Chapter 6

HIGHER ORDER VISUAL OBJECT REPRESENTATIONS: A FUNCTIONAL ANALYSIS OF THEIR ROLE IN PERCEPTION AND ACTION

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OVERVIEW AND SCOPE

A Functional Analysis of Visual Object Representations

This chapter reviews research on the neural organization of higher order visual object representations. “Objects,” in this context, refer to common everyday things we routinely grasp and use, such as forks, phones, cups, books, and brushes. Successful processing of such everyday objects involves visual recognition, grasping, and functional use—and all in a way that can be driven by internally generated action goals. In order for objects to be used according to their function (and to satisfy internal action goals), high-level visual representations must integrate with nonvisual information (e.g., motor information, conceptual representations, action goals). High-level visual object representations might be initially defined as those representations that are *about* visual properties of objects and that are able to productively interface with both (upstream) earlier visual processes and (downstream) representations that are not about visual properties of objects.

A *functional analysis* of high-level visual processing studies visual representations through the lens of the computational goals that characterize the broader neural systems of which visual representations are component parts; “computational” is used here in the sense of Marr (Marr & Poggio, 1976). By analogy, the computational goal of the digestive system is to extract energy and eliminate waste. The individual organs that make up the digestive system do not each recapitulate that broader computational goal: The mouth contributes its function, the stomach its function, the small intestine its function, and so on. “Digestion” describes what the entire system does, with all component parts working together. The analogue to digestion herein is functional object use; there are several ways in which this analogy offers useful structure. First, if the broader goal of a brain network is functional object use, any region that is a part of that network will instantiate a process that *contributes* to functional object use, while no one brain region will instantiate a complex function such as functional object use. To look for the computational goal that defines the whole system in any given region or stage of processing would be a mereological error (for discussion, see Mahon, 2020). Second, the structure of a given stage of processing in the digestive pathway anticipates the needs of the next processing stage. The stomach is “designed” so that it expects food that has been processed by the mouth in a particular way; the

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structure of the mouth (vis-à-vis processing food) *anticipates* what will be demanded by the stomach in order for the computations of the stomach to run smoothly. And so it goes on down the processing chain.[1] Understanding what the processes downstream to a brain region expect and what the processes upstream to the region anticipate provides useful constraints on what the region itself is doing. Third, the structure in the digestive system is innate—which processes are supported by which organs, which organs are directly connected, and the overall computational goal that defines the system is all hardwired. One does not learn to grow teeth with certain shapes in order to make it possible for the outputs of the mouth to be appropriate inputs to the stomach. If there were selective pressures that shaped the organization of high-level visual representations, such pressures would not operate over specific regions; selection pressures operate on the *entire* system (Gould and Lewontin, 1972). By hypothesis, I argue this is the case for the separable brain networks that support domain-specific knowledge systems (Mahon and Caramazza, 2011; Mahon 2020).

Premeditated Perception: An Overlooked Use Case Scenario of Visual Processing

Consider the following example from everyday behavior: You decide to make a sandwich. You navigate to the kitchen, and on the way, all manner of objects are perceived but probably not noticed as such (perhaps because they are where they always are). In the kitchen you get the bread and a plate and the peanut butter. You open a drawer to take out a knife. For the first time in this extended series of inner mental states and outward actions, you visually perceive the knife. In this example, the visual perception of the knife was not the initial impetus for thinking about a knife; the initial activity of "knife" was caused by internally generated representations (e.g., an action subgoal of needing a knife, in order to spread the peanut butter, to make the sandwich, to not be hungry, and so on). The knife was sought (and *then* perceived) because it was *already* represented as being a useful part of a broader action goal. I refer to this as *premeditated perception*.

Premeditated perception can be contrasted with what I refer to as the *surprise paradigm*. The surprise paradigm subsumes most experimental research on visual object recognition across a range of tasks (e.g., viewing, naming, *n*-back, incidental tasks) and, for the most part, all the studies to be reviewed herein. The methodological maxim of the surprise paradigm is that participants should not be able to anticipate (explicitly or implicitly) what will be the next stimulus on any given trial. In that way, strategies (explicit or implicit) do not confound an interpretation of *why* the brain is activated in the way that it is. Within the tradition of the surprise paradigm, studies of visual processing have generally emphasized identification as the goal of visual perception.

The limitation of the surprise paradigm is that it does not capture an important use case scenario that is common to everyday behavior: Objects are often already identified before they are perceived. Consider the role of "the process of identification of the knife" in the extended sequence of making a sandwich described earlier. The motor-relevant information about how to use the knife to satisfy the goal of spreading peanut butter was represented independently of, and likely to some extent *before*, perception of the knife. However, and as will be developed herein, access to motor-relevant information about object use is predicated on individuation of the knife *as such* (i.e., as the object that is the substrate of the intended action). In such cases, the first "input" to the system is not vision but a representation of the action goal and how an object should be manipulated to accomplish that goal.

Of course, perception is not always premeditated, and object-associated actions are derivable (cold) upon visual identification of objects. In fact, pantomime of object use to visual presentation of objects, out of context, is a core test to assess apraxia (Rothi et al., 1991; see Volume 1, Chapter 8, this handbook). To continue the example above, imagine that upon opening the kitchen

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[1] Of course, there is no intentionality on the part of the mouth or stomach—or the pressures that constrained their organization. The terms "anticipate," "expect," "design," and "demand" are equally metaphors when talking about digestion as when talking about brain regions.

drawer, you discover there are no clean knives, and, rather than do the dishes, you reason (de novo) that a spoon would do just fine for spreading peanut butter, so you grasp the spoon (see Munoz-Rubke et al., 2018). The argument here is that we usually do not discover what we will do with objects by looking at them; in such contexts, representations of what will be done with the object in the service of current action goals are available as priors on perception (see also Wu, 2008). This has implications when thinking about the architecture of high-level visual representations and the dynamics of how those representations interface with object use systems on the one hand and early perceptual processes on the other hand.

I have suggested two methodological approaches to constrain a discussion of high-level visual representations. First, whatever the organization of the system may be, it must be such that it is consistent with the two use case scenarios just sketched: premeditated perception and the surprise paradigm. Use case scenarios, carefully applied (Gould & Lewontin, 1979), can place constraints on models of the organization and processing dynamics of the system. I have also argued that, in order to infer the nature of processes supported by individual brain regions supporting high-level visual processing, it is necessary to consider the computational stance (Marr & Poggio, 1976) of the broader network in which those regions are embedded.

Why Focus on Just Manipulable Objects?

Manipulable objects, or tools, are defined herein as handheld objects that are manipulated in a manner that is constrained by the physical structure of the object and that implements the function of the object (for discussion, see Mahon et al., 2007). Visual processing of graspable and manipulable objects covers only a small subset of the range of inputs that the human visual system processes. Similarly, we touch and grasp and manipulate many things that are not, by this definition, manipulable objects (e.g., a thermostat, a pebble, a kitten). The reason for focusing on manipulable objects is that doing so provides a clear view of broader organizational principles that, I argue, apply to high-level visual representations broadly.

The theoretical framework that drives this review is that there is an innate structure that constrains the development and functioning of a limited number of domain-specific learning and knowledge systems (Caramazza & Shelton, 1998; Martin, 2016; Spelke & Kinzler, 2007). Other construals of domain specificity (Downing et al., 2006; Kanwisher et al., 1997) emphasize that what is innate are semantic categories. In the view developed herein (see Mahon and Caramazza, 2011), categories describe sets of things in the world. To say that a brain region is specialized for a category is, at best, shorthand for saying the region is specialized for a computation that is required of processing of items from one category and not items from other categories. Being clear about what brain regions are specialized *for* has important implications for the types of evidence that would be considered to support or refute a hypothesis of domain specificity.

The term “manipulable objects” describes the set of things in the world for which it is necessary to integrate visual, motor, and conceptual representations in the service of the computational goal that subsumes the various use case scenarios that characterize the functioning of the system. The network of regions that support the representation and integration of visual, motor, and conceptual representations about manipulable objects is, by hypothesis, an innately constrained domain-specific learning and knowledge system. That system is defined by the computational goal of making predictions about how first-person actions will change the state of the world to bring it into alignment with action goals (Mahon, 2020). Some of the processes that make up that system will be engaged by things that are not manipulable objects but that require some of the same processing. For instance, grasping a half-peeled banana in a way that allows one to take a bite would, by hypothesis, draw on some of the processes that make up the domain-specific system for reasoning about how first-person actions will affect the world. Imagine a functional magnetic resonance imaging (fMRI) experiment showed that viewing a half-peeled banana led activity of brain regions that were independently defined as being involved in representing manipulable objects (i.e., tools). Such an observation would be problematic for the view that equates domain specificity with category specificity—indeed, such an observation could be taken (rightly) as evidence against the view that the brain regions in question are specialized for manipulable objects (Gauthier et al., 1999). By contrast, such an observation would confirm a theory that explained the cause of neural specificity for manipulable objects in terms of the unique intersection of processing needs demanded for successful interactions with that class of things in the world.

