66 Concepts and Object Domains

YANCHAO BI

ABSTRACT Domain effects have been studied extensively for object perceptual and conceptual processes. Decades of neuroimaging research have identified domain differences in widely distributed brain systems, including various higher-level sensory and motor systems. Investigations of the mechanisms underlying such differences have led to a more detailed understanding of and questions about the computational nature of these regions and their functional roles in object knowledge representation in general. In this chapter, I review recent findings on the variables associated with the response and connectivity profiles of three different domain-preferring clusters in higher ventral visual cortex. The findings reveal the joint effects of visual features and connectivity patterns and an intriguing interaction between input modality and object domain. The available evidence motivates a line of theoretical analyses about the nature of domain-relevant response systems and their relationship with input systems (e.g., vision). A promising hypothesis is that the manner in which bottom-up input information is translated into different response systems for different domains constrains the nature of representation at various object-processing levels.

How does the human brain represent what we know about objects in the world, such as a mouse, a table, or an ax? One hypothesis gleaned from neuropsychological and neuroimaging studies is that the object domains of evolutionary salience, such as animals, tools, and conspecifics, is an important dimension along which object knowledge is organized (Caramazza & Shelton, 1998). Brain lesions may lead to relatively disproportionate deficits in the knowledge of certain domains (Capitani, Laiacona, Mahon, & Caramazza, 2003; Warrington & Shallice, 1984). Stimuli of different domains elicit relatively different strengths of activation in multiple brain regions, including perceptual systems such as higher-order visual cortex, auditory cortex, motor cortex, and so-called higher-order association cortex (see reviews in Brefczynski-Lewis & Lewis, 2017; Martin, 2016).

Objects belonging to various domains systematically differ in many aspects, such as their physical appearance, their movement, the sound they produce, whether and how they can be manipulated, the type of function they serve for humans, and whether and what emotional responses they induce. All of these differences can potentially play a role in accounting for the neuropsychological and functional magnetic resonance imaging (fMRI) findings of domain differences (e.g., Warrington & McCarthy, 1987). In this chapter, I discuss current notions, findings, and the new questions that have emerged.

I first introduce the consensus framework underlying the brain basis of object knowledge representation, which incorporates a domain dimension, focusing on the ventral visual pathway (ventral occipitotemporal cortex, or VOTC); I then discuss how recent empirical patterns pose new challenges for the existing theories. I go on to present a theoretical analysis of the effect of an important domain difference—that is, the manner in which sensory systems map onto the corresponding response systems, on local computations for different domains, and then describe the outstanding questions.

Canonical View of Object Knowledge Representations and the Effects of Object Domains

Decades of neuroimaging studies have consistently localized object-knowledge representations to widely distributed brain regions across the temporal, frontal, and parietal cortices (Binder, Desai, Graves, & Conant, 2009; Mahon & Caramazza, 2011; Martin, 2007). The activations in regions that loosely belong to the sensorimotor cortices are commonly interpreted as representing attributes of corresponding modalities (e.g., form, color, motion, sound, action, and emotion; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017; Martin, 2016). In this distributed-representation framework of object concepts, within each modality, brain subclusters showing a varying degree of sensitivity to objects of different domains have been consistently reported. The higher-order visual cortex includes clusters that show different preferences for pictures of different domains, with a broad animate/inanimate distinction (Chao, Haxby, & Martin, 1999; Grill-Spector & Weiner, 2014; Kanwisher, 2010; Konkle & Caramazza, 2013). In the auditory cortex, clusters have been found that are differentially sensitive to the sounds of people (voices and speech), man-made sounds, and natural sounds (Brefczynski-Lewis & Lewis, 2017). For the action system (prefrontal, inferior frontal, and inferior parietal regions), stronger activation is elicited by small manipulable objects (Lewis, 2006; Martin, Wiggs, Ungerleider, & Haxby, 1996). These domain-preferring nodes distributed in different modality-specific processing streams are linked together by brain connections to form domain-specific networks.

Object Domain Distributions in the Ventral Visual Pathway: Nodal Representations and Connection Structures

Domain organization has been most extensively studied in the VOTC. From the ventral medial to the lateral occipitotemporal cortex, gradients of three clusters showing stronger sensitivity to pictures of three domains of objects have been consistently obtained: the medial-anterior fusiform gyrus/parahippocampal gyrus (medFG/PHG, or the parahippocampal place area, PPA; Epstein & Kanwisher, 1998), which prefers places and large objects; the lateral-posterior fusiform gyrus (latFG; Chao, Haxby, & Martin, 1999), which prefers animals; and the lateral occipitotemporal cortex (LOTC; Bracci, Cavina-Pratesi, Ietswaart, Caramazza, & Peelen, 2012), which prefers tools (figure 66.1; e.g., Konkle & Caramazza, 2013; see reviews in Bi, Wang, & Caramazza, 2016; Bracci, Ritchie, & de Beeck, 2017; Grill-Spector & Weiner, 2014; Peelen & Downing, 2017).

