Opinion

# Trends in Cognitive Sciences



# Does the brain's ventral visual pathway compute object shape?

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A rich behavioral literature has shown that human object recognition is supported by a representation of shape that is tolerant to variations in an object's appearance. Such 'global' shape representations are achieved by describing objects via the spatial arrangement of their local features, or structure, rather than by the appearance of the features themselves. However, accumulating evidence suggests that the ventral visual pathway – the primary substrate underlying object recognition – may not represent global shape. Instead, ventral representations may be better described as a basis set of local image features. We suggest that this evidence forces a reevaluation of the role of the ventral pathway in object perception and posits a broader network for shape perception that encompasses contributions from the dorsal pathway.

# The communicative power of shape

If you were to visit the Wadi Sura caves in southwestern Egypt, you would be confronted with a series of familiar images: people holding hands and dancing, drawings of elephants and giraffes, as well as other depictions of prehistoric life. What is physically painted on the walls, however, is extremely minimal – stick figures for the people and a few coarse outlines for the animals. Nevertheless, the communicative power of shape information is such that these images can be readily identified by a child even 7000 years later.

Shape information is the central property by which humans recognize objects. With few costs, humans can recognize objects by their shape in the absence of other visual information [1–3]. Even infants and young children classify objects by their shapes [4–7] and do so across variations in other features [8,9]. However, despite the importance of shape in object recognition, accumulating evidence suggests that shape plays a surprisingly small role in explaining the organization and functioning of the **ventral visual pathway** (see Glossary) – the primary neural substrate supporting object recognition. In this opinion article, we explore the hypothesis that the ventral pathway may not represent a complete object shape, and we present evidence that supports this proposal.

# Global representations of shape

As the Wadi Sura cave paintings demonstrate, human representations of shape are remarkably abstract [10,11], with the individual elements of the shape bearing little physical resemblance to the object they are intended to depict. Instead of a veridical representation of the real world, human shape representations reflect an object's **global shape** structure. Global shape refers to an object-centered representation that describes the overall form of the object via the spatial arrangement, or structural description, of **local features** while remaining tolerant to variations among the features themselves (Figure 1A) [12–14]. Such a representation is largely independent from the visual properties that are typically thought to define shapes, such as contours and 3D surfaces. As a consequence of this independence, global shape representations

### Highlights

Decades of behavioral research have shown that shape information is crucial for object recognition.

However, recent studies demonstrate that neurons in the ventral pathway are highly sensitive to small image changes that do not disrupt the identity of an object, and that the distributed pattern of ventral neuronal responses represents local features rather than a complete shape.

Instead, a growing list of studies propose that global shape information may be computed in the dorsal visual pathway and transmitted to the ventral visual pathway.

A review of neuropsychology patient studies reveals that shape perception may be preserved following damage to the ventral pathway. This includes studies reporting a double dissociation in which global shape representations are impaired following dorsal damage whereas local feature representations are impaired following ventral damage.

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generalize across 2D and 3D formats, making them effective for interpreting shape from simple drawings on a wall to 3D objects in the world. Indeed, as stick figure depictions of the human form show, shape can often be conveyed with extremely impoverished features provided that the features are arranged appropriately. Perception of global shape is only disrupted, then, when the spatial structure of an object is not visible [15], such as when an object is shown from the side or from a foreshortened viewpoint (Figure 1B).

Due to its abstract nature, global shape supports object recognition under a range of conditions. For instance, many studies have shown that global shape allows for viewpoint-tolerant recognition because it preserves the identity of an object across disruptions to its retinal image, such as from changes in orientation [16,17] or partial occlusion [18–20]. Global shape is also crucial for basic-level object categorization (e.g., 'dog') because exemplars within a category (e.g., poodle, corgi) typically share the same global shape while varying in their local features (e.g., form of the snout, ears) [21–23]. Unsurprisingly, object recognition performance declines drastically when the spatial structure of an object is not visible, such as in cases of foreshortening [24]. In these cases, an observer must rely on diagnostic local features or incorporate additional cues (e.g., depth) to recognize objects.

