions in the BOLD signal, rather than to the template incorrectly describing cortical organization. Large blood vessels (draining veins) can cause modulations in the BOLD signal which differ from the responses elicited by local neural activity (Lee et al., 1995; Dagli et al., 1999; Menon, 2002; Olman et al., 2007). Hence to correctly infer brain organization from fMRI scans, it is important to distinguish large-vessel artifacts from local cortical activity. One particularly large blood vessel, the transverse venous sinus (~5 mm diameter), frequently lies in close proximity to the hV4 map, causing a significant artifact in many functional MRI measurements (Winawer et al., 2010) (Fig. 4). In some subjects, imaging artifacts caused by the sinus have limited the ability to measure portions of the hV4 map, especially on the lateral aspect of the map exactly where the lower visual field representation is hypothesized to be located. By identifying imaging artifacts such as those caused from the transverse sinus, one can explain some of the subject-to-subject differences in the observed hV4 maps.

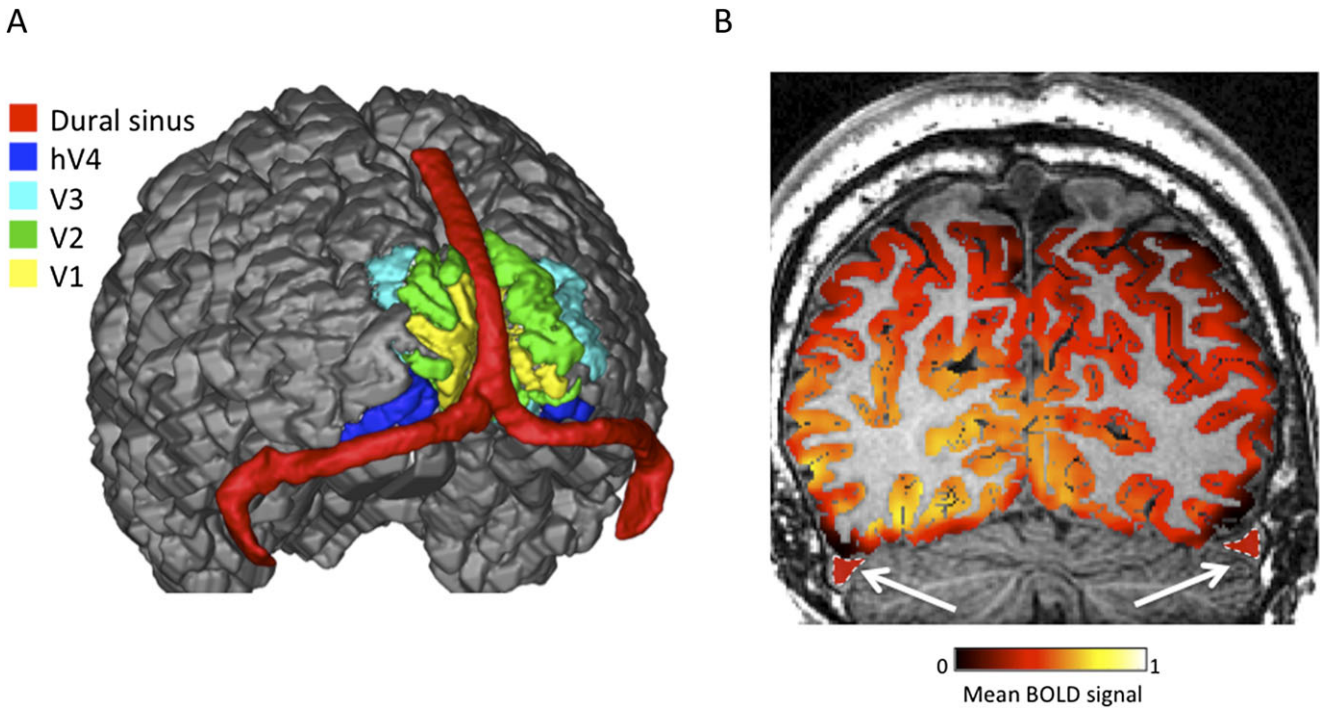

Fig. 4. HV4 and the dural sinuses. (**A**) Rendering of the cortex viewed from behind. Several visual field maps and the dural sinus are shown in solid colors. The hV4 map (blue) is close to the transverse venous sinus (red), which can cause signal dropout and other artifacts in fMRI scans, interfering with measurement of part of the hV4 map in some subjects. (**B**) A map of the fMRI signal intensity visualized on an anatomical coronal slice. White arrows point to the transverse sinus. The functional map is limited to the gray matter. Gray matter regions near the transverse sinus have low signal intensity (black) (after Winawer et al., 2010, with permission from the Association for Research in Vision and Ophthalmology).