The nature of the domain differences in these regions has been at the heart of discussions about higher-order visual cortex and knowledge representation. The following types of (nonmutually exclusive) hypotheses regarding these differences have been entertained: (1) They compute certain bottom-up visual properties that are correlated with or diagnostic of different domains (e.g., Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Levy, Hasson, Avidan, Hendler, & Malach, 2001; Nasr, Echavarria, & Tootell, 2014; Srihasam, Vincent, & Livingstone, 2014), (2) they are multimodal or amodal (abstract conceptual) domain-specific representations (e.g., Ricciardi, Bonino, Pellegrini, & Pietrini, 2013), and (3) they are driven by the innate brain connections that connect modality-specific representations across different systems for processing a given domain (Mahon & Caramazza, 2011). I will briefly review the following evidence relating to these three notions: whether certain low-level visual features that tend to associate with certain object domains activate these clusters in the absence of object-domain knowledge; whether nonvisual stimuli of the corresponding object domains, even in the case of total visual deprivation (congenitally blind individuals), activate these clusters; and whether they are connected with different brain regions in other sensory/motor systems. The overall findings are summarized in table 66.1 and figure 66.1.

Preference to Navigation-Related Objects in the Medial-Anterior Fusiform Gyrus/Parahippocampal Gyrus

Is this region activated by certain visual features associated with large objects and places? The answer is yes. The lower-level visual properties that have been shown to associate with PPA activation include rectilinear shape (Nasr, Echavarria, & Tootell, 2014), peripheral vision (Levy et al., 2001), and large real-world size (Konkle & Oliva, 2012). Scrambled images of houses, presumably keeping only the low-level visual features and blocking other domain-relevant information that depends on recognition, elicit response patterns similar to those of normal house pictures, with stronger activation in the medFG/PHG areas (Coggan, Liu, Baker, & Andrews, 2016).

Is this region activated by nonvisual stimuli of the corresponding domain and in congenitally blind individuals? The answer is also yes. Compared with various control conditions, this area was more strongly activated when the subjects haptically explored Lego scenes; listened to sounds associated with landmarks, such as the ringing of a church bell; or made semantic judgments on visually presented names of famous sites ("Was the Colosseum constructed before 500 AD?") or size judgments on the auditory names of large nonmanipulable objects (e.g., Adam & Noppeney, 2010; Fairhall & Caramazza, 2013; He et al., 2013; Wolbers, Klatzky, Loomis, Wutte, & Giudice, 2011). In congenitally blind individuals, this region was also more strongly activated when they explored Lego scenes relative to Lego abstract objects (Wolbers et al., 2011) and when they performed size judgment tasks on auditory words of large nonmanipulable objects compared with tools and animals (He et al., 2013).

Brain connectivity pattern Currently, two major types of brain connections are measured noninvasively: white matter structural connectivity, using diffusion tensor imaging (DTI; Le Bihan et al., 2001), and resting-state functional connectivity (rsFC), which is measured by the degree of synchronization (correlation of the activity time course) at rest using functional imaging (Friston, Frith, Liddle, & Frackowiak, 1993; Smith, 2012). The PPA was found to be functionally connected with regions encompassing other scene/large object-sensitive clusters, including the retrosplenial cortex (RSC) and the transverse occipital sulcus (TOS; He et al., 2013). Testing the relationship between the connectivity pattern and domain-preference functional responses, Saygin et al. (2012) showed that a fusiform voxel's domain preference (scenes relative to faces) could be predicted from its structural connectivity patterns with the rest of the brain. Visual experience has minimal influence on the rsFC pattern, the structural connectivity pattern, or the relationship between the structural connectivity pattern and the functional preference for large objects in this area (Wang et al., 2015, 2017). Finally, the properties of the long-range structural connections of the PPA are associated with visual recognition performances of places and large objects (Gomez et al., 2015; Li et al., 2018).

Preference to Small Manipulable Objects (Tools) in the Lateral Occipitotemporal Cortex

Is this region activated by certain visual features associated with tools? The presence of an elongated shape seems sufficient to activate the LOTC (Chen, Snow, Culham, & Goodale, 2017). However, having more elongation features is not necessary to induce preferential activity in this region. It is also activated by items with a very distinct visual shape, such as hands (Bracci et al., 2012; Bracci & Peelen, 2013; Striem-Amit, Vannuscorps, & Caramazza, 2017). Training novel objects to be used as tools results in stronger activation here than pretraining, although the visual properties remain identical before and after training (Weisberg, van Turrennout, & Martin, 2007).