# Neural locus of shape perception

Given their importance for object recognition, shape representations have long been thought to arise from the hierarchy of processing stages along the ventral visual pathway. The ventral pathway is typically considered to project from posterior occipitotemporal portions of the inferior temporal lobe (IT), encompassing the lateral occipital cortex (LO), to anterior portions, encompassing the fusiform gyrus. Object information in the ventral pathway is ultimately propagated to the anterior temporal lobe (ATL), which contains a multimodal **semantic representation of objects**.

Decades of research have shown that the ventral pathway is causally involved in object recognition. The responses of the ventral pathway are correlated with performance on object recognition tasks [25,26], and disruption of the ventral pathway (from damage or stimulation) impairs recognition [27–29]. Indeed, object-selective regions in the ventral pathway can be reliably localized by contrasting intact object images against images in which the appearance of the object has been substantially scrambled (e.g., Figure 1A, left vs. Figure 1B, left) [30–32]. The crucial question, however, is whether the ventral pathway supports object recognition by computing global shape.

Despite the behavioral evidence that object recognition relies on an object-centered global shape representation, few studies have shown that the ventral pathway explicitly computes such a representation [33–35]. Instead, extensive fMRI and electrophysiology research show that the ventral pathway is sensitive to shape-orthogonal properties such as position, orientation, and illumination [36–40]. Moreover, the majority of studies that do provide evidence of shape sensitivity in the ventral pathway primarily document the coding of local features such as contours or the form of individual object parts [41-45], or of shape statistics such as curvilinearity [46-49]. In many cases, sensitivity to local features is stronger than to the overall spatial arrangement of features [50–53]. In general, these studies find that a greater proportion of ventral pathway neurons are sensitive to local features than complete shapes [40,52], that spurious changes to an object's image cause release from neural adaptation [36,54], and that there is reliable multivariate coding for identity-orthogonal properties in the ventral pathway of humans and monkeys [38,39]. Indeed, object-selective regions can only be localized if the scrambled image contrast sufficiently disrupts the appearance of local features (Figure 1B, left). Scrambled object images that preserve local features elicit similar activation to intact object images in the ventral pathway (e.g., Figure 1A, left vs. Figure 1B, middle [55-57]).

#### Glossary

Dorsal visual pathway: a series of visual processing areas that project approximately from the occipital cortex to superior portions of the parietal cortex. The dorsal pathway is most commonly associated with visuospatial processing and action.

Global shape: an object-centered representation that describes the overall form of an object via the spatial arrangement of object's features, or structural description. Provided that the object's structure is visible, global shape defined percepts are tolerant to variations in the appearance of an object across viewing conditions and across category exemplars. Global shape can often be conveyed with little information, as in the case of stick figures.

Local features: the specific or individual properties of an object's visual appearance, which may include the composition of its contours or the form/ geometry of its component parts. The appearance of a local feature may vary across changes in object orientation or across category exemplars.

**Object-trained deep neural network (DNN):** a hierarchically organized computational model consisting of multiple layers capable of object recognition. Across layers, a DNN transforms visual input into progressively more complex visual features. DNNs learn diagnostic object features after being trained to identify objects through supervised or unsupervised methods.

#### Semantic object representations:

an object representation that is independent of the sensory information that comprises the object. Such a representation may be activated equally well across modalities, such as through visual, auditory, or text input.

#### Ventral visual pathway: a

hierarchically organized series of visual processing areas projecting from posterior occipitotemporal portions of the inferior temporal lobe (IT), encompassing the lateral occipital cortex (LO), to anterior portions, encompassing the fusiform gyrus. The ventral pathway is most commonly associated with complex visual pattern recognition.





