



What drives the organization of object knowledge in the brain?

Citation

Mahon, Bradford Z., and Alfonso Caramazza. 2011. "What Drives the Organization of Object Knowledge in the Brain?" *Trends in Cognitive Sciences* 15 (3): 97–103.
<https://doi.org/10.1016/j.tics.2011.01.004>.

Published version

<https://doi.org/10.1016/j.tics.2011.01.004>

Link

<http://nrs.harvard.edu/urn-3:HUL.InstRepos:41384856>

Terms of use

This article was downloaded from Harvard University's DASH repository, and is made available under the terms and conditions applicable to Open Access Policy Articles (OAP), as set forth at

<https://harvardwiki.atlassian.net/wiki/external/NGY5NDE4ZjgzNTc5NDQzMGIzZWZhMGFIOWI2M2EwYTg>

Accessibility

<https://accessibility.huit.harvard.edu/digital-accessibility-policy>

Share Your Story

The Harvard community has made this article openly available.
Please share how this access benefits you. [Submit a story](#)

Published in final edited form as:

Trends Cogn Sci. 2011 March ; 15(3): 97–103. doi:10.1016/j.tics.2011.01.004.

What drives the organization of object knowledge in the brain?

The distributed domain-specific hypothesis

Bradford Z. Mahon^{1,2} and Alfonso Caramazza^{3,4}

¹ Department of Brain and Cognitive Sciences, Meliora Hall, University of Rochester, Rochester, NY, USA 14627

² Department of Neurosurgery, 601 Elmwood Ave, University of Rochester Medical Center, Rochester, NY, USA, 14642

³ Department of Psychology, William James Hall, 33 Kirkland Street, Harvard University, Cambridge, MA 02138

⁴ Center for Mind/Brain Sciences, University of Trento, Palazzo Fedrigotti, Corso Bettini 31, I-38068 Rovereto (TN), Italy

Abstract

Various forms of category-specificity have been described at both the cognitive and neural levels, inviting the inference that different semantic domains are processed by distinct, dedicated mechanisms. Here we argue for an extension of a Domain-Specific interpretation to these phenomena that is based on network-level analyses of functional coupling among brain regions. On this view, domain-specificity in one region of the brain emerges because of innate connectivity with a network of regions that also process information about that domain. Recent findings are reviewed that converge with this framework, and a new direction is outlined for understanding the neural principles that shape the organization of conceptual knowledge.

Category-specificity as a means to study constraints on brain organization

Brain damaged patients with category-specific semantic impairments have conceptual level impairments that are specific to a category of items, such as animals, fruit/vegetables, nonliving things or conspecifics. Detailed analysis of those patients (see Box 1) suggests that conceptual knowledge is organized according to domain-specific constraints^{1, 2}. According to the Domain-Specific Hypothesis², there are innately dedicated neural circuits for the efficient processing of a limited number of evolutionarily motivated domains of knowledge. This interpretation of the neuropsychological phenomenon of category-specific semantic deficits has been extended to interpret results from functional Magnetic Resonance Imaging (fMRI) in healthy subjects^{3, 4}. Much of the research using fMRI to study category-specificity has focused on the pattern of responses in the ventral visual pathway, which projects from early visual areas to lateral and ventral temporal-occipital regions, and processes object shape, texture, and color in ways that are relatively invariant to viewpoint, size, and orientation^{5–7}. Different regions within the ventral pathway preferentially respond

Address for Correspondence: Bradford Z. Mahon, mahon@rcbi.rochester.edu, Alfonso Caramazza, caram@wjh.harvard.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

to images of faces, animals, tools, places, written words, and body parts^{4, 6, 8–13}; see also, 13–15.