Is this region activated by nonvisual stimuli of the corresponding domain and in congenitally blind individuals? The LOTC's selectivity to tools has been reported when subjects made judgments about or generated names for object sounds, such as the sound of *sawing wood* (Doehrmann, Naumer, Volz, Kaiser, & Altmann, 2008; Lewis, Brefczynski, Phinney, Janik, & DeYoe, 2005; Tranel, Grabowski, Lyon, & Damasio, 2005), or written or spoken tool names (the word *saw*; e.g., Noppeney, Price, Penny, & Friston, 2006; Peelen et al., 2013). For congenitally blind individuals, LOTC's selectivity to tools was reported when the participants performed object-size judgment tasks according to the auditory names of tools compared

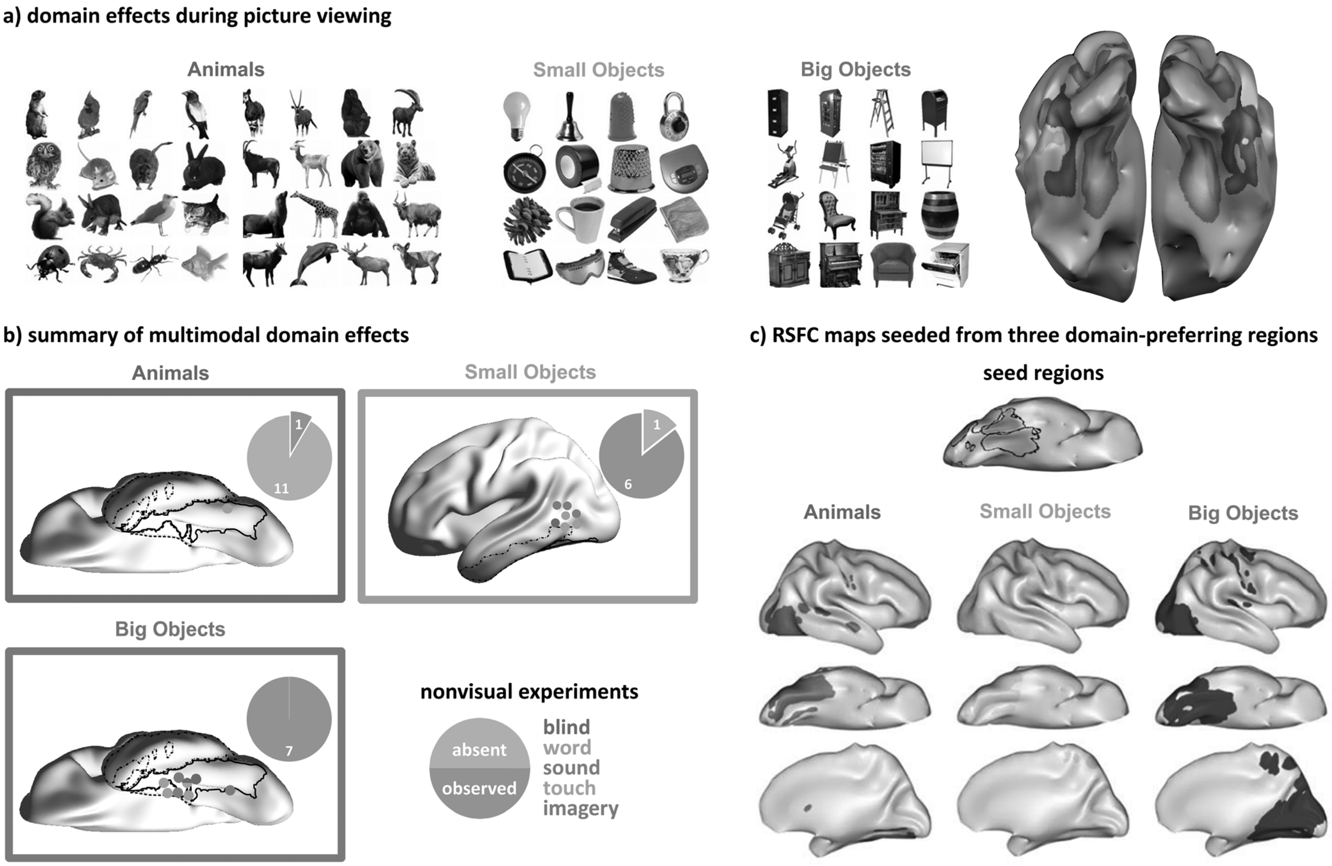

FIGURE 66.1 The functionality and connectivity pattern of the VOTC domain-preferring clusters. *A*, Visual experiments: the three domain-preferring clusters in VOTC that associate with viewing pictures of large objects, small manipulable objects, and animals. Adapted from Konkle and Caramazza (2013). *B*, Nonvisual experiments: The two artifact clusters in (*A*) show consistent domain effects in nonvisual experiments, whereas the animal cluster tended not to show preference to animals when the stimuli were nonvisual. The color dots on the brain map correspond to the studies summarized in Bi et al. (2016, table 1), with different colors indicating different types of nonvisual input. Pie charts show the number of studies in which nonvisual domain effects were observed (*red*) or absent (*blue*). *C*, The resting-state functional connectivity patterns that associate with the three domain-preferring clusters. Adapted from Konkle and Caramazza (2017). (See color plate 79.)

with the names of animals and large nonmanipulable objects (Peelen et al., 2013).