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Figure 1. Object images with intact and disrupted global shapes. (A) Examples of airplanes where the spatial arrangement of features is preserved. Despite radically different local features, a common spatial arrangement, or structure, elicits the same percept of shape. (B) Examples of airplanes where the spatial arrangement of features is disrupted or partially occluded via foreshortening.

Several studies have directly explored the degree to which the ventral pathway represents complete object shapes or simply local features. One study showed that individual neurons of the ventral pathway radically change their response to feature changes that are nearly imperceptible to human observers [58]. Specifically, the researchers identified the preferred (high firing rate) and non-preferred (low firing rate) images for individual neurons in monkey IT (Figure 2A, top). They then applied extremely small perturbations to the images that left the identity of the object intact (Figure 2A, bottom). Despite the subtlety of these perturbations, these alterations qualitatively changed the response profile of neurons. For instance, a neuron with a preferred selectivity to pipe gauges, and not dogs, would, following these perturbations, respond to the images of dogs as strongly as, or even more strongly, to images of gauges (Figure 2B,C). Thus, as other studies have also shown [40,45,59], individual neurons in the ventral pathway are highly sensitive to variations in image features, even when those features do not change the perceived shape of the object.

Although individual neurons may represent local featural information, the representation of complete shapes may arise from the population-level activity of many neurons. To test this possibility, another study measured the behavioral response of humans, as well as the multivariate response of the ventral pathway, to images that preserved complex local features of the objects while disrupting their spatial arrangement (Figure 3A) [60]. Human observers, unsurprisingly, could discriminate between naturalistic images where the spatial arrangement was intact and novel images where the arrangement, but not the features, was disrupted (Figure 3A, top). However, the multivariate responses of the ventral pathway, as measured using both human fMRI data and a model of monkey IT, did not discriminate between the two image types (Figure 3A, middle).





Figure 2. Slight image perturbations change the firing rate of individual ventral neurons. (A) Example of a clean preferred (red) and non-preferred (blue) image categories for an individual neuron, as well as non-preferred images with various degrees of perturbation as specified by  $\varepsilon$ . (B) Raster plot illustrating the firing rate of the neuron in response to its preferred category (red), as well as to a non-preferred category (blue) following different degrees of perturbation. (C) The normalized (norm.) firing rate to preferred images (dashed red line) and non-preferred images (solid blue line) following different degrees of perturbation. By  $\varepsilon = 10$ , the firing to the non-preferred image category exceeds the preferred image category. Figure adapted, with permission, from [58].

The authors concluded that, instead of representing objects as complete shapes, the population activity of the ventral pathway represents objects as a collection or 'basis set' of features where the precise arrangement of features is irrelevant.

Even the large-scale organization of the ventral pathway is better described by features than by object shape. For instance, another series of studies re-rendered naturalistic object images into a texture-like representation, known as 'texforms', that retained the visual statistics of the images while disrupting the shapes of the objects and making them unrecognizable to human observers (Figure 3B, top) [61,62]. They found that these unrecognizable texform images, nevertheless, elicited the same large-scale organization as real objects in the ventral pathway, with the neural





Figure 3. Greater sensitivity to local features than global shape in the ventral pathway. (A) Example stimuli and results from [60] as measured behaviorally from human observers (top), the human ventral visual pathway (middle), and deep neural networks (DNNs, bottom). Each image triplet depicts the multidimensional scaling (MDS) of image similarities. The top two images of each triplet depict synthetic images where the arrangement of features has been scrambled, and the bottom image of each triplet depicts the original image where the arrangement of features remains intact. The distances between each image in a triplet reflect their similarities. (Top) Human observers readily grouped feature scrambled images together and discriminated them from intact images. By contrast, the multivariate responses of the

(Figure legend continued at the bottom of the next page.)



topography functionally corresponding to the dimensions of animacy and real-world size (Figure 3B, bottom). These findings are consistent with the scrambling experiments described earlier, as well as with many other studies that find that images that retain the features or texture statistics of images elicit comparable univariate and multivariate responses to those elicited by their real-world counterparts [63,64]. Thus, although shape is the principal cue by which humans recognize objects, and local features and textures are generally considered to be unnecessary for object recognition, it is these latter properties that best describe the large-scale organization of the ventral pathway.

