

## Review

## ‘What’ Is Happening in the Dorsal Visual Pathway

Erez Freud,<sup>1,2,\*</sup> David C. Plaut,<sup>1,2</sup> and Marlene Behrmann<sup>1,2</sup>

The cortical visual system is almost universally thought to be segregated into two anatomically and functionally distinct pathways: a ventral occipitotemporal pathway that subserves object perception, and a dorsal occipitoparietal pathway that subserves object localization and visually guided action. Accumulating evidence from both human and non-human primate studies, however, challenges this binary distinction and suggests that regions in the dorsal pathway contain object representations that are independent of those in ventral cortex and that play a functional role in object perception. We review here the evidence implicating dorsal object representations, and we propose an account of the anatomical organization, functional contributions, and origins of these representations in the service of perception.

## Two Cortical Visual Pathways

One of the most influential conceptualizations within cognitive neuroscience asserts that the cortical visual system is segregated into two anatomically and functionally distinct pathways: the **ventral visual pathway** and the **dorsal visual pathway** (see [Glossary](#)). This division of labor, articulated in a seminal paper [1], and first inferred from lesion studies in monkeys and then in humans, proposes that the ventral pathway represents object shape and identity (‘what’), whereas the dorsal pathway represents object location or spatial relationships (‘where’). Roughly a decade later, in a revision of this framework [2], the functions of the two pathways were redefined not primarily by their input attributes, but instead by their output requirements, the key distinction being the role of the dorsal pathway in supporting visuomotor control (‘how’) rather than spatial representations *per se*.

A fundamental division of labor between the ventral and dorsal pathways has been supported by decades of research employing a range of diverse methods including neuropsychological investigations (e.g., [3–5]), single-unit recording (e.g., [6–9]), behavioral psychophysics (e.g., [10–13]), and functional imaging (e.g., [14–17]; [18] for review). Nonetheless, both the early ‘what’ versus ‘where’, and the more updated ‘what’ versus ‘how’ distinctions between the pathways, continue to be subject to challenge. One recent challenge focuses on the extent to which the dichotomy between the two pathways holds, given the distributed nature of **object representations** [19]. For example, in contrast to the prediction of the what/where segregation, the spatial properties of an object, including its position, size, and pose, can be reliably decoded from ventral cortex [20,21]. In complementary fashion, and also in contrast with the prediction of the what/how segregation, ventral visual pathway representations appear to be modulated by motor attributes, in the absence of visual feedback and even before movement initiation [22,23].

In the same way as the existing distinctions are coming under challenge with respect to ventral cortex, the same is true for dorsal cortex, with growing evidence of non-action-based (i.e., effector-independent) perceptual representations in the posterior regions of the dorsal pathway in both humans and non-human primates [24–35]. The aim of the current paper is to

## Trends

In both human and non-human primates, the posterior portion of the dorsal pathway generates object-based representations that are unrelated to action planning or execution.

Patients with extensive lesions to the ventral pathway still generate object representations in the dorsal pathway, and evince perceptual sensitivity to object structural information.

Neuropsychological investigations with patients, and lesion studies with non-human primates, have demonstrated that a lesion to the posterior part of the parietal cortex leads to perceptual deficits, particularly in 3D perception and in the perception of structure from motion.

<sup>1</sup>Department of Psychology, Carnegie Mellon University, Pittsburgh, PA, USA

<sup>2</sup>Center for the Neural Basis of Cognition, Carnegie Mellon University and the University of Pittsburgh, Pittsburgh, PA, USA

\*Correspondence: [efreud@andrew.cmu.edu](mailto:efreud@andrew.cmu.edu) (E. Freud).

examine this latter challenge – namely, the role of the dorsal visual pathway in object perception and the extent to which dorsal object representations serve vision-for-perception in addition to the well-established vision-for-action [2]. To this end we first review the evidence for object representations in the dorsal pathway, and then propose that dorsal cortex subserves an anatomically defined gradient in which more-posterior and medial regions support more-perceptual representations, and more-anterior and lateral regions are more tuned to action-oriented representations.

### Independent Object-Selective Representations in the Dorsal Visual Pathway

Investigations of both human and non-human primates have revealed object-related neural activity in the dorsal pathway that is independent of action planning or execution [36–39]. Importantly, while much of the object-selective activation overlaps with the visuomotor system [7,40] and probably reflects object representations that are in the service of action [41], at least some of the activation is dissociable from the visuomotor regions and is located more posteriorly or caudally within the parietal lobe [18,27,40,42–44]. This latter pattern of activation dovetails with the recent identification of a parietomedial temporal subdivision of the dorsal pathway, distinct from the parieto–premotor pathway, and which projects to the ventral pathway and may subserve visuospatial processing [42].