In typical fMRI measurements, the artifacts do not span so large an area as to obscure the entire map; nonetheless, in any individual subject, an inability to accurately measure part of the map may preclude determining whether the map is responsive to the contralateral hemifield (180 deg), as predicted by Wade et al. (2002), *versus* responsive to less than a complete hemifield, say 135 deg, as predicted by Hansen et al. (2007). If, however, one considers a group of subjects, the problem is different because the alignment between the sinus artifact and the cortical maps varies across individuals. The interpretation of Winawer et al. (2010) was that when artifacts did not preclude a clear measurement of the hV4 map, the map extended to the lower vertical meridian, consistent with the hV4/VO model, but not the V4v/V4d model. A prediction from this work is that imaging methods which eliminate this artifact will show more consistent representation of the lower vertical meridian in the hV4 map across subjects.

Anatomical regularities: HV4 and the posterior transverse collateral sulcus

A more recent observation that contributes to a much more consistent characterization of the hV4 map is that its location is highly regular with respect to the sulcal patterns in ventral occipital cortex (Witthoft et al., 2013). The boundary between hV4 and VO-1 was identified by Brewer et al. (2005) as an eccentricity reversal (blue region in Fig. 2A). Witthoft et al. (2013) showed that part of this eccentricity reversal, and hence the hV4/VO-1 boundary, nearly always lies in a particular sulcus, the posterior transverse collateral sulcus (ptCoS). This observation was shown to be consistent across a large group of subjects, and provides an important constraint on how one identifies the hV4 map. One of the hV4 boundaries, the one shared with V3v, is relatively easy to identify by functional data because visually evoked fMRI signals in V3v are reliable and robust. Witthoft et al. (2013), by providing an anatomical landmark to locate a second boundary, effectively boxes in hV4 as well as VO-1, so that a large portion of each map can be reliably found in nearly every observer, just as V1 can be found in every observer because it always lies on the calcarine sulcus.

Taking advantage of this anatomical landmark, Witthoft et al. (2013) analyzed the functional data within hV4 and its neighbors and produced a useful schematic of the retinotopic map in hV4 and VO (Fig. 5). The schematic highlights an important point about the hV4/VO boundary, also observed by Brewer et al. (2005): namely, there is a rotation in the orientation of the iso-eccentricity lines and the iso-polar angle lines at the hV4 boundary. This rotation reflects the fact that the boundary between these maps is also a boundary between map clusters (Wandell et al., 2005). Across V1, V2, V3, and hV4, which are part of a single map cluster, the eccentricity bands are in register so that the foveal representations are all near to one another at the occipital pole. In contrast, there is a discontinuity in the eccentricity bands at the hV4/VO-1 boundary. The precise arrangement at the boundary between the map clusters varies across subjects, as indicated by the two example templates in Fig. 5. Having an anatomical landmark to identify one of the hV4 boundaries (the ptCoS) aids the development of a more precise template of the map organization at this boundary, which in turn facilitates identifying maps consistently across subjects. Moreover, it allows for educated guesses about the location of hV4 and VO-1