Different computational goals are associated with different visual categories or classes of things in the world, such as tools, faces, places, living animate things, body parts, numbers, and printed words. By hypothesis, the organization of high-level visual representations of those classes of stimuli are subject to constraints imposed by downstream and upstream systems. For instance, the computational goal of face recognition is not functional use—we do not grasp and use faces. We do infer the emotional and mental contents of the mind behind the face—such inferences are hungry for very particular types of information (Carroll & Conway, 2020; Changizi, Zhang, & Shimojo, 2006; Gauthier et al., 1999). By hypothesis, the processing need of inferring emotional and mental states of others is the type of high-level computational goal that could define the domain-specific network, of which visual recognition of faces is just one component process.

By analogy, one does not learn how to grow teeth with a certain type of structure so that the stomach gets the right type of inputs. Similarly, there is no "learning" involved in the stomach being connected to the small intestine on the one end and the esophagus on the other end. The same is the case for the brain: The arrangement of the many processes/regions that make up a domain-specific system is not "learned."[2] Connectivity is what is innate about domain specificity (Mahon & Caramazza, 2011). We have referred to this framework as the distributed domain-specific hypothesis (Mahon & Caramazza, 2009, 2011; Mahon et al., 2007, 2009; Martin, 2007). In this view, the structure of high-level processing is (innately) constrained by connectivity between high-level visual areas of the brain and other parts of the brain that process nonvisual information. Understanding the systems with which high-level visual representations interact, and the computational goals of those interactions, thus becomes central to elucidating the nature of high-level visual representations. Although a broader discussion of domain specificity is beyond the scope of this review, a growing literature has tested predictions made by a connectivity-constrained approach (Bouhali et al., 2014; Bracci & Peelen, 2013; Bracci et al., 2012; Büchel et al., 1998; Q. Chen et al., 2017; Dehaene & Cohen, 2007; Gallivan, Chapman, et al., 2013; Garcea et al., 2019; Hutchison et al., 2012; Lee et al., 2019; Mahon et al., 2007; Martin, 2006, 2007, 2016; Osher et al., 2016; Riesenhuber, 2007; Saygin et al., 2012, 2016; Walbrin & Almeida, 2021).

WHAT THE FIELD KNOWS

A Network of Brain Regions Supports Functional Object Use

In a series of papers, Alex Martin and colleagues (Chao & Martin, 2000; Chao et al., 1999) described a set of brain regions that exhibit differential neural responses when naming, identifying, or just viewing manipulable objects, compared with a range of various baseline categories (animals, faces, houses). That finding has been broadly replicated (e.g., Garcea & Mahon, 2014; Noppeney et al., 2006). Color Plate 9A (see color insert) is an fMRI map representing one such replication. The regions in Color Plate 9 are color-coded according to the types of deficits exhibited by patients who have focal lesions involving those regions. The functional–anatomic correlation schematized in Color Plate 9B, based on fMRI and neuropsychological data, is an idealization: (a) The contrast map in Color Plate 9A shows regions that express *differential* neural responses to manipulable objects, compared with visual stimuli generally; (b) lesions in individual patients rarely

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[2] The claim is not that there is no learning or that experience and learning are not needed for typical development. The digestive system needs food to develop properly; processing food in this analogy is like the brain processing information. What is not learned (in any sense of the word) is: i) *which* organs/regions carry out *which* processes, and ii) how those regions/organs are organized to form a coherent processing system.

respect the neat functional boundaries suggested by the fMRI map; and (c) patients' deficits are often not *selective* to the processes indicated by the coloring of the schematic. Nonetheless, the schematic shown in Color Plate 9 is a useful structure with which to organize and understand a broad range of findings that have been reported; the arguments to be developed herein do not depend on the idealization implied by that schematic.

The ventral and lateral occipitotemporal areas highlighted in Color Plate 9 support visual recognition and identification (see the following discussion and references). However, a number of brain regions that exhibit clear and differential responses to the visual presentation of manipulable objects may not process visual information per se. For instance, included in the set of regions that are automatically engaged when naming and identifying manipulable objects are action-relevant frontal and parietal areas. Patients with focal lesions to those motor relevant areas can have reaching, grasping, or object-use impairments but do not have visual agnosias or object-identification or conceptual impairments (see following sections).

The empirical observations summarized in Color Plate 9 have motivated a series of questions that have driven much research over the past 2 decades. First, which regions of the parietal cortex represent *action* representations and which represent *visual object* representations? Second, what are the channels of visual processing that support access to action representations and visual object representations? Third, if the integrity of processing in parietal and frontal motor-relevant areas is not necessary for visual recognition, then why are those motor areas active? And fourth, if ventral and lateral occipitotemporal areas support visual recognition, then why is there neural specificity in those regions for a class of things (manipulable objects) defined, at least in part, by motor-relevant dimensions (i.e., relation of the manner of manipulation to structure and function)? This chapter will review empirical findings in the service of constraining answers to those questions and clarifying the type of experimental evidence that would address them going forward.

Ventral and Dorsal Visual-Processing Streams

One of the most important discoveries over the past several decades is that there are multiple channels of cortical visual processing that can be traced to different types of retinal ganglion cells and their projection patterns into the lateral geniculate nucleus and other subcortical visual structures. Parvocellular, magnocellular, and koniocellular pathways are optimized to process different aspects of visual information (Carroll & Conway, 2020; Livingstone & Hubel, 1988; Merigan & Maunsell, 1993). For instance, for equivalent eccentricities, receptive fields within the parvocellular pathway tend to be smaller and biased toward processing lower temporal frequencies than receptive fields within the magnocellular pathway (Derrington & Lennie, 1984). Parvocellular pathways are important for resolving fine-grained detail (i.e., information contained in high-spatial frequencies), as well as contrast created by color boundaries involving red and green wavelengths. Magnocellular pathways are optimized for processing lower spatial frequencies at high temporal frequencies and are sensitive to subtle differences in luminance—that is, global shapes moving fast. Koniocellular pathways (Hendry & Reid, 2000) have small receptive fields, are sensitive to blue/yellow contrast, and—notably—have substantial projections from the lateral geniculate nucleus directly to extrastriate areas as well as primary motion area MT/V5 (Sincich et al., 2004). The broad point is that "visual information" coming into the primary cortical visual areas starts off highly stratified, both in terms of anatomical pathways and functionally in terms of the type of information for which the pathways are optimized.

The proposal of a ventral–occipital–temporal route of visual processing in the service of perception and a dorsal occipital-parietal route in the service of visual localization was initially formulated on the basis of neuropsychological evidence and neurophysiological research with nonhuman primates (Schneider, 1969; Ungerleider & Mishkin, 1982). Goodale, Milner, and colleagues (Goodale & Milner, 1992) built on the distinction between "what" versus "where" (ventral vs. dorsal; Ungerleider & Mishkin, 1982) to propose a division of labor between "what" versus "how and where" (for further discussion on how best to characterize the two streams, see Freud et al., 2016; Merigan & Maunsell, 1993; Pisella et al., 2006; Schenk, 2006; Xu, 2018).

The ventral processing stream projects from V1, a first stage of cortical visual processing, through ventral occipital and temporal cortices to anterior regions of the temporal lobe. All ganglion cell types (parvocellular, magnocellular, and koniocellular) project through the geniculostriate pathway into the ventral processing pathway (Conway, 2018; Livingstone & Hubel, 1988). The ventral stream extracts a viewpoint and context-invariant visual representation that supports access to stored knowledge about that object; I will review evidence later in support of the hypothesis that the ventral pathway is the only pathway to a conceptual interpretation of the visual input.