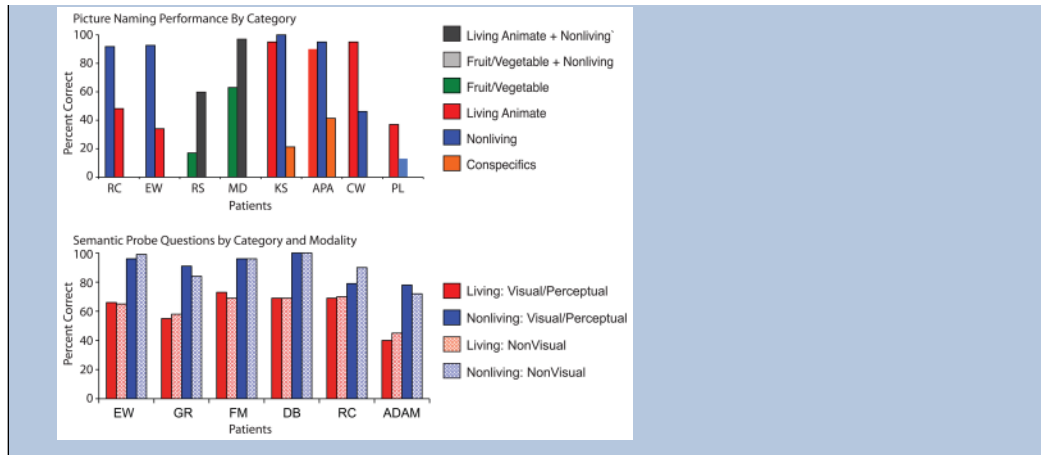
Box 1

Cognitive Neuropsychological Evidence for Domain-Specific Constraints

Patients with category-specific semantic deficits may be differentially, or even selectively impaired for knowledge of animals, plants, conspecifics, or artifacts (for review see¹¹). The knowledge impairment cannot be explained in terms of a differential impairment to a sensory or motor-based modality of information. While discussion and debate continues as to whether non-categorical dimensions of organization may lead to category-specific brain organization, there is consensus that the phenomenon itself is ‘categorical’.

There are important parallels between the neuropsychological literature on category-specific semantic deficits and the findings from functional neuroimaging and neurophysiology. First, the categories that emerge from the neuropsychological literature map onto the categories that emerge in functional imaging and neurophysiology. This indicates that the different methods and populations are tracking the same underlying property of brain organization. Second, the resistance of category-specific deficits to be explained by dimensions of organization that do not include semantic category² parallels the same pattern that has emerged in imaging and neurophysiology⁶⁰. It is clearly the case that the brain is organized by sensory and motor modalities, and it is also the case that different sensory and motor modalities participate to varying extents in the representation of items from different categories. However, the existence of category-specificity in imaging⁴, neurophysiology⁶⁷, and neuropsychology¹¹ cannot be explained exclusively by appeal to modality-based principles of organization. This suggests that the dimensions of brain organization that express themselves as phenomena of category-specificity (across methods and populations) are in fact domain-specific constraints on brain organization. Finally, there is emerging neuropsychological evidence for endogenous constraints on brain organization, including the existence of category-specific semantic deficits tested at age 16 after stroke at one day of age⁶⁸.

There are also parallels between the patterns of category-specific semantic deficits, and psychophysical studies of putatively specialized routes for processing specific classes of visual stimuli. For instance, New and colleagues⁶⁹, using a change detection paradigm demonstrated a significant advantage for living animate stimuli. Thorpe and colleagues⁷⁰ have demonstrate extremely rapid and accurate detection of face and animal stimuli. Almeida and colleagues⁶⁵ have shown that conceptual information about manipulable objects can be extracted from stimuli that are putatively not processed by the ventral visual pathway. These and other findings may indicate experimental ways of isolating domain-specific networks.



The existence of consistent topographic biases by semantic category in the ventral stream raises fundamental questions about the principles that determine brain organization^{4, 10–12, 16, 17}. To date, the emphasis of research on the organization of the ventral stream has been on the stimulus properties that drive responses in a particular brain region, studied in relative isolation from other regions. This approach was inherited from well-established traditions in neurophysiology and psychophysics where it has been enormously productive for mapping psychophysical continua in primary sensory systems. It does not follow that the same approach will yield equally useful insights for understanding the principles of the neural organization of conceptual knowledge. The reason is that unlike the peripheral sensory systems, the pattern of neural responses in higher order areas is only partially driven by the physical input – it is also driven by how the stimulus is interpreted, and that interpretation does not occur in a single, isolated region. The ventral object processing stream is the central pathway for the extraction of object identity from visual information in the primate brain – but what the brain does with that information about object identity depends on how the ventral stream is connected to the rest of the brain.

Here, we focus on visual object recognition, as this has been the aspect of object knowledge and processing that has been studied in greatest depth; however, similar principles would be expected to apply to other modalities as appropriate. We argue that there are innately determined patterns of connectivity that mediate the integration of information from the ventral stream with information computed by other brain regions. Those channels are at the grain of a limited number of evolutionarily relevant domains of knowledge. We further suggest that what is given innately is the connectivity, and that specialization by semantic category in the ventral stream is driven by that connectivity. The implication of this proposal is that the organization of the ventral stream by category is relatively invariant to visually based, bottom up, constraints. This approach corrects an imbalance in explanations of the causes of the consistent topography by semantic category in the ventral object-processing stream by giving greater prominence to endogenously determined constraints on brain organization.