Brain connectivity pattern The results from the rsFC analysis showed that the LOTC is intrinsically linked with the parietal cortex along the intraparietal sulcus and the inferior frontal regions that have been implicated in tool processing (Konkle & Caramazza, 2017; Peelen et al., 2013), which does not seem to be affected by visual deprivation (Wang et al., 2015). DTI studies showed that the pMTG tool region, which roughly corresponds to the LOTC, is structurally connected with the parietal and frontal tool-related regions and lesions affecting the connections between the LOTC and the frontal tool clusters (inferior frontal and ventral premotor cortex) associated with tool conceptual deficits (Bi et al., 2015).

Preference to Animate Items in the Latfg

Is this region activated by certain visual features associated with animate items? Curvature and fovea processing have been suggested to associate with activation in this territory (Hasson et al., 2002; Srihasam, Vincent, & Livingstone, 2014). Nonetheless, after controlling for various visual properties, including shape, texture, and picture size, animal pictures still activate this region more strongly than well-matched man-made objects (Proklova, Kaiser, & Peelen, 2016).

Is this region activated by nonvisual stimuli of the corresponding domain and in congenitally blind individuals? Studies using nonvisual stimuli have failed to observe animal preferences relative to other domains using object sounds (e.g., Adam & Noppeney, 2010; Lewis et al., 2005) or written or spoken animal names (e.g., He et al., 2013; Noppeney, Price, Penny, & Friston, 2006; but see Chao, Haxby, & Martin, 1999). That is, this region is not more strongly activated when subjects listen to animal sounds (e.g., a barking sound) or names (e.g., the word *dog*) relative to nonanimal sounds or words (e.g., a church bell or the word *church*). In congenitally blind participants, listening to animal names does not activate this region more strongly than other objects (He et al., 2013; Wang et al., 2015).

Brain connectivity pattern In sighted individuals, this region is intrinsically functionally connected with the bilateral occipital and posterior ventral temporal cortex, the superior temporal sulcus, and the somatosensory and motor cortex (Konkle & Caramazza, 2017). Visual deprivation has a significant impact on the rsFC pattern of this region; in the congenitally blind, it is additionally connected with the primary and secondary auditory, the bilateral superior parietal, and the inferior frontal regions (Wang et al., 2015).

Support and Challenges Associated with Current Theories

In the first section, I presented three (non–mutually exclusive) notions: the bottom-up visual property account, the amodal domain-specific property account, and the connectivity-constraint account. Each notion is consistent with some of the results reviewed above (see table 66.1). The coexistence of the specific visual feature effects and nonvisual domain effects in the two artifact clusters (medFG/PHG and LOTC) reflects the close interactions between visual and domain representations, which may be optimized for real-world behavior (see discussions in Bracci, Ritchie, & de Beeck, 2017; Proklova et al., 2016). The results showing stronger connectivity between domain-preferring regions across various brain systems and the predictive nature of the connectivity pattern for the local domain-preference response are consistent with the connectivity-constraint account for domain distribution in the VOTC (Mahon & Caramazza, 2011) and the

TABLE 66.1 Summary of the effects of stimuli properties on the domain distribution in the higher-order visual cortex.

		Places and large objects in the medFG/PHG	Small manipulable objects in the LOTC	Animals in the latFG
Visual (view visual features)	Sighted (sufficient, not necessary)	Rectilinear	Elongation	Curvature
Visual (view object pictures)	Sighted	Yes	Yes	Yes
Words (listen to object names)	Sighted	Yes	Yes	Mostly no
	Blind	Yes	Yes	Mostly no
Auditory (listen to object sounds)	Sighted	Yes	Yes	No
	Blind	—	—	—
Tactile (haptic exploration of objects)	Sighted	Yes	—	—
	Blind	Yes	—	—

general notion that connection determines function (Passingham, Stephan, & Kötter, 2002).

None of the accounts, in their current forms, explains the intriguing differences in the input modality effects across domains. When objects are presented in nonvisual modalities, such as haptic or sound, large objects still activate the medFG/PHG and tools LOTC while the latFG no longer has domain preference for animals. Why would hearing the sound of a church bell and the sound of sawing, or hearing the words *church* and *saw*, preferentially activate the two artifact VOTC regions but hearing the barking sound or the word *dog* does not activate the latFG? Does this mean that the nature of representation (format and content) of these three domain-preferring clusters differs, with the animal cluster being more "visual" (representing properties of animals that are primarily sensed through the visual modality), whereas other parts of the VOTC actually represent nonvisual properties (Peelen & Downing, 2017)? If yes, why are there such differences across domains?

Updated Proposal: Further Considerations of Stimulus-Response Mapping

A possible solution for the current empirical package is offered in Bi, Wang, and Caramazza (2016). The central points are that (1) the brain is wired to efficiently map sensory information to response systems that are optimal for survival; (2) the mechanism of mapping is tightly related to the nature of each information system being mapped; (3) different object domains entail mapping sensory information with different types of response systems, and thus the mechanisms of mapping may differ; and (4) the representations that map across systems are more readily accessed from multiple modalities.