By contrast, the dorsal visual-processing pathway projects from V1, as well as from subcortical structures, to the dorsal occipital cortex and posterior parietal cortex, as well as to motion-sensitive area MT/V5. The dorsal stream supports fast-motion processing and the online transformation of visual information into motor parameters in support of obstacle avoidance, pointing, eye movements, and ballistic reaching and grasping. With respect to visual object processing, the dorsal stream supports online analysis of object location and volumetric properties (e.g., size, orientation) that are relevant to *concurrently* unfolding object-directed actions. The dorsal stream receives little direct parvocellular input and is dominated by magnocellular and koniocellular inputs. Importantly, the dorsal stream receives substantial direct subcortical projections that bypass V1, via both nongeniculostriate and geniculo–extrastriate pathways (Lyon et al., 2010; Schmid et al., 2010; Sincich et al., 2004). It also bears emphasizing that there is mixing of parvocellular and magnocellular inputs already in V1 (Conway, 2018; Merigan & Maunsell, 1993; Schiller et al., 1990).

The ventral stream supports seeing, as we experience it, while the dorsal stream supports visual processing for concurrently unfolding actions. When we look at the world, we do not see raw qualia of colors and lines—or even shapes—but rather a book, a chair, a loved one; we see the world as the ventral stream delivers it, parsed and interpreted. By contrast, the dorsal stream is constantly calculating how the movements of our body will interface with the world as it is, which is not always as we see it. When you walk across a room and manage to not bump into the table and chairs, you might assume (if you were to ask yourself) that you did not bump into the furniture because it was seen. This is a reasonable assumption because we can and do act on the basis of our phenomenological visual experience. But, in addition, and behind the screen of what we *experience* as vision, our movement through the world is guided by a kind of semantically uninformed lidar powered by the dorsal stream.

Another important distinction between the dorsal and ventral streams relates to different reference frames for visual processing: The ventral stream processes information in allocentric (i.e., object-centered) reference frames while the dorsal stream represents visual information in egocentric reference frames (Schenk, 2006). That distinction resonates with the thesis that the ventral stream supports perception (which must be invariant to viewpoint and perspective) while the dorsal stream supports unfolding actions (which must be calibrated to the reference frame of the effector, such as the starting position of the hand).

One way to dissociate processing across the ventral and dorsal visual pathways is to study visual illusions. By definition, visual illusions drive a wedge between our phenomenological visual experience and the actual structure of the visual input. Some visual illusions trick perception (i.e., phenomenology) more so than they trick the motor system when an action is directed toward the illusory stimulus. In an early demonstration along those lines, Aglioti and colleagues (1995) used the Ebbinghaus/Tichner Illusion to dissociate processing across the dorsal and ventral pathways. In that illusion, a central disc appears larger when surrounded by smaller discs, compared with when larger discs surround it. One simply cannot look at such stimuli without experiencing the illusion—it is as compulsory as seeing any other (clear) difference in size between objects. In one experimental condition, Aglioti and colleagues measured the amount of illusory "distortion" in the *perception* of the central disc. In a separate condition, they instructed participants to reach out and grasp the central disc with their thumb and index finger; during the reach-to-grasp movement, participants' grip apertures were measured using a motion-tracking system. It is known that during a reach-to-grasp action, the maximum grip aperture (in flight to the target) scales linearly with the true size of the grasp target. In that way, Aglioti and colleagues were able to measure the amount of illusory distortion that was present in the grip aperture (as an index of dorsal-stream processing). What they found was that while the illusory distortions were present to a small extent in grip apertures, the magnitude of those distortions was smaller than their magnitude during the perceptual task. The broad takeaway is that the systems that support grip scaling for object grasping are resilient, at least to some extent, to the illusory distortions that are unavoidable for phenomenological vision (for discussion and debate, see Franz, 2001; Milner & Dyde, 2003).

Neuropsychological Dissociations Between Ventral and Dorsal Processing

Neuropsychological observations remain some of the most compelling and stark dissociations between dorsal and ventral stream processes. Over a series of papers, Goodale, Milner, and their colleagues described the performance of patient D. F., who has bilateral lesions to lateral occipital cortex in the ventral stream, caused by anoxic injury (for location of the lateral occipital cortex, see Color Plate 9). Her low-level visual processing, color perception, receptive and productive language, executive function, attention, and memory were all intact—her principal deficit consisted of a dense visual form agnosia. She was unable to make simple judgments about whether a pencil was oriented horizontally or vertically, failed to match visually presented stimuli, and could not copy simple line drawings (despite being good at drawing from memory). Remarkably, when D. F. reached to grasp an object or post a card through a slot, her reach direction, grip aperture, and wrist orientation naturally accommodated to the target (Goodale et al., 1991). The point is not that her object-directed actions were normal; rather, her spontaneous object-directed actions were broadly accurate vis-à-vis the location and orientation of the grasp target, despite an inability to identify the grasp target (or make any other *perceptual* judgments about the target's shape or orientation). More broadly, D. F. had no difficulty performing "spontaneous" visuomotor actions, such as playing catch, making eye movements to visual onsets, or hiking along a difficult path.

Other neuropsychological findings provide contrast between the pattern of impairment observed in D. F. (who had *lateral* occipitotemporal lesions) and the consequences of lesions that involve the *ventral* occipitotemporal cortex (see also Volume 1, Chapter 7, this handbook). Lesions that involve the lingual gyrus and collateral sulcus (posterior medial occipitotemporal structures) are associated with achromatopsia when they involve more posterior segments and color agnosia when they involve more anterior aspects (Miceli et al., 2001; Stasenko et al, 2014; for convergence from fMRI, see Cant & Goodale, 2007; Simmons et al., 2007). Patients with achromatopsia have difficulty with color perception and naming but do not necessarily have difficulty with knowledge of the typical colors of things (e.g., knowing that the sky is blue). By contrast, patients with color agnosia can be spared for color perception but impaired for knowledge that (for instance) the grass is green, the sky is blue, or that a watermelon is a different color on the inside than on the outside (see also Siuda-Krzywicka et al., 2019). One well-studied patient with a lesion involving the collateral sulcus demonstrated an impairment for processing surface-texture properties with spared processing of visual form (Cavina-Pratesi et al., 2010). Convergent evidence from fMRI (Gallivan et al., 2014) suggests that inferences about objects' material composition and weight are supported by processing in the collateral sulcus and adjacent structures (see following sections for further discussion). Furthermore, recall that patient D. F., who had lesions to posterior *lateral* occipital areas, had no difficulty with color perception or color knowledge. This points to an important distinction between ventral aspects of the occipitotemporal cortex and lateral aspects of the occipitotemporal cortex. The ventral occipitotemporal cortex processes surface-texture properties while the lateral occipitotemporal cortex supports analysis of visual form.

In contrast to the performance of patient D. F., patients with posterior parietal lesions can be impaired for object-directed reaching or grasping while perception and identification remain intact (Goodale & Milner, 2013; Pisella et al., 2000; Ungerleider & Mishkin, 1982). We know in such cases that perception is intact because such patients can report (accurately) what they see (e.g., name objects, report aspects of their orientation). More posterior or caudal aspects of the intraparietal sulcus (IPS), including dorsal occipital cortex and area V6A in the parieto-occipital sulcus (Fattori et al., 2012), support the transport component of reach-to-grasp actions (Culham et al., 2003); more anterior regions in the posterior parietal cortex, including the anterior IPS (aIPS), support hand shaping for object grasping (Binkofski et al., 1998). Further confirmation of a role of posterior parietal areas in supporting visual processing in the service of concurrently unfolding actions is provided by transcranial magnetic stimulation studies with healthy participants: Transient disruption to the posterior parietal cortex can impair spontaneous corrections to ongoing actions when the visual stimulus's location is changed during the reach (Desmurget et al., 1999).

The Role of Conceptual Processing in Functional Object Grasping

The dorsal stream supports visuomotor transformations in the service of concurrently unfolding actions. That thesis can be caricatured as saying that *all* object-directed actions depend on dorsal stream processing or that actions depend on *only* dorsal stream processing or that actions are not dependent (*at all*) on information computed by the ventral stream. Those caricatures are all nonstarters, and, I would argue, experiments are not needed to know that they are nonstarters. This is because object-directed grasps can be (and often are) tuned to what is being grasped and the broader goal motivating the grasp. *End-state comfort* refers to the observation that functional object-directed grasps anticipate how the object will be manipulated once it is in hand (Rosenbaum et al., 1990). Functional object grasps are normative with respect to what will happen after the object is grasped: typically, what will happen after the grasp is functional object use. But that need not always be the case, and the accommodation of grasps in those contexts is equally informative. For instance, consider the different ways in which one typically grasps a knife depending on whether one is picking it up to pass it to someone or to cut an apple. When grasping a knife to cut an apple, the knife will be grasped by the handle in a way that supports the subsequent cutting action; that is the "typical" use of the knife. By contrast, when picking up a knife to hand to someone, one would grasp the knife by the blade and thus hand the person the handle. Thus, (a) functional grasps flexibly accommodate to what will be done with the object once it is in hand, and (b) the distinction between the blade and the handle is not given by the perceptual input—it is a conceptually mediated distinction (Creem & Proffitt, 2001), which means that functional grasping is dependent on a prior conceptual analysis of the visual input.