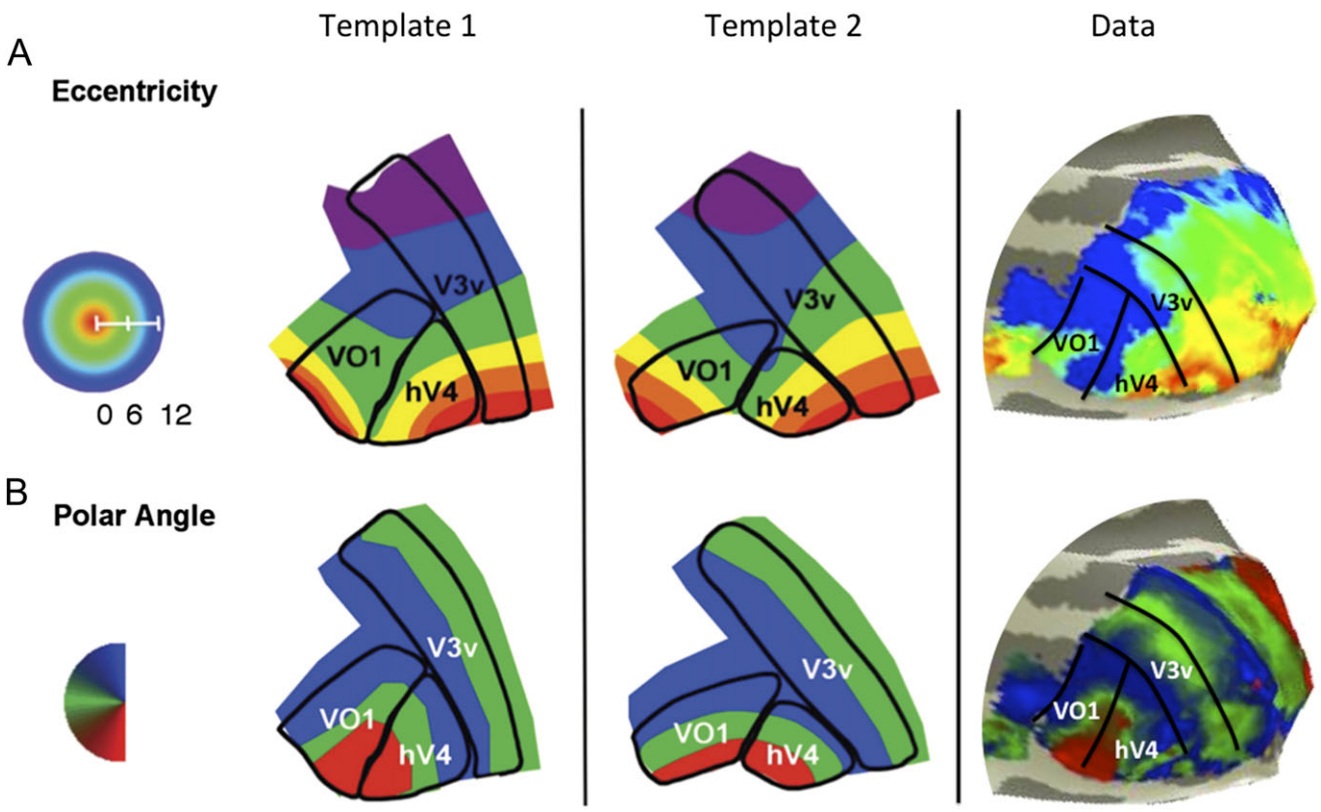

Fig. 5. Retinotopy in and around hV4. The left and middle panels are schematic diagrams of the organization of retinotopic data in V3v, hV4, and VO-1. The hV4/VO-1 boundary is identified by a reversal in the eccentricity map (here, green), upper panels (**A**), whereas the V3v/hV4 boundary is identified by a polar angle reversal (blue, bottom, (**B**)). In some cases, the angle maps bend sharply at the hV4/VO-1 boundary, as in the left example, and in some cases they do not, as in the middle column. The right column shows an example subject to compare to the schematic. It is more similar to the left schematic than the middle schematic. After Witthoft et al. (2013), by permission of Oxford University Press.

in cases where no retinotopy data are available, for example patient data where only anatomical images have been collected. It can also be used in conjunction with automated parcellation schemes relying on models or probabilistic atlases (Abdollahi et al., 2014; Wang et al., 2014). Nonetheless, fully automated, computational tools for identifying retinotopic properties from the anatomy, like those developed for V1–V3 (Benson et al., 2012; Benson et al., 2014), do not yet exist for hV4 and the VO maps.

Population receptive fields

For a decade and a half following the development of functional MRI, the dominant method for measuring retinotopic maps was the traveling wave method, also called phase-encoded retinotopy (Engel et al., 1994; Sereno et al., 1995; Engel et al., 1997). Over the last decade, measurements of responses within retinotopic maps have begun to incorporate newer computational tools, especially population receptive models, or pRF models (Yoshor et al., 2007; Dumoulin and Wandell, 2008; Kay et al., 2008 reviewed by Wandell & Winawer, 2015). The pRF method, building on earlier fMRI (Tootell et al., 1997; Smith et al., 2001) and LFP (Victor et al., 1994) studies, estimates not only the center position (x,y) in the visual field that most effectively produces a BOLD response but also the spatial extent of the visual field that a cortical region is sensitive to (pRF size). The pRF parameters reveal regularities both between and within visual field maps. Within any map, the more peripheral a pRF center, the larger (on average) the pRF size (Dumoulin & Wandell, 2008; Amano et al., 2009; Winawer et al., 2010; Kay et al., 2013*a*), a pattern also observed in single unit electrophysiology measurements in nonhuman animals. This relationship between eccentricity and pRF size can be well fit by a line that passes approximately through the (0,0) point (Fig. 6A). Using the line fits to these data, one can visualize the pRF sizes in the visual field for the different retinotopic maps (Fig. 6B). Moreover, pRF size at a given eccentricity tends to increase across the visual field maps. For example, the pRF sizes in hV4 are considerably larger than those in V1–V3, consistent with the notion that the scale of spatial pooling in ventral occipital cortex is larger than it is in V1–V3.

pRF models have begun to move beyond the description of the receptive field as a two dimensional Gaussian, incorporating more visual computations including task. For example, a recent pRF model showed that compared to V1 and V2, hV4 spatial summation across contrast patterns is more highly saturated (the response amplitude does not increase as much as the stimuli increase in size) (Kay et al., 2013*a*). Furthermore, compared to V1, hV4 is more sensitive to variations in contrast amplitude across the image (second order contrast) (Kay et al., 2013*b*). PRF models that account for task show that spatial tuning is shifted by attention in hV4 more than in V1–V3, and less than in lateral, temporal, and parietal maps (Klein et al., 2014). Similarly, pRF models could also be constructed to test theories about encoding of eye position

