## A Game of Perception and Action: Do we have two distinct visual systems?

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October, 2023

Over the course of several decades, a body of prominent research has illuminated the functional specialization of the human visual system, delineating its distinct roles in perception and action. Two fundamental pathways within the brain—the dorsal and ventral visual streams govern this understanding. The original theory of the two visual systems was first put forward by Ungerleider and Mishkin (1982), who coined the term what/where model. By studying macaque brain, they unveiled the anatomical partitioning of the primary visual cortex into these two pathways. Then, they proposed that the ventral stream is specialized in the conceptual attributes of visual perception—identifying 'what' the object is—whereas the dorsal stream is specialized in the spatial aspects of vision—identifying 'where' the object is. This division was subsequently elucidated by Goodale and Milner (1992), who conducted a series of observations on patients with specific brain lesions and articulated 'two visual systems' model. Their work underscored a functional dichotomy: the dorsal stream controls the unconscious vision for action, playing a pivotal role in guiding movements, while the ventral stream provides conscious perception of objects.

The visual system dissociation hypothesis was very influential: it induced a considerable amount of research and also has been debated over the past three decades. In this essay, we explore the two visual system model, scrutinizing it from diverse scientific perspectives. We first revise the anatomical and functional description of the two visual streams. Then, we delve into the lesion studies, neuroimaging investigations, and laboratory-based tests, discussing the separation of the two visual functions. Finally, we acknowledge critical viewpoints that have emerged in recent discourse concerning the

distinct functional specialization of the dorsal and ventral streams.

The primary visual cortex is situated within the occipital lobe—back of the cranium. Anatomically, the neural structures projecting from the occipital lobe towards the temporal lobe and the parietal lobe give rise to the two fundamental visual pathways. Accordingly, the neurotypical functioning of the visual system is encapsulated by the dual roles of object recognition and motor guidance. The visual information flowing from area V1 in the primary visual cortex to the temporal lobe including hippocampus, traversing the ventral stream, is used in the realm of visual recognition, typically entailing memory. On the other hand, visual information flowing from area V1 towards the parietal lobe and the motor cortex, traversing the dorsal stream, is used for the guidance of visually coordinated movements.

Goodale and Milner (2018) particularly articulate a functional division between the dorsal and ventral streams in terms of the task they accomplish. This interpretation underscores that the two visual streams use different visual cues for their specialized visual tasks as opposed to the idea that they receive two types of input i.e., object vs spatial information. Moreover, the dorsal stream, responsible for the control of visually guided movements, operates primarily outside the realm of conscious visual awareness, yet involves in non-conscious visual processing, based on the observations in patient cases (A. D. Milner, 1998).

The foundation of our understanding that visual perception and action is dissociable in the brain is rooted in compelling neuropsychological evidence. Notably, patients who have sustained damage to specific regions within the primary visual cortex, as a result of stroke, tumor, injury etc, exhibited impairments on one visual task more rather than the other. Such phenomenon is evident in the case of patient D.F, who was diagnosed with visual form agnosia—inability to recognize objects (D. Milner & Goodale, 2006). What piqued the interest of Goodale and Milner in this instance was the striking observation that D.F.'s visuomotor skills remained remarkably proficient despite her severe impairment in visual recognition. For instance, she could efficiently reach out to grasp objects even though she could not identify them. This observation led to the hypothesis that damage to the ventral stream disrupted object recognition, while the dorsal stream, although impaired to some extent, retained the ability to manage visuomotor functions.

In contrast to visual form agnosia, patients afflicted with Balint syndrome (Bálint, 1909), exhibit deficits in visuomotor control. Symptoms include optic ataxia (inability to accurately reach and grasp objects), simultanagnosia

(incapacity to attend to multiple objects simultaneously), and oculomotor apraxia (inability to voluntarily shift the gaze). These impairments, stemming from bilateral parietal damage and resulting in dorsal stream lesions, characterize Balint syndrome (Jakobson et al., 1991). Intriguingly, if the ventral stream remains intact in such patients, their object recognition abilities remain relatively unaffected, while visuomotor and visuospatial challenges persist, underscoring the distinct roles of these two visual pathways in our cognitive processes.