End-state comfort implies that a representation of the action associated with an object's functional use (praxis) constrains the initial grasp (Creem & Proffitt, 2001; Milner, 2017). A representation of what will be done with the object once it is in hand (praxis) can only be accessed via a conceptual interpretation of the object—it is not derivable bottom-up from the visual input (for a different view, see Jarry et al., 2013). If the ventral stream, as I will argue, is the only pathway from visual input to a conceptual interpretation, then functional object grasps (i.e., grasps that display end-state comfort) imply that actions are constrained by processing supported by the ventral stream. This was already suggested by early formulations of the two visual systems proposal (Carey et al., 1996; Goodale et al., 1994; Milner, 2017). The implication is that functionally appropriate object-directed actions depend (necessarily) on inputs supplied by both the ventral and the dorsal streams.

Compelling experimental evidence for a role of the ventral stream in functional object-directed actions is provided by the difficulties with object-directed action that are exhibited in the setting of ventral stream lesions. Perhaps most saliently, D. F. did not exhibit effects of end-state comfort when grasping objects: She grasped common objects in a manner that accommodated to the volumetric properties of the object but was not functional and reflected no understanding of *what* was being grasped. She did not exhibit end-state comfort because she was not able to access representations of object function and praxis from visual input. That she still had intact representations of object function and object-associated praxis was demonstrated by the fact that, once the object was in hand, D. F. recognized it through tactile cues, adjusted her grasp accordingly, and could demonstrate the correct manipulation (Carey et al., 1996). D. F.'s behavior, when informed only by visual inputs, thus reflects a dorsal stream without access to a conceptual interpretation of the object.

Convergent evidence for a direct role of ventral stream processing in supporting actions was offered in the context of an important early critique of how to distinguish between the dorsal and ventral pathways (Pisella et al., 2006). Pisella and colleagues argued that, in the context of parietal lesions, pointing performance to visual targets' locations was better when patients point to the *remembered* location of a no-longer-visible target than when they point to the location of a *currently* visible target. That observation supports the idea that the dorsal stream is concerned with real-time visual information in the service of concurrently unfolding actions; representing the prior location of a target would have to depend on processes extrinsic to the dorsal stream, which Pisella and colleagues argued is supported by the ventral stream.

Grasping Without Meaning: What Can the Dorsal Stream Do on Its Own?

A particularly stark demonstration of grasping without meaning comes from cortically blind patients who can perform visually guided reaches and grasps to stimuli presented in their hemianopic (blind) visual field—so-called action blindsight (Danckert & Rossetti, 2005). Cortical blindness results from lesions that deafferent or directly lesion the primary visual (striate) cortex. As noted above, there are multiple channels of visual input that bypass the primary visual cortex. Thus, a lesion that deafferents or directly lesions the primary visual cortex renders a patient cortically blind for the corresponding areas of their visual field; such lesions can leave intact nongeniculostriate and geniculo–extrastriate pathways that bypass the primary visual cortex. The practical implication is that the inability of cortically blind patients to "see" in some (or all) of their visual field does not mean that there is no processing of visual information for the blind region. For instance, a patient who had bilateral lesions affecting the early visual cortex and complete cortical blindness could walk down a hallway cluttered with obstacles without bumping into them (de Gelder et al., 2008).

In the setting of object-directed grasping actions, Perenin and Rossetti (1996) described a patient who could orient her wrist and who demonstrated relatively preserved grip scaling when grasping objects in the blind field. Prentiss, Schneider, and colleagues (Prentiss et al., 2018) subsequently described a quadrantanopic patient who was at chance to perceptually judge the orientation of a handle presented in his blind quadrant but was able to spontaneously orient his wrist when the handle was the target of a grasp (see color insert, Color Plate 10).

Those types of findings indicate that subcortical projections bypassing the early visual cortex (Lyon et al., 2010; Schmid et al., 2010) are sufficient to support grip scaling and wrist orientation. Such inputs are sufficient to support actions, but those actions are deprived of a conceptual interpretation of what is being grasped. Another important, and positive, thesis that can be extrapolated from research on action blindsight is that the dorsal stream is able to process the volumetric properties, location, and orientation of graspable objects, independent of processing in the geniculostriate pathway (which includes the ventral stream). Those findings suggest substantial processing within the dorsal stream of the visual structure, or shape, of objects—a topic to which I return later.

Another source of evidence for the generalization that the dorsal stream can compute "graspability" in the absence of a conceptual interpretation of the object is provided by studies using the psychophysical technique of continuous flash suppression (CFS). CFS is a type of interocular suppression in which a stimulus can be rendered invisible for prolonged periods of time. Fang and He (2005) showed that CFS-suppressed (i.e., invisible) images of elongated tools drive neural responses in the dorsal occipital and posterior parietal cortex to the same extent as do visible images of the same stimuli. By comparison, neural responses in the ventral stream were eliminated for CFS-suppressed stimuli. Almeida and colleagues (2008) showed that when CFS-suppressed images are used as primes in a behavioral priming paradigm, CFS-suppressed images of tools facilitate the subsequent categorization of elongated tool targets, whereas CFS-suppressed images of vehicles, animals, and faces do not facilitate the categorization of vehicle, animal, or face targets, respectively. Within that paradigm, Almeida and colleagues (2010) subsequently found that identity priming (e.g., hammer priming hammer) was not larger than category-congruent priming (e.g., hammer priming saw), consistent with the inference that the dorsal stream has no access to *what* the object is. In another follow-up, it was found that any elongated CFS-suppressed stimulus was an effective prime for an elongated tool target (e.g., a snake, or even a bar, would prime a tool as well as another elongated tool would; Almeida et al., 2014; see also Sakuraba et al., 2012).

The findings from CFS-based priming studies collectively suggest that elongation, in the absence of any semantic content or semantic interpretation, is a visual feature processed by the dorsal visual pathway independent of processing within the ventral stream. J. Chen and colleagues (2018) used task-based fMRI and effective functional connectivity to distinguish “toolness” from elongation. The authors found that ventral stream regions process toolness (i.e., as a category) independent of elongation, while mid and posterior IPS regions process elongation independent of toolness. The authors further found that toolness drove connectivity from ventral to dorsal regions, whereas elongation drove connectivity from dorsal to ventral regions. Other research (Garcea et al., 2012; Handy et al., 2003) may point to asymmetries between the left and right posterior parietal areas in processing object elongation.

Functional Neuroimaging Evidence for Conceptually Mediated Access to Object-Directed Actions

I have argued that the posture of the object-directed action system is to compute object grasps in a manner that anticipates what will be done with the object. In the setting of premeditated perception, what will be done with the object is represented independently of (and often before) perception. In other circumstances (the surprise paradigm), accessing representations of praxis depends on a visually driven conceptual interpretation. I have also reviewed evidence that the dorsal stream, on its own, is not able to access a conceptual interpretation of the visual input. That combination of findings (and background assumptions) implies that functional object grasping requires a conceptual interpretation of the visual input (ventral stream) in order to constrain real-time visuomotor processing (dorsal stream). The system’s design (by hypothesis) enables it to represent what will be done with the object (praxis) *before* the object is grasped and (often, but not necessarily) before the object is perceived. Indeed, in the context of everyday actions, what will be done with the object is the initial motivation for grasping the object in the first place: We grasp objects to use them *because* we already have an action goal that implicates that object (see also Wu, 2008).

The question then becomes this: Which aspects of parietal-based object-directed action processing depend on a conceptual interpretation of the visual input? Or, under the assumption (argued for earlier) that the ventral stream is the sole pathway to a conceptual interpretation of visual input, the question can be reformulated (for discussion, see Mahon & Wu, 2015): Which parietal-based object-directed action representations depend on ventral stream processing? As noted earlier (see Color Plate 9), when participants view or name manipulable objects during functional neuroimaging, there is activity that includes multiple dissociable motor-relevant regions that (separably) support reaching, grasping, and praxis.

