Dorsal-Ventral Stream Interactions in Visual Object Representation Processing

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Abstract

The brain' s visual system processes visual information about objects through dorsal and ventral pathways. The ventral pathway is primarily responsible for the "what" aspect of object visual recognition processing, whereas the dorsal pathway is mainly responsible for the "where" aspect of object visuospatial and motion processing. However, multiple interactive neural connections exist between the dorsal and ventral pathways, suggesting functional interactions between the two in visual object representation processing. On the one hand, the ventral pathway alone cannot compute the global shape of objects; information regarding global shape represented in the dorsal pathway must converge with information regarding local features represented in the ventral pathway to support invariant visual object information processing. On the other hand, in goal-directed thought and behavior, the dorsal pathway needs to extract and maintain object visual information from the ventral pathway in real time to achieve adaptive visual object information processing. The former constitutes a primarily feature-driven (bottom-up) functional integration, while the latter constitutes a primarily task-driven (top-down) functional integration. Future research should further investigate the effects of attention on global shape representation in the dorsal pathway, the mechanisms by which object familiarity modulates the integration of global shape and local features, how visual working memory resists interference to maintain processing of goal-directed stimuli, the influence of endogenous memory information on adaptive visual object representation, as well as the developmental mechanisms of the dorsal-ventral pathways and their impact on the interaction between the two.

Full Text

Preamble

The visual system processes object information through dorsal and ventral pathways. The ventral pathway, projecting from V1 through V2 and V4 to the inferior temporal cortex (ITC), is known as the "what" pathway and primarily handles object recognition. The dorsal pathway, projecting from V1 through V2 and V3 to the posterior parietal cortex (PPC), is known as the "where" pathway and mainly specializes in visuospatial and motion processing to serve visually guided actions (Freud et al., 2020; Freud et al., 2016; Lima et al., 2023; Mahon, 2023). While substantial evidence supports this functional segregation, mounting research reveals multiple reciprocal neural connections between these pathways, suggesting significant functional interactions in visual object representation (Freud & Behrmann, 2020; Garcea et al., 2018; Goldstein-Marcusohn et al., 2024; Vinci-Booher et al., 2022; Yang et al., 2020).

Invariant and adaptive visual processing represent two key mechanisms for object representation in the brain (Xu, 2018b). Invariant processing refers to the visual system's ability to maintain stable representations of object features despite changes in viewing conditions (e.g., perspective, size), enabling object recognition and categorical judgments (Ayzenberg & Behrmann, 2024; Nestmann et al., 2022; Xu & Vaziri-Pashkam, 2022). Adaptive processing, conversely, involves the dynamic selection and temporary storage of object information to meet individual goals and task demands (Xu, 2018a, 2018b, 2024). Traditional views held that invariant object processing is accomplished solely by the ventral pathway (Kravitz et al., 2013). However, recent findings indicate that the ventral pathway requires integration of global shape information represented in the dorsal pathway to achieve invariant processing (Ayzenberg & Behrmann, 2022a, 2023a, 2023b, 2024). Moreover, through visual working memory (VWM), the dorsal pathway can dynamically extract and temporarily store object information from the ventral pathway to support adaptive visual representations (Taylor & Xu, 2022; Vaziri-Pashkam et al., 2019; Xu, 2018a, 2018b, 2023a). Elucidating the interaction mechanisms between dorsal and ventral pathways in visual object representation not only advances our understanding of object cognition but also holds important implications for artificial intelligence modeling of object recognition and clinical research on object perception disorders.

This paper first introduces the structural composition and fiber connections of the dorsal and ventral pathways to establish the anatomical basis for information exchange between them. It then examines: (1) the functional segregation and integration mechanisms in invariant object representation, and (2) the dynamic integration mechanisms through which the dorsal pathway extracts and represents object information from the ventral pathway via VWM during goal-directed adaptive processing. Finally, it discusses key issues requiring further investigation.

2. Structural Composition and Fiber Connections of Dorsal and Ventral Pathways

The structural organization and fiber connections of the dorsal and ventral pathways are illustrated in Figure 1 [Figure 1: see original paper], showing human (a) and monkey (b) brains. In the human dorsal pathway, visual information is transmitted forward from V3A/B to the PPC. The human PPC comprises a continuous band of multiple regions distributed along and around the intraparietal sulcus (IPS), arranged from posterior to anterior as IPS0/V7 and IPS1-IPS5 (Kastner et al., 2017; Kravitz et al., 2013). In monkeys, the dorsal pathway transmits visual information through V3 to the PPC, which from posterior to anterior includes the caudal intraparietal area (CIP), lateral intraparietal area (LIP), ventral intraparietal area (VIP), medial intraparietal area (MIP), and anterior intraparietal area (AIP) (Freud et al., 2016; Kastner et al., 2017).