Interestingly, and counterintuitively, as revealed by fMRI in humans, representations of objects in the posterior dorsal pathway [i.e., IPS1 (intraparietal sulcus 1) and IPS2, Figure 1] appear to be relatively insensitive to various image transformations, even in a passive fixation task in which no action is required (e.g., size, retinal position, and viewpoint) [24]. This is especially surprising because invariance is considered to be both characteristic of ventral object representations [45,46] and a necessary component for successful object recognition. This evidence suggests that the posterior aspects of the parietal cortex are sensitive to object shape, even in the context of non-action based tasks. One possibility is that object-based responses in the dorsal pathway might reflect the obligatory implicit extraction of **affordance** information – in other words, again in the service of action [47]. This alternative is not likely, however, given that, the invariance to transformations holds for 2D objects that lack clear action-affordance associations [24]. In addition, the dorsal object-based response is not an artifact of attentional modulation [36], eye-movements [48], or non-shape depth cues because dorsal object sensitivity is observed even for 2D objects that lack depth information [38] and when eye-movements and attention are carefully controlled [24,49] (Box 1 for further discussion).

One obvious interpretation of the dorsal object-selectivity is that it might simply be a consequence of the anatomical and functional coupling between dorsal and ventral regions [19,42,50], perhaps via the vertical occipital fasciculus which connects the pathways posteriorly [51,52] or via the efferent projections that run from the posterior parietal lobe to the hippocampal formation and to parahippocampal areas in the ventral pathway [42,53] (Box 2). Indeed, the neural responses to action observation [54] as well as 3D object processing [27] in the ventral pathway are influenced by neural responses in the dorsal pathway [27,54], and the reverse (i.e., changes in dorsal pathway activation by ventral pathway responses) likely holds as well [55,56].

The key question, then, is whether the dorsal pathway is merely a downstream recipient of ventral cortex activation or whether it plays an independent, functional role in object perception. To support the latter interpretation, two criteria must be met. First, object representations in the dorsal pathway should be dissociable from those generated by the ventral pathway – specifically, these representations ought to be generated even in a situation in which ventral pathway representations are largely compromised. Second, object representations in the dorsal pathway ought to make some contribution to **visual perception**, indicating that these representations are necessary for intact perception.

### Glossary

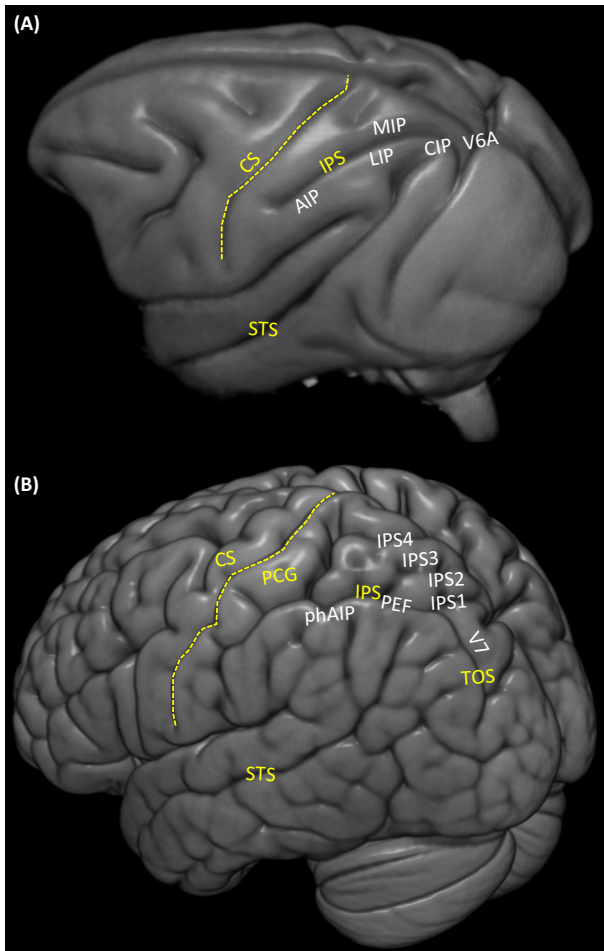
**Affordance:** a set of potential actions that are offered to the organism by the environment/object. According to Gibson [126], the process of object perception automatically includes the extraction of affordance values.

**Dorsal visual pathway:** this pathway extends from the primary visual cortex (V1) in the occipital lobe to the parietal lobe. The dorsal pathway is subdivided by the intraparietal sulcus (IPS) into several main sectors including the superior parietal lobule, inferior parietal lobule, and the supramarginal gyrus.

**Object representation:** the response from a group of neurons that captures information about an object that is present in the input. A neural object representation can be derived for the purpose of action and/or perception.

**Ventral visual pathway:** this pathway extends from the primary visual cortex (V1) in the occipital lobe and courses through the occipitotemporal cortex to the anterior part of temporal lobe. The ventral pathway can be subdivided into early visual regions, the lateral aspect of the occipital and temporal lobes, and the ventral temporal cortex.