Experimental tests are needed that dissociate the different parietal-based action processes that are engaged upon the visual presentation of a manipulable object and, specifically, to test which of those parietal-based action processes depend on inputs that come by way of the ventral visual pathway.

One way to test which parietal object-directed action representations depend on prior ventral stream processing is to manipulate stimulus attributes that bias processing away from the dorsal stream and toward the ventral stream. The segregation of visual processing at subcortical levels within the visual system, reviewed earlier, provides the leverage needed to accomplish this. As noted, the parvocellular pathway differentially projects to the ventral compared to the dorsal visual pathway (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993) and shows greater sensitivity for high spatial frequencies, low temporal frequencies, and heterochromatic red/green isoluminant boundaries. In a series of fMRI studies with healthy, typically developed participants (see color insert, Color Plate 11), we titrated images of tools and a baseline category (animals) so that the visual images were defined by visual dimensions that are not “seen” by the dorsal pathway (e.g., high spatial frequency, red/green isoluminant contrast). We found that stimuli biased toward processing in parvocellular channels (and by extension the ventral stream) continue to activate inferior, but not superior, parietal areas.

In one study (Mahon et al., 2013), participants saw images of manipulable objects (i.e., tools) and animals that had been filtered to contain only high or only low spatial frequency information. Whole-brain contrasts were computed to identify voxels exhibiting increased blood oxygen level-dependent contrast for tool stimuli compared with animal stimuli, *separately* for the low and for the high spatial frequency stimuli. Because the dorsal pathway has low sensitivity for information contained in high spatial frequencies, it can be inferred that tool preferences in the parietal cortex for stimuli defined by high spatial frequencies depend on inputs that come by way of the ventral stream. We found that tool preferences for stimuli defined by high spatial frequencies no longer activate regions along the posterior IPS, superior parietal cortex, and dorsal occipital cortex—that is, the regions of parietal cortex associated with classic “dorsal” stream processing that are routinely shown to be differentially engaged by graspable objects compared with various baselines. Rather, stimuli defined by high spatial frequency information led to tool preferences restricted to the aIPS and the supramarginal gyrus (Mahon et al., 2013). The same pattern was observed when using temporal frequency (Kristensen et al., 2016), as well as red/green isoluminant color contrast (Almeida et al., 2013), to bias visual processing toward the ventral stream (see Color Plate 11).

In a fourth, and conceptually independent, test (Garcea et al., 2016), we reasoned that any parietal-based representations that depend on inputs from the ventral stream will be “washed” of information about the visual-field location in which the stimulus was presented. In other words, action representations that result from prior processing in the ventral stream should exhibit resilience to the visual hemifield in which the stimuli were presented. We found that the amplitude of neural responses to graspable and manipulable objects in the left inferior parietal lobe was not modulated according to whether the stimuli were presented in the left or the right visual fields (Color Plate 11). This was in contrast to neural responses to tools in superior and posterior parietal areas, which were modulated by the hemifield of presentation (always stronger contralateral to the hemifield of presentation).

The four independent findings (Color Plate 11) just reviewed support the hypothesis that access to object-directed action representations from visual presentation of objects, indexed by activity in the *inferior* parietal lobule, is dependent on prior processing in ventral stream structures. In addition, the studies summarized in Color Plate 11 support specific inferences about the areas of the parietal cortex for which activity depends (by hypothesis) on inputs from the ventral pathway. An implication is that a major function of the ventral stream is to support access to object manipulation (i.e., praxis) from visual input. Representations of object manipulation constrain the initial object-directed grasp, with the consequence that the initial object-directed grasp displays end-state comfort (with respect to the subsequent manipulation). Note that in contexts of premeditated perception, the system represents the object-associated praxis information *before* perceiving the object. Thus, in contexts of premediated perception, praxis information need not be accessed (cold) from the visual input, and the role of perception is, by hypothesis, to tune the fit of already-represented action representations to the visual properties of the object at hand.

While beyond the scope of the current chapter (see Volume 1, Chapter 8, this handbook), it is likely that a deeper understanding of the role of the ventral stream in accessing actions will prove valuable for understanding the causes of some forms of upper limb apraxia. Limb apraxia refers to a deficit in skilled and coordinated use of the hand and arm, for instance when using objects, and which cannot be explained by disruption to primary sensory or motor processes. The difficulty exhibited by some patients with apraxia may be traceable to disrupted connectivity from temporal lobe structures to parietal areas that represent object-directed actions (Binkofski & Buxbaum, 2013; Goodale et al., 1994; Kalénine et al., 2010). Upper limb apraxia is classically associated with damage to the supramarginal gyrus of the inferior parietal lobule; however, it may be that damage that disconnects the supramarginal gyrus from the left posterior middle temporal gyrus is a key determinant of ideational or conceptual apraxia, in which actions remain fluent but are inappropriate to the object (e.g., using a knife to comb one's hair).

QUESTIONS AND CONTROVERSIES

Keeping Clear on Terminology

Across different discussions in the literature, the terms "ventral" and "dorsal" are sometimes used in

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Visual processing initiates, already at the retina, as physiologically, anatomically, and functionally separable channels of processing. A complex series of subcortical and cortical stages of processing, with both feedforward and feedback connectivity, yields "high-level" visual representations that integrate and abstract across those initially separate channels of visual input (e.g., Conway, 2018; Livingstone and Hubel, 1998). High-level visual representations are invariant to certain surface transformations of the visual input (e.g., viewpoint, size, lighting). And, while high-level visual representations are "about" visual properties of objects, their format is such that they are able to productively interface with representations computed by nonvisual systems of the brain (e.g., conceptual processing, motor planning).

The brain network that collectively supports functional object grasping and manipulation includes high-level visual representations of manipulable objects. The past 2 decades have seen an explosion of research into the occipitotemporal and frontoparietal areas that support the integration of visual and motor information, respectively, in the service of functional object use. On the one hand, functional neuroimaging studies indicate that the entire frontoparieto-occipitotemporal network is automatically engaged when viewing manipulable objects, even in the absence of an intention to act on the object. On the other hand, cognitive neuropsychological studies of patients with focal brain injuries indicate that functional object use can be decomposed into separable processes/regions, including specialization for visual shape processing, color and surface-texture processing, conceptual interpretation, name retrieval, transport of the hand to the grasp target, shaping of the hand to match the volumetric properties of the grasp target, complex object manipulation (praxis), and representation of action goals. Ongoing research is using functional neuroimaging in patients with focal brain lesions to understand how damage to one part of the complex network that supports functional object use affects processing in anatomically remote but functionally connected regions within that network.

an anatomical sense and sometimes used in a functional or computational sense. Anatomically, the ventral stream is located ventrally in the brain (i.e., the "bottom" of the brain). Computationally, ventral processes are concerned with extracting visual representations that are invariant to transformations in the input (e.g., point of view, lighting, distance, context)—ventral stream computations generate a stable sensory footing for seeing. "Dorsal," used in the anatomical sense, refers to the dorsal projection of the visual system (dorsal occipital, posterior parietal cortex—i.e., the "top" of the brain). "Dorsal," in the computational sense, refers to visual processing that is in the service of ballistic and concurrently unfolding actions (e.g., hand actions, eye movements, locomotion around obstacles). Understood computationally, processing in the dorsal stream is driven entirely by the visual input—a dorsal visual analysis of the visual input is (on its own) agnostic about what the stimulus is. Similarly, dorsal stream computations are not (by hypothesis) invariant to distance, point of view, and orientation, as veridical representation of those dimensions is needed to transform visual inputs into accurate motor outputs.

An implication of these terminological issues is that the dorsal stream is not coextensive with the parietal cortex: Neural activity in the parietal cortex is not ipso facto dorsal stream activity ("dorsal" understood computationally). Likewise, the ventral stream (understood computationally) does not stop at the anterior temporal lobe. There is a rich literature on the role of lateral inferior frontal areas in supporting the maintenance of behaviorally relevant categories during analysis by occipitotemporal areas (Rainer et al., 1998) and selecting among alternative representations (Thompson-Schill et al., 1997). If processing in the occipitotemporal cortex is dependent on inputs from extratemporal regions, then, computationally, why exclude those extratemporal regions from a processing model of what ventral stream computations do? As a concrete example, Bar and colleagues (2006) have argued that an important input to the ventral stream is via the orbital frontal cortex, which, by hypothesis, has direct access to a rough first-pass magnocellular visual analysis of the visual input that is dominated by low spatial frequencies. That gestalt visual shape representation serves (by hypothesis) to guide slower, more detailed (and parvocellular-dominated) processing in the ventral stream.