In the human ventral pathway, visual information is transmitted through hV4 to the lateral occipital cortex (LOC) at the occipitotemporal junction, then forward to the ventral occipitotemporal cortex (VOTC) of the ITC—including the fusiform gyrus (FG) and other regions—and the anterior temporal lobe (ATL) (Ayzenberg & Behrmann, 2022a; Kravitz et al., 2013). In monkeys, the ventral pathway transmits visual information through V4 to the posterior (TEO) and anterior (TE) regions of the inferior temporal area (IT) (Kravitz et al., 2013). Neuroanatomical and non-invasive diffusion magnetic resonance imaging (dMRI) studies (Takemura et al., 2019) demonstrate extensive and dense neural connections between the dorsal and ventral pathways. In humans, the vertical occipital fasciculus (VOF) connects ventral occipital regions (hV4) with dorsal visual areas (V3A/B) (Takemura et al., 2019), while the posterior vertical pathway connects the ITC with extensive posterior-to-anterior regions of the PPC (Bullock et al., 2019; Vinci-Booher et al., 2022). In monkeys, the VOF connects V3 and V4 (Takemura et al., 2024), and extensive regions between IPS and IT are connected by the inferior longitudinal fasciculus (ILF) (Roumazeilles et al., 2020). These multiple reciprocal connections provide the anatomical substrate for functional interactions between dorsal and ventral pathways in visual object representation.

3. Functional Segregation and Integration in Invariant Object Representation

Studies in humans (Ayzenberg & Lourenco, 2022; Ayzenberg, Simmons, et al., 2023) and non-human primates (Guo et al., 2022) reveal functional segregation in object representation: the dorsal pathway encodes global shape while the ventral pathway encodes local features. Because global shape representation is object-centered and describes an object’ s overall structure through the spatial arrangement of local features, it exhibits tolerance to changes in those features (Figure 2) [Figure 2: see original paper] (Ayzenberg & Behrmann, 2022a). This property makes global shape representation a critical organizational feature supporting invariant object processing. Consequently, the ventral pathway must integrate global shape information from the dorsal pathway to accomplish invariant object representation.

3.1 Functional Segregation in Visual Object Representation

Extensive evidence supports functional segregation between dorsal and ventral pathways. First, the ventral pathway shows greater sensitivity to local features than to global shape. For instance, when images are subjected to subtle, imperceptible local perturbations that do not affect object identity recognition, single neurons in monkey IT exhibit strong and dense firing responses (Guo et al., 2022), indicating high sensitivity to local feature changes even when they do not alter perceived identity. However, for synthetic images with scrambled local feature arrangements, both human fMRI multivariate responses in ventral visual cortex and computational modeling outputs from monkey IT fail to distinguish them from intact natural images, despite human observers easily differentiating the two categories (Jagadeesh & Gardner, 2022). Thus, at both single-neuron and population levels, the ventral pathway represents objects not as complete shapes but as collections of features whose precise spatial arrangement does not substantially affect representation outcomes. Similarly, "Texforms" images—which degrade object contours and shapes to unrecognizable levels while preserving texture statistics—activate the same large-scale functional maps in the ventral pathway as intact natural images (e.g., broad cortical regions encoding object size and animacy), even though human observers cannot recognize them (Long et al., 2018; Wang et al., 2022). This suggests that local features, rather than global shape, better characterize functional activation patterns across large cortical regions in the ventral pathway.

Second, the dorsal pathway can independently represent global shape. Unlike the ventral pathway, the dorsal pathway shows greater activation for intact object images compared to images with scrambled local features (Freud, Culham, et al., 2017). Transcranial magnetic stimulation (TMS) and lesion studies demonstrate that temporary deactivation or damage to dorsal cortex impairs perception of global shape, including configural processing (Zachariou et al., 2017), perception of inter-feature relationships (Thomas et al., 2012), and visuospatial perception (Medina et al., 2020). Although ventral cortex is central to object recognition, dorsal cortex remains sensitive to three-dimensional (3D) structure representation even after ventral damage (Freud, Ganel, et al., 2017). Riddoch et al. (2008) found a double dissociation between lesion location and functional deficits: patients with ventral cortex lesions show impaired local feature perception but intact global shape perception, whereas those with dorsal cortex lesions exhibit the opposite pattern. Recent computational vision research has proposed a quantitative model describing object local feature arrangements through internal symmetry axes—the "shape skeleton" (Ayzenberg et al., 2022; Ayzenberg & Lourenco, 2022). This model effectively explains how the human visual system represents global shape for object recognition (Ayzenberg et al., 2019; Ayzenberg & Lourenco, 2019; Destler et al., 2019; Wilder et al., 2019). Studies show that shape skeletons better predict dorsal pathway response patterns and can independently explain response variance compared to other visual models (Ayzenberg & Behrmann, 2022b; Ayzenberg et al., 2022).

Thus, the dorsal pathway primarily represents global shape while the ventral pathway is sensitive to local features, with both contributing to object representation. The critical question concerns how these pathways interact to achieve invariant object processing. Given that the ventral pathway is central to object recognition and invariant representation is its hallmark, Ayzenberg and Behrmann (Ayzenberg & Behrmann, 2022a, 2024; Ayzenberg, Simmons, et al., 2023) propose that the dorsal pathway independently computes global shape representations early in processing and transmits this information to the ventral pathway to support invariant object representation.