The Distributed Domain-Specific Hypothesis

A domain-specific neural system is a network of brain regions¹¹ in which each region processes a different type of information about the same domain or category of objects^{2, 18}. The types of information processed by different parts of a network may be sensory, motor, affective or conceptual. The range of potential domains or classes of items that may have dedicated neural circuits is restricted to those with an evolutionarily relevant history that could have biased the system toward a coherent organization. A second important

characteristic of domain-specific systems is that the computations that must be performed over items from the domain are sufficiently ‘eccentric’¹⁹, so as to merit a specialized process. In other words, the coupling across different brain regions that is necessary for successful processing of a given domain is different in kind from the types of coupling that are needed for other domains of knowledge.

For instance, the need to integrate motor-relevant information with visual information is present for tools and other graspable objects and less so for animals or faces. In contrast, the need to integrate affective information, biological motion processing, and visual form information is strong for conspecifics and animals, and less so for tools or places. Thus, our proposal is that domain-specific constraints are expressed as patterns of connectivity among regions of the ventral stream and other areas of the brain that process nonvisual information about the same classes of items. For instance, specialization for faces in the lateral fusiform gyrus (fusiform face area^{20–22}) arises because that region of the brain has connectivity with the amygdala and the superior temporal sulcus (among other regions) which are important for the extraction of socially relevant information and biological motion. Specificity for tools and manipulable objects in the medial fusiform gyrus is driven, in part, by connectivity between that region and regions of parietal cortex that subserve object manipulation^{23–26}. Connectivity-based constraints may also be responsible for other effects of category-specificity in the ventral visual stream, such as connectivity between somatomotor areas and regions of the ventral stream that differentially respond to body parts^{27–29} (extrastriate body area), connectivity between left lateralized frontal language processing regions and ventral stream areas specialized for printed words (visual word form area^{30, 31}), and connectivity between regions involved in spatial analysis and ventral stream regions showing differential responses to highly contextualized stimuli, such as houses, scenes, and large nonmanipulable objects (parahippocampal place area³²).

The Role of Visual Experience

According to the Distributed Domain-Specific Hypothesis, the organization by category in the ventral stream is not only a reflection of the visual structure of the world; it also reflects the structure of how ventral visual cortex is connected to other regions of the brain^{11, 23, 33}. However, visual experience and dimensions of visual similarity are also critical in shaping the organization of the ventral stream (e.g.,^{34, 35}) — after all, the principal afferents to the ventral stream come from earlier stages in the visual hierarchy³⁶.

While recent discussion has discussed non-visual dimensions that may be relevant in shaping the organization of the ventral stream^{4, 6, 7}, many accounts differentially weight the contribution of visual experience in their explanation of the causes of category-specific organization within the ventral stream. A number of hypotheses have been developed, and we merely touch on them here to illustrate a common assumption: that the organization of the ventral stream reflects the visual structure of the world, as interpreted by domain-general processing constraints. Thus, the general thrust of those accounts is that the visual structure of the world is correlated with semantic category distinctions in a way that is captured by how visual information is organized in the brain. One of the most explicit proposals is that there are weak eccentricity preferences in higher order visual areas that are inherited from earlier stages in the processing stream. Those eccentricity biases interact with our experience of foveating some classes of items (e.g., faces) and viewing others in the relative periphery (e.g., houses)³⁷. Another class of proposals is based on the supposition that items from the same category tend to look more similar than items from different categories, and similarity in visual shape is mapped onto ventral temporal occipital cortex¹⁷. It has also been proposed that a given category may require differential processing relative to other categories, for instance in terms of expertise³⁸, visual crowding³⁹, or the relevance of visual information for categorization⁴⁰. Still other accounts appeal to ‘feature’ similarity and distributed feature

maps⁴¹. Finally, it has been suggested that multiple, visually-based, dimensions of organization combine superadditively to generate the boundaries among category-preferring regions¹². Common to all of these accounts is the assumption that visual experience provides the necessary structure, and that a visual dimension of organization *happens to be* highly correlated with semantic category.

While visual information is important in shaping how the ventral stream is organized, recent findings indicate that visual experience is not necessary in order for the same, or similar, patterns of category-specificity to be present in the ventral stream. In an early PET study, Büchel and colleagues⁴² showed that congenitally blind subjects show activation for words (presented in Braille) in the same region of the ventral stream as sighted individuals (presented visually). Pietrini and colleagues⁴³ used multi-voxel pattern analyses to show that the pattern of activation over voxels in the ventral stream was more consistent across different exemplars within a category, than exemplars across categories. More recently, we⁴⁴ have shown that the same medial-to-lateral bias in category preferences on the ventral surface of occipital temporal cortex that is present in sighted individuals, is present in congenitally blind subjects. Specifically, nonliving things, compared to animals elicit stronger activation in medial regions of the ventral stream (see Figure 1).