**Visual agnosia:** a neuropsychological condition, usually the result of a lesion in the ventral visual pathway, in which the patient has impaired object recognition that cannot be accounted for by a reduction in visual acuity, a general loss of knowledge, or impaired intelligence. Visual object agnosia is usually subdivided into visual form agnosia (also known as a *apperceptive agnosia*) and *associative agnosia*. Visual form agnosia is characterized by a striking visual impairment in which the patients cannot even distinguish between simple shapes such as a circle and a square (e.g., in the context of matching task) or even copy simple shapes. *Associative agnosia* is a selective impairment in the recognition of visual stimuli, despite apparently relatively preserved visual perception of the stimuli [127]. We note that there is ongoing controversy about the validity of the *apperceptive/associative* distinction.



**Figure 1. Visuomotor and Perceptual Representations in the Dorsal Pathway.** The macaque (A) and human (B) brain from a lateral view. The arrangement of functional areas along the dorsal pathway (white text) is schematically depicted as defined by electrophysiological studies (monkeys) [44] and fMRI studies (humans) [105]. Yellow text refers to anatomical landmarks. In the monkey brain, the AIP is assumed to support the transformation of visual information to motor plans [7]. LIP is involved in computations related to eye movement, and the more posterior regions (CIP) mediate perceptual representations [27,38]. In the human brain, visuomotor transformations are supported by the phAIP and other regions along the lateral aspect of the IPS [14,18]. The ‘what’ subpathway is thought to comprise the more-posterior and medial regions (V7, IPS1, IPS2), which derive perceptual representations of object shape [24–26]. See text for more details and references. Abbreviations: AIP, anterior intraparietal; CIP, caudal intraparietal; CS, central sulcus; IPS, intraparietal sulcus; LIP, lateral intraparietal; MIP, medial intraparietal; PCG, precentral gyrus; PEF, parietal eye field; phAIP, putative human AIP; STS, superior temporal sulcus; TOS, transverse occipital sulcus. Brain reconstructions are based on the INIA19 template [106] and on the ICBM 152 MNI template [107], and were rendered using MRICroGL software ([www.mccauslandcenter.sc.edu/mricrogl/home](http://www.mccauslandcenter.sc.edu/mricrogl/home)).

**Visual perception:** the process by which visual information from the environment is derived and interpreted. Visual perception can be measured by a variety of methods including, for example, having an observer judge features of input such as size, depth, color, and shape, judge similarity between inputs, or report recognition of information in a visual display.

#### Trends in Cognitive Sciences

#### Box 1. Caveats in the Investigation of Dorsal Object Representations

The study of the nature of object representations in the dorsal pathway and their behavioral significance is still subject to significant caveats that compel caution in the interpretation of behavioral and neural data. First, in most studies of non-human primates, sensitivity of a neural population to features or objects is measured after the animals were trained using specific actions (e.g., saccadic match to sample task). This training could lead to stimulus-specific activity which relates to the action and not to the stimulus *per se*, as demonstrated by a study showing that selectivity to color could be found in the LIP (lateral intraparietal), despite the fact that color is not represented in the dorsal pathway [108]. Importantly, this caveat is also relevant to human studies because participants are typically asked to report their perceptual experience using a specific action.

Another limitation is that it is hard to definitively tag a specific neural representation as a ‘perceptual’ or ‘visuomotor’ representation because object representations are surely needed for both functions. This problem is predominantly apparent in studies that measure the neural response without perceptual-behavioral assessments (e.g., [24]) (or vice versa, e.g., [79]). Correlational and neuropsychological studies that map the relation between the content or the representations and the observed behavior (perceptual or visuomotor) can provide some insights in this domain, but, nevertheless, given the interconnection between the two pathways, some of these results may still reflect propagation of information between the two pathways.

Finally, given the well-established role of the dorsal pathway in object 3D processing (see text for details), it worth mentioning that the investigation of object representations along this pathway can benefit from the use of real 3D objects. Some initial results already demonstrate that both visuomotor [109,110] and perceptual behaviors [111,112] are shaped by object realness, and this dimension can also alter the nature of the neural representations in the dorsal pathway [113].