3.2.1 LOC as a Neural Locus for Functional Integration

The lateral occipital cortex (LOC) is a critical region for object recognition in the ventral pathway, subdivided along the posterior-anterior axis into the lateral occipital cortex (LO) and posterior fusiform gyrus (pFs) (Grill-Spector et al., 1999). LO exhibits the highest shape sensitivity in the ventral pathway and shows greater representational similarity to posterior dorsal pathway regions (V3a-IPS0) than to other ventral regions (Freud, Culham, et al., 2017). This similarity persists even for complex objects like faces, where LO and posterior dorsal regions show greater representational alignment than other ventral regions (Ai et al., 2023), possibly reflecting shared representations of facial configural properties (Zachariou et al., 2017). Although these regions belong to different pathways, their similar representational structures provide a neural basis for LO to receive global shape projections from the dorsal pathway (Ayzenberg, Simmons, et al., 2023). As part of the ventral pathway, LOC follows a posterior-anterior processing hierarchy (Lerner et al., 2002; Wurm & Caramazza, 2022), with posterior LO being more sensitive to local features and anterior pFs more sensitive to global properties and more stable invariant representations across size and position changes. Studies show that LO can decode shape skeleton information, whereas no evidence for shape skeleton representation is found in pFs (Lescroart & Biederman, 2013), suggesting that pFs may primarily be sensitive to semantic-level information (Ayzenberg et al., 2022). Therefore, LOC participates as a whole in dorsal-ventral functional integration. Specifically, after receiving rapid projections of global shape information from the dorsal pathway, LOC integrates this with local feature information as processing advances along the hierarchy, ultimately achieving invariant object representation (Ayzenberg, Simmons, et al., 2023; Liu et al., 2017; Nestmann et al., 2021).

3.2.2 Temporal Advantage of Dorsal Pathway Visual Processing

Electrophysiological studies in humans and non-human primates reveal a latency advantage for dorsal pathway visual processing. For example, single-cell recordings in monkeys show that IPS neurons exhibit selectivity for 2D shapes approximately 30–40 ms after stimulus onset, whereas V4 latency is about 60–70 ms (Janssen et al., 2008). Similarly, for 3D shape selectivity, IPS latency is about 50 ms compared to 110 ms in IT (Theys et al., 2012). Human EEG

(Regev et al., 2018) and MEG (Liu et al., 2017) studies also show that dorsal pathway decoding of global shape (IPS latencies of 60 ms and 50 ms, respectively) precedes ventral pathway decoding (LOC latencies of 200 ms and 130 ms). This temporal advantage may arise because the dorsal pathway receives fast-transmitted, coarse, low-contrast, low-spatial-frequency object information via the magnocellular pathway (Ayzenberg, Simmons, et al., 2023), while the ventral pathway receives slower-transmitted, fine, high-contrast, high-spatial-frequency information via the parvocellular pathway (Collins et al., 2019; Wang et al., 2023). Studies show that dorsal pathway sensitivity to coarse object information emerges as early as 50 ms post-stimulus, whereas ventral sensitivity to fine information appears at 70 ms (Collins et al., 2019). Critically, TMS and fMRI studies indicate that coarse object information transmitted through the magnocellular pathway is sufficient for computing global shape (Ayzenberg, Simmons, et al., 2023; Wang et al., 2023).

3.2.3 Dorsal-to-Ventral Transmission of Global Shape Supports Invariant Representation

Ayzenberg and Behrmann (2022b) used fMRI to directly investigate dorsal pathway influences on ventral pathway global shape representation. They found that the posterior intraparietal sulcus (pIPS), primarily including IPS0, computes object part relations and exhibits object category decoding comparable to LOC. Importantly, mediation and multivariate effective connectivity analyses revealed that pIPS multivariate responses mediate LOC' s global shape representation and show significant effective connectivity with LOC, with pIPS global shape processing preceding and predicting LOC processing. However, fMRI' s limited temporal resolution precludes definitive conclusions about the timing and directionality of dorsal-ventral interactions. To address this, Ayzenberg and Simmons et al. (2023) employed high-density EEG, which offers high temporal precision and spatial resolution. Their results showed that pIPS information decoding (approximately 66 ms) preceded LOC decoding (approximately 94 ms), with dorsal pathway activity predicting ventral pathway responses in a time-dependent manner.

In summary, functional segregation between dorsal and ventral pathways necessitates that ventral invariant object processing integrates global shape information from the dorsal pathway. Specifically, coarse object information from primary visual cortex is rapidly transmitted via the magnocellular pathway to pIPS, where early-stage global shape representations are formed and transmitted to LOC. There, they integrate with fine local feature information arriving via the parvocellular pathway before propagating forward along the ventral pathway to complete invariant object representation. This process constitutes a primarily feature-driven (bottom-up) object information processing mechanism.