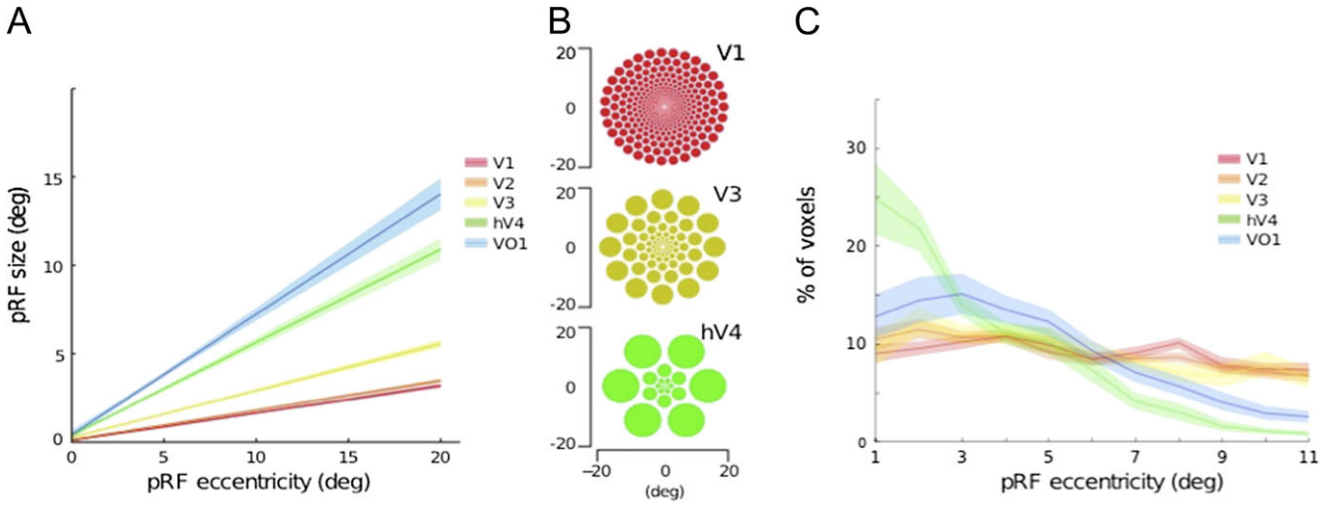

Fig. 6. Population receptive field parameters in hV4 and nearby maps. (**A**) Population receptive field size as a function of eccentricity in several human retinotopic maps. Two clear trends are evident. First, the population receptive field size increases with eccentricity within each map. Second, the population receptive field size differs between maps, with the smallest pRFs in V1, and much larger pRFs in ventral occipital maps (hV4, VO-1). Adapted from Kay et al. (2013*a*). (**B**) The spatial array of pRFs using the parameters in panel A. The radius of each circle is the apparent receptive field size at the appropriate eccentricity. Reprinted with permission from Winawer and Horiguchi (https://archive.nyu.edu/handle/2451/33887). (**C**) A histogram showing the fraction of voxels whose pRF center is located within different eccentricity bins. In hV4, most of the voxels have pRFs within a few degrees of the fovea. This pattern differs from the V1–V3 maps.

(Merriam et al., 2013) and spatial reference frames (d'Avossa et al., 2007; Crespi et al., 2011).

Visual field coverage

Aggregating pRF parameters across voxels from a single map shows another important difference between hV4 and V1–V3: the hV4 map has a more limited representation of the periphery than V1–V3. In hV4, unlike V1–V3, most of the pRF centers are within 3–4 deg of the fovea, with much sparser representation beyond that (Fig. 6C). This observation is consistent with the hypothesis that ventral visual cortex is largely specialized for recognition processes that depend heavily on foveal and parafoveal vision (Ungerleider & Mishkin, 1982; Goodale & Milner, 1992; Ungerleider & Haxby, 1994; Levy et al., 2001; Malach et al., 2002). HV4, situated between V3 and other ventral visual areas, may be the earliest (most posterior) visual field map to reflect this foveal bias. The foveal bias in hV4 is also evident in retinotopic maps visualized on the cortical surface, as the length of the hV4 map (fovea to periphery) is greatly reduced compared to V1–V3 (Fig. 2A and 2B, Fig. 5). The foveal bias can be quantified by the cortical magnification function (CMF): the amount of surface area devoted to each degree in the visual field as a function of eccentricity. In the central fovea (0.5 deg), the CMF in hV4 is larger than in V1, but at one degree and beyond, the CMF in hV4 is smaller than V1, consistent with enhanced representation of the central visual field in hV4 (Harvey & Dumoulin, 2011).

Another useful way to visualize retinotopic data within visual field maps is by a coverage map. A coverage map can be made either by plotting a point at the location of each voxel's (x,y) coordinate in the visual field (Fig. 7A and 7B), or by computing the envelope of the pRFs from within a map (Fig. 7C and 7D). The latter method, by accounting for the entire pRF of each voxel, shows all the regions in the visual field that the map is responsive to.

Coverage plots from several groups show that within the central 5–6 deg, the retinotopic representations in hV4, like V1, span both the upper and lower visual fields. However, the degree to which hV4 responds to the entire contralateral hemifield varies considerably across individual subjects, as is especially clear in the Arcaro et al. (2009) and Winawer et al. (2010) plots (7a,c). Furthermore, the plots pooling across subjects show that the hV4 map has little coverage of the peripheral visual field compared to V1 (Fig. 7B and 7D).