# Evidence from neural network models

One way to understand the underlying dimensions of the ventral pathway is to examine the types of computational models that best explain its response profile. Over the past decade deep neural networks (**DNNs**) have emerged as the best existing models of human object recognition and ventral pathway processing. When trained to recognize objects, through supervised or unsupervised methods, DNNs exhibit a functional organization similar to the hierarchy of the ventral pathway, wherein early layers exhibit selectivity for simple visual features, such as oriented gratings, whereas later layers exhibit selectivity for complex object features, such as parts of a face [65]. When designed with connectivity constraints, the representations in later DNN layers even exhibit a topographic organization similar to that of category-selective areas of the ventral pathway – with separate clusters dedicated to objects and faces [66]. Beyond qualitative similarities, DNNs provide strong statistical descriptions of the ventral pathway [26,67–70], with their statistical fits approaching or, even surpassing, the inter-subject noise-ceiling – the theoretical upper limit for any model fit – in some brain areas [71,72]. Using image-synthesis techniques, object-trained DNNs have even been able to describe the selectivity of ventral pathway neurons and drive their responses higher than any naturalistic image tested [73–75].

However, despite a strong correspondence between the internal representations of DNNs and the response profile of the ventral pathway, DNNs exhibit fundamental differences in their object recognition behavior compared to humans. Specifically, DNNs do not consistently categorize objects on the basis of shape, and instead seem to primarily rely on local features [4,76] or texture statistics [77,78]. Moreover, imperceptible perturbations to the object image that would not fool a human (i.e., adversarial images) can radically change the response of a DNN [79]. Even when DNN training explicitly emphasizes shape by decorrelating texture information from the category label, the models continue to exhibit a bias for local object features [4,80].

How can DNNs, on the one hand, provide such a strong match to the ventral pathway, while, on the other hand, exhibit such a poor match to human behavior? One obvious possibility is that DNNs are simply poor models of the ventral pathway, and different architectures or training regimens would enhance their neural and behavioral predictivity. Indeed, despite their impressive fit to the ventral pathway, DNNs often leave a significant amount of variance unexplained. However, an alternative possibility is that DNNs are, in fact, good models of the ventral pathway, and that the ventral pathway simply exhibits little sensitivity to global shape. Indeed, like the ventral pathway, the responses of DNNs were insensitive to disruptions of an object's spatial configuration but were sensitive to the local features of the objects (Figure 3A, bottom) [60]. Similarly, the responses of DNNs to texforms predicted ventral pathway responses to the corresponding

<sup>(</sup>middle) ventral pathway and (bottom) DNNs showed no such grouping, with equal distances between each image. (B) Example stimuli and results from [61]. (Top) Texform examples are shown alongside their real-world counterparts for animate/inanimate and large/small categories. (Bottom) Ventral pathway activation maps for the original images and their texform counterparts. Although unrecognizable by human observers, texforms elicit the same large-scale topographic organization along the dimensions of object animacy and size as real-world objects.



### Local shape properties in the ventral pathway

We have suggested that the ventral pathway does not represent the global shape of objects, but, instead, represents objects via a basis set of local features. However, this does not mean that the ventral pathway is not crucial for object recognition. As described above, there is overwhelming evidence that the ventral pathway is causally involved in object recognition. Indeed, the feature representations of the ventral pathway are sufficient for recognition in many contexts. For instance, humans are adept are recognizing familiar objects from small image patches that show one or two diagnostic features [82,83], and an extensive literature has shown that object identities can be readily decoded from the multivariate response of the ventral pathway [84,85]. Moreover, DNNs have illustrated that accurate recognition of naturalistic images can be achieved by relying almost exclusively on learned features [86].