4. Functional Integration in Adaptive Object Representation

As described above, dorsal pathway global shape representations in early visual processing stages support ventral invariant processing, enabling rapid object recognition and providing a stable, detailed analysis of the visual environment. However, indiscriminate availability of massive visual input would distract attention and disrupt task execution. Therefore, at any given moment, the visual system must exclude most task-irrelevant information and select only a small subset of relevant information to support cognitive processes such as task planning and problem-solving, thereby accomplishing goal-directed tasks (Xu, 2018a, 2018b, 2023a). For example, when viewing "a cat wearing a red bow," the invariant visual system faithfully reflects the cat's visual features, maintaining general invariance across contexts and tasks. In contrast, the adaptive visual system highlights different features based on the observer' s focus: when identifying the animal, it emphasizes the "cat" conceptual attribute; when determining the bow' s color, it emphasizes the "red" attribute (Xu, 2018b). Thus, adaptive object representation is a task-based, goal-directed process requiring a functional integration platform that can dynamically select and represent object visual information processed in the ventral pathway. The PPC in the dorsal pathway likely serves this critical role.

4.1 PPC and Adaptive Object Representation

The PPC in the dorsal pathway is ideally suited for adaptive visual representation (Xu, 2018a, 2018b, 2020). In terms of cortical topography, regions along the IPS from posterior to anterior subserve distinct functions. Posterior regions V3A/V3B/IPS0 (homologous to monkey CIP) primarily process spatial information (Alizadeh et al., 2018; Medina et al., 2020). Anterior regions IPS3/IPS4/IPS5, the human parietal grasp region (AIP), and the human parietal reach region (MIP) participate in motor execution of eye movements, grasping, and reaching (Kastner et al., 2017). Critically, intermediate regions IPS1/IPS2 (LIP), which substantially overlap with the superior intraparietal sulcus (sIPS) (Figure 1a) (Bettencourt & Xu, 2016b; Xu, 2018a), are primarily involved in cognitive processing of object visual information (Xu, 2018a, 2018b, 2020) and participate in storing and encoding object visual information (Lefco et al., 2020). Finally, the superior parietal lobule (SPL) and right temporal parietal junction (TPJ) flanking the IPS primarily control attention and facilitate flexible shifting (Oğlin et al., 2024; Xu, 2018a). This arrangement places sIPS(LIP), which subserves cognitive processing, amidst regions handling visuospatial information, action, and attentional control. Through attentional control mechanisms, this region can determine which visual information is selected and processed, storing and flexibly representing it in VWM to meet task demands.

4.2 sIPS(LIP) Supports Adaptive Object Representation

Adaptive object representation requires two key features (Xu, 2018a, 2018b): robust attentional control and task modulation to focus on goal completion and resist distractor interference, and storage and representation of task-relevant information in VWM to maintain information temporarily when visual stimuli are no longer present for further cognitive processing.

First, sIPS(LIP) visual processing is modulated by attention and task demands (Taylor & Xu, 2024; Vaziri-Pashkam & Xu, 2019). For example, many LIP neurons in monkeys show selectivity for object visual features only when they are task-relevant (Seideman et al., 2022). Human fMRI multivoxel pattern analysis (MVPA) shows that visual features such as shape (Xu & Jeong, 2015), color (Yu & Shim, 2017), and category (Bracci et al., 2017) can be decoded in IPS only when they are task-relevant or attended, whereas LOC encodes task-irrelevant shapes (Xu, 2010) and shows weaker distractor suppression than sIPS (Vaziri-Pashkam & Xu, 2017). Moreover, sIPS object classification accuracy remains stable under distractor interference and correlates with individual behavioral performance (Bettencourt & Xu, 2016a; Xu, 2024). Patient R.V. with sIPS damage cannot perform appropriate hand movements according to task requirements (Goodale, Meenan, et al., 1994), and patients with reversible sIPS lesions show dramatically reduced accuracy in identifying cued target stimuli when competing distractors are present during early lesion stages (day 4 post-lesion), but exhibit normal distractor resistance after recovery (day 107 post-lesion) (Gillebert et al., 2011). Finally, task demands and stimulus features jointly modulate visual information encoding in LIP neurons (Ibos & Freedman, 2016) and visual representation strength in sIPS (Long & Kuhl, 2018; Vaziri-Pashkam & Xu, 2017). For instance, Taylor and Xu (2024) used multidimensional scaling analyses to project representational dissimilarity matrices encompassing all task-category combinations onto a two-dimensional space. Results showed that within-task category representational geometry was more similar than between-task geometry in sIPS, with category representations distributed similarly across tasks. In contrast, LOC and VOTC showed greater similarity for representations of objects from the same category, with category geometry unaffected by task. Thus, both category and task jointly shape sIPS representational geometry, whereas LOC and VOTC geometry is dominated primarily by object category, demonstrating that sIPS not only selects information according to task goals but also represents it further.