What's next to hV4?

It is easiest to find a boundary when one knows what is on both sides of it. In the case of the hV4 map, two of the boundaries meet this criterion. The posterior/medial boundary is shared with V3v and is clearly marked by a polar angle reversal at the upper vertical meridian (Fig. 5B, blue). The anterior boundary is shared with VO-1 and is defined by an eccentricity reversal at a peripheral representation (Fig. 5A, blue/green). What about the other side of hV4? In the template in Fig. 5 and the data shown in Fig. 2, the other side of hV4 is unlabeled. This is the ventral/lateral side of hV4, which tends to lie on or near the inferior occipital gyrus. The cortex on this side of hV4 contains a face selective region (Fig. 8). This region tends to lie on or near the inferior occipital gyrus and is sometimes called the occipital face area or inferior occipital gyrus-faces (Halgren et al., 1999; Rossion et al., 2003; Weiner & Grill-Spector, 2010). Whether or not this face patch directly abuts hV4 is not known, so it may not mark the precise border of hV4. Face areas, unlike visual field maps, do not (yet) have well described internal structure, and hence there is not a clear template that the researcher can use to decide where a face area begins and ends; instead, common practice is to use thresholded statistical maps, such that the size and boundaries of the area are dependent on signal-to-noise ratios in the measurement and the choice of contrast categories.