### Box 2. Anatomical and Functional Connectivity Between the Pathways

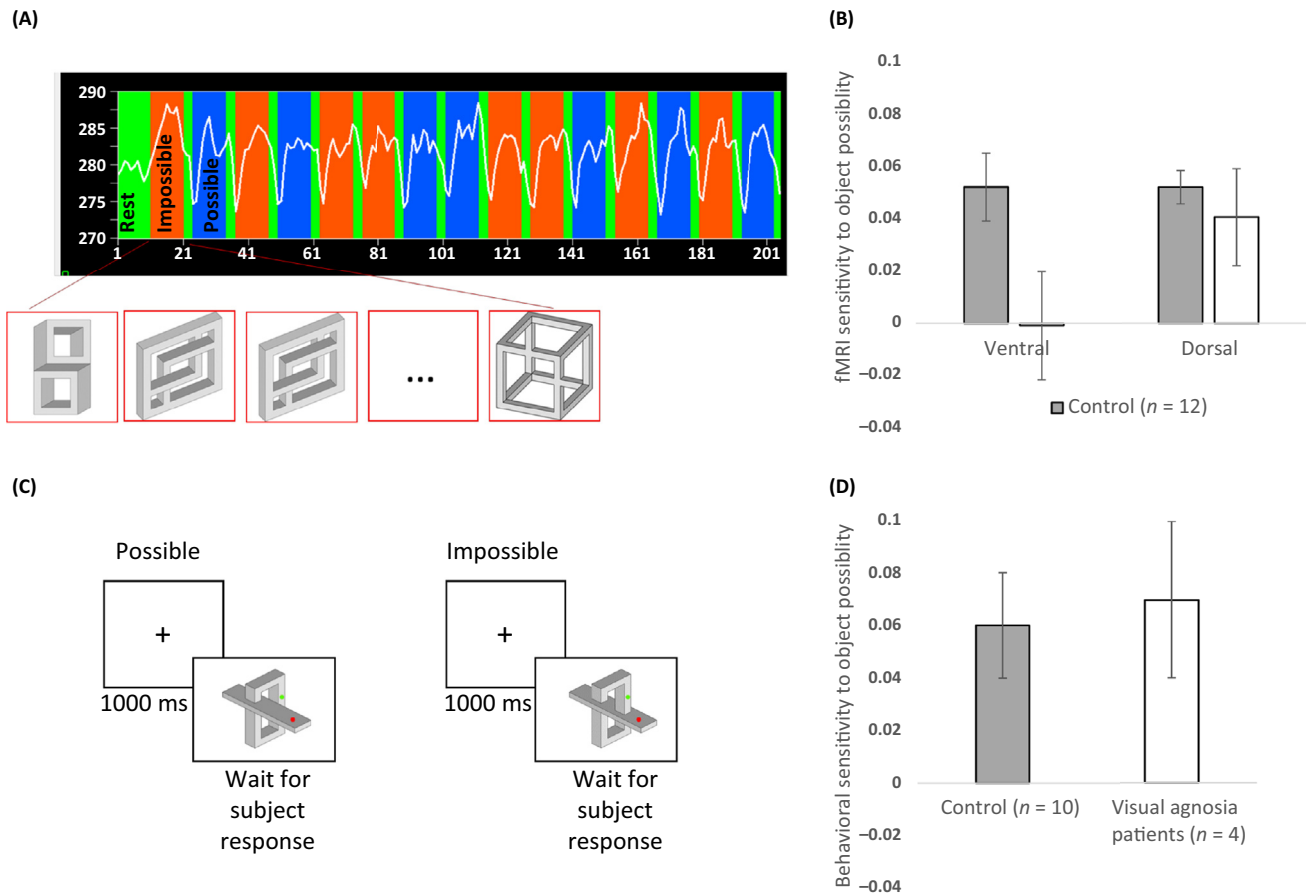
The dorsal and the ventral pathway are anatomically connected to each other by several major groups of axons. The parietomedial temporal pathway travels the caudal part of the inferior parietal lobule (ciPL, dorsal pathway) to the hippocampal formation and to parahippocampal areas which are part of the ventral pathway [114]. In addition to these direct connections, the ciPL is connected to these regions through a set of indirect connections that travel through limbic regions [115,116]. Importantly, the hippocampal formation is known to be involved in complex spatial processing and navigation, and the dorsal pathway input might also be engaged in such computations [42]. The lateral surfaces of the dorsal and ventral pathway are connected by two additional tracts: the posterior arcuate fasciculus (pAF) and the vertical occipital fasciculus (VOF) [51,117].

In addition to the anatomical connections between the two pathways, imaging studies have documented strong functional connections between the two pathways. For example, based on the anatomical infrastructure of the VOF [52], regions in intermediate visual areas in the dorsal (V3A/B) and ventral (hV4/VO-1) pathways are connected and exchange visual information. Moreover, strong functional connectivity between the two pathways was found in higher-level regions such as the posterior parietal cortex and the lateral occipital complex. Interestingly, this functional connectivity was modulated by the validity of the perceptual input (i.e., possible vs. impossible objects) [30]. Another study, which utilized effective functional connectivity analysis, showed that dorsal pathway activation was correlated with activation in the anterior ventral pathway [54] in a perceptual task that included action observation. Taken together, these findings further suggest that the two pathways are interconnected both functionally and anatomically, and these connections might be important in the process of object recognition. Future investigation employing advanced analytical methods (e.g., dynamic causal modeling [118]) may further clarify how object representations are shaped in the two pathways as a function of the connections between the two pathways.

