Review

'What' Is Happening in the Dorsal Visual Pathway

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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.

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.

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

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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.