There is also strong evidence that the ventral pathway contributes to aspects of shape perception, namely the perception of local shape elements. In particular, decades of research has shown that LO, and its homolog in monkeys, posterior IT, is particularly sensitive to properties of shape. In monkeys, posterior IT exhibits a precise code for shape contours, as well as for 3D surfaces [41,59,87]. Moreover, LO seems to represent shape cues across different formats, including motion signals [88–91]. There is also evidence that LO plays a role in perceptual organization and supports the visual completion of disconnected contours [92–94]. Finally, studies have found that the large-scale organization of the ventral pathway is well described by shape statistics such as curvilinearity [47,48,95]. These shape statistics are not sufficient to describe the form of an individual object, but, like texforms, may suffice to describe large-scale object groupings such as animacy. Thus, although the ventral pathway may primarily represent local object properties, it nevertheless contributes to shape perception and plays a crucial role in object recognition. Additional research will be necessary to fully describe the nature of local features in the ventral pathway and how they combine to form an object representation.

### A broader network for shape perception

If the ventral pathway does not compute global shape information, how are humans ultimately able to represent shape in the service of object recognition? We suggest several possibilities that require additional investigation. One possibility is that local featural information from the ventral pathway is recombined at later, more anterior stages of processing, such as ATL. Indeed, ATL has been shown to represent objects as combinations of features from earlier visual areas [96,97], and single-unit recording from ATL neurons shows invariant responses to specific object identities across large variations in the type of image or even the modality of the input [98,99]. In this view, there are no intermediate representations of shape; instead, semantic object concepts are formed directly from combinations of features, much like in DNNs.

However, an alternative possibility is that global shape is computed in visual areas outside the ventral pathway and integrated with the feature representations of the ventral pathway to form a complete object representation. In particular, accumulating evidence has shown that the **dorsal visual pathway**, which has been historically implicated in visuospatial processing and action [100,101], represents object information and interacts with the ventral pathway to support

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recognition (Figure 4) [102,103]. Indeed, there is a long history of neuropsychological patients with parietal damage who exhibit object recognition deficits [104]. Like the ventral pathway, scrambling of object information elicits reliable activation in the dorsal pathway [30,31]. Moreover, the identity of an object can be decoded from the multivariate response of dorsal regions across variations in viewpoint and category exemplar [105–108]. Crucially, there is evidence that the dorsal pathway is a source of input to the ventral pathway [109,110]. Intracranial recordings from humans show that object information is present in the dorsal pathway earlier than the ventral pathway [111], and temporary inactivation of the dorsal pathway in monkeys reduces activity in the ventral pathway during object perception tasks [112]. Moreover, recent work using high-density electroencephalography (EEG), a technique with high temporal precision and spatial resolution sufficient to distinguish dorsal and ventral pathways, found that decoding of object category in the dorsal pathway precedes and predicts that of the ventral pathway [113]. Together these findings suggest that the dorsal pathway transmits object information to the ventral pathway [113].



Figure 4. An expanded brain network for object recognition. In this schematic depiction of the visual system, the ventral pathway (V1 to ATL) acts much like a DNN (bottom) – extracting increasingly complex local object features, but not a complete shape. Instead, structural information describing the global shape of an object, but not its individual features (top; depicted as a red skeleton), may be computed in dorsal visual pathway regions such as IPS. This information is then sent to the ventral pathway to form a complete object representation. Abbreviations: ATL, anterior temporal lobe; DNN, deep neural network; IPS, intraparietal sulcus; L1–L6, layers 1–6; LOC, lateral occipital complex; V1–V4, visual areas 1–4.