Humans engage in different types of responses to different object domains. A typical response to a large, stable object is to go around it (useful for navigation), a response to a tool is to manipulate it in a certain way for a specific function, a response to an animal is to fight or take flight, and a response to other humans would primarily be social. That is, for different object domains, the visual information is primarily mapped onto different nonvisual response systems (figure 66.2; see also figure 1 in Peelen & Downing, 2017). These different target systems may have different types of relationships with the visual system. For instance, the correspondence between manipulation and physical form, such as shape and size, which can be computed through the visual system, may be relatively transparent. Object parts made by humans are of certain shapes and sizes to be manipulated in certain ways using effectors (e.g., elongation for grasping). When mapping visual information onto manipulation information, it can happen at a visual form element level for which corresponding units in the motor system also exist (figure 66.2, midlevel), rather than wait until the object-specific form and manipulation representations, on which mapping can of course also happen based on stored (conceptual) knowledge (figure 66.2, object-specific level). For mapping to the spatial navigation response system, certain shape (e.g., chunky, rectilinear) properties may associate with properties such as "being stable," indicating potential navigation landmarks, and trigger specific navigation actions such as going around or stepping over. Such crossmodal mapping on these midlevel form elements makes them *multimodal*. For animals, however, the type of response (fight or flight) is not associated with specific form features. Being big or small, round or long does not necessarily indicate whether an animal is dangerous or not. Thus, the translation from the visual form information associated with animals to the fight/flight response system does not appear to operate on the same (midlevel) element level as artifacts or through similar mapping mechanisms. The level upon which it operates is unknown—it could be at earlier specific visual detector levels (see below) and/or at later stages (e.g., whole-object [conceptual knowledge] level associations or combinations of multiple types of visual cues, such as shape/motion/color). As a result, in common midlevel "form" elements, the information content could be multimodal for those associated with large objects and small, manipulable objects but not with animate things.

This proposal does not add additional assumptions to the overall framework of object representation. It simply considers the nature of different types of object information and the corresponding crossmodality relationships for major object domains in greater depth. By attributing the VOTC domain effects to the midlevel visual (form) system, this proposal also readily explains why certain low-level visual features might be sufficient to activate these clusters.

Outstanding Questions

This updated proposal highlights the influence of the mapping principles between sensory and response systems in shaping the representation properties in each system. It frames a line of questions to be tested: (1) What is the information content at these domain-preferring regions? Does the "multimodal" domain effect indeed reflect the same types of form representation? (2) The updated proposal argues that the mapping between different object properties may happen on multiple levels and depend on the relationships between the two types of information. What are the mechanisms of