With regard to the first criterion, the object-selective representations of the dorsal and ventral pathways exhibit some distinct properties. This is true in non-human primates in that the presentation of 3D objects generates neural responses in the dorsal pathway that have shorter latencies than those measured from the ventral pathway, undermining the possibility that the former representations result from the cascaded projection from the ventral pathway [41,57]. Similarly, in an event-related potential (ERP) study in humans, neural responses following action observation were observed in parietal regions after only 120 ms, whereas ventral pathway activation emerged later after 380 ms [54]. In addition, when visual awareness to a stimulus is reduced by continuous flash suppression, the object-selective activation is profoundly reduced in the ventral but not in the dorsal pathway [58].

The separability of dorsal versus ventral object representations is necessary, but not sufficient, to support the conclusion that the dorsal pathway plays a functional role in perception. Some support for a functional role of the dorsal cortex is provided by the significant correlation between the activation profile in dorsal pathway and behavioral performance [25,27,29,59]: for example, in one study, perceptual classification of the surface texture and arrangement of object parts was correlated with dorsal pathway activation [29]. In addition, complex patterns, including those of individual faces, engage dorsal area IPS, and the ensuing IPS activation pattern was correlated with the performance of participants in a visual search task [25].

Perhaps the strongest evidence for the independence of dorsal object representations comes from lesion studies in humans and non-human primates: patients with lesions to the ventral pathway still retain some sensitivity to 3D structural object representations, as reflected in their perceptual abilities [26] and blood oxygen level-dependent (BOLD) activation in the intact dorsal pathway (Figure 2). Moreover, even for JW, a patient with extensive bilateral ventral lesions who was perceptually impaired even relative to other patients with **visual agnosia**, intact residual sensitivity to structural information was found. Consistently, close scrutiny of the fMRI profile of patient DF, an agnostic individual with extensive ventral damage, reveals dorsal object-selectivity bilaterally in response to objects compared with scrambled versions of object [5]. These findings suggest that dorsal pathway representations can be generated independently in the absence of a fully functional ventral pathway.



Trends in Cognitive Sciences

**Figure 2. Object Representation in the Dorsal Pathway.** Experimental details and results from [26]. (A,B) Neural sensitivity to object 3D structural information in two patients with visual agnosia and controls in the ventral and dorsal pathway. (A) Pictures of possible and impossible objects were presented while participants completed a 1-back task. (B) The fMRI BOLD signal evoked by possible and impossible objects was measured in regions along the dorsal and ventral pathways. Sensitivity scores were calculated such that positive values reflect stronger activation for impossible objects compared to possible ones. In controls, regions of interest (ROIs) in ventral and dorsal pathways were sensitive to object possibility, as is evident from the greater response evoked by impossible than by possible objects. Patients with visual agnosia also exhibited preserved sensitivity to this information in the dorsal, but not in the ventral, pathway. (C,D) Behavioral sensitivity to object 3D information in patients and controls. (C) Participants performed pairwise depth classifications on two dots that were located on the stimuli. (D) Sensitivity to object possibility was reflected by better performance for possible objects (sensitivity values that are greater than zero). A similar level of sensitivity to object possibility was observed in patients with visual agnosia and controls.

The reverse, but complementary, pattern is that perceptual impairment – specifically of 3D objects and global form perception – results from dorsal pathway lesions, as shown in humans and non-human primates [27,43,60–63]. For example, in humans, patients with posterior parietal lesions exhibited marked perceptual deficits, particularly for 3D objects defined from binocular and monocular depth cues [63]. Correspondingly, non-human primate lesion studies that aimed to explore the causal role of dorsal regions in 3D perception showed that deactivation of the dorsal area CIP (caudal intraparietal) led to perceptual impairments related to 3D disparity perception as well as to decreased inferotemporal ventral activation [27].

### ‘What’ in the Dorsal Visual Pathway?

Taken together, the findings reviewed thus far indicate that dorsal object representations are dissociable from those generated in the ventral pathway, and play an independent and functional role in visual perception. In light of the above, we propose that visual perception should not be

considered as the product of computations carried out solely by the ventral pathway, but instead as the joint outcome of the two pathways, both of which contribute to the representation of 'what' is perceived.

Importantly, this view does not undermine the well-established functional role of the dorsal pathway in spatial and visuomotor control, nor the importance and centrality of the ventral pathway to visual perception in general, and to object recognition in particular. In fact, the accumulation of evidence suggests that the dorsal pathway is composed of several subpathways [42], and that at least one of these pathways has a functional, and probably necessary, role in object perception.