Although these studies on category-specificity in blind individuals represent only a first pass analysis of the role of visual experience in driving category-specificity in the ventral stream, they indicate that visual experience is not necessary in order for category-specificity to emerge in the ventral stream. This fact raises an important question – if visual experience is not needed for the same topographical biases in category specificity to be present in the ventral stream, then, what drives such organization? One possibility, as we have suggested, is innate connectivity between regions of the ventral stream and other regions of the brain that process affective, motor, and conceptual information.

Connectivity as an innate domain-specific constraint

A critical component of the distributed domain-specific hypothesis is the notion of connectivity. The most obvious candidate to mediate such networks is white matter connectivity. However, it is important to underline that functional networks need not be restricted by the grain of white matter connectivity, and perhaps more importantly, task- and state-dependent changes may bias processing toward different components of a broader anatomical brain network. For instance, connectivity between lateral and orbital prefrontal regions and ventral temporal-occipital cortex^{45, 46} is critical for categorization of visual input. It remains an open question whether multiple functional networks are subserved by this circuit, each determined by the type of visual stimulus being categorized. For instance, when categorizing manipulable objects, connectivity between parieto-frontal somatomotor areas and prefrontal cortex may dominate, while when categorizing faces other regions may express stronger functional coupling to those same prefrontal regions. Such a suggestion would generate the expectation that while damaging prefrontal-to-ventral stream connections may result in difficulties categorizing all types of visual stimuli, disruption of the afferents to prefrontal cortex from a specific category-preferring area could lead to categorization problems selective to that domain. The neural basis of the connectivity that supports domain-specific neural systems is, admittedly, in need of further development and articulation. Below, we will return to expectations that may be drawn from this account.

Evidence for Innate Constraints

By ‘innate constraints’ on brain organization is meant those aspects of brain organization that are initiated and constrained in their development and outcome by genetics. The signature of innate structure is similarity across individuals, both within a species and

potentially, across species. 'Innate' does not imply 'present-from-birth,' although present-from-birth strongly suggests an innate contribution. Maturation in the context of the right types of experience may be necessary for the expression of innate structure, and interactions between innate and experiential factors can jointly constrain outcome⁴⁷. This is particularly the case for mental processes, as there would be nothing to process without the content provided by experience. Several threads of evidence show that genetic variables capture similarity in functional brain organization as it relates to the presence of domain-specific neural circuits.

Twin Studies

Two recent reports highlight greater neural or functional similarity between monozygotic twin pairs than between dizygotic twin pairs (for discussion see ^{48, 49}). The strength of these studies is that experiential contributions are held constant across the two types of twin pairs. In a fMRI study, Polk and colleagues⁵⁰ studied the similarity between twin pairs in the distribution of responses to faces, houses, pseudowords, and chairs in the ventral stream. The authors found that face and place-related responses within face and place selective regions, respectively, were significantly more similar for monozygotic than for dizygotic twins. In the second study, Wilmer and colleagues⁵¹ studied the face recognition and memory abilities⁵² in monozygotic and dizygotic twin pairs. The authors found that the correlation in performance on the face recognition task for monozygotic twins was more than double that for dizygotic twins. This difference was not present for control tasks of verbal and visual memory, indicating selectivity in the genetic contribution to behavioral abilities (see also ref⁵³).

Congenital Prosopagnosia

Further evidence for a genetic contribution to face recognition abilities comes from congenital prosopagnosia, a developmental disorder in which individuals may have selective impairments for recognizing faces⁵⁴. A recent study by Thomas and colleagues⁵⁵ found that congenital prosopagnosia was associated with reduced structural integrity of the inferior longitudinal fasciculus, which projects from the fusiform gyrus to anterior regions of the temporal lobe. Reduced structural integrity was also observed for the inferior fronto-occipital fasciculus which projects from ventral temporal-occipital cortex to frontal regions. Such observations of reduced integrity of major white matter tracts linking posterior temporal-occipital cortex with other brain regions underlines the strength of a network-level analysis in understanding the constraints that shape the organization of knowledge in the ventral stream.

Nonhuman Primates

An expectation on the view that innate constraints shape category-specificity in the ventral stream is that such specificity, at least for some categories, may also be found in nonhuman primates. It is well known, using neurophysiological recordings that preferences for natural object stimuli exist in monkey inferior temporal cortex^{35, 56}, comparable to observations with similar methods in awake human subjects¹⁵. More recently, functional imaging with macaques⁵⁷ and chimpanzees⁵⁸ suggests that at least for the category of faces, comparable clusters of face preferring voxels can be found in temporal cortex in monkeys as are observed in humans.