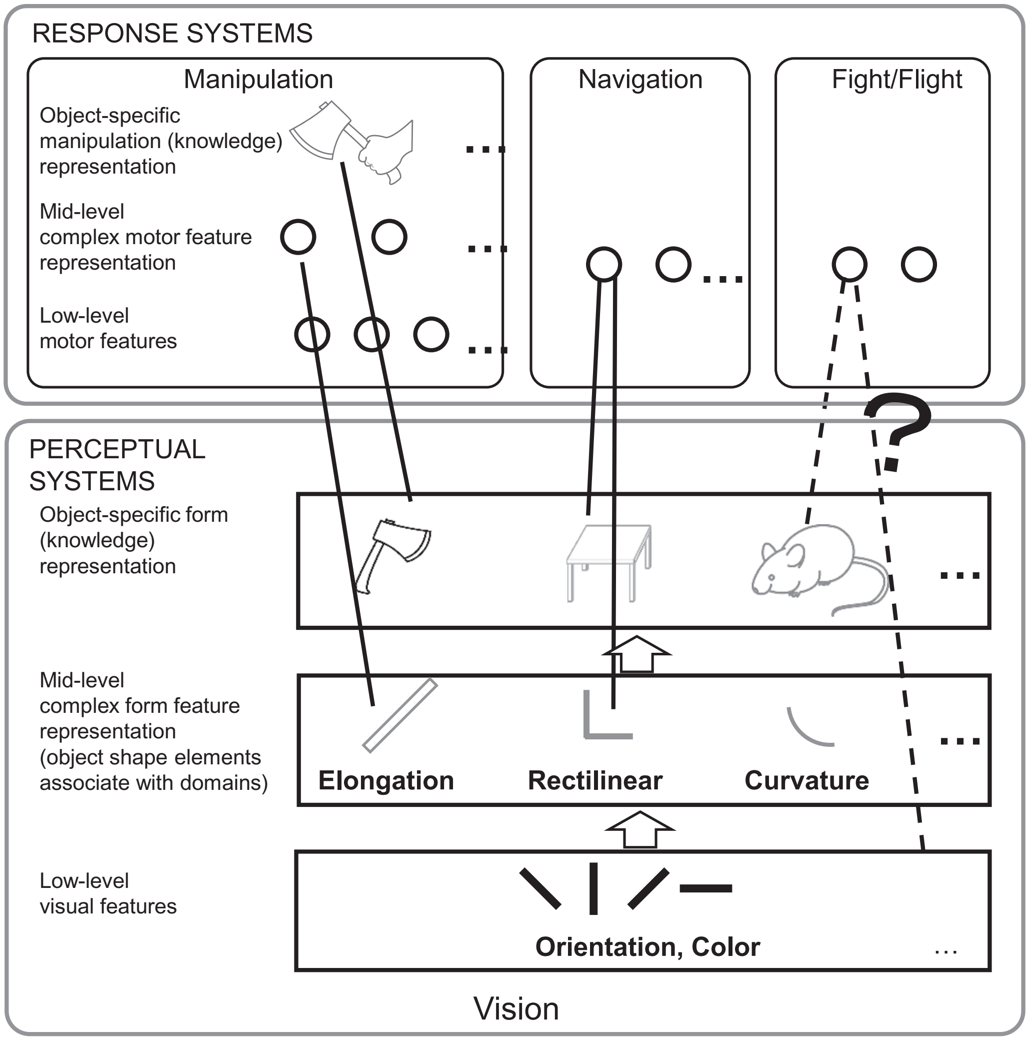

FIGURE 66.2 A schematic sketch of the updated proposal about object-domain representation. Only the example perceptual and response systems are shown. The main point is that the mapping between the perceptual representations and various response systems (corresponding to different object domains) may happen at different levels, depending on the relationships between systems. Note that the representation structures in the navigation and fight/flight response systems are highly simplified.

these mappings (see recent analyses of binding through connection patterns and/or region pattern interactions; Anzellotti & Coutanche, 2018; Fang et al., 2018)? (3) How early is the "domain" influence? Studies of domain representation have focused on the cortical sites where the domain difference is most visible, such as the so-called higher-order cortex. Recent neurophysiological evidence from nonhuman primates has discovered neurons in the primary visual and motor systems that are tuned to features much more complex than previously thought, such as those selective to predators (e.g., snakes) in the pulvinar (Le et al., 2013), curvatures in V1 (Tang et al., 2018), and complex actions in the primary motor cortex (Graziano, 2016). While the complex feature space for objects is large and undetermined (Kourtzi & Connor, 2011), those that are optimized for domain detection and triggering specific stimulus-response mappings might be good candidates for the effective functional units.

Conclusions

For a long time, the field of object processing has aimed to determine whether domain differences originate from bottom-up effects or innate domain-specific circuits. These discussions have led to a more detailed understanding and new questions about the functionalities and connectivity patterns of a range of cortical regions, especially the higher-level visual cortex. I wish to highlight a further dimension: the nature of the interface between different systems. After all, how the brain parses the physical world is driven by the need for optimal responses for survival, which is different for these object domains. How exactly this mapping process affects the regional representations and the connection mechanisms remains to be discovered.

Acknowledgments

I thank Alfonso Caramazza and Xiaoying Wang for the constant discussions about the topic in this chapter. I also thank Xiaosha Wang, Tao Wei, and Wei Wu for comments on earlier drafts and Yuxing Fang for the help in producing figure 66.2. This work has been supported by the Fulbright Visiting Scholar Program.

REFERENCES

Adam, R., & Noppeney, U. (2010). Prior auditory information shapes visual category-selectivity in ventral occipito-temporal cortex. *NeuroImage, 52*(4), 1592–602.

Anzellotti, S., & Coutanche, M. N. (2018). Beyond functional connectivity: Investigating networks of multivariate representations. *Trends in Cognitive Sciences, 22*(3), 258–269.

Bi, Y., Han, Z., Zhong, S., Ma, Y., Gong, G., Huang, R., … Caramazza, A. (2015). The white matter structural network underlying human tool use and tool understanding. *Journal of Neuroscience, 35*(17), 6822–6835.

Bi, Y., Wang, X., & Caramazza, A. (2016). Object domain and modality in the ventral visual pathway. *Trends in Cognitive Sciences, 20*(4), 282–290.

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex, 19*(12), 2767–2796.

Bracci, S., Cavina-Pratesi, C., Ietswaart, M., Caramazza, A., & Peelen, M. V. (2012). Closely overlapping responses to tools and hands in left lateral occipitotemporal cortex. *Journal of Neurophysiology, 107*(5), 1443–1456.

Bracci, S., & Peelen, M. V. (2013). Body and object effectors: The organization of object representations in high-level visual cortex reflects body-object interactions. *Journal of Neuroscience, 33*(46), 18247–18258.

Bracci, S., Ritchie, J. B., & de Beeck, H. O. (2017). On the partnership between neural representations of object categories and visual features in the ventral visual pathway. *Neuropsychologia, 105*(June), 153–164.

Brefczynski-Lewis, J. A., & Lewis, J. W. (2017). Auditory object perception: A neurobiological model and prospective review. *Neuropsychologia, 105*, 223–242.

Capitani, E., Laiacona, M., Mahon, B., & Caramazza, A. (2003). What are the facts of semantic category-specific deficits? A critical review of the clinical evidence. *Cognitive Neuropsychology, 20*(3/4/5/6), 213–261.

