

Letter

Third Visual Pathway,
Anatomy, and Cognition
across SpeciesKevin S. Weiner^{1,2,*} and
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Pitcher and Ungerleider [1] proposed extending the two visual pathway model to include a third visual pathway (TVP) for social perception. The TVP is consistent with the lateral stream as previously referenced in the human neuroimaging literature [2–4] (Figure 1). The authors use a variety of evidence in support of the TVP, including examples of homology between human and macaque. Although we agree with their general proposal of the TVP, we offer additional anatomical and functional findings that suggest differences in the TVP between species and in the functional roles of the TVP beyond social perception.

Is V5/MT the Entry Point of the TVP?

The authors highlight that neural signals reach the superior temporal sulcus (STS) via V5/MT (Figure 1B), a cortical region involved in processing visual motion. However, recent research shows that a nearby face-selective region located above V5/MT in the human posterior STS (pSTS-faces; Figure 1B), which was a main focus of the opinion article, is connected to the far periphery of V1/V2 [5]. These connections bypass V5/MT and serve as evidence suggesting that V5/MT may not be the sole entry point of the TVP. Functionally, these connections likely contribute to the peripheral visual field bias in pSTS-faces described by the authors. Interestingly, like humans, macaques also have a cortical area above V5/MT that is connected to the periphery of V1/V2 [6]. However, unlike humans, this area is not face-selective in macaques, which we expand on further at the end of this Letter.

Future studies can examine if there are parallel anatomical and functional subroutes within the TVP across species – some that include V5/MT and some that do not.

Is Motion a Necessary Factor of the TVP?

If V5/MT is not the sole entry point of the TVP, then it is unlikely that defining functional properties of the TVP 'is dependent on the use of moving visual stimuli' ([1] p.2). For example, a region selective for static objects (area LO of the lateral occipital complex) that overlaps two retinotopic maps, LO-1 and LO-2, is often associated with the ventral stream. However, recent findings situate both maps in the lateral stream (Figure 1A,C). Intriguingly, these two maps have been causally implicated in the perception of stationary, not moving, stimuli: transcranial magnetic stimulation to LO-1 disrupts orientation, but not shape, discrimination, and vice versa for LO-2 [7]. Thus, motion may not be a necessary defining factor of the TVP, which can be explored in future research. More broadly, the definition of the TVP will require reconsideration of which areas presently assigned to either the dorsal or ventral streams are located within the TVP (including the extrastriate body area, as mentioned by the authors), as well as whether the TVP contains functional properties that are distinct from, or are an integration of, both streams [2,8].

Multimodal Processing within the TVP?

While the authors stress the role of the TVP for social perception and motion processing, we also highlight that the TVP is likely critical for other types of visual processing (as discussed in the previous paragraph), as well as for multimodal processing that is not necessary for social perception. For example, previous findings show that regions situated posterior and anterior to V5/MT are also multimodal. Object-selective regions posterior to V5/MT show preferential responses for haptic

presentations of objects [9], while body-selective regions posterior and anterior to V5/MT also show preferential neural responses when participants move their own body parts – movements that do not necessarily convey social meaning [10]. Thus, although 'no simple one-word description' ([1] p.9) encompasses the functions of the TVP, many are likely to be (i) multimodal, (ii) non-visual in nature, or (iii) relatively low-level (e.g., orientation discrimination in LO-1 as discussed in the previous paragraph) compared with more complex neural computations underlying social perception.

Are Anatomical Differences in the TVP Functionally Meaningful between Species?

Classic anatomical criteria such as connectivity and cytoarchitecture (e.g., the neural hardware considered to perform computations underlying cognitive function) have been used to parcellate different brain areas from one another. A majority of these approaches are observer-dependent. Modern observer-independent approaches [11] (Figure 1D) are automated and statistically determine boundaries between adjacent areas. These approaches have not yet parcellated a large cortical expanse of the TVP anterior to human V5/MT [11]. Thus, immediate open questions are: (i) How far anteriorly does the TVP extend across species? (ii) What is the relationship between functional and cytoarchitectonic parcellations of the TVP between species? (iii) What are the similarities and differences of that relationship between species? For example, while cortex superior to V5/MT has shared connectivity to peripheral V1/V2 in both species [5,6], only in humans is it face-selective, potentially resulting from cytoarchitectonic differences of the TVP between species.

