

Does the dorsal pathway derive intermediate shape-centred representations?

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Vannuscorps et al. (2021) present a case study of a young woman named Davida, who has a highly selective visual disorder. The authors conducted an impressive set of complementary experiments and provided evidence that Davida perceives 2D shapes, bounded by sharp, high contrast edges, to be flipped along their own axes and/or orientated along their shape-centred coordinates (90° , 180° , 270°). However, these unique deficits were not found for perception of 3D stimuli, stimuli that are strongly blurred, implied by motion, or defined by low luminance contrast with the background. To explain these results, the authors proposed the existence of an intermediate stage of processing in the visual system termed “intermediate shape-centred representation” (ISCR) that represents bounded areas of the visual field in a shape-centred frame of reference. These ISCRs are computed in parallel based on different visual cues before being integrated and mapped onto higher frames of reference to support visuoperceptual and visuomotor behaviours.

Accordingly, Davida’s case reflects a failure in the transition of ISCR to higher frames of references, as she is unable to integrate computations of axis correspondence and axis polarity for high contrast stimuli, presumably represented by the parvocellular system, even though her computations of tilt magnitude/direction remain intact. Here, we discuss an outstanding question regarding the proposed ISCR. Namely, what neural basis can support the computations of these intermediate, shape-bounded representations? Vannuscorps et al. (2021) proposed that regions LO1 and LO2 of the ventral pathway can subservise this function (p. 16) and the Davida’s specific deficit may be a result of deficient dorsal to ventral flow of information (p. 17). Here, we offer an extended view and claim that ISCRs might not be a unique property of the ventral visual pathway and can also reflect computations carried out by regions in the posterior parietal cortex (PPC), which are part of the dorsal visual pathway. We then suggest that these dorsal

intermediate representations are subsequently projected to higher regions along both pathways to support perception and action.

The neural basis of intermediate shape-centred representations (ISCR)

Given the behavioral focus of the Vannuscorps et al. (2021) investigation, the neural basis of the ISCR remains unclear. Vannuscorps et al. speculate that computations carried out by the ventral pathway, particularly by regions LO1 and LO2 (i.e., V4 in monkeys) can promote these representations. This proposal relies on the anatomical location of these regions (between retinotopic early visual cortices and high-level cortices), their functional properties (i.e., segregated representations of shapes which are based on different visual cues) and their connectivity profile (to the ventral and dorsal pathways). While the properties mentioned above support the plausible role of these ventral regions in ISCR computations, we should also consider whether regions in the dorsal pathway and specifically in the PPC can also derive similar, shape-centred representations.

In recent years, accumulating evidence shows that the dorsal pathway computes shape information that might contribute not only to visuomotor control but also to perceptual behaviours (Freud et al., 2016, 2020). Concretely, posterior parts of the dorsal pathways were found to be sensitive to shape information (Bracci & Op de Beeck, 2016; Freud, Culham, et al., 2017). These dorsal representations are correlated with perceptual behaviours (Freud, Culham, et al., 2017) and reflect semantic similarities among objects (Bracci & Op de Beeck, 2016; Jeong & Xu, 2016). In accordance with the proposed properties of the ISCRs, shape sensitivity in the PPC was found to be independent of image transformations and largely invariant to changes in

orientation or size (Konen & Kastner, 2008), which parallels the response patterns found in the ventral pathway.

Notably, regions in the PPC (i.e., IPS0 - also known as V7- and IPS1) share several key characteristics with the LO1-LO2 complex, supporting the hypothesis that these regions might compute intermediate shape-centred representations. First, anatomically, these regions are situated between the early visual cortex (V1-V3) and higher-level regions (e.g., IPS2-4, anterior IPS). This location might account for their varied connectivity profile. Specifically, anatomical (Greenberg et al., 2012) and functional (Ayzenberg & Behrmann, 2021; Hutchison & Gallivan, 2018) connections exist between the PPC and regions in the ventral and dorsal pathways. Consistently, reversible inactivation of the caudal IPS in monkeys led to functional changes in regions in cortex IT (Van Dromme et al., 2016), further establishing functional coupling between the PPC and regions in the occipitotemporal cortex. Thus, the PPC is well-suited to transfer the ISCR to subsequent computations in higher regions along the dorsal and ventral pathways.

Second, it was demonstrated that PPC regions are sensitive to different visual cues, including structure from motion (Erlikhman et al., 2018), depth cues (Georgieva et al., 2009; Orban, 2011), 3D structural information (Freud et al., 2015; Freud, Ganel, et al., 2017) and the spatial layout of object parts (Ayzenberg & Behrmann, 2021). Importantly, the above-mentioned sensitivity to 3D structural information and to the spatial geometry of objects is likely necessary to generate shape-centred representations which are invariant to image transformation.

Third, the hypothesis that regions outside the ventral pathway also generate ISCR is consistent with Vannuscorps et al. (2021) proposal that ISCR are derived separately by the magnocellular and parvocellular systems. Particularly, input to the ventral pathway is received from all types of ganglion cells. In contrast, the dorsal pathway receives most of its input from

the magnocellular (Merigan & Maunsell, 1993) and the koniocellular systems (Almeida et al., 2013). Although this separation is relative rather than binary (Nassi et al., 2006), it further supports the assumption that different cortical regions are involved in the computations of ISCR. Particularly, it is plausible the dorsal pathway computes ISCRs based on magnocellular inputs, while the ventral pathway computes these representations based on parvocellular inputs. Accordingly, in line with that proposed by Vannuscorps et al. (2021), one hypothesis is that ventral pathway computations are impaired in Davida, as her deficit is highly specific to the processing of stimuli presumably processed by the parvocellular system.

Finally, it is also worthwhile to consider what is the functional role of the ISCR that are presumably computed by the PPC. Clearly, shape representations derived by the PPC can be essential for computations carried out by the anterior regions of the dorsal pathway, the nexus of visuomotor control (Culham & Valyear, 2006; Goodale & Milner, 1992). Importantly, however, the functional contribution of the PPC is not limited to visuomotor control (see above). For example, given the rapid nature of the magnocellular input to these regions, it is plausible that PPC derives ISCR representations before ventral regions (that rely on parvocellular input) (Collins et al., 2019). Thus, PPC representations might facilitate object recognition by scaffolding or constraining the representations derived by the ventral pathway (Bar et al., 2006). Recent findings support this notion by showing that information about the spatial organization of object parts is uniquely encoded by the PPC and then communicated to ventral regions (Ayzenberg & Behrmann, 2021).

To conclude, the idea that the visual cortex computes intermediate shape-centred representations is compelling and can account for Davida's unique neuropsychological profile as well as other behavioural and neuroimaging observations. We propose that the neural basis of

these representations is not limited to the ventral visual pathway and might reflect computations carried out in multiple cortical loci across the two visual pathways.

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