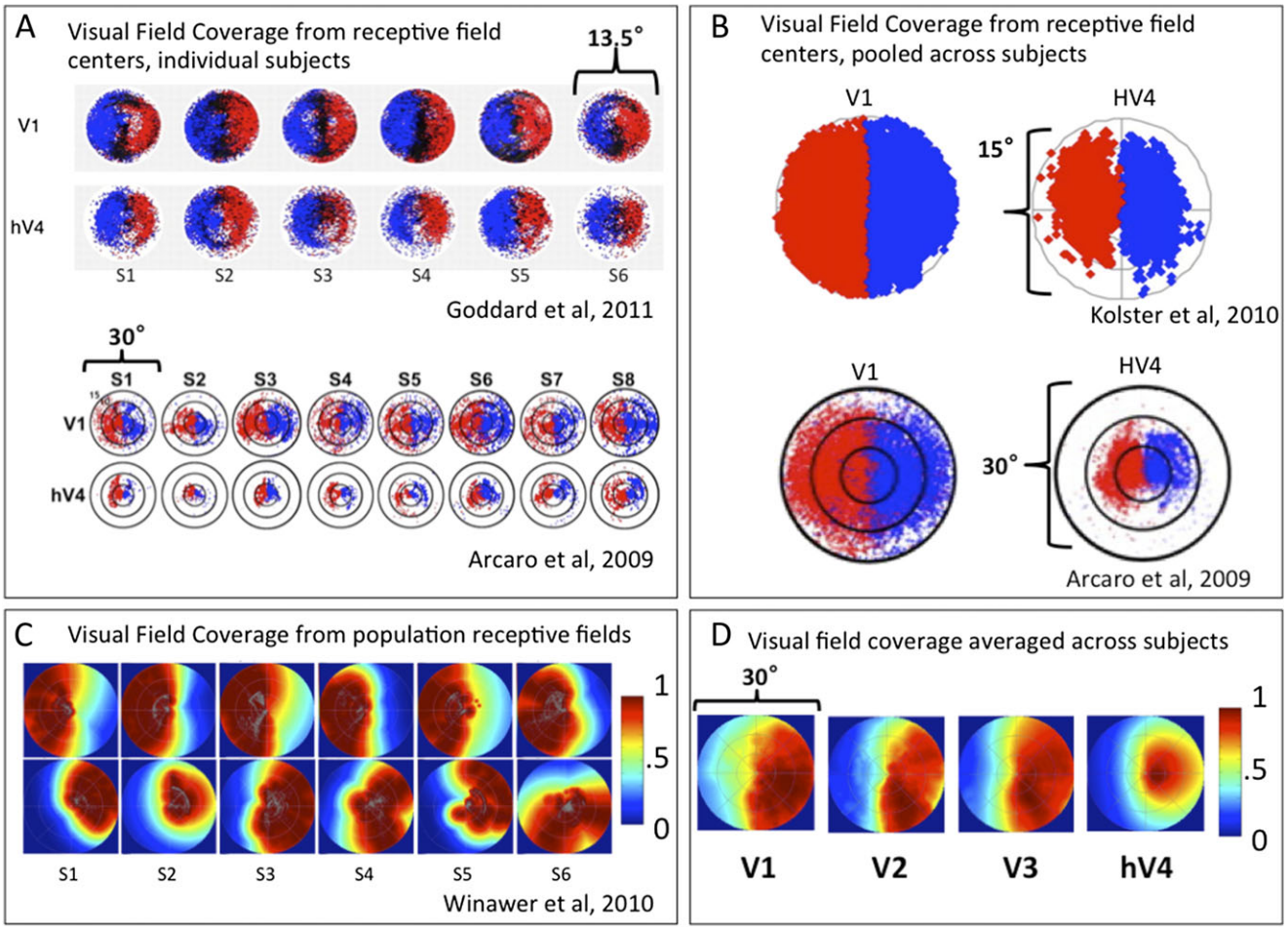

Fig. 7. Visual field coverage in hV4 and V1. (**A**) Two studies plot the (*x*,*y*) position within the visual field of each voxel within the V1 map or the hV4 map. Goddard et al. (2011) plot left hemisphere voxels in red and right hemisphere voxels in blue. The stimulus extent is 13.5 deg diameter. In both V1 and hV4, visual field coverage includes most of the contralateral hemifield, though the hV4 coverage of the periphery is sparser. Plots from Arcaro et al. (2009) show a similar pattern, although the color scheme is opposite, and the stimulus extent is larger (30 deg diameter). The hV4 responses are sparse in the periphery and variable across subjects, but cover much of the central 8–10 deg. Upper panel reprinted from Goddard et al. (2011), with permission from the Association for Research in Vision and Ophthalmology. Lower panel reprinted from Arcaro et al. (2009) with permission from the Society for Neuroscience. (**B**) Similar to A, but pooled across observers (Kolster et al., $n = 11$; Arcaro et al., $n = 8$). (**C**) Visual field coverage is computed as the envelope of the pRFs within a visual area (Winawer et al., 2010). The color bar indicates the height of the envelope at each point in the visual field, ranging from 0 to 1. Gray dots indicate pRF centers. Coverage varies across individuals. For many subjects, the hV4 map covers most of the contralateral visual field. (**D**) Coverage maps averaged across ($n = 16$) observers and hemispheres (pRFs from the right hemisphere are flipped across the *y*-axis), measured by one of the authors (NW), for V1–V3 and hV4. In each area, the coverage maps span most of the contralateral hemifield, though the coverage is more foveally biased in hV4.

In the hV4/VO work by Brewer et al. (2005), measurements to face stimuli and object stimuli were made both within and next to the hV4 and VO maps. Consistent with the reports of a face area on the inferior occipital gyrus, these authors also reported a greater response to face stimuli than object stimuli in the region next to hV4.

While face patches in ventral visual cortex are not yet associated with visual field maps in humans, they do lie in parts of the brain showing a strong preference for the fovea. Place selective patches, within the collateral sulcus by contrast, show a strong preference for the periphery (compare Figs. 1 and 8). This relationship between eccentricity preference and category selectivity in humans was initially observed by Levy et al. (2001), who argued for a single large eccentricity representation in visual cortex which encompassed both the posterior visual field maps (through V8/V4v) and more anterior regions which contained category selective responses but lacked a strong polar angle representation (Malach et al., 2002). They proposed that category selectivity and the attendant computations were built on top of parts of cortex which had the most relevant information. For example, face recognition requires high resolution, foveal vision, and therefore face selectivity will be found in anterior portions of visual cortex which have that information. Subsequent research has altered some aspects of this picture, showing multiple eccentricity representations in visual cortex (Wandell et al., 2005), clear polar angle representations extending along the occipital branch of the collateral sulcus, and a partial overlap between place selectivity and the visual field maps anterior to hV4 (Arcaro et al., 2009). Moreover, face- and place-selective areas can be characterized with the same kind of receptive field mapping used to study retinotopic maps (Witthoft et al., 2014;

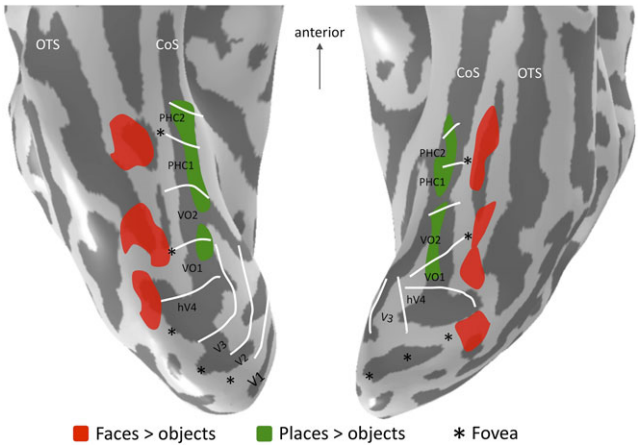

Fig. 8. Stimulus selectivity in ventral occipital cortex. The locations of face selective and place selective visual areas are shown relative to ventral visual field maps. Lateral to hV4, there is a face-selective region (red) on the inferior occipital gyrus. There are additional face-selective regions next to the VO-2 map and the PHC maps on the fusiform gyrus. Place-selective responses (green) overlap the VO-1/2 and PHC-1/2 maps. Figure provided courtesy of Kevin Weiner, after Grill-Spector and Weiner (2014), with permission from Nature Publishing Group.