Having established that the dorsal pathway is engaged in the service of object perception, several questions emerge. For example, (i) to what extent do these representations vary along the extent of the dorsal pathway? (ii) What are the precise properties that define the perceptual object representations in the dorsal pathway and how do they contribute to perception? We suggest below brief answers to these questions and then set out several challenges for future studies (see Outstanding Questions).

#### Perceptual (Caudal–Medial) to Motor (Rostral–Lateral) Representational Gradient

The dorsal pathway covers extensive portions of the parietal lobe and also some parts of the occipital lobe. Given this anatomical scope, it is not surprising that dorsal representations are not monolithic and may be shaped as a function of anatomical location and connectivity to other brain circuits [42]. Previous studies have already recognized the heterogeneity of neural representations in the dorsal pathway and have demonstrated that, under visually guided tasks or action observation tasks, more-posterior parts of the dorsal pathway are more sensitive to the spatial location of the objects, to object identity, and to gaze-centered representations, while more-anterior parts, which are closer to motor cortex, are more sensitive to effector (e.g., hand) information and to movement type (e.g., grasping versus reaching) [22,64–70] (for similar proposals in the context of ventral pathway representations see [71,72]). In line with a recent anatomical model [42], this posterior–anterior gradient is likely not limited to the caudal–rostral axis, but may also be mapped on the medial–lateral axis. In particular, the more caudal–medial regions of the dorsal pathway (i.e., V7, IPS1–2 in humans; CIP in non-human primates) (Figure 1) are strongly connected to early visual cortex [73] and to ventral cortex [42], and represent more-visual or perceptual properties of the input. By contrast, the more-rostral part of the dorsal pathway (i.e., phAIP in humans, AIP in non-human primates), connected to the sensorimotor system [73] and coupled to motor regions, is shaped in service of visuomotor behaviors. These observations support the idea that parietal cortex plays a key role in transforming visual representations into motor representations.

This functional perception–action continuum is also well supported by empirical findings from investigations with non-human primates. Several monkey physiology studies have found that the more-posterior dorsal area CIP is causally involved in perceptual processes related to classifications of 3D objects [27,43], and deactivation of this region does not result in any visuomotor deficits [43]. By contrast, the dorsal anterior intraparietal area (AIP) and area F5a in the ventral premotor cortex (PMv), both of which play a role in object grasping, have neurons that respond selectively to 3D shapes. Furthermore, in both of these regions 3D-shape selective neurons are colocalized with neurons showing motor-related activity during object grasping in the dark. These findings support the conclusion that these more-anterior neural responses subserve action-based responses rather than perception *per se* [74]. Correspondingly, the activation profile of neurons in the AIP was correlated with behavior only after the perceptual choice was already made, suggesting that this region was not involved in 3D shape discrimination *per se* [75].

### Box 3. Hemispheric Specialization of the Dorsal Pathway

The lateralization of tool-sensitivity to the left hemisphere [119] in right-handed individuals raises important questions about hemispheric differences in dorsal object representations [120,121]. Hemispheric differences are known to modulate visual representations in the ventral pathway. For example, greater face sensitivity is usually observed in the right hemisphere, while the left ventral pathway exhibits greater sensitivity to written words [122,123], although this lateralization is graded rather than absolute. It is not clear to what extent similar lateralization applies to perceptual representations in the posterior part of the dorsal pathway.

Neuropsychological findings provide some support for hemispheric specialization of the dorsal pathway. In a recent study, perceptual impairments following a parietal lesion were observed among patients with right, but not left, hemisphere lesions [62]. These observations are compatible with early neuropsychological investigations (see text for details [63]) and also with previous studies demonstrating that visual functions associated with the parietal cortex, such as visual attention [124] and mental rotation abilities [125], are usually more dominant in the right than left hemisphere. Hence, visual representations in the dorsal pathway may be shaped not only as a function of anatomy within each hemisphere (see main text for details) but also between hemispheres (left, motor; and right, spatial).

Consistent with the transformation from more-sensory to more motor-representations is the well-established dorsal activation to images of man-made tools compared to other classes of objects (e.g., [65,66]). This activation profile appears tied to the tool's associated motor programs (i.e., affordance) [76,77], although there is perhaps also some sensitivity to the visual attributes shared by different types of tools, such as elongation [78,79]. Also compatible with the tuning for visually guided action, this tool-preferred activation, although bilateral, is typically more robust in the left hemisphere [80] (Box 3 for further discussion on hemispheric specialization). The tool sensitivity along the dorsal pathway also corresponds to the caudal (perceptual)–rostral (motor) organization: whereas pictures of graspable objects and pictures of tools evoke similar responses in the posterior part of the parietal cortex, tools evoke greater BOLD activation than graspable objects in the anterior regions [81]. This pattern of activation might suggest that the visual representations in the anterior part of the IPS are tightly coupled with the motor programs associated with specific tools, whereas more-posterior regions are not constrained in the same manner.