Of course, this line of argument can easily become a slippery slope, such that the whole brain becomes part of the ventral stream; anatomical structures and pathways are important guardrails on delineation of dorsal and ventral stream processes. The point is that it is not just anatomy being read out of the functional neuroimaging data. It is anatomy plus some reverse inference about the computations supported by that anatomy (Poldrack, 2011). Consider the above arguments from fMRI that praxis representations are accessed via a ventral stream analysis of the input (Almeida et al., 2013; Mahon et al., 2013). That inference depends on an observation and an independent assumption. The observation is that inferior parietal areas are active in experimental contexts that bias processing of the visual stimulus toward the ventral stream. The independent assumption is that activity of those inferior parietal areas indexes access to praxis representations. The strength of the inference thus comes down, in part, to the strength of that underlying assumption (in this context, that assumption is arguably well supported; see evidence and discussion in Q. Chen et al., 2018). This situation is very common in fMRI: One concludes that a process is involved in an fMRI experimental paradigm because that process is assumed to be supported by the region(s) active in the study.

The implication is that when neural activity in a region of the parietal cortex is taken to be a signature of dorsal stream processing, it is important to recognize that there is an independent assumption behind that inference. These issues come to the fore in the next section, which is focused on the issue of whether the dorsal stream (understood computationally) supports perceptual processing of visual information (as indexed by neural activity in the posterior parietal cortex).

Where Do Object-Directed Action and Visual Object Representations in the Parietal Cortex Come From?

There are two broad issues to be addressed in this section. The first issue concerns the relevant parcellation of the parietal cortex into regions that represent object-directed action representations versus visual object representations. The second issue concerns which object-directed action and visual representations in the parietal cortex are computed by the dorsal stream (understood computationally) and which depend on inputs from the ventral stream.

Within the parietal cortex, there are at least three dissociable processes that collectively support functional object use: the reach and transport phase of the hand to the object (dorsal occipital cortex, posterior IPS), shaping of the hand to grasp the object (aIPS), and praxis (what is done with the object once it is in hand—supramarginal gyrus; see Color Plate 9 and, e.g., Binkofski et al., 1998; Q. Chen et al., 2016, 2018; Culham et al., 2003; Fattori et al., 2012; Konen et al., 2013).[3] Lesions to those regions lead (among other difficulties) to deficits with actions but not with perception or identification (see data and reviews in Goodale & Milner, 1992; Mahon & Caramazza, 2005, 2008; Negri et al., 2007; Rothi et al., 1991). The aIPS supports hand shaping for grasping and is known to be heavily interconnected with premotor areas (Konen et al., 2013; Kravitz et al., 2011; Rizzolatti & Matelli, 2003). One of the arguments developed herein is that processing in the aIPS must be integrated with representations of surface texture and the inferred material composition and weight distribution of objects, supported by ventral-medial occipitotemporal structures (see Milner, 2017; van Polanen & Davare, 2015).

Freud and colleagues (Freud, Culham, et al., 2017) have argued that more posterior regions of the IPS represent abstract 3D visual representations of objects. If those visual object representations are a product of dorsal stream processing (understood computationally), then the classic model of the dorsal stream needs revision (see discussion in Freud et al., 2020). An alternative is that those posterior parietal representations are dependent on inputs from the ventral stream (Kravitz et al., 2011; Xu, 2018). There is broad agreement that the dorsal stream (understood computationally) occupies a subset of dorsal cortex (understood anatomically).

In one early and influential study, James and colleagues (2002) tested whether object representations in the posterior parietal and occipitotemporal cortex abstract across different viewpoints of the same object. Testing whether visual object representations are invariant to surface transformations of the visual input, including the major transformation of viewpoint, is a key test of whether they could support perception. James and colleagues leveraged the phenomenon of repetition priming within fMRI, which refers to the reduction of neural response when a stimulus is repeated multiple times. The generally received logic is that if the neural signal in a region is attenuated to repeated presentations of the same item, then that region represents something about that stimulus that was common across the repeated presentations (for broader discussion and alternative interpretations of repetition priming, see Grill-Spector et al., 2006). For instance, if the visual stimulus (of an object) is exactly the same image across the two presentations, then the expectation is that there should be adaptation in both early and late visual areas. This is because both low-level and high-level visual information repeats when it is the same exact image. Consider, however, if on the first presentation a hammer is shown from one viewpoint and, on the second presentation, the same hammer is shown from an angle that differs by 45 degrees from the first presentation. In that situation, regions will show reduced responses to the second presentation only if they contain visual representations that are common across the different viewpoints; such regions would be, for instance, regions that represent object structure in object-centered coordinates, regions that support retrieval of the object name, or regions that represent praxis. Stated in terms of invariance: Adaptation will be seen across different viewpoints only in regions in which processing achieves invariance across viewpoint. Applying that logic to the ventral and dorsal visual pathways, James and colleagues reasoned there should be repetition priming across viewpoints in the ventral but not in the dorsal stream. They found that ventral stream areas

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[3] In important respects, processing is unlikely to be so completely segregated—for instance, hand-shape information can be discerned in the dorsal occipital cortex (V6A; Fattori et al., 2012). The core argument remains, even with such mixing of response properties across regions, as long as different regions express dissociable biases in processing.

exhibited adaptation across different viewpoints of the same object, consistent with a role in supporting perceptual analysis. By contrast, posterior parietal and dorsal occipital areas did not exhibit adaptation across different viewpoints of the same object. The authors argued that those data suggest that the dorsal stream computes visual object representations that are specific to the particular viewpoint of the object, consistent with the idea that the dorsal stream processes (veridical) visual information in the service of action.

In a subsequent broad and highly influential empirical investigation on this topic, Konen and Kastner (2008b) used fMRI in healthy participants to test for size and viewpoint invariance across occipitotemporal and posterior parietal areas. Those authors found signatures of invariance in the lateral occipital cortex, which aligns with the understanding of that region as supporting visual perception of form. Importantly, subregions of the posterior IPS also exhibited similar patterns of invariance—specifically subregions IPS1 and IPS2, which have been implicated in working memory and active manipulation of information (Konen & Kastner, 2008a; see also Jeong & Xu, 2016; for evidence of behaviorally relevant abstract representations of object identity in posterior parietal cortex, see Xu, 2018). The posterior parietal areas that exhibit invariance to surface transformations can be independently defined based on retinotopic coordinates (of remembered visual targets during a delayed saccade task; Konen & Kastner, 2008a); those findings collectively underscore the visual nature of the representations in posterior parietal areas.

The question becomes this: Do visual representations in posterior parietal cortex depend on processing in the dorsal stream (understood computationally) or on inputs that come by way of the ventral stream? Different theoretical approaches can be distinguished on this issue. Freud and colleagues (Freud, Culham, et al., 2017) found that posterior parietal and dorsal occipital cortex activity related to shape processing was correlated with visual recognition performance. Furthermore, neural signatures of visual shape representations in the posterior parietal cortex were found to be present in individuals with ventral stream lesions and deficits for visual shape perception (Freud, Ganel, et al., 2017). Those findings support the argument that posterior parietal shape representations are *not* dependent on ventral stream processing. In a similar line, Konen and Kastner (2008a) argued that the parietal cortex (like the ventral stream) contains a hierarchically organized processing stream. They further argued that the fact that visual information is represented, at least to some extent, in retinotopic coordinates in parietal cortex suggests that retinotopic coordinates could be a common substrate for the integration of information between the posterior parietal cortex and the ventral stream.