Such common patterns of neural organization for some classes of items in monkeys and humans could, of course, be entirely driven by dimensions of visual similarity, which are known to modulate responses in IT cortex⁵⁹. However, even when serious attempts have been made to reduce such responses to dimensions of visual similarity, taxonomic structure emerges over and above the contribution of known visual dimensions. For instance,

Kriegeskorte and colleagues⁶⁰ used multi-voxel pattern analysis to compare the similarity structure of a large array of different body, face, animal, plant, and artifact stimuli in monkey IT cortex and human temporal-occipital cortex. The similarity among the stimuli was measured in terms of the similarity of the patterns of brain responses they elicited, separately on the basis of the neurophysiological data (monkeys)⁵⁶ and fMRI data (humans). The similarity structure that emerged revealed a tight taxonomic structure common to monkeys and humans, and which could not be reduced to known dimensions of visual similarity.

Next Steps

Specialization of function in the brain is clearest at the level of primary sensory and motor areas that have a physical organization in the brain that projects topographically onto a psychophysical continuum, such as retinotopy, tonotopy, or somatotopy. At the other end of the continuum, there are aspects of human cognition that have eluded neat parcellation in the brain, such as the neural instantiation of the abstract and recursive systems that make human thought and metacognition possible. Somewhere in the middle live conceptual representations – they interface with and draw on the sensory and motor systems and at the same time require the flexibility characteristic of symbolic representations⁶¹. We have outlined a framework for understanding the causes of category-specific organization in the brain that is based on the idea that there are innate patterns of connectivity that constrain the distribution of category-specific neural regions. This proposal fully embraces a hierarchical view of the organization of conceptual knowledge³: the organization of the ventral stream reflects the final product of a complex tradeoff of pressures, some of which are expressed locally within the ventral stream and some of which are expressed as connectivity to the rest of the brain. Our suggestion is that connectivity to the rest of the brain is the first, or broadest, principle according to which the ventral stream comes to be organized by semantic category.

While there is striking overlap in the semantic categories that may dissociate under conditions of brain damage and which show consistent topographic organization in the ventral stream (see Box 1), there is a large disconnect between the lesion locations in patients with category-specific deficits and the patterns of neural activation observed with fMRI. In particular, category-specific semantic deficits are not typically associated with focal lesions to category-preferring regions within the ventral stream. This suggests that what is damaged in patients with category-specific semantic deficits are the broader neural circuits that are specialized for the impaired domain of knowledge. Damage to multiple regions within that domain-specific neural circuit could lead to a category-specific deficit by disrupting or disorganizing the broader network. Furthermore, damage to regions that serve to integrate processing across the whole domain, such as the anterior temporal lobes^{62, 63} for the domains of animals and conspecifics, may particularly disrupt functioning throughout the broader network.

A second direction for research that is encouraged by the Distributed Domain-Specific Hypothesis is to characterize the patterns of both anatomical and functional connectivity within domain-specific neural circuits. The expectation is that there will be a tight coupling between patterns of connectivity and the locations of category-preferring regions. In this regard it is important to note that regions expressing connectivity with category-specific regions within the ventral stream are not necessarily ‘downstream’ from visual object recognition, and do not necessarily represent ‘more developed’ or ‘more processed’ information than what is computed in the ventral stream. Stimuli are processed through multiple routes in parallel, such as subcortical processing of emotional face stimuli^{20, 21} and dorsal stream processing of manipulable objects^{64, 65}. Thus, one exciting possibility is that

fast but coarse analysis of the visual input that bypasses the geniculate striate pathway may ‘cue’ or ‘bias’ processing within the ventral stream according to the content of the stimulus to be processed⁴⁵, analogous to attentional modulation of early visual responses.

A third way in which the Distributed Domain-Specific Hypothesis may be tested is to explore the connectivity of all of the categories that show selective responses in the ventral stream. For instance, an expectation that may be generated is that stimuli from different domains, such as hands and tools may live next to each other in the ventral stream because both would be predicted to have connectivity to somatomotor cortex. In other words, the way in which representations are organized in the ventral stream should follow patterns of connectivity, such that they are organized according to similarity metrics represented in other parts of the brain, rather than (only) by dimensions of visual similarity.

