

## Letter

### An expanded neural framework for shape perception

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A longstanding perspective in neuroscience is that the output of the ventral visual pathway is a shape-based representation that supports object recognition across many contexts. In our Opinion paper [1], we questioned this claim and suggested that the ventral pathway, instead, represents local object features and that global shape representations arise through interactions with the dorsal pathway. In her commentary, Xu [2] raises several important questions that must be addressed for our hypothesis to be tractable.

#### Sensitivity to local features does not exclude the possibility of global shape

Xu [2] points out that representations of local features and global shape may coexist within the ventral pathway. However, large-scale investigations of global and local representations have found little evidence of global shape representations in the ventral pathway (e.g., [3]). In fact, despite the enduring belief that the ventral pathway contains ‘invariant’ neural populations, decades of research have provided little indication for their existence [4]. Moreover, although large-scale resections of the ventral pathway cause object recognition impairments, it is not clear whether these impairments are rooted in a shape perception deficit *per se*. As we describe in our Opinion [1], even patients with integrative agnosia and extensive temporal lobe damage still exhibit a capacity to match objects on the basis of their shapes. Furthermore, if global shape is represented alongside local features, then, at a minimum, the ventral

pathway should be sensitive to the spatial arrangement of features, even if the appearance of the features does not vary. Jagadeesh and Gardner [5] provided such a test and found no sensitivity to the arrangement of features in the ventral pathway.

Xu [2] does raise a specific concern with Jagadeesh and Gardner’s [5] results, namely that their scrambled stimuli were still recognizable and, therefore, their results may reflect amodal completion of shape. Amodal completion is the process of filling in missing or partially occluded elements of an object. Although there is evidence that ventral and dorsal pathways are capable of amodal completion, this process may not be relevant to Jagadeesh and Gardner [5] as their stimuli did not have any missing elements. Moreover, this proposal is inconsistent with evidence from Long *et al.* [6], who found that unrecognizable images that maintained the texture statistics of their recognizable counterparts (i.e., texforms), elicited the same pattern of ventral activity as recognizable images. If shape is the primary organizing principle of the ventral pathway, texforms should not elicit the same organization as real objects.

#### The ventral pathway accomplishes transformation-tolerant recognition

A key finding from visual neuroscience is that the multivariate response of the ventral pathway can support some transformation-tolerant decoding of object identity. Xu [2] suggests that because such changes alter the appearance of local features, the ventral pathway must represent global shape. However, the success of decoding across some transformations does not illuminate how decoding is achieved. Indeed, as we highlight in our Opinion [1], deep neural network models also exhibit some transformation tolerance even though they do not represent shape. Moreover, there are many examples where the ventral pathway does not exhibit transformation tolerance [4] and, as the

previous section illustrated, there are cases where the ventral pathway exhibits tolerance where it should not, such as when images are rendered as texforms.

Finally, many studies find comparable transformation tolerance in both dorsal and ventral pathways, raising the question of where such representations are computed. For example, Xu and colleagues [7] found significant object decoding across spatial frequencies in both ventral and dorsal pathways. Xu [2] suggests that transformation-tolerant representations in the dorsal pathway arise via input from the ventral pathway. However, this suggestion is at odds with electrophysiological studies that show that object and shape information is present in the dorsal pathway earlier than the ventral pathway [8,9] and that inactivation of dorsal regions impairs processes typically ascribed to the ventral pathway, such as configural face perception [10].

#### Can representations of global shape be explained by attention?

Given that attention is a function of the dorsal pathway, Xu [2] asks whether representations of shape in the dorsal pathway can be explained by attentional processing. However, it is important to understand what exactly is meant by ‘attention’. One definition is that attention results in the selection of a target stimulus over competing distractors and, therefore, attention may highlight an object’s global form over its features. However, for this to be true, global shape information would need to be represented in the first place. An alternative account suggests that shared attention to visual features supports their binding into a complete shape. This type of attentional process may help to determine which features belong to the same object, but it does not explain how the features are arranged – such as when objects share similar features but have different arrangements (e.g., cup vs

bucket). Perceptual grouping of features may also occur pre-attentively. For instance, patients with hemispatial neglect, a visual attention disorder, are still influenced by grouped features even when some of the features fall in the unattended hemispace [11]. Moreover, object-sensitive regions of the dorsal pathway are well described by computational models of global shape that do not implement any process akin to attention [12].

### Concluding remarks

Although additional research is still needed to understand the nature of object representations in the visual system and the contributions of the dorsal pathway, the extant data force a reconsideration of the neural framework for visual object

processing, expanding it beyond the ventral pathway.

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