One study directly tested whether the dorsal pathway computes object-centered global shape information and interacts with the ventral pathway to support object recognition [106]. Given the sensitivity of the dorsal pathway to spatial information, it was hypothesized that the dorsal pathway may compute the spatial arrangement among the parts of an object, but not the features of the parts themselves. Using a functional localizer that contrasted the arrangement of the parts with the features of the parts, regions in the dorsal pathway were found that were selective for object-centered part arrangements, but not other properties represented by the dorsal pathway (e.g., allocentric relations). Importantly, the response of these regions could be used to decode the category of real-world objects (e.g., airplanes, lamps), with performance comparable to that of the ventral pathway. Moreover, whereas the ventral pathway was best described by feature representations from a DNN, the dorsal pathway was best described by a model of global shape that ignores local feature information, known as the shape skeleton (Figure 4), suggesting that recognition in each pathway is likely accomplished using different visual properties [107,114]. Finally, mediation analyses and effective connectivity analyses suggested that the dorsal pathway mediates representations of shape in the ventral pathway, which is consistent with research suggesting that the dorsal pathway transmits information to the ventral pathway.

Related work has found that dorsal regions are more sensitive to the spatial configuration of features in a face (e.g., the positions of eyes), whereas ventral regions are more sensitive to the features themselves (e.g., the appearance of the eyes) [115]. Importantly, this study found that the dorsal and ventral pathways were functionally connected during configural face perception, and that inactivation (from transcranial magnetic stimulation; TMS) of dorsal regions impaired performance on configural face perception tasks. Indeed, several studies have shown that applying TMS to the dorsal pathway impairs perception of global, but not local shape properties [116,117]. There are also many studies showing that patients with bilateral damage to the dorsal pathway experience simultanagnosia (also known as Balint's syndrome) - an inability to perceive multiple objects [118,119]. These patients often also have difficulty perceiving the relations between object parts, thereby impairing perception of global form [120-123]. However, it is important to note that these studies used figures with disconnected elements (e.g., Navon figures), which may be particularly challenging for simultanagnosia patients who are unable to attend to multiple objects. Thus, additional research using a wider selection of stimuli, as well as tighter controls for attention-related processing, will be necessary to understand the degree to which the dorsal pathway contributes to global shape. Nevertheless, these studies suggest that global shape information may arise in the dorsal pathway and interact with the ventral pathway to form a complete object representation (Figure 4).

# Reconciling data from neuropsychology patients

If global shape is crucial for object recognition, and the ventral pathway does not represent global shape, why then are patients so impaired at object recognition following damage to the ventral pathway? Indeed, one class of deficit – integrative agnosia – specifically relates to patients' inability to perceive the arrangement of features [34,124,125]. Although more data will be necessary to address this question fully, we would highlight a few possibilities.

First, although the ventral pathway may not compute global shape information itself, it is still the primary area underlying object recognition [110,126]. Indeed, studies showing that the dorsal pathway contributes to object recognition find that these contributions occur via interactions with the ventral pathway [106,112,115,127]. Thus, damage to the ventral pathway may disrupt both the object processing that occurs in the ventral pathway and the connectivity to object processing centers in the dorsal pathway [109,128].



Second, although object agnosia is most commonly ascribed to ventral pathway damage [100,129], we would point out that the specific types of deficit and their severity vary widely with the location and extent of damage [130,131]. For instance, there are several cases where patients with object agnosia and extensive damage to the ventral pathway can nevertheless distinguish objects on the basis of shape [125,127,132,133]. In one of these cases, a patient with bilateral ventral damage could discriminate between objects on the basis of shape when they were presented as silhouettes, but not when local features were included [125]. This finding suggests that the damage impaired their ability to integrate shape with local features rather than their ability to perceive shape itself. Another study found a double dissociation between patients, such that a patient whose damage was situated more in the dorsal pathway exhibited a deficit in perceiving global shape, but not in perceiving local features, whereas a patient with damage localized to the ventral pathway exhibited a deficit in perceiving local features, but not global shape [132]. There are also cases where circumscribed lesions to the ventral pathway, seemingly in the absence of dorsal damage, lead to deficits in global shape perception [128]. However, it is possible that the deficits in this case are related to disrupted connectivity between dorsal and ventral pathways. Indeed, this patient also sustained damage to the corpus callosum as well as to subcortical white matter tracts leading to the ventral pathway. However, additional causal experiments will be necessary to identify the precise network that supports global shape representations. Nevertheless, the body of research from neuropsychology patients necessitates a more nuanced view of the relations between shape perception and processing in the ventral pathway.