Another important perspective is that of Xu (2018). She argued that, while ventral stream representations achieve invariance in order to provide a stable basis for perception, the role of the posterior parietal cortex is to process visual representations in a manner that is tuned to the current task—adaptive visual processing. A premise of Xu's proposal is that the posterior parietal visual representations that are invariant to surface transformation are dependent on connectivity with occipitotemporal areas. Within the framework of Xu, abstract visual object representations in the posterior parietal cortex are not the result of processing in the dorsal pathway; they are dependent (necessarily) on ventral stream processing. According to that proposal, the observation that posterior parietal visual object representations exhibit invariance to transformations of the visual input is not contrary to the classical construal of the dorsal stream (understood computationally). That analysis is consistent with a recent combined fMRI and neuropsychological study of a patient with a focal ventral lesion and associated visual agnosia (Freud & Behrmann, 2020). The authors found that shape sensitivity was reduced not only in the ventral stream but also bilaterally in the posterior parietal cortex. As discussed by Xu (2018), there are a number of anatomical pathways that could support that type of integration between posterior parietal cortex and ventral stream. For instance, the anatomical location of the vertical occipital fasciculus (Yeatman et al., 2014), connecting posterior parietal areas to posterior occipitotemporal areas, could support cross-talk of visual representations between occipitotemporal and posterior parietal cortex.

To sum up, it is clear that visual shape processing occurs not just in the ventral stream, in the service of perception, but also in the parietal cortex, in support of multiple functions. Those functions include action (grasping) and the flexible maintenance and manipulation of task-relevant information. It is an open issue whether those posterior parietal visual shape representations (or perhaps some of them) are processed by the dorsal stream or are, rather, dependent on inputs from the ventral stream. The empirical evidence and theoretical arguments briefly reviewed underline the importance of being consistent in the use of the term "dorsal." If posterior parietal visual object representations depend on connectivity with (and inputs from) the occipitotemporal cortex, then the hypothesis of a dorsal pathway specialized for real-time analysis of vision in the service of action may live alongside an enriched understanding of the role of the posterior parietal cortex in supporting adaptive visual processing (Milner, 2017; Xu, 2018). The alternative view is that all visual object representations in the posterior parietal cortex depend on dorsal stream (understood computationally) processing. In this alternative, the classical understanding of the "dorsal" stream would be in need of revision.

Stepping back, one may note that the impaired perceptual abilities that attend ventral stream lesions indicate that dorsal stream visual representations are not sufficient to support explicit perceptual judgments. Along those lines, Freud and colleagues have argued that the 3D visual object representations that are computed by the dorsal stream are too coarse to support perception (Freud, Ganel, et al., 2017). That is consistent with the generally low acuity of the available inputs to the dorsal stream—namely that it receives little parvocellular input (Merigan & Maunsell, 1993).

Another important and constraining neuropsychological observation is that patient D. F. had difficulty grasping objects in a volumetrically appropriate manner if they did not have a principal axis of elongation (Carey et al., 1996). That observation is relevant to the earlier discussion in this chapter that elongation may be a visual property to which dorsal processes are differentially sensitive (Almeida et al., 2010; J. Chen et al., 2018; Handy et al., 2003).

An area ripe for additional experimental work is to use fMRI to study how visual object representations in different subregions of the posterior parietal cortex are (or are not) modulated by lesions to the ventral stream. On the one hand, there is evidence that visual representations in the parietal cortex are independent of the integrity of ventral stream processing (see Freud, Ganel, et al., 2017; James et al., 2003); on the other hand, there is evidence that posterior parietal representations are modulated by ventral lesions (Freud & Behrmann, 2020).

One takeaway from this discussion may be that the relevant distinction between the dorsal and ventral streams is not vision for action versus vision for perception; rather, the distinction is visual analysis for concurrent action versus visual analysis for conceptual interpretation. The dorsal stream supports concurrently unfolding actions based on bottom-up "aconceptual" real-time analysis of visual input, whereas the ventral stream supports interpretations of visual input and re-representations of past visual stimuli and is the only way to access conceptual representations from visual input. By hypothesis, the dorsal stream supports concurrently unfolding actions with richer 3D visual representations than previously thought (Freud et al., 2020). It could be that such parietal-based visual object representations, however abstract and rich they may be, are proprietary to the dorsal stream—and hence cut off from perceptual and conceptual processing in the ventral stream. This construal allows that the posterior parietal cortex may both support visual object processing intrinsic to the dorsal stream (understood computationally) and be heavily interconnected with the ventral stream and thus able to represent visual information in a task-dependent and flexible manner. Actions that cannot be "computed" bottom-up from the visual input (e.g., end-state comfort, praxis) must be accessed via ventral visual pathways analysis of the visual input.

I have argued that some visual object representations in the posterior parietal cortex are dependent on inputs from the ventral stream and that some visual object representations are a result of, and proprietary to (Mahon & Wu, 2015), processing in the dorsal stream (understood computationally).

This opens up a new possibility of dorsal–ventral interactions: By hypothesis, the visual object representations that are computed by the dorsal stream (understood computationally) guide ventral stream analysis of the perceptual cues that need to be parsed to be able to direct the correct action to the correct part of the correct object. I explore recent empirical findings in line with this hypothesis in the next section.

A Connectivity-Based Account of Specialization of Function in the Occipitotemporal Cortex

In order to grasp an object by the appropriate part and with the appropriate force, several dissociable types of high-level visual representations must be integrated. For instance, information about shape and three-dimensional structure is important for supporting a conceptual interpretation that yields, for instance, the distinction between the handle of a knife and its blade. The broader action goals that drive behavior (e.g., pass the knife to a friend or use it to cut an apple) constrain how an object-directed action will be directed toward the relevant part of the object. Visual cues about the surface texture of the object and, by inference, the material composition and thus weight distribution of the object must also be integrated with shape information so that the object is grasped with the appropriate grip strength and at the appropriate location.

In the context of everyday behavior, object grasps are conceptually informed and constrained—they are calibrated to both what it is that is being grasped (conceptual interpretation of the visual input) and why the object is being grasped (action goals). As noted, the aIPS supports hand shaping in the service of object-directed grasping (Binkofski et al., 1998; Culham et al., 2003; Mruczek et al., 2013). I also argued that the dorsal pathway, on its own, computes semantically uninformed object grasps, at least for objects with a principal axis of elongation. The dorsal stream, on its own, does not have access to information about what the object is or the object's material composition and weight distribution. Medial occipitotemporal structures, including the collateral sulcus and lingual gyrus, support analysis of surface-texture properties and inferences about material composition (Cavina-Pratesi et al., 2010; Gallivan et al., 2014).

The medial fusiform and adjacent collateral sulcus also exhibit differential neural responses to tools (or small manipulable objects) compared with animals, faces, and printed words (Chao et al., 1999; Mahon et al., 2007; Noppeney et al., 2006). By hypothesis (Mahon, 2020), category preferences for tools in the medial fusiform gyrus and collateral sulcus are a reflection of the interactions that allow the system to direct the correct actions to the correct parts of the correct objects. In this view, neural responses to tools in the medial fusiform gyrus are shaped, in part, by inputs from the aIPS. It is plausible that the aIPS modulates responses in the ventral stream because the aIPS is able to represent that there is a graspable object in the field via an independent dorsal stream analysis (Almeida et al., 2010; Carey et al., 1996; Fang & He, 2005; Prentiss et al., 2018). This proposal bears structural similarities to that of Bar and colleagues (2006), who argued that a fast magnocellular analysis leads to biasing signals from the orbital frontal cortex on ventral stream processes. The difference is that while Bar and colleagues' proposal was about the role of such biasing signals in supporting identification, the proposal here is that the biasing signals coming by way of the aIPS into the ventral stream are focused on driving perceptual inferences that are relevant for an action toward that object (see also van Polanen & Davare, 2015). Because differential neural responses to manipulable objects are observed in medial occipitotemporal areas even in tasks that do not involve action (Chao et al., 1999; Mahon et al., 2007), the current hypothesis must assume that such biasing signals from the aIPS to the ventral stream occur, at least to some extent, in an obligatory manner (i.e., independent of task context).

