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A step toward understanding the human ventral visual pathway

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Goddard E. A step toward understanding the human ventral visual pathway. *J Neurophysiol* 117: 872–875, 2017. First published June 29, 2016; doi:10.1152/jn.00358.2016.—The human ventral visual pathway is implicated in higher order form processing, but the organizational principles within this region are not yet well understood. Recently, Lafer-Sousa, Conway, and Kanwisher (*J Neurosci* 36: 1682–1697, 2016) used functional magnetic resonance imaging to demonstrate that functional responses in the human ventral visual pathway share a broad homology with the those in macaque inferior temporal cortex, providing new evidence supporting the validity of the macaque as a model of the human visual system in this region. In addition, these results give new clues for understanding the organizational principles within the ventral visual pathway and the processing of higher order color and form, suggesting new avenues for research into this cortical region.

color vision; fMRI; macaque inferior temporal cortex; natural images; ventral visual pathway

THE VENTRAL VISUAL PATHWAY shows strong responsiveness to complex form and is suggested to play a critical role in visual object identification and categorization (Grill-Spector and Weiner 2014). For example, previous work has identified that the human ventral temporal cortex contains subregions that have face-biased or place-biased responses (Levy et al. 2001). Lafer-Sousa et al. (2016) used functional magnetic resonance imaging (fMRI) to measure cortical responses while subjects viewed chromatic and achromatic movie clips to compare the locations of face-, place-, and color-biased responses within the human ventral visual pathway. Thirteen subjects viewed the natural movie clips, which comprised 3-s clips grouped into 18-s blocks according to their content (face, bodies, scenes, objects, or scrambled objects) and color (full color or grayscale). While the subjects viewed these stimuli, partial-head functional volumes (including the ventral surface of the temporal lobe) were acquired. On the basis of these data, the authors defined face-biased voxels [where the blood oxygen level-dependent (BOLD) response to face blocks was greater than for objects], along with placebiased voxels (which showed a higher response to places than objects) and color-biased voxels (with a higher response to color than to grayscale blocks, grouped across content). They identified face-biased and place-biased regions in their analyses, as demonstrated previously (Levy et al. 2001), but sandwiched between these regions, they also found regions of color-biased responses (see Fig. 1).

This arrangement is strikingly similar to the layout the authors found previously in inferior temporal (IT) cortex in the macaque (Lafer-Sousa and Conway 2013), providing further evidence of functional homology between these regions. Together, the data from macaque and human neuroimaging offer new clues for understanding the processing of color and form by these regions.

Functional homology between the human ventral pathway and macaque IT cortex. Visual neuroscience has a rich history of using primate models, such as macaque, to investigate neuronal response properties. Establishing the homology between these primate models and the human visual system is a critical step in accurately applying such models, for which neuroimaging is a powerful tool. Lafer-Sousa et al. (2016) report that along the ventral visual pathway in humans, the organization of functional responsiveness to faces, color, and objects is broadly consistent with the organization of these functional properties in macaque IT cortex, identified by the authors in previous work (Lafer-Sousa and Conway 2013). Lafer-Sousa et al. (2016) plot the macaque and human data side-by-side in Fig. 9 of their paper, illustrating the commonalities in the organization of functional responses despite anatomical differences between the species in this region of cortex, particularly in the relative expansion of the cortical surface ventral to the superior temporal sulcus (STS) in humans. This functional homology provides new evidence that macaque IT cortex is a suitable model of the ventral visual pathway in humans by confirming that the human ventral visual pathway and macaque IT cortex not only show similar response properties but also are comparable in their internal organization. Strengthening the case for functional homology of these regions is important for confirming the validity of macaque IT cortex as an animal model for the human ventral visual pathway, particularly since the ventral visual pathway is adjacent to area V4, an earlier visual area for which the homology between humans and macaques breaks down. Specifically, in macaque V4, the upper and lower halves of the contralateral hemifield representation are split, located on the ventral and dorsal surfaces of the occipital cortex respectively, whereas in humans, there is a single hemifield representation on the ventral surface (Goddard et al. 2011; Winawer and Witthoft 2015).