Perhaps the most pressing issue that must be addressed by the Distributed Domain-Specific Hypothesis is whether connectivity drives specialization by category, as we have proposed, or whether specialization of function is present independently of connectivity, and the connectivity emerges later. One way to empirically address this is to test individuals who are blind since birth. Sensory deprivation will remove the influence of local constraints, presumably expressed over short-range bottom up connections from earlier visual regions, but would not be expected to fundamentally alter the ‘longer range’ connections. Combining detailed analysis of connectivity in such individuals with analysis of the location of category-preferring regions in the ventral stream may ground inferences about whether connectivity in fact drives the location of category-preferences in the ventral stream. In particular, the regions specialized for printed words may offer a means to test this issue, as there is no motivation for presuming specialization of function to be innately present for printed words in the human brain. Yet, because there are regions that are consistently specialized for printed words, the expectation would be that this specialization is driven by connectivity between the ventral stream and regions of the brain involved in linguistic processing. The prediction can be made that subject-by-subject variation in the location of the visual word form area (tested with Braille) in congenitally blind individuals will match up with subject-by-subject variation in connectivity between that region of the ventral stream and other language processing regions of the brain.

The core of our proposal, that specialization in a region of the brain is driven, in part, by constraints on how that information will ultimately be used in the service of behavior, is not new. It is well established that visual processing bifurcates into a dorsal stream for object directed action and spatial processing and a ventral stream for the extraction of object identity⁶⁶. The two visual system model places important restrictions on plasticity of function within the visual system. Analogously, the Distributed Domain-Specific Hypothesis places new limits on plasticity of function within the ventral object processing stream, and suggests that the key to describing those limits lies in the patterns of connectivity between the ventral stream and other category-specific brain regions.

References

1. Capitani E, Laiacona M, Mahon BZ, Caramazza A. What are the facts of category-specific deficits? A critical review of the clinical evidence. *Cognitive Neuropsychology* 2003;20:213–261. [PubMed: 20957571]
2. Caramazza A, Shelton JR. Domain specific knowledge systems in the brain: The animate-inanimate distinction. *Journal of Cognitive Neuroscience* 1998;10:1–34. [PubMed: 9526080]
3. Caramazza A, Mahon BZ. The organization of conceptual knowledge: The evidence from category-specific semantic deficits. *Trends in Cognitive Sciences* 2003;7:354. [PubMed: 12907231]

4. Martin A. The Representation of Object Concepts in the Brain. *Annual Review of Psychology* 2007;58
5. Miceli G, et al. The dissociation of color from form and function knowledge. *Nature Neuroscience* 2001;4:662–667.
6. Grill-Spector K, Malach R. The human visual cortex. *Annual Review of Neuroscience* 2004;27:649–677.
7. Cant JS, et al. fMR-adaptation reveals separate processing regions for the perception of form and texture in the human ventral stream. *Exp Brain Res* 2009;192:391–405. [PubMed: 18815774]
8. Allison T, et al. Human extrastriate visual cortex and the perception of faces, words, numbers, and colors. *Cereb Cortex* 1994;4:544–554. [PubMed: 7833655]
9. Chao LL, et al. Attribute-based neural substrates in posterior temporal cortex for perceiving and knowing about objects. *Nature Neuroscience* 1999;2:913–919.
10. Kanwisher N. Domain specificity in face perception. *Nature* 2000;3:759–763.
11. Mahon BZ, Caramazza A. Concepts and Categories: A Cognitive Neuropsychological Perspective. *Annual Review of Psychology* 2009;60:1–15.
12. Op de Beeck HP, et al. Interpreting fMRI data: maps, modules and dimensions. *Nat Rev Neurosci* 2008;9:123–135. [PubMed: 18200027]
13. Pitcher D, et al. Triple dissociation of faces, bodies, and objects in extrastriate cortex. *Curr Biol* 2009;19:319–324. [PubMed: 19200723]
14. Bentin S, et al. Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience* 1996;8:551–565. [PubMed: 20740065]
15. Kreiman G, et al. Category-specific visual responses of single neurons in the human medial temporal lobe. *Nat Neurosci* 2000;3:946–953. [PubMed: 10966627]
16. Cantlon JF, et al. Cortical representations of symbols, objects, and faces are pruned back during early childhood. *Cerebral Cortex*. In Press.
17. Haxby JV, et al. Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 2001;293:2425–2430. [PubMed: 11577229]
18. Carey, SSE. Domain specific knowledge and conceptual change. In: Hirschfeld, LSG., editor. *Mapping the Mind: Domain Specificity in Cognition and Culture*. Cambridge Univ. Press; 1994. p. 169-200.
19. Fodor, J. *Modularity of Mind*. MIT; 1983.
20. Pasley BN, et al. Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron* 2004;42:163–172. [PubMed: 15066273]
21. Vuilleumier P, et al. Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience* 2004;7:1271–1278.
22. Martin A, Weisberg J. Neural foundations for understanding social and mechanical concepts. *Cognitive Neuropsychology* 2003;20:575–587. [PubMed: 16648880]
23. Mahon BZ, et al. Action-related properties shape object representations in the ventral stream. *Neuron* 2007;55:507–520. [PubMed: 17678861]
24. Valyear KF, Culham JC. Observing Learned Object-specific Functional Grasps Preferentially Activates the Ventral Stream. *J Cogn Neurosci*. 2009
25. Noppeney U, et al. Two distinct neural mechanisms for category-selective responses. *Cerebral Cortex* 2006;16:437–445. [PubMed: 15944370]
26. Rushworth MFS, et al. Connection patterns distinguish 3 regions of human parietal cortex. *Cerebral Cortex* 2006;16:1418–1430. [PubMed: 16306320]
27. Astafiev SV, et al. Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature Neuroscience* 2004;7:542–548.
28. Orlov T, et al. Topographic Representation of the Human Body in the Occipitotemporal Cortex. *Neuron* 2010;68:586–600. [PubMed: 21040856]
29. Peelen MV, Caramazza A. What Body Parts Reveal about the Organization of the Brain. *Neuron* 2010;68:331–333. [PubMed: 21040838]
30. Dehaene S, et al. The neural code for written words: a proposal. *Trends in Cognitive Sciences* 2005;9:335–341. [PubMed: 15951224]