The emerging perspective, then, substantiated by many studies as reviewed above, is one of a gradient of representation mapping more-visual to more action-based properties along the caudal–rostral and also the medial–lateral dorsal pathway. The heterogeneity of representations and variation along this gradient might account for some of the puzzling inconsistencies in the literature. As noted above, representational invariance (i.e., resilience to different image transformation such as retinal size, location, and viewpoint) is one of the signatures of object representations in the ventral pathway [45,82–85] but is also noted in some [25], albeit not all [41,49], investigations of the properties of the dorsal pathway. The inconsistencies between invariance versus sensitivity to visual transformations might reflect differences in the organization or homology of the parietal cortex across species [48,86,87] or differences in experimental techniques (fMRI vs. electrophysiological recording). However, and relevant to the issue at hand, they might also reflect differences between the regions that are often differently sampled along the rostral–caudal axis in the various investigations. This last possibility is supported by the finding that comprehensive mapping of adaptation (reduction in BOLD signal with repetition of the same stimulus) along the rostral–caudal axis uncovers invariant object representations only in the posterior (i.e., IPS1, IPS2) but not in the anterior part (i.e., IPS3, IPS4) of the IPS [24].

#### Dorsal Pathway Contribution to Perception – The Case of 3D Perception

The evidence thus far suggests that regions of the dorsal pathway (especially more-posterior and medial regions) contribute functionally to perception and may be computed independently of ventral cortex involvement. Two remaining important questions, then, concern what precisely is the nature of the dorsal neural representations, and why it is that, if object representations can be generated by dorsal cortex, patients with ventral lesions continue to be (sometimes

profoundly) impaired at object recognition. While much of this is still poorly understood and obviously requires further investigation (see Outstanding Questions), converging evidence suggests that the dorsal pathway may play a unique role in 3D depth perception ([26,41,60,88,89]; [74,90] for review). Many studies have demonstrated that regions along the dorsal pathway are sensitive to depth information induced from a multiplicity of depth cues, including disparity [88,91], motion [87] and texture cues [89,92], and, to a lesser extent, from shading cues [92]. Importantly, dorsal pathway sensitivity to depth information can reflect the processing of object-based 3D structure defined from monocular depth cues, as is evident from the data showing greater activation for impossible objects that have invalid 3D structure [26,30], and from an fMRI study that found differential dorsal pathway responses for position information processing and for object 3D structure processing [93]. Finally, regions along the dorsal pathway were also found to be involved in mental rotation [94], which requires the derivation of 3D structure.

While the derivation of a volumetric, 3D representation is entirely sensible in the service of visuomotor control [41], 3D information can both facilitate and contribute to object recognition as well. 3D depth information is particularly important for the derivation of an object structural description in the face of variations in viewing conditions and, consequently, may play a useful role in object perception [95] although this information may not suffice for fine-grained object recognition.

Accordingly, 3D representations, some in the service of perception, were also observed in non-human primate studies showing that dorsal object representations have shorter latencies but are not as detailed as the corresponding ventral representations [27,49,74]. These findings may provide important clues about the contribution of the dorsal pathway to visual perception. In particular, dorsal object representations may provide coarse (albeit necessary) input to the ventral pathway about object structure and global form, potentially from the rapid propagation of magnocellular signals. Such a mechanism could account for the residual perceptual abilities found in patients with visual agnosia [26], and also for the perceptual deficits associated with parietal lesions [60,62]. This assumption is compatible with neuropsychological investigation in which patients with occipitoparietal (i.e., dorsal pathway) and occipitotemporal (i.e., ventral pathway) lesions were asked to identify objects defined from disparity. While patients with occipitotemporal lesions were able to detect the existence of an object, but not to identify it, patients with occipitoparietal lesions were not even able to detect the object [63]. This observation (also see [27,43,60,62]) further suggests that the representations in the dorsal pathway play an important role in 3D perception, but nevertheless are not sufficient, in and of themselves, to support normal object recognition.

The findings of 3D representations in the dorsal pathway mesh well with the claims of a perceptual–motor gradient. In particular, 3D object representations are found in non-human primates in both the anterior part of the parietal cortex (AIP) as well as in more-posterior parts of it (CIP; LIP). However, while AIP representations were found not to be engaged in a 3D perceptual object discrimination task, and only in service of visuomotor control [75], object representations in the more-posterior CIP were associated with perceptual behavior [27].

#### Dorsal Pathway Contribution to Perception – Beyond 3D Structure

Dorsal pathway representations may encode and contribute to the perception of spatial properties beyond 3D structure. For example, in a same–different face detection task, configural but not featural processing of faces was uncovered in the posterior dorsal pathway, as demonstrated by the BOLD activation profile. This activation was also correlated with perceptual performance and led to greater functional connectivity with the fusiform face area (FFA; perhaps via medial anatomical pathway [42]). Moreover, when transcranial magnetic stimulation (TMS)



was applied to these regions, there was selective interference of configural processing, further suggesting the dorsal pathway processing is essential for the intact perception of object spatial information [35].