Concluding Remarks

The opinion article by Pitcher and Ungerleider offers an exciting opportunity to better understand not only homologous

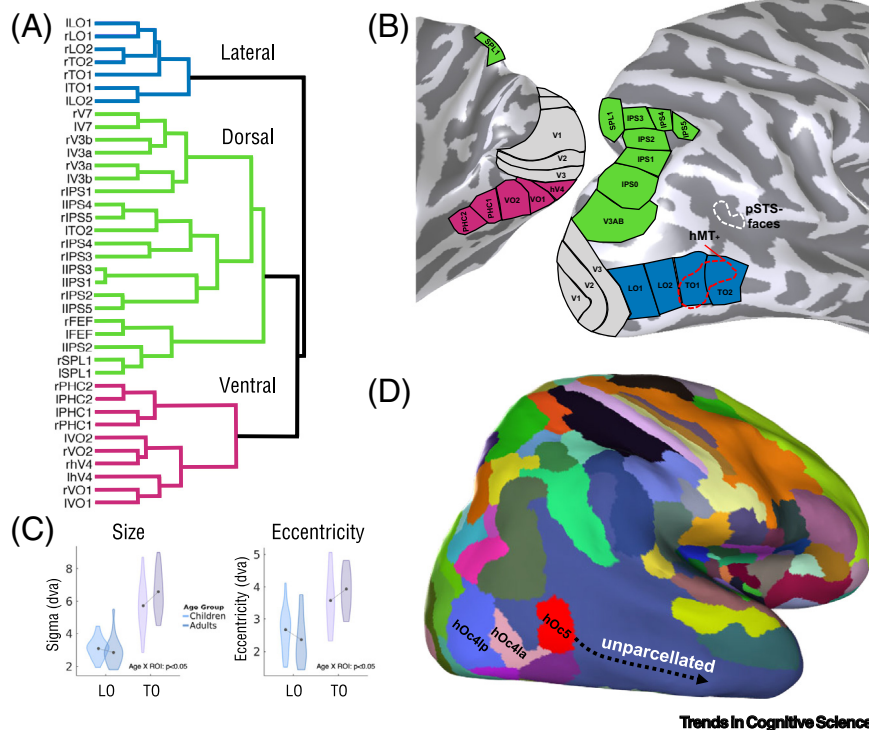


Figure 1. Additional Functional and Anatomical Features of the Third Visual Pathway (TVP) in Humans. (A) Visual cortex comprises many retinotopic representations of the visual field, commonly referred to as visual field maps. Functional connectivity analyses [3] among 22 of these maps found a triple dissociation among lateral, ventral, and dorsal visual field maps, supporting the three cortical pathways proposed by Pitcher and Ungerleider [1]. (B) Views of an inflated cortical surface show the anatomical position of these visual field maps colored according to the three streams identified in panel A (early visual areas in gray). A face-selective region within the posterior superior temporal sulcus (pSTS-faces, broken line white outline) and human motion-selective complex (hMT+, broken line red outline, which includes V5/MT) are also depicted. (C) Population receptive field data in children and adults of lateral stream maps in lateral occipital (LO) and temporal occipital (TO) cortices show development in which both receptive field size (sigma) and distance from the fovea (eccentricity) change with age [4]. Such development has not been observed in ventral stream maps, further functionally dissociating the TVP from the ventral stream. Images reproduced under Copyright Clearance (number 5017221436750). (D) Observer-independent cytoarchitectonic parcellation of the human cerebral cortex [11]. A large portion of the TVP in front of human (h) occipital area hOc5 (red, the cytoarchitectonic homolog of human V5/MT) is cytoarchitectonically unparcellated in humans using observer-independent methods. hOc4lp and hOc4la are proposed cytoarchitectonic homologs of LO-1 and LO-2, respectively. Image generated from <https://jubrain.fz-juelich.de/apps/cytoviewer2/cytoviewer-main.php> [11]. Abbreviations: dva, degrees of visual angle; FEF, frontal eye field; hOc, human occipital (this is a neutral nomenclature used in observer-independent cytoarchitectonic approaches [11]); hV4, the 'h' stands for human and V4 refers to the fourth visual area (hV4 is often used as a label because the homology between hV4 and macaque V4 is still heavily debated); IPS, intraparietal sulcus; LO, lateral occipital; PHC, parahippocampal cortex; ROI, region of interest; SPL, superior parietal lobule; TO, temporal occipital; V1, V2, V3, etc., a well-accepted nomenclature in which V stands for visual and each number refers to a subsequent area in the visual processing hierarchy; VO, ventral occipital.

areas and networks between species, but also areas and networks that are likely uniquely human and contribute to uniquely human aspects of cognition. Although the concept of pathways in visual cortex is contentious, it is difficult to argue against the impact of Ungerleider and

Mishkin's original model [12]. Altogether, we write this letter respectfully acknowledging Ungerleider's enormous contribution to understanding visual pathways and cortical areas from anatomical, neural, and fMRI studies across species. In addition to those groundbreaking

contributions, we emphasize the impact that the proposed modification of a TVP by Pitcher and Ungerleider will have for decades to come.

Acknowledgments

We thank Kalanit Grill-Spector, Jonathan Winawer, and two anonymous reviewers for useful comments on previous versions of this Letter.

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<https://doi.org/10.1016/j.tics.2021.04.002>

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