Second, sIPS(LIP) participates in VWM storage and representation (Kastner et al., 2017; Lefco et al., 2020). Neurophysiological studies in monkeys show that LIP neurons sustain shape representations during VWM delay periods (Fitzgerald et al., 2011; Sereno & Maunsell, 1998). Human fMRI studies demonstrate that sIPS activation during working memory tasks correlates positively with VWM capacity (Bettencourt & Xu, 2016b; Sheremata et al., 2018). Importantly, during VWM delay periods, the presence or predictability of distractors does not affect sIPS decoding ability or behavioral performance but significantly impacts decoding in early visual cortex (Bettencourt & Xu, 2016a; Xu, 2020). This suggests that sIPS maintains more robust VWM representations than early visual cortex when VWM is perturbed, preserving information maintenance against interference. Lesion (Berryhill & Olson, 2008) and TMS (Tseng et al., 2010) studies further show that damage to this region impairs VWM storage and encoding. In summary, sIPS is crucial for VWM storage and representation, particularly given its close correlation with behavioral performance and resistance to interference, making it well-suited for adaptive object representation.

Thus, sIPS(LIP) functions as a high-level cognitive hub associated with attention and VWM (Kastner et al., 2017). This region can select and temporarily maintain task-relevant object visual information to support adaptive processing. However, unlike ventral invariant processing, which requires dorsal global shape support, dorsal adaptive processing requires object information represented in the ventral pathway (Xu, 2018a, 2018b).

4.3 Dorsal Pathway Extraction and Utilization of Ventral Object Information

Human neuroimaging (Vaziri-Pashkam & Xu, 2019) and monkey neurophysiological studies (Borra & Luppino, 2017; Theys et al., 2015) show that PPC representations of visual object information are highly robust, encompassing single features (color, size, texture) and complex features (identity, object category) (Freedman & Ibos, 2018), independent of spatial and action information (Xu, 2018a, 2018b). Multiple lines of evidence indicate that visual object information represented in PPC originates from the ventral pathway.

First, LOC provides invariant visual object information to IPS to support goal-directed task completion. As previously discussed, LOC is not only a key region integrating global shape and local feature information in the ventral pathway but also exhibits invariance to object size and viewpoint (Nestmann et al., 2022; Xu & Vaziri-Pashkam, 2022). Importantly, IPS1-2 show similar invariance to object features as LOC, suggesting that integrated visual information from LOC may support adaptive processing in IPS1-2 (Konen & Kastner, 2008; Vaziri-Pashkam & Xu, 2019). Neuropsychological studies show that LOC damage impairs invariant visual information processing (Milner, 2017). For example, patient D.F., when asked to insert a T-shaped object into a T-shaped slot, appears limited to using visual information from a single orientation (vertical or horizontal axis of the slot) to guide wrist rotation (Goodale, Jakobson, et al., 1994). Due to LOC damage preventing integration of information about both slot axes, only local feature and orientation information from a single axis could be transmitted to IPS. Consequently, when the slot' s horizontal axis served as the guiding orientation, the patient consistently aligned the object's vertical axis with the slot' s horizontal axis, resulting in task failure. Thus, invariant object information represented in LOC is crucial for supporting IPS in goal-directed tasks (Xu, 2018a, 2018b).

Second, structural connections and information flow exist from FG to IPS. dMRI studies (Jitsuishi & Yamaguchi, 2020) identify a dedicated fiber bundle (IPS-FG bundle) directly connecting IPS and FG. Further analysis shows that IPS1–2 are tightly connected with multiple FG subregions involved in color analysis and object recognition at different processing levels. Therefore, the IPS-FG bundle can meet the demands of various cognitive functions (e.g., VWM) for dorsal-ventral integration. For example, fMRI studies show increased functional connectivity between FG and IPS when viewing tool images (Chen et al., 2018). Dynamic causal modeling (DCM) analyses of fMRI data examining effective connectivity during tool knowledge representation reveal that functional knowledge tasks enhance connectivity strength between primary visual cortex and FG, whereas manipulation knowledge tasks strengthen connections from primary visual cortex to FG and then to IPS (Kleineberg et al., 2018). This suggests that more abstract knowledge about object identity and function is first decoded in the ventral pathway, then partially transmitted to the dorsal pathway for further representation according to task demands, ultimately completing visually guided actions (Mahon, 2023).

Third, the PPC top-down modulates and reshapes object representations in the ventral pathway. Research suggests that the dorsal pathway not only top-down selects and extracts object visual information from the ventral pathway to support goal-directed behavior but also monitors task execution in real-time and dynamically adjusts and reshapes ventral object representations according to dorsal feedback signals, thereby enhancing information availability and object recognition ability (Budisavljevic et al., 2018). Studies using representational dissimilarity matrices (RDMs) measured similarity between VOTC and PPC representations during VWM encoding and maintenance phases (Xu, 2023b). Results showed that VOTC representations during the maintenance phase were more similar to PPC representations during the encoding phase than to VOTC' s own encoding-phase representations. Further analysis indicated that VOTC automatically encoded extensive perceptual information during the encoding phase, with its RDM driven primarily by object visual features. When partial object information was encoded by PPC according to task demands and maintained in VWM, VOTC' s RDM during the maintenance phase closely followed task-relevant features in PPC. Thus, PPC not only directly acquires object information from VOTC but also top-down modulates and reshapes VOTC content related to VWM to better achieve cross-pathway integration in visual representation.