Structure from motion, or the extraction of the shape of the object by exploiting the different velocities of different points on the surface of the object in the input (for review see [96]), may also be derived by dorsal cortex. Studies in humans and in non-human primates have shown that movement-selective regions (middle temporal area, MT; and medial superior temporal area, MST), that are considered to be part of the dorsal pathway (but see [97] who suggests that these regions may construct a third, dissociated, pathway), are involved in the extraction of shape from motion, and that this sensitivity is beyond simple sensitivity to optic flow or sensitivity to local stimulus components [98]. The derivation of shape from motion appears to engage regions in the posterior parietal cortex in humans [87,99], and comparison between patients with occipitoparietal and occipitotemporal lesions showed that patients with occipitoparietal lesions were selectively impaired in extracting 3D structure from motion and in the detection of global motion patterns. These patients were, however, still able to successfully detect local motion and to extract 2D shape from motion, further pointing to the involvement of the dorsal pathway in the perception of 3D structure from motion. By contrast, patients with an occipitotemporal lesion were still able to extract 3D structure from motion, despite their impairment in recognition of these shapes [63]. This pattern of behavior further demonstrates that, at least under some conditions, object recognition is achieved by an integration of dorsal and ventral representations [96].

#### Origin of the Dorsal ‘What’ Representations

We have suggested that the caudal–rostral and medial–lateral object representation axes may derive from the differential connectivity patterns to visual (early visual cortex and ventral cortex) and motor cortices, respectively. In addition to these anatomical constraints, dorsal object representations might also rely on functional associations between motor and perceptual experiences. Despite the paucity of research in this field, some initial support for this hypothesis comes from developmental studies showing that tool sensitivity is evident in the dorsal pathway early in life [100], but that this sensitivity undergoes further refinement between the ages of 4 and 8 years [101], suggesting that sensitivity to objects in the dorsal pathway may continue to be shaped by motor experience and learning. This conclusion also converges with recent studies showing that visual perception is shaped and modulated by motor and exploration experiences during infancy. For example, the level of motor development in infants was found to be correlated with better 3D object representation [102] and with face preference [103]. Moreover, when infants aged 3 months were trained to self-produce reaching movements directed to objects, their spontaneous face preference increased as well [104]. The neural underpinnings of the perceptual–motor axis and its ontogenetic basis is still unknown and, although connectivity constraints may play a key initial role in establishing functional organization, interactions between perceptual and visuomotor representations along the dorsal pathway may emerge with experience and learning. Much research is still necessary to understand the underpinnings of the gradient, and its maturation and increasing refinement over the course of development.

#### Concluding Remarks and Future Directions

The claim segregation and functional independence of the visual dorsal and ventral cortical pathways has provided one of the most influential frameworks for understanding the visual system over the past four decades, although the exact nature of the segregation has been re-evaluated, revised, and reconsidered over this time. Recent empirical evidence calls into question the binary distinctions between the two pathways, and suggests that the dorsal pathway is involved in – and is possibly even necessary for – visual perception. Moreover, widespread empirical findings indicate that object representations are not monolithic even within

#### Outstanding Questions

There is ongoing controversy concerning the nature of object representations in the dorsal pathway. Are dorsal object representations invariant with respect to different visual transformations such as size, position and pose? Does representational invariance follow the caudal–rostral axis of the occipitoparietal lobe?

The caudal–rostral representational axis proposed here demands further characterization. Does sensitivity to object shape decrease as one moves forward on the axis? Correspondingly, does sensitivity to visual elements relevant to visuomotor control increase as a function of being more anterior along the axis?

Despite the accumulating evidence for the necessary involvement of the dorsal pathway in object perception, it is not yet clear what unique contribution to visual perception is offered by these cortical regions beyond 3D structural representations – and how these dorsal representations interact with and alter ventral pathway representations?

The developmental trajectory of the ventral pathway and its associated perceptual processes has been intensively characterized in the last decade. Surprisingly, only a handful of studies have investigated the development of visual object representations in the dorsal pathway. Additional investigations along these lines could answer several important questions. What are the environmental pressures and life experiences that shape dorsal object representations? Is the perceptual contribution of object representations in the dorsal pathway changed as function of age and experience?

the dorsal pathway, and are differentially shaped along the perceptual (caudal–medial)–motor (rostral–lateral) axis, with the more-caudal–medial regions being responsive to the visual properties of the input and the more-rostral–lateral regions tuned more in the service of the visuomotor output. In light of the emerging evidence, visual perception should be studied not simply as a function of one (ventral) ‘what’ pathway, but instead as the joint outcome of the processing and coordination of different ‘what’ regions in both cortical visual pathways.

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