Kay et al., 2015). Nonetheless, the general point that there is large-scale eccentricity structure in visual cortex, and that the visual field maps and category selective regions are in register with this eccentricity structure and one another has been borne out by subsequent research.

Another intriguing proposal is that there are additional visual field maps next to hV4 on or near the inferior occipital gyrus. One group has reported two maps in this region, which they call phPIT (putative human posterior inferior temporal area) to be consistent with maps described in the macaque literature (Kolster et al., 2010; Abdollahi et al., 2014). Because the maps described by Kolster and colleagues are small, and because they are in a location where transverse sinus artifacts will sometimes interfere with fMRI measurements (Winawer et al., 2010), routinely measuring these maps is a challenge. Nonetheless, if the description of these maps is correct, it would help constrain the interpretation of retinotopic data in the vicinity of hV4, which in turn would further clarify the organization of visual areas in ventral occipital cortex. Because a face area and retinotopic maps have been separately reported to exist near the same boundary of hV4, a question arises as to whether they overlap: is the occipital face area in the phPIT maps? Recent estimates that combine data across studies suggest that they do overlap (Janssens et al., 2014); confirmation from within-subject analyses would further strengthen this observation.

Stimulus selectivity within and near hV4

As we discussed in the introduction, one of the motivations for identifying visual field maps is to characterize the computations and representations within them. The earliest studies of visual responses in macaque V4 (Zeki, 1973) and its putative homolog in humans (Lueck et al., 1989) indicated that the area was sensitive to color. Subsequent studies with more precise definitions of the boundaries of hV4 and VO-1/2 have confirmed that these ventral occipital maps respond robustly to color exchanges (Wade et al., 2002; Brewer et al., 2005), or to the addition of chromatic contrast on a luminance pattern (Wade et al., 2008). In contrast, the region anterior to dorsal V3 appears to respond minimally to chromatic contrast (Wade et al., 2008), though a small color-related activation was noted in group averaged analyses. This is the location one would expect to find a dorsal V4 if the human maps were organized similarly to the macaque maps. The fact that robust responses were observed for chromatic stimuli in the region anterior to ventral V3 but not the region anterior to dorsal V3 supports the conclusion that these two regions do not comprise a single map, thus arguing against the V4v/V4d proposal (Hansen et al., 2007). Similarly, when subjects viewed either full color movie segments or matched achromatic movie segments, there was a larger response to the color segments in hV4 and VO-1, but not in the location of putative dorsal V4 (Goddard et al., 2011).

Several studies have sought to quantify ventral occipital responses to color in terms of stimulus properties. For example, Brouwer and Heeger (2009) examined how cortical responses vary with stimulus hue. Using a color encoding model and multivariate decoding methods, Brouwer and Heeger showed that color representations in hV4 and VO-1 differed from V1–V3 and from lateral occipital maps. In hV4 and VO-1, summary measures of multivoxel responses revealed a pattern of neural similarity between colored stimuli that more closely matched perceptual similarity, compared to other visual field maps. These results suggest a link between color perception and the representation of color in ventral occipital maps.

Measurements of temporal frequency encoding also indicate a link between responses in the ventral occipital maps and color perception. As the temporal frequency of chromatic patterns increases, the responses in the VO-1 map decrease sharply; the response to 7.5 Hz flicker is much lower than to 1.5 Hz flicker. In V1, responses to luminance patterns and red-green chromatic patterns are relatively constant up to about 10 Hz (Liu & Wandell, 2005). These authors point out that the pattern in VO-1 matches the psychophysical phenomenon that rapidly flickering lights lose their color appearance. The pattern in hV4 was intermediate between the pattern in V1 and in VO-1. Similarly, the fMRI response in VO-1 does not distinguish between a rapidly flickering equiluminant stimulus (25 Hz) and its nonflickering, fused control (Jiang et al., 2007). The fact that VO-1 does not distinguish these stimuli matches observers' inability to distinguish the stimuli. In contrast, V1 responds much more robustly to the high frequency flicker than the static control. As in the Liu and Wandell study, the hV4 response is intermediate between the VO-1 and the V1 responses.

Together, many studies now implicate both hV4 and the VO-1/2 maps in color vision. These same studies do not find a similar level of color-selective responses in dorsal areas adjacent to V3d. Because the hV4 map borders the VO-1 map, it is difficult to know whether lesions to one of the maps or both of the maps explain cortical color blindness. These studies do not indicate that hV4 and VO-1 are the only regions involved in encoding color. Indeed, it is likely that color representations are distributed throughout much of the visual pathways. Rather, the studies show that color responses within hV4 and the VO maps are robust and that the representations within these maps more closely match behavior than representations in several other cortical visual areas.