In summary, PPC' s anatomical structure and functional characteristics make it an ideal integration platform for dynamically selecting object visual information processed in the ventral pathway to meet task demands. The VWM supported by sIPS(LIP) ensures temporary storage and representation of task-relevant information, making visual representation content more strongly controlled by attention and protected from distraction, thereby enabling dynamic integration of adaptive object information. This process constitutes a primarily task-driven (top-down) visual object information processing mechanism.

5. Summary and Outlook

The division of the visual system into anatomically and functionally segregated dorsal and ventral pathways represents one of cognitive neuroscience’ s most influential theoretical frameworks. However, multiple reciprocal neural connections between these pathways suggest substantial functional interactions. On one hand, the ventral pathway cannot independently represent global shape —critical for invariant visual processing—and must receive global shape information from pIPS(IPS0) to integrate with local feature information in LOC, supporting invariant object representation. On the other hand, the PPC serves as a dynamic integration platform that can flexibly select appropriate object visual information from the ventral pathway based on task demands and temporarily store it in VWM supported by sIPS(IPS1-2), enabling goal-directed adaptive visual processing. Thus, functional interactions between dorsal and ventral pathways exist in visual object representation: the former represents a primarily feature-driven (bottom-up) integration providing stable, veridical, and detailed environmental representations, while the latter represents a primarily task-driven (top-down) integration enabling flexible and effective interaction with the external world.

Although the interaction mechanisms between dorsal and ventral pathways in visual object representation are becoming clearer, several key issues require further investigation.

First, the influence of attention on dorsal pathway global shape representation. Xu (2023a) proposed that global shape representation might be an epiphenomenon of attentional processing rather than an intrinsic property of dorsal object representation. Attentional processes during object perception are generally considered to involve both feature-driven bottom-up and cognitively controlled top-down components (Katsuki & Constantinidis, 2014). The former participates in automatic integration of visual features (e.g., shape, color, size) in early stages (75-100 ms), while the latter allocates attentional resources according to task goals in later stages (after 250 ms) (Conci et al., 2011; Schneider et al., 2012). However, global shape decoding in pIPS (66 ms) (Ayzenberg, Simmons, et al., 2023) precedes the onset of feature integration (75 ms) (Conci et al., 2011), suggesting that global shape representation may be completed earlier. The mechanisms of attentional involvement in dorsal global shape representation remain unclear. Evidence indicates that during target selection from competing distractors, attention preferentially processes global shape over local features (Grüner et al., 2021), suggesting that global shape salience automatically attracts attentional resources. Notably, shape skeletons—describing global shape structural information—not only highlight global shape features (Ayzenberg & Lourenco, 2019, 2022) but are also primarily represented in V3 (Ayzenberg et al., 2022; Lescroart & Biederman, 2013). V3 primarily processes low-spatial-frequency information transmitted via the magnocellular pathway (Felleman et al., 1997) and participates in representing salient features in visual scenes that are crucial for bottom-up attentional guidance (Katsuki & Constantinidis, 2014). This suggests that bottom-up attention may still participate in global shape representation. Future research could systematically manipulate shape skeleton salience (e.g., varying distances between skeletal axes in 10% increments) (Ayzenberg & Lourenco, 2019) to examine dynamic V3 activation changes and investigate whether bottom-up attention affects global shape representation. Additionally, while pIPS (especially IPS0) shows selective activation for global shape with natural objects (Ayzenberg, Simmons, et al., 2023), its information processing is shaped by both attentional processes (Katsuki & Constantinidis, 2014; Riddle et al., 2019). However, existing evidence indicates that pIPS sensitivity to global shape is unaffected by task difficulty or attentional resource allocation (Arsenovic et al., 2022), and attentional distribution does not alter the posterior-anterior gradient of shape sensitivity in dorsal and ventral pathways (peaking at V3b/IPS0 and LOC, respectively) (Goldstein-Marcusohn et al., 2024). This suggests pIPS global shape representation may not be modulated by top-down attention. Future studies should employ orthogonal designs manipulating both shape salience (guiding bottom-up attention) and task goals (guiding top-down attention) to investigate the combined mechanisms of attentional modulation of dorsal global shape representation.