31. Martin A. Shades of Déjerine - Forging a Causal Link between the Visual Word Form Area and Reading. *Neuron* 2006;50:173–190. [PubMed: 16630825]
32. Bar M, Aminoff E. Cortical analysis of visual context. *Neuron* 2003;38:347–358. [PubMed: 12718867]
33. Riesenhuber M. Appearance isn't everything: News on object representation in cortex. *Neuron* 2007;55:341–344. [PubMed: 17678848]
34. Op de Beeck HP, et al. Discrimination training alters object representations in human extrastriate cortex. *J Neurosci* 2006;26:13025–13036. [PubMed: 17167092]
35. Tanaka K, et al. Coding visual images of objects in the inferotemporal cortex of the macaque monkey. *Journal of Neurophysiology* 1991;66:170–189. [PubMed: 1919665]
36. Felleman DJ, Van Essen DC. Distributed hierarchical processing in primate visual cortex. *Cerebral Cortex* 1991;1:1–47. [PubMed: 1822724]
37. Levy I, et al. Center-periphery organization of human object areas. *Nature Neuroscience* 2001;4:533–539.
38. Gauthier I, et al. Activation of the middle fusiform 'face area' increases with expertise in recognizing novel objects. *Nat Neurosci* 1999;2:568–573. [PubMed: 10448223]
39. Rogers TT, et al. Fusiform activation to animals is driven by the process, not the stimulus. *Journal of Cognitive Neuroscience* 2005;17:434–445. [PubMed: 15814003]
40. Mechelli A, et al. Semantic Relevance explains category effects in medial fusiform gyri. *NeuroImage* 2006;3:992–1002. [PubMed: 16343950]
41. Tyler LK, et al. Do semantic categories activate distinct cortical regions? Evidence for a distributed neural semantic system. *Cognitive Neuropsychology* 2003;20:541–559. [PubMed: 20957584]
42. Buchel C, et al. A multimodal language region in the ventral visual pathway. *Nature* 1998;394:274–277. [PubMed: 9685156]
43. Pietrini P, et al. Beyond sensory images: Object-based representation in the human ventral pathway. *Proc Natl Acad Sci U S A* 2004;101:5658–5663. [PubMed: 15064396]
44. Mahon BZ, et al. Category-Specific Organization in the Human Brain Does Not Require Visual Experience. 2009;63:397–405.
45. Kveraga K, et al. Magnocellular projections as the trigger of top-down facilitation in recognition. *Journal of Neuroscience* 2007;27:13232–13240. [PubMed: 18045917]
46. Miller EK, et al. Neural correlates of categories and concepts. *Current Opinion in Neurobiology* 2003;13:198–203. [PubMed: 12744974]
47. Lewontin, R. *The Triple Helix: Genes, Organisms, and Environment*. Harvard University Press; 2000.
48. Park J, et al. Face Processing: The Interplay of Nature and Nurture. *Neuroscientist* 2009;15:445–449. [PubMed: 19535815]
49. Zhu Q, et al. Heritability of the Specific Cognitive Ability of Face Perception. *Current Biology* 20:137–142.
50. Polk TA, et al. Nature versus nurture in ventral visual cortex: a functional magnetic resonance imaging study of twins. *J Neurosci* 2007;27:13921–13925. [PubMed: 18094229]
51. Wilmer J, et al. Human face recognition ability is specific and highly heritable. *Proceedings of the National Academy of Sciences* 2010;107:5238–5241.
52. Duchaine B, Nakayama K. The Cambridge Face Memory Test: Results for neurologically intact individuals and an investigation of its validity using inverted face stimuli and prosopagnosic subjects. *Neuropsychologia* 2006;44:576–585. [PubMed: 16169565]
53. Zhu Q, et al. Heritability of the Specific Cognitive Ability of Face Perception. *Current Biology* 2010;20:1–6. [PubMed: 20036540]
54. Duchaine BC, YG, Butterworth EJ, Nakayama K. Prosopagnosia as an impairment to face specific mechanisms: elimination of the alternative hypotheses in a developmental case. *Cognitive Neuropsychology* 2006;23:714–747. [PubMed: 21049351]
55. Thomas C, et al. Reduced structural connectivity in ventral visual cortex in congenital prosopagnosia. *Nat Neurosci* 2009;12:29–31. [PubMed: 19029889]