Although the earliest descriptions of the fourth visual area in macaque and in human emphasized color selectivity, many subsequent studies have implicated macaque V4 (Gallant et al., 1993; Pasupathy & Connor, 2002) and hV4 (Dumoulin & Hess, 2007; Hansen et al., 2007; Bouvier et al., 2008; Konen & Kastner, 2008) in attention as well as the encoding of texture, form, and surfaces. One proposal is that V4, in both human and macaque, plays a key role in

communication between the early visual areas and inferotemporal cortex, especially in the selection of stimulus features (Roe et al., 2012). In this view, V4 selection is important for both feedforward processing (recognition) and feedback (attention). The human visual maps anterior to hV4—VO-1/2—have also been implicated in stimulus specific processing other than color, including objects (Brewer et al., 2005) and scenes (Arcaro et al., 2009).

Summary and future directions

Since its discovery, hV4, as well as its neighboring VO maps, has attracted significant attention. One reason is its location. It is situated between the early maps (V1–V3) and many of the ventral occipital and temporal visual areas that are critical for recognition, including regions that are highly responsive to objects (Malach et al., 1995), faces (Kanwisher et al., 1997), scenes (Epstein et al., 1999), and words (Cohen et al., 2000). A clearer definition of the location and organization of hV4 and VO cortex is an important step toward characterizing the ventral pathway in human visual cortex. Another reason it has attracted attention is the response properties within the map, for example, its responsiveness to color and other surface properties (Wada et al., 2014), as well as its role in attention (Hansen et al., 2007). The hV4 and VO maps also differ qualitatively from the earlier visual field maps, V1–V3, in that lesions to V1–V3 result in partial visual field blindness (scotomas) (Inouye, 1909; Holmes, 1918; Horton & Hoyt, 1991*a*,*b*), whereas lesions to hV4 and VO do not; instead, lesions to hV4 and VO cause selective perceptual deficits (Meadows, 1974*b*; Zeki, 1990; Bouvier & Engel, 2006). In other respects, the hV4 and VO maps differ quantitatively from the V1–V3 maps. For example, the population receptive fields measured with fMRI are larger and more foveally biased. Together, the location and stimulus properties of hV4 suggest that it is likely to play an important role in coordinating signals between the early retinotopic maps and the various downstream visual areas involved in recognition and appearance.

We have reviewed multiple claims about the organization of the fourth visual field map and its neighbors, and believe that the preponderance of the evidence favors the proposal with an hV4 hemifield map on the ventral surface, VO-1/2 maps anterior to hV4, and LO-1/2 maps on the lateral surface. The evidence comes from retinotopic data, anatomical regularities, and stimulus selectivity. Yet, we believe that further progress is needed to understand the organization of ventral occipital cortex, especially in the form of more quantitative models and better data. One path forward will be to specify competing models in more computational terms, and to solve models on publicly available data sets using shared code. Tools for automated fitting of the V1–V3 maps (Benson et al., 2014) rely on the publicly available Freesurfer software (http://surfer.nmr.mgh.harvard.edu). Extending these models to additional field maps on the ventral surface, and testing the models on public data sets as they become available such as the Human Connectome Project (Van Essen et al., 2013), will likely facilitate better agreement between labs and more certain conclusions. Furthermore, extending automated tools to not just fit templates to data, but to do model comparison, will help resolve between competing proposals.

While our understanding of the organization of cortical areas defined using fMRI has increased, the field has also made progress in mapping the connections between them. Recent work using DTI measurement of white matter in conjunction with new validation methods, has shown that one particular tract, the vertical occipital fasciculus, connects ventrolateral visual field maps (hV4, VO) with dorsal visual field maps (V3A/B) (e.g., Pestilli et al., 2014). It is notable that these dorsal and ventral maps all contain contiguous hemifield representations, in contrast to the adjacent maps, V2 and V3, which split the quarterfields into dorsal and ventral halves. A representation of the full hemifield in hV4 and VO on the ventral side, and V3A/B on the dorsal side is desirable properties if these areas are important information centers communicating between the ventral and dorsal streams.

A second type of connectivity metric measures population receptive fields in one brain area with reference to a second brain area, rather than with reference to the stimulus (Heinzle et al., 2011; Haak et al., 2012). For example, the response in a V3 voxel could be described as a surface Gaussian within V1, such that the weighted sum of the V1 voxel time series predicts the time series in the V3 voxel of interest. Such methods have the potential to increase our understanding of how visual areas communicate with one another, for example quantifying how large a surface area in one map is sampled by each point in another map. Applying such models to ventral visual field maps (e.g., Baldassano et al., 2012) offers a complementary approach to fiber tractography. There can be little doubt that the better understanding of visual cortex connectivity will help clarify the surface arrangement of the multiple maps, and their inputs and outputs.

Yet, accurate fitting of retinotopic maps is as much a means as an end. We hope that better agreement between groups about where the maps lie and how they are organized will allow for more rigorous tests of what the maps do, and why so many of them exist (Barlow, 1986).

Acknowledgment

We thank Jennifer M. Yoon for helpful comments. Funding from NIH Grant EY022116 (JW); and EY02988, EY02391501, and EY019279 in support of NW (PI Kalanit Grill-Spector).

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