Moreover, neuroimaging studies provide a better understanding of the visual system by unraveling the activation patterns within the brain during various visual tasks. While early investigations hinted at a general separation between the dorsal and ventral streams, with the former being implicated in visuomotor tasks and the latter in object recognition, recent findings suggest a more complex and highly distributed functional structure (Gallivan & Culham, 2015). For instance, fMRI studies of Cavina-Pratesi et al. (2018) reveal a broader activation of brain regions during visuomotor tasks involving grasping, reaching, and pointing than previously anticipated, i.e., extending beyond the dorsal stream. Particularly in pointing task, their rationale centers on the communicative nature of the task, which require both object recognition and coordinated movement, leading to activation in the lateral occipito-temporal cortex. This finding underscores the intricate nature of the interaction between the two visual streams and challenges simplistic distinctions.

In another fMRI study (Zachariou et al., 2014), it is noted that both ventral and dorsal stream regions are activated during shape perception tasks even though the location-based tasks appear to be mainly controlled by the dorsal stream. This finding reinforces the adaptability and interplay between these pathways in accordance with the specific demands of the task at hand.

Furthermore, a significant contribution to our evolving understanding of visual processing comes from a study that synthesized resting state fMRI data from participants in the Human Connectome Project (Haak & Beckmann, 2018). Based on a statistical analysis over 22 visual brain regions, the study reveal the presence of not two, but three distinct visual streams. Intriguingly, it is proposed that the ventral stream bifurcates into two substreams—one projecting along the ventral surface into the temporal lobe and the other traversing along the lateral surface. These findings challenge the conventional model and emphasize the need for a more nuanced perspective on the functional organization of the human visual system.

In addition to neuropsychological and neuroimaging studies, laboratory-based tests encompassing psychophysical assessments and experiments involving visual illusions provide a wealth of insights into the intricacies of visual processing. Notably, visual illusions such as Ebbinghaus figures, Sander's parallelogram, and the Müller-Lyer illusion serve as potent tools to show the context-dependency of visual perception and the dissociation between perception and action. For instance, the Ebbinghaus illusion consists of two identically sized circles—one surrounded by larger circles and the other surrounded by smaller ones. Owing to the context-driven nature of perception, the circle surrounded by smaller circles appears larger than its counterpart enveloped by larger circles. Intriguingly, the dorsal stream, tasked with processing object size for motor actions, does not fall for this illusion: individuals instructed to reach for both objects employ an identical grip size, transcending the perceptual discrepancy present in the ventral stream (Aglioti et al., 1995).

On the other hand, some visual priming experiments give further insight into the interaction between the two visual systems. For instance, the Continuous Flash Suppression (CFS), a technique effectively suppresses the perception of a static image presented to one eye through the rapid presentation of changing patterns to the other eye, is posited to deactivate the ventral stream while preserving the dorsal stream's functionality. In a CFS study conducted by Almeida et al. (2008), participants' performance in detection and discrimination tasks is evaluated while primed with images of different object categories, including tools, vehicles, and animals. Surprisingly, their findings reveal that manipulable objects are especially used in object categorization by the dorsal stream processing, shedding light on the intricacies of the interaction between perception and action.

These investigations naturally provoke questions concerning the independence between the dorsal and ventral stream processing in various visual tasks (Hebart & Hesselmann, 2012). Contrary to the prevailing two-system model, a growing body of research challenges the idea of a rigid division between vision for perception and vision for action. For instance, an increasing number of studies now propose that the dorsal stream is also involved in object perception (Freud et al., 2020; Zachariou et al., 2014), contradicting the initially proposed distinction between the two visual streams. Recent advancements in brain imaging studies and computational approaches adopt a more flexible, dynamic, and context-dependent perspective on visual processes, departing from a simple distinction (de Haan et al., 2018).

In this essay, we delved into the prevailing two visual system model that posits the dorsal stream governs visually guided actions while the ventral stream controls object perception. Extensive exploration through neuropsychological inquiries into visual conditions, neuroimaging investigations, and laboratory-based tests has unveiled the multifaceted nature of the human visual system. On the other hand, researchers persistently examine such a modular theory from diverse perspectives, refraining from simplistic theory to account for the vast complexities inherent to the brain and cognitive processes. In summation, how the brain orchestrates and intertwines the fragments of the visual system into a unified visual experience remains one of the most profound problem in neuroscience and under active research.

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