To summarize, by hypothesis, differential neural responses to manipulable objects (i.e., tools) in the medial fusiform gyrus and collateral sulcus arise from two intersecting constraints: (a) access to surface-texture and material properties via a ventral stream analysis of the visual input and (b) inputs from dorsal stream regions that represent that there is a graspable[4] object in the field (see Mahon, 2020). Early evidence consistent with that view was reported by a study from our group in which we distinguished between tools and arbitrarily manipulated objects. Tools were defined as objects for which there is a direct mapping between structure, function, and the grasping and manipulation actions associated with use (e.g., fork, hammer). Arbitrarily manipulated objects are as equally graspable as tools but have variable (i.e., arbitrary) relations between structure, function, and manner of manipulation (e.g., wallet, book). The nature of the distinction between tools and arbitrarily manipulated object is such that the same action(s) (e.g., functional grasp, praxis) would be evoked for the same tool across presentations, whereas different actions would be evoked for arbitrarily manipulated objects (because arbitrarily manipulated objects, by definition, do not have stereotyped patterns of object-associated use). We found that although there was stimulus-specific repetition priming in posterior parietal and dorsal occipital areas for both tools and arbitrarily manipulated objects, there were repetition priming effects only for tools (and not for arbitrarily manipulated objects) in anterior and inferior regions of the parietal cortex (for a similar pattern in the parietal cortex, distinguishing tools from nontool graspable objects, see also Mruczek et al., 2013). Critically, we also found that the pattern of repetition priming in the medial fusiform gyrus for tools and arbitrarily manipulated objects tracked the pattern observed in inferior parietal areas rather than the pattern observed in posterior and superior parietal areas (Mahon et al., 2007). There was greater repetition priming for tools than for arbitrarily manipulated objects in the medial fusiform gyrus. This was initial evidence that neural responses in occipitotemporal areas track motor-relevant properties of objects: Repetition priming in the medial fusiform is an echo of what is happening in the inferior parietal lobule (see also Gallivan, Chapman, et al., 2013).

Stepping back, one can extrapolate several predictions from the proposal that neural responses to "tools" in medial ventral stream regions are the result of joint inputs from the ventral and dorsal visual pathways. First, there should be privileged connectivity between the medial fusiform gyrus and aIPS, a prediction that has been confirmed across a number of studies (Amaral et al., 2021; Q. Chen et al., 2017; Gallivan, McLean, et al., 2013; Garcea & Mahon, 2014; Garcea et al., 2018; Mahon et al., 2007; Stevens et al., 2015). The presence of functional connectivity between tool-preferring regions of the ventral occipitotemporal cortex and parietal cortex is independent evidence that those temporal and parietal areas are in fact part of a network and not (just) independently driven by common visual inputs.

A second (and untested) prediction, within the surprise paradigm, is that the emergence of responses that code graspability in the aIPS should temporally precede (and be yoked to) tool-specific responses emerging in the collateral sulcus. In other words, there may be an initial response to surface-texture properties in the collateral sulcus that is not stronger for manipulable objects than nonmanipulable objects—this would represent a ventral stream analysis of surface-texture properties (without inputs from parietal areas). In parallel, the aIPS is computing (conceptually uninformed) grasps, but only for stimuli that are graspable. At some point in processing time after stimulus onset, responses in the collateral sulcus become stronger for tools than for animals and faces. The time point at which that occurs is predicted to be dependent on, and tightly yoked to, responses in the aIPS that (aconceptually) compute graspability.

Perhaps one of the strongest predictions that can be generated is that lesions to the aIPS should have a direct modulatory effect on neural responses in the medial fusiform gyrus and collateral sulcus. Specifically, lesions to the aIPS should affect neural responses to tool stimuli in those medial occipitotemporal areas, but not responses to other classes

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[4] "Graspable" is used here in a sense that is different from "manipulable." Manipulation refers to object use that fulfills the function of the object and that is constrained by the structure of the object. Graspable refers to whether the object is of a size and shape that (aconceptually) affords a grasp with the hand. Because praxis is accessed via conceptual interpretation of the visual input, the dorsal stream (in this construal) does not represent that there is a "manipulable" object in the field but rather (merely) that an object is graspable (with no representation of what is graspable).

of stimuli in the same region. Garcea and colleagues (2019) tested this using a technique termed voxel-based lesion activity mapping (VLAM). VLAM is similar to the well-established approach of voxel-based lesion symptom mapping (VLSM; Bates et al., 2003). In VLSM, each patient from a large group contributes a lesion mask and a performance measure on at least one neuropsychological task. The likelihood of any voxel being lesioned across the group is correlated with performance on the neuropsychological task. VLSM thus provides a map of where lesions affect performance in the reference neuropsychological task. By contrast, in VLAM analyses, each patient contributes a lesion mask and a whole-brain map of stimulus-evoked activity, for instance, a whole-brain map of differential neural responses to tool stimuli compared to animal stimuli. Garcea and colleagues found that the amplitude of tool responses in the medial fusiform gyrus and collateral sulcus was inversely related to the presence of lesions in the aIPS (see color insert, Color Plate 12). By contrast, the amplitude of neural responses to place stimuli in the same collateral sulcus and medial fusiform regions was not modulated by lesions to the aIPS. The category specificity of that finding suggests a form of dynamic diaschesis, a concept initially proposed by Price and colleagues (2001).

Garcea and colleagues' (2019) findings indicate that neural responses to tools in the ventral stream are dependent on the integrity of processing in the left aIPS, which is what would be predicted if tool responses in that ventral stream region are driven by the intersection of two constraints—one coming through the ventral visual hierarchy and one coming from the aIPS via the dorsal stream.

In a complementary test of causal influences of the parietal cortex on ventral occipitotemporal responses to manipulable objects, Lee and colleagues applied transcranial direct current stimulation (tDCS) to the left parietal cortex before healthy participants completed an fMRI study (Lee et al., 2019). During the fMRI study, the participants saw images of tools, faces, and places. The authors found that tDCS to the parietal cortex modulated multivariate decoding of responses to tools in the collateral sulcus and medial fusiform gyrus. However, tDCS to the parietal cortex did not modulate neural responses to place stimuli in the same area of the ventral stream, again indicating tool specificity in parietal-to-ventral modulation. An important follow-up study that could be carried out would be to use transcranial magnetic stimulation *during* fMRI to test whether concurrent stimulation to parietal tool-preferring regions up- or downregulates responses in occipitotemporal areas independently defined as tool preferring (medial fusiform gyrus, collateral sulcus, and left posterior middle temporal gyrus).

QUESTIONS AND CONTROVERSIES SUMMARY

- The parietal cortex represents object-directed actions and visual object representations. Which parietal action and object representations depend on analysis of the visual input by the ventral stream?
- Is it a valid assumption that access to a conceptual interpretation of the visual input depends (necessarily) on processing within the ventral stream?
- There is neural specificity in the ventral visual pathway for visual stimuli that are defined by motor- or action-relevant dimensions (i.e., tools). Is neural specificity for tools in the ventral stream dependent on real-time inputs that come from the dorsal visual pathway that code that there is a graspable object in the field?
- Is elongation a visual property that is processed in a privileged manner by the dorsal visual pathway?

CONCLUSION

This review has emphasized the roles played by high-level visual representations when thinking about, visually recognizing, grasping, and using everyday objects according to their function to satisfy action goals. Functional object use subsumes all of those activities, and as a complex behavior, functional object use is not supported by a single process in the brain or a single brain region. Functional object use involves the coordinated interactions of dissociable processes supported by anatomically dissociable regions. Those regions are distributed across all the major lobes of the brain. More narrowly, this review has contrasted the types of high-order visual object representations that are generated across occipitotemporal and occipitoparietal areas. Specifically, the focus has been on the role of high-level visual representations in accessing nonvisual information (e.g., concepts, motor-relevant information) and in supporting interactions between the ventral and dorsal visual pathways.

The theoretical framing of this review was motivated by the idea that in order to derive inferences about the organization of a complex system, it is important to be clear on the use case scenarios of the system. The logic is straightforward: Whatever the organization of the system may be, it must be able to accommodate those use case scenarios. The role of this type of functional analysis is to define what must minimally be explained: Plausibility is not a criterion to accept a theory, but implausibility is sufficient justification to reject one (Gould & Lewontin, 1979).

I have also argued that the field has overemphasized identification as the use case scenario for visual processing; that approach can exclude consideration of how objects are perceived in context. It is not uncommon that, the first time an object is visually perceived in an everyday context, the identity of the object has already been individuated by an internally generated action goal. One opens the silverware drawer and thus perceives the knife *because* one needed a knife in the first place. The knife, as the useful object needed to accomplish the ongoing work, was present in mind before it was visually perceived. Of course, the particular knife in the drawer need not be explicitly represented in order for the system to represent a knife as being the object that is needed for the work. However, in order to then grasp a particular knife in a way that supports using it for a specific goal, it is necessary to represent how the properties of that particular knife can be interpreted through the lens of an action goal. I have argued that the ventral stream is the only pathway from visual inputs to a conceptual interpretation. Indeed, the role of visual perception in this context may not be identification per se but something more like tuning the perceptual inputs to current action goals and, in turn, tuning the specific actions that will be required to still meet those goals to the available perceptual inputs.

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