Clustering of functional preferences in the ventral visual pathway. As we piece together evidence from visual field mapping and functional preference in the ventral visual pathway, it remains unclear to what extent these regions of different functional preferences (including eccentricity and object

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Fig. 1. Comparison of approximate locations of the face-, place-, and color-biased regions reported by Lafer-Sousa et al. (2016) with visual field maps along the ventral visual pathway. A: an inflated cortical surface (MNI average brain, rendered using MATLAB 2013a and the toolbox mni2fs) is viewed from below, on which the right-hemisphere collateral sulcus (CoS), fusiform gyrus (FG), and mid-fusiform sulcus (MFS) are labeled. The approximate locations of lower and upper meridian representations (white and black dashed lines, respectively) and fovealrepresentations (asterisks) are drawn on the inflated surface of the right hemisphere with reference to the data in Fig. 2 of Winawer and Witthoft (2015) and Fig. 3 of Grill-Spector and Weiner (2014). B: schematic illustration of the arrangement of the right-hemisphere visual field maps V1 to PH-2 on a flattened cortical surface (as described by Arcaro et al. 2009). C: illustration of the approximate location of the face-, place-, and colorbiased regions (drawn with reference to Fig. 9 of Lafer-Sousa et al. 2016) in relation to the areas defined in B. Since Lafer-Sousa et al. (2016) did not include visual field mapping beyond hV4, the estimated alignment of their data with the visual field maps is based on anatomical landmarks.

category) form continuous maps for each feature or whether they comprise a series of distinct clusters. DiCarlo et al. (2012) suggest that in macaque IT, behavioral goals may be a better spatial organizing principle than visual field maps. Similarly, Kravitz et al. (2013) argue that the ventral visual pathway is likely a group of highly connected visual areas responsive to higher order object properties, where each has distinct patterns of connectivity to other brain regions and subserves slightly different behavioral functions, such as the identification of faces, objects, scenes, tools, and written words. Many of the gradients in functional preference are spatially aligned and likely to be interrelated. For example, Grill-Spector and Weiner (2014) note that the gradients from face-preferring to scene-preferring, and foveally biased to peripherally biased, along with other functional gradients, are each lateral-to-medial gradients across the mid-fusiform sulcus (MFS; see Fig. 1).

Interestingly, the color-preferring regions identified by Lafer-Sousa et al. (2016) do not create another lateral-tomedial gradient. Instead, the color-preferring regions lie in the center of these other gradients, with non-color-preferring regions on either side (see Fig. 1). Of particular relevance to the issue of gradients within the ventral visual pathway, Lafer-Sousa et al. (2016) found a dissociation of color and object category preference: the color-biased regions were not strongly biased for object category, and object-category-biased regions (on either side of the color-biased regions) were not strongly biased for color (although see caveats below). The authors also found a similar dissociation in macaque (Lafer-Sousa and Conway 2013). This provides evidence against the notion that there is a smooth transition from face-preferring to placepreferring neural responses across the cortical surface. Instead, these results suggest that there is some clustering of feature preferences within the ventral visual pathway, with discontinuities in object-category preference across the cortical surface. To better understand the functional organization of the ventral visual pathway, we need to continue to not only identify the arrangement of functional preference for eccentricity, object category, color, and other features but to also understand how these feature preferences interact.

Separation of color and form in the ventral visual pathway? The clustered arrangement of color preference and objectcategory preference reported by Lafer-Sousa et al. (2016) also raises the debate of the extent to which color and form information is processed separately by the ventral visual pathway. Early electrophysiology studies arguing for the segregation of color and form signals in subregions of V1 and V2 were typically based on describing biases for color, orientation, or direction of movement, but Gegenfurtner (2003) demonstrated that these biases were accompanied by residual responses to nonpreferred stimulus dimensions. In a recent review, Rentzeperis et al. (2014) concluded that evidence from behavioral and neurophysiological studies largely favors an integrated coding of color and form, where there is not a strict segregation between neurons or areas that are sensitive to color and those sensitive to form. Rentzeperis et al. (2014) argue that since the brain likely uses population codes to represent stimulus features, rather than relying on the responses of a small number of neurons, the presence of weak responses to a nonpreferred stimulus dimension may nonetheless carry significant information about that dimension that is used by the brain.