56. Kiani R, et al. Object category structure in response patterns of neuronal population in monkey inferior temporal cortex. *J Neurophysiol* 2007;97:4296–4309. [PubMed: 17428910]
57. Tsao DY, et al. A cortical region consisting entirely of face-selective cells. *Science* 2006;311:670–674. [PubMed: 16456083]
58. Parr LA, et al. Face Processing in the Chimpanzee Brain. *Current Biology* 2009;19:50–53. [PubMed: 19097899]
59. Op de Beeck H, Wagemans J, Vogels R. Inferotemporal neurons represent low-dimensional configurations of parameterized shapes. *Nature Neuroscience* 2001;4:1244–1252.
60. Kriegeskorte N, et al. Matching categorical object representations in inferior temporal cortex of man and monkey. *Neuron* 2008;60:1126–1141. [PubMed: 19109916]
61. Mahon BZ, Caramazza A. A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *J Physiol Paris* 2008;102:59–70. [PubMed: 18448316]
62. Damasio H, et al. Neural systems behind word and concept retrieval. *Cognition* 2004;92:179–229. [PubMed: 15037130]
63. Patterson K, et al. Where do you know what you know? The representation of semantic knowledge in the human brain? *Nature Reviews* 2007;8:976–987.
64. Fang F, He S. Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nature Neuroscience* 2005;8:1380–1385.
65. Almeida J, et al. Unconscious processing dissociates along categorical lines. *Proc Natl Acad Sci U S A* 2008;105:15214–15218. [PubMed: 18809923]
66. Goodale MA, Milner AD. Separate visual pathways for perception and action. *Trends in Neurosciences* 1992;15:20–25. [PubMed: 1374953]
67. Kriegeskorte N, et al. Matching categorical object representations in inferior temporal cortex of man and monkey. *Neuron* 2008;60:1126–1141. [PubMed: 19109916]
68. Farah MJ, Rabinowitz C. Genetic and environmental influences on the organization of semantic memory in the brain: Is “living things” an innate category? *Cognitive. Neuropsychology* 2003;20:401–408. [PubMed: 20957577]
69. New J, et al. Category-specific attention for animals reflects ancestral priorities, not expertise. *Proc Natl Acad Sci U S A* 2007;104:16598–16603. [PubMed: 17909181]
70. Thorpe S, et al. Speed of processing in the human visual system. *Nature* 1996;381:520–522. [PubMed: 8632824]

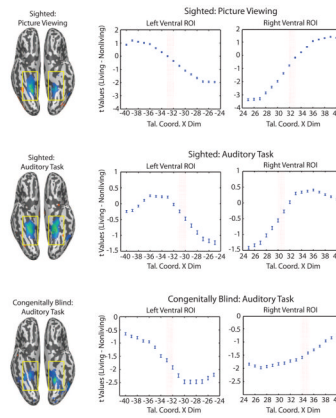


Figure 1. Congenitally blind and sighted participants were presented with auditorily spoken words of living things (animals) and nonliving things (tools, nonmanipulable objects) and were asked to make size judgments about the referents of the words. The sighted participants were also shown pictures corresponding to the same stimuli in a separate scan. For sighted participants viewing pictures, the known finding was replicated that nonliving things such as tools and large nonmanipulable objects lead to differential neural responses in medial aspects of ventral temporal-occipital cortex. This pattern of differential BOLD responses for nonliving things in medial aspects of ventral temporal-occipital cortex was also observed in congenitally blind participants and sighted participants performing the size judgment task over auditory stimuli. These data indicate that the medial-to-lateral bias in the distribution of category-specific responses does not depend on visual experience. For details of the study, see ref⁴⁴.