Second, mechanisms by which object familiarity modulates integration of global shape and local features. Although substantial evidence supports dorsal pathway independent representation of global shape, some studies find that patients with dorsal cortex damage but intact ventral cortex (e.g., R.V.) show minimal object recognition deficits (Goodale, Meenan, et al., 1994; Goodale & Milner, 2023; Milner & Goodale, 2006). If global shape representation is crucial for object recognition, why this discrepancy? One hypothesis suggests that stimuli in these studies were familiar to patients, who could recognize and categorize objects using local features alone without recruiting dorsal global shape information (Ayzenberg & Behrmann, 2023b). Ayzenberg and Blauch et al. (2023) trained deep neural networks (DNNs) on shape stimuli presented to patients in Goodale and Meenan et al. (1994) and found that a shallow feedforward DNN model (CORnet-Z) easily classified these stimuli as curved versus straight shapes (Ayzenberg, Blauch, et al., 2023). Since DNNs do not represent global shape but are highly sensitive to local features (Baker et al., 2023; Baker et al., 2018; Jarvers & Neumann, 2023), this suggests that DNNs can classify these objects even without global shape representation. Human fMRI studies also show that when images containing few diagnostic object parts are presented, people can identify objects with high accuracy while ventral cortex shows strong activation (Holzinger et al., 2019; Ullman et al., 2016). As DNNs are optimal computational models of human ventral pathway object recognition (Ayzenberg & Behrmann, 2022a), and both DNN and human ventral representations of local features are shaped by experience (Ayzenberg & Behrmann, 2024; Doerig et al., 2023), local features may have high information availability for familiar objects. However, this advantage disappears for novel, unfamiliar objects. For example, DNNs require far more samples and training trials than humans for novel object recognition, with poorer training outcomes (Zador, 2019). Human infant studies show that 6-month-old infants can categorize objects based on global shape after exposure to a single sample (one-shot learning) (Ayzenberg & Lourenco, 2022), with skeletal models of global shape providing the best fit for infant behavioral performance (Ayzenberg & Lourenco, 2019). This indicates that infants rely primarily on global shape to develop object recognition abilities with minimal perceptual experience or language involvement. Notably, despite sparse visual worlds, infants' object categorization abilities match or exceed many state-of-the-art DNNs (Ayzenberg & Behrmann, 2024), suggesting DNNs may lack important structural features or appropriate learning objectives (e.g., samples maximizing global shape structure display), limiting their rapid development. Integrating skeletal models into convolutional neural networks (CNNs) significantly improves performance on visual perception tasks, with classification performance more closely approximating human performance (Rezanejad et al., 2019). Future research should incorporate constraints on local feature spatial arrangement into DNN architectures to improve biological plausibility and dorsal pathway correspondence while enhancing recognition accuracy and training efficiency. Integration of findings from infant development, computational modeling, and brain lesion studies is also needed to investigate how object familiarity changes during learning affect mechanisms integrating global shape and local features.

Third, mechanisms by which VWM resists interference to maintain goal-directed stimulus processing. A key mechanism of adaptive visual object processing is the ability to maintain representations of current task goals in VWM despite interference (distracting stimuli or non-targets) (Xu, 2024). Studies show that multiple brain regions (including PFC, PPC, VOTC, and early visual cortex) represent both targets and distractors during VWM delay periods (Christophel et al., 2018; Olmos-Solis et al., 2021; Rademaker et al., 2019; van Loon et al., 2018; Xu, 2024). How does VWM effectively resist interference to maintain current target representations? One view suggests that the visual system prevents interference by suppressing activity unrelated to current task goals (Olmos-Solis et al., 2021). However, Xu (2024) found that interference resistance does not depend on distractor suppression but on separating target and distractor representations in VWM to prevent mutual interference, as distractor changes do not affect PPC target classification accuracy. The author proposed that PPC employs orthogonalization to represent different information streams processed in parallel in VWM, separating target and distractor representations. However, this orthogonalization does not appear to apply to VOTC, where target classification accuracy is significantly affected by distractor changes, possibly because VOTC, as a core object recognition region, must veridically reflect the external environment rather than flexibly respond to task demands. Notably, VOTC represents distractors more strongly than targets during VWM encoding, whereas PPC shows equivalent representation levels for both, suggesting that PPC suppresses distractor representations to some degree while selecting and extracting information from VOTC (Xu, 2024). Thus, PPC may resist VWM interference through both suppression and orthogonalization, with the latter being more adaptive as it can simultaneously accommodate representations of both targets and distractors in VWM. However, Xu (2024) only presented distractor images continuously during the delay period without including target search and selection processes, which may have precluded clear detection of suppression. Future studies could add target search demands or increase task difficulty to Xu (2024)' s experimental procedure to investigate the dynamic mechanisms of orthogonalization and suppression for resisting interference in VWM.

Additionally, research suggests that multiple brain regions involved in VWM representation follow a representational gradient: anterior PFC provides more abstract, goal- or task-related information; posterior VOTC and early visual cortex encode stimulus content (e.g., category information); and intermediate PPC encodes both task relevance and object category (Olmos-Solis et al., 2021). This suggests that PPC, as a functional integration platform, can integrate object category information from the ventral pathway with task relevance information from PFC to form a unified, goal-directed priority map that preferentially processes target information relevant to current tasks while ignoring irrelevant distractors in VWM (Olmos-Solis et al., 2021; Ritz & Shenhav, 2024). Future research must further investigate how PPC integrates information from PFC and the ventral pathway to construct priority maps in VWM.