However, it is important to acknowledge that it is much rarer for patients with dorsal pathway damage to experience severe object recognition deficits, even when they have simultanagnosia. Given the purported importance of shape information to object recognition, how can this be? One interesting possibility is that, for most of everyday life, the feature representations of the ventral pathway are sufficient to recognize familiar objects. As we mentioned previously, humans can recognize familiar objects from image patches that show only a few diagnostic features [82,83], and DNNs illustrate how models with sufficient object experience can complete many object recognition tasks in the absence of shape representations. Indeed, like in DNNs, the feature representations of the ventral pathway are shaped by extensive experience [134–136], leading to selective responses to extremely familiar categories such as faces, places, and words. It was only using novel objects or 'adversarial examples' that the visual limitations of DNNs were discovered. Thus, there may be 'adversarial' examples that better reveal the limitations of patients with dorsal lesions. One interesting possibility is that dorsal representations of shape may be invoked when encountering new objects or in contexts where the diagnostic features of familiar objects are not available. Indeed, global shape information from the dorsal pathway may be especially crucial when learning new object identities [137], such as early in development when children have little object experience [4,8].

# **Concluding remarks**

We have laid out the hypothesis that the ventral visual pathway may not be involved in computing a complete shape representation, as has long been assumed in much of the vision sciences literature. We have presented evidence that the ventral visual pathway, at both single-unit and population-activity levels, exhibits greater sensitivity to local features than to complete shapes. As in DNNs, a set of local features may, nevertheless, be sufficient to recognize familiar objects that humans encounter in day-to-day life [83], but may be insufficient when learning new objects or encountering objects in novel contexts. Instead, object-centered global shape information may be computed by the dorsal visual pathway and transmitted to the ventral pathway to support object recognition across a larger range of contexts [106].

#### Outstanding questions

Under what conditions is global shape and input from the dorsal pathway necessary for object recognition?

How do the ventral and dorsal pathways interact when an observer learns new object identities, such as early in development?

Is a basis set of local features sufficient to explain the response properties of category-selective regions in the ventral pathway? In particular, how might the current framework account for representations of categories such as faces in the ventral pathway?

How do representations of global shape based on the spatial arrangement of features intersect with other indicators of global form, such as those based of Gestalt grouping rules?

What are the precise temporal dynamics and information processing stages of global shape processing? How is shape information propagated from dorsal to ventral pathways?



Nevertheless, this hypothesis requires additional data and raises many further questions (see Outstanding questions). Although we have shown that the neuropsychological literature provides mixed evidence for global shape representations in the ventral pathway, the current account must nevertheless be reconciled with the findings that patients are more impaired at object recognition following damage to the ventral than the dorsal pathway. Under what conditions are global shape and input from the dorsal pathway necessary for object recognition? Future patient work should use a broader set of stimuli that allow researchers to carefully disambiguate the visual properties patients rely on when perceiving objects [138]. Moreover, the current account must also be reconciled with a key property of the ventral pathway: category selectivity. Are shape representations necessary to explain the selectivity for categories such as faces, places, and words? Alternatively, might local feature descriptors, such as those implemented by DNNs, be sufficient [66,75]? Finally, our conceptualization of global shape intersects with the rich literature in Gestalt psychology on the perceptual grouping of local features to form a complete shape [139]. Are such perceptual grouping rules supported by the same mechanisms that compute global shape? Alternatively, might there be distinct mechanisms that underlie the many documented perceptual grouping rules [133]?

Thus, although further research will be necessary to understand how the brain computes robust shape representations in the service of object recognition, we believe the extant data provoke a reconsideration of the role of the ventral pathway in forming such representations.

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#### **Declaration of interests**

No interests are declared.

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