Although Lafer-Sousa et al. (2016) demonstrate a clear dissociation in the biases of the color and object categorypreferring subregions of the ventral visual pathway, further work is needed to test how these biases affect the stimulus related information represented by the populations of neurons in these subregions. Lafer-Sousa et al. (2016) note that adaptation and multivariate pattern analysis could be applied to reveal further information about the dissociation between color and form information. In particular, multivariate pattern analysis could be used to link the biases with the population codes for these stimulus features in future work.

Emergence of higher order color representations. If ventral temporal cortex is specialized for "high-level" form information, then it is unsurprising that complex, naturalistic stimuli induce stronger responses and sample a greater range of functional responsiveness of ventral temporal cortex. This relates to a more general point of how we can best characterize the response properties of higher level areas. Reduced stimuli allow easier control of features of interest and can be used to generate models of response properties that are tested with more natural stimuli (Rust and Movshon 2005). However, as we progress from V1 to mid-level areas like V4, and to higher level areas, "building" response properties from the bottom up becomes progressively more complicated, and acquiring sufficient data to constrain such models becomes untenable (DiCarlo et al. 2012).

For higher order areas then, it may be necessary to use naturalistic, rather than simplified, stimuli to explore the area's range of functional responses. This point has been raised by previous fMRI studies investigating the response properties of human ventral temporal cortex. One example is the work presented by Haxby et al. (2011), who compared individuals' BOLD responses evoked by a full-length movie and by simpler, static stimuli in abstract, high-dimensional model spaces, designed to summarize the responses of ventral temporal cortex. They found that when data were in the model space constructed using responses to movies, classifiers could be trained to discriminate the simpler static stimuli, but not the other way around. This suggests that the richer movie stimulus evokes responses that vary along a greater number of relevant stimulus dimensions, and so more effectively capture the range of functional responses within the ventral temporal cortex.

Interestingly, in a subset of subjects, Lafer-Sousa et al. (2016) compared naturalistic and reduced stimuli in their ability to identify color-preferring voxels in visual and inferior temporal cortex. They measured preference for chromatic over achromatic stimuli by using both naturalistic movie clips (chromatic and achromatic versions, matched for luminance) and drifting gratings (colored, equiluminant gratings and gratings defined by a 50% luminance contrast). They found that analyzing the responses to grating stimuli yielded a larger number of color-preferring voxels in early visual cortex, whereas analyzing the responses to movie clips yielded a larger number of color-preferring voxels in the

central and anterior color-biased regions (Cc and Ac). In their posterior color-biased region (Pc, including hV4 and VO), both stimulus types produced similar results.

This dissociation may simply reflect a lower overall responsiveness in the central and anterior color-based regions (Cc and Ac) to the reduced grating stimuli so that the difference effect is no longer revealed when simple stimuli are used. Alternatively, the dissociation might be indicative of a qualitatively different representation of color in higher order areas, such as the central and anterior color-biased regions (Cc and Ac). Brouwer and Heeger (2013) have previously demonstrated that color responses reflect color categories in hV4 and VO-1 [both within the posterior color-biased region (Pc) of Lafer-Sousa et al. 2016], but not in earlier visual areas. Beyond hV4, it seems likely that the neural response to color would continue to transform qualitatively to represent color information that is relevant to object and scene recognition (for example, see Bartels and Zeki 2000), and to integrate information from vision with memory and language systems. Future work may reveal the nature of how visual color information is transformed beyond hV4 within the ventral visual pathway and how color information in these regions interacts with object and scene representations.

Overall, the findings of Lafer-Sousa et al. (2016) provide evidence of functional homology between the human ventral visual pathway and macaque IT, and offer new insights into the functional organization of this cortical region. Additionally, the regions of color-biased responses provide a new starting point for region-of-interest-based research into higher order color representations, which will likely be best revealed by measuring neural responses to complex, naturalistic stimuli.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author.

AUTHOR CONTRIBUTIONS

E.G. prepared figures; E.G. drafted manuscript; E.G. edited and revised manuscript.

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