Fourth, the influence of endogenous memory information on adaptive visual object representation. Xu (2018a, 2018b) appropriately integrated various PPC cognitive functions into adaptive visual object representation, but these visual information sources primarily concerned exogenous information about current objects processed in the ventral pathway. In fact, PPC can also retrieve and extract relevant long-term stored episodic and semantic memory information from the medial temporal lobe (MTL) (Brown et al., 2018; Humphreys et al., 2022; Ramanan et al., 2018) and the anterior temporal lobe (ATL) in the ventral pathway (Humphreys et al., 2022), processed by the lateral intraparietal sulcus (lIPS) and angular gyrus (AnG) (Humphreys et al., 2022; Humphreys et al., 2021). AnG can temporarily buffer and integrate this information (Humphreys et al., 2021; Kuhnke et al., 2023; Ramanan et al., 2018), while lIPS, part of the frontoparietal control network, is regulated by top-down executive control from prefrontal cortex (PFC) and can select and manipulate endogenous information in AnG according to current task demands (Humphreys et al., 2022; Humphreys et al., 2021; Sestieri et al., 2017). Thus, lIPS and AnG processing of endogenous information is similar to sIPS VWM functions for exogenous information. Given their anatomical proximity to sIPS, they may constitute different components of the adaptive visual object representation system. However, mechanisms by which brain regions processing endogenous information participate in adaptive visual object representation of exogenous information remain poorly understood (Xu, 2018a, 2018b). Studies show that networks retrieving endogenous memory information (centered on lIPS and AnG) and networks searching external visual input (centered on sIPS) exhibit functional competition (Sestieri et al., 2017; Sheremata et al., 2018), and similar competition exists among anterior, posterior, and middle subregions of AnG (Humphreys et al., 2020; Humphreys et al., 2022). DTI analyses reveal that anterior and posterior AnG connect with broad ventral pathway regions (primary visual cortex, FG, ATL), while middle AnG connects with MTL, suggesting AnG receives both current perceptual information and long-term episodic and semantic memory (Humphreys et al., 2022). Future research must clarify the relationship between AnG' s multimodal spatiotemporal information input buffering mechanisms (Humphreys et al., 2022) and information selection and manipulation in lIPS and sIPS, which is crucial for explaining PPC mechanisms of adaptive visual representation of both endogenous and exogenous information.

Fifth, developmental mechanisms of dorsal and ventral pathways and their impact on functional interactions. Studies in humans and non-human primates show that dorsal and ventral pathways develop at different rates (Stiles et al., 2020). For example, infant studies (under 12 months) show that the dorsal pathway typically develops earlier than the ventral pathway in both structure and function (Ciesielski et al., 2019; Natu et al., 2021). Conversely, in older children (preschool and school age), the ventral pathway develops faster than the dorsal pathway (Vinci-Booher et al., 2022), possibly because infants primarily use blurry vision and motion sensitivity to prioritize development of holistic 3D shape representation (Ayzenberg & Behrmann, 2024). Moreover, the "low-resolution" dorsal magnocellular pathway develops earlier than the ventral parvocellular pathway (Hammarrenger et al., 2003), leading infants to categorize objects based on dorsal global shape rather than local features (Ayzenberg & Lourenco, 2022). As object perception experience accumulates, ventral pathway development accelerates, establishing distinct category-selective regions and conferring ventral pathway advantages in visual processing in older children (Srihasam et al., 2014). How does this asynchronous development affect functional interactions in object representation? Research shows that ventral pathway processing advantages drive dorsal pathway development. For example, fMRI studies show that when adults (20-30 years) perceive 3D objects formed by coherently rotating dots, PPC activation increases, whereas children (5-6 years) show enhanced activation only in occipital V3a and ventral lingual gyrus, indicating immature PPC spatial motion processing that requires ventral pathway support (Klaver et al., 2008). dMRI studies also show that ventral pathway white matter tracts reach adult levels in 5-8-year-old children, whereas dorsal pathway tracts remain immature with a more protracted developmental trajectory (Vinci-Booher et al., 2022). Since perceptual input is a major driver of white matter development (Maurer & Lewis, 2018) and visual information flows from ventral to dorsal pathways via connecting fiber bundles (Vinci-Booher et al., 2022), dorsal pathway microstructural development may be driven by ventral pathway information. However, few studies have directly examined whether early dorsal pathway development in infancy drives ventral pathway development. Research shows that from birth to 6 months, human infants' dorsal pathway develops faster than the ventral pathway in myelination and synaptogenesis, possibly related to rapid development of dorsal motion perception abilities that support ventral object recognition (Ayzenberg & Behrmann, 2024; Natu et al., 2021). Studies also show that as frontoparietal attention networks develop between 3-6 months postnatally, infants' fixation times on simple stimuli (e.g., black-and-white geometric patterns) decrease while fixation times on complex stimuli and features (e.g., faces and objects) increase, with correspondingly enhanced ventral pathway activation (Reynolds, 2015), suggesting that ventral pathway functional enhancement may be supported and driven by dorsal attention networks. Thus, dorsal-ventral interactions are dynamic and bidirectional across development: dorsal pathway early development drives and supports later ventral development in infancy, while ventral pathway maturation supports dorsal development in childhood. Future research must examine how these directional interactions in infancy and childhood affect functional integration in invariant and adaptive object processing.

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