Caramazza, A., & Shelton, J. R. (1998). Domain-specific knowledge systems in the brain: The animate-inanimate distinction. *Journal of Cognitive Neuroscience, 10*(1), 1–34.

Chao, L. L., Haxby, J. V, & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience, 2*(10), 913–919.

Chen, J., Snow, J. C., Culham, J. C., & Goodale, M. A. (2017). What role does "elongation" play in "tool-specific" activation and connectivity in the dorsal and ventral visual streams? *Cerebral Cortex,* March, 1–15.

Coggan, D. D., Liu, W., Baker, D. H., & Andrews, T. J. (2016). Category-selective patterns of neural response in the ventral visual pathway in the absence of categorical information. *NeuroImage, 135*, 107–114.

Doehrmann, O., Naumer, M. J., Volz, S., Kaiser, J., & Altmann, C. F. (2008). Probing category selectivity for environmental sounds in the human auditory brain. *Neuropsychologia, 46*(11), 2776–2786.

Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature, 392*(6676), 598–601.

Fairhall, S. L., & Caramazza, A. (2013). Brain regions that represent amodal conceptual knowledge. *Journal of Neuroscience, 33*(25), 10552–10558.

Fang, Y., Wang, X., Zhong, S., Song, L., Han, Z., Gong, G., & Bi, Y. (2018). Semantic representation in the white matter pathway. *PLoS Biology, 16*(4), e2003993.

Friston, K. J., Frith, C. D., Liddle, P. F., & Frackowiak, R. S. (1993). Functional connectivity: The principal-component analysis of large (PET) data sets. *Journal of Cerebral Blood Flow & Metabolism, 13*, 5–14.

Gomez, J., Pestilli, F., Witthoft, N., Golarai, G., Liberman, A., Poltoratski, S., … Grill-Spector, K. (2015). Functionally defined white matter reveals segregated pathways in human ventral temporal cortex associated with category-specific processing. *Neuron, 85*(1), 216–228.

Graziano, M. S. A. (2016). Ethological action maps: A paradigm shift for the motor cortex. *Trends in Cognitive Sciences, 20*(2), 121–132.

Grill-Spector, K., & Weiner, K. S. (2014). The functional architecture of the ventral temporal cortex and its role in categorization. *Nature Reviews Neuroscience, 15*(8), 536–548.

Hasson, U., Levy, I., Behrmann, M., Hendler, T., & Malach, R. (2002). Eccentricity bias as an organizing principle for human high-order object areas. *Neuron, 34*(3), 479–490.

He, C., Peelen, M. V, Han, Z., Lin, N., Caramazza, A., & Bi, Y. (2013). Selectivity for large nonmanipulable objects in scene-selective visual cortex does not require visual experience. *NeuroImage, 79*, 1–9.

Kanwisher, N. (2010). Functional specificity in the human brain: A window into the functional architecture of the mind. *Proceedings of the National Academy of Sciences of the United States of America, 107*(25), 11163–11170.

Konkle, T., & Caramazza, A. (2013). Tripartite organization of the ventral stream by animacy and object size. *Journal of Neuroscience, 33*(25), 10235–10242.

Konkle, T., & Caramazza, A. (2017). The large-scale organization of object-responsive cortex is reflected in resting-state network architecture. *Cerebral Cortex, 27*(10), 4933–4945.

Konkle, T., & Oliva, A. (2012). A real-world size organization of object responses in occipitotemporal cortex. *Neuron, 74*(6), 1114–1124.

Kourtzi, Z., & Connor, C. E. (2011). Neural representations for object perception: Structure, category, and adaptive coding. *Annual Review of Neuroscience, 34*, 45–67.

Lambon Ralph, M. A., Jefferies, E., Patterson, K., & Rogers, T. T. (2017). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience, 18*, 42–55.

Le, Q. Van, Isbell, L. A., Matsumoto, J., Nguyen, M., Hori, E., Maior, R. S., … Nishijo, H. (2013). Pulvinar neurons reveal neurobiological evidence of past selection for rapid detection of snakes. *Proceedings of the National Academy of Sciences of the United States of America, 110*(47), 19000–19005.

Le Bihan, D., Mangin, J., Poupon, C., Clark, C., Pappata, S., & Molko, N. (2001). Diffusion tensor imaging: Concepts and applications. *Journal of Magnetic Resonance Imaging, 66*(13), 534–546.

Levy, I., Hasson, U., Avidan, G., Hendler, T., & Malach, R. (2001). Center-periphery organization of human object areas. *Nature Neuroscience, 4*(5), 533–539.

Lewis, J. W. (2006). Cortical networks related to human use of tools. *Neuroscientist, 12*(3), 211–231.

Lewis, J. W., Brefczynski, J. A., Phinney, R. E., Janik, J. J., & DeYoe, E. A. (2005). Distinct cortical pathways for processing tool versus animal sounds. *Journal of Neuroscience, 25*(21), 5148–5158.

Li, Y., Fang, Y., Wang, X., Song, L., Huang, R., Han, Z., … Bi, Y. (2018). Connectivity of the ventral visual cortex is necessary for object recognition in patients. *Human Brain Mapping, 39*(7), 2786–2799.

Mahon, B. Z., Anzellotti, S., Schwarzbach, J., Zampini, M., & Caramazza, A. (2009). Category-specific organization in the human brain does not require visual experience. *Neuron, 63*(3), 397–405.

Mahon, B. Z., & Caramazza, A. (2009). Concepts and categories: A cognitive neuropsychological perspective. *Annual Review of Psychology, 60*, 27–51.

Mahon, B. Z., & Caramazza, A. (2011). What drives the organization of object knowledge in the brain? *Trends in Cognitive Sciences, 15*(3), 97–103.

Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology, 58*, 25–45.

Martin, A. (2016). GRAPES—Grounding representations in action, perception, and emotion systems: How object properties and categories are represented in the human brain. *Psychonomic Bulletin and Review, 23*(4), 979–990.

Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature, 379*(6566), 649–652.

Nasr, S., Echavarria, C. E., & Tootell, R. B. H. (2014). Thinking outside the box: Rectilinear shapes selectively activate scene-selective cortex. *Journal of Neuroscience, 34*(20), 6721–6735.

Noppeney, U., Price, C. J., Penny, W. D., & Friston, K. J. (2006). Two distinct neural mechanisms for category-selective responses. *Cerebral Cortex, 16*(3), 437–445.

Passingham, R. E., Stephan, K. E., & Kötter, R. (2002). The anatomical basis of functional localization in the cortex. *Nature Reviews. Neuroscience, 3*, 606–616.

Peelen, M. V., Bracci, S., Lu, X., He, C., Caramazza, A., & Bi, Y. (2013). Tool selectivity in left occipitotemporal cortex develops without vision. *Journal of Cognitive Neuroscience, 25*(8), 1225–1234.

Peelen, M. V., & Downing, P. E. (2017). Category selectivity in human visual cortex: Beyond visual object recognition. *Neuropsychologia, 105*, 177–183.

Proklova, D., Kaiser, D., & Peelen, M. V. (2016). Disentangling representations of object shape and object category in human visual cortex: The animate-inanimate distinction. *Journal of Cognitive Neuroscience, 28*(5), 680–692.

Ricciardi, E., Bonino, D., Pellegrini, S., & Pietrini, P. (2013). Mind the blind brain to understand the sighted one! Is there a supramodal cortical functional architecture? *Neuroscience and Biobehavioral Reviews, 41*, 64–77.

Saygin, Z. M., Osher, D. E., Koldewyn, K., Reynolds, G., Gabrieli, J. D. E., & Saxe, R. R. (2012). Anatomical connectivity patterns predict face selectivity in the fusiform gyrus. *Nature Neuroscience, 15*(2), 321–327.

Smith, S. M. (2012). The future of fMRI connectivity. *NeuroImage, 62*, 1257–1266.

Srihasam, K., Vincent, J. L., & Livingstone, M. S. (2014). Novel domain formation reveals proto-architecture in inferotemporal cortex. *Nature Neuroscience, 17*(12), 1776–1783.

Striem-Amit, E., Vannuscorps, G., & Caramazza, A. (2017). Sensorimotor-independent development of hands and tools selectivity in the visual cortex. *Proceedings of the National Academy of Sciences, 114*(18), 4787–4792.

Tang, S., Lee, T. S., Li, M., Zhang, Y., Xu, Y., Liu, F., … Jiang, H. (2018). Complex pattern selectivity in macaque primary visual cortex revealed by large-scale two-photon imaging. *Current Biology, 28*(1), 38–48.

Tranel, D., Grabowski, T. J., Lyon, J., & Damasio, H. (2005). Naming the same entities from visual or from auditory stimulation engages similar regions of left inferotemporal cortices. *Journal of Cognitive Neuroscience, 17*, 1293–1305.

Wang, X., He, C., Peelen, M. V, Zhong, S., Gong, G., Caramazza, A., & Bi, Y. (2017). Domain selectivity in the parahippocampal gyrus is predicted by the same structural connectivity patterns in blind and sighted individuals. *Journal of Neuroscience, 37*(18), 4705–4716.

Wang, X., Peelen, M. V., Han, Z., He, C., Caramazza, A., & Bi, Y. (2015). How visual is the visual cortex? Comparing connectional and functional fingerprints between congenitally blind and sighted individuals. *Journal of Neuroscience, 35*(36), 12545–12559.

Warrington, E. K., & McCarthy, R. A. (1987). Categories of knowledge. *Brain, 110*(5), 1273–1296.

Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain, 107*(3), 829–853.

Weisberg, J., van Turrennout, M., & Martin, A. (2007). A neural system for learning about object function. *Cerebral Cortex, 17*(3), 513–521.

Wolbers, T., Klatzky, R. L., Loomis, J. M., Wutte, M. G., & Giudice, N. A. (2011). Modality-independent coding of spatial layout in the human brain. *Current Biology, 21*, 984–989.