Neural Representations for Object Perception: Structure, Category, and Adaptive Coding

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Abstract

Object perception is one of the most remarkable capacities of the primate brain. Owing to the large and indeterminate dimensionality of object space, the neural basis of object perception has been difficult to study and remains controversial. Recent work has provided a more precise picture of how 2D and 3D object structure is encoded in intermediate and higher-level visual cortices. Yet, other studies suggest that higher-level visual cortex represents categorical identity rather than structure. Furthermore, object responses are surprisingly adaptive to changes in environmental statistics, implying that learning through evolution, development, and also shorter-term experience during adulthood may optimize the object code. Future progress in reconciling these findings will depend on more effective sampling of the object domain and direct comparison of these competing hypotheses.

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INTRODUCTION

Object perception is critical for understanding and interacting with the world. Our ability to perceive objects is amazingly rapid, robust, and accurate, given the extreme computational difficulty of extracting object information from natural images (Dickinson 2009). The neural coding mechanisms underlying this remarkable ability have been a subject of intense study for half a century. Yet the fundamental principles of object processing in the brain remain uncertain and controversial. In contrast, other aspects of visual perception have been satisfyingly explained at a mechanistic level. For example, scholars widely accept that visual motion is represented by populations of neurons tuned for direction and speed in areas MT (middle temporal) and MST (middle superior temporal) and in other parts of the dorsal visual pathway (McCool & Britten 2007). But, in the ventral visual pathway (Ungerleider & Mishkin 1982, Felleman & Van Essen 1991), we have no comparable consensus on the coding dimensionality for objects. In fact, studies of ventral pathway function often avoid the question of what specific information is encoded by neural responses, somewhat comparable to studying MT neurons without knowing about direction tuning.

The reason for this gap in understanding is the difficulty of adequately sampling the enormous input domain for ventral pathway neurons. Object space is simply too high dimensional to study in the same way as other visual subdomains. Motion coding can be studied by sampling neural responses to stimuli along a few obvious dimensions such as direction and speed. These responses can be fit with mathematical tuning functions that capture the motion information conveyed by the neural responses. This basic ability to characterize the information encoded by neurons has been the foundation for spectacular work on perceptual causality and decision-making in the dorsal motion pathway (McCool & Britten 2007).

This basic approach cannot be applied in the same way to the ventral object pathway. The dimensionality of the object domain is too high to sample comprehensively, and it is unknown: There is no single, obvious way to represent a complex object with neural responses. As a result, the standard approach has been to sample object space randomly, with arbitrary sets of real or photographic objects. Such experiments have provided seminal insights into ventral pathway function, including the discovery of face-processing neurons (Desimone et al. 1984) and the description of columnar organization in inferotemporal cortex (Fujita et al. 1992). But because sampling is sparse and incomplete, these experiments cannot elucidate the specific information conveyed by neural responses; they cannot determine the coding dimensions of object-selective neurons, and they cannot constrain mathematical models of neural tuning in those dimensions.

This review describes three recent trends in the ongoing effort to grapple with the high dimensionality of object space. First, investigators have recently attempted to parameterize object structure and quantify neural tuning in structural dimensions. Second, others have attempted to quantify the relationship of neural responses to object categories. Third, recent studies have addressed the dynamic nature of ventral pathway coding, in the hope that object representation can be understood in terms of

Ventral pathway:

pathways in the

object-related

texture

shape, color, and

one of the two main

primate visual cortical

hierarchy; the ventral pathway processes

information, including

Annu. Rev. Neurosci. 2011.34:45-67. Downloaded from www.annualreviews.org by Medical Research Council (UK) on 10/17/14. For personal use only. the learning mechanisms that generate neural codes during development and that recalibrate coding on shorter timescales.

STRUCTURAL CODING

The classic approach to neural coding is to parameterize stimuli along one or more dimensions, to sample neural responses comprehensively along those dimensions, and to fit those responses with mathematical functions to describe how neurons encode information along those dimensions. In the object domain, this approach is problematic because the dimensionality of objects is (a) vast, necessitating the use of very large stimulus sets to cover the domain with some level of completeness, and (b) indeterminate, requiring novel experimental and analytical designs to test hypotheses about neural coding dimensions for objects. Nevertheless, progress has been made in quantifying neural tuning in structural dimensions across large sets of parametrically varying object stimuli.

Boundary Fragment Coding in Intermediate Cortex

Problems of sampling and stimulus parameterization are more tractable at intermediate processing stages such as area V4 because receptive fields are smaller and thus the complexity of object information encoded by neurons is correspondingly lower. Attempts to understand object coding in area V4 have partially extrapolated from what is known about structural representation in early visual cortex. Thus, V4 has been studied with grating stimuli (Gallant et al. 1993), contour stimuli (Pasupathy & Connor 1999, 2001), and natural object photographs (David et al. 2006). In all three cases, the scale and complexity of stimuli have been increased commensurate with V4 receptive field sizes, which are on the same order as retinal eccentricity (i.e., at 3° eccentricity, receptive field diameter is roughly 3°).

Responses in early visual cortex can be well characterized with tuning models in the

orientation/spatial frequency domain that account for phase invariance (David & Gallant 2005). Such models capture less variance at the V4 level (David et al. 2006), which suggests that additional dimensions are represented in V4. A number of studies have shown that V4 neurons are sensitive not only to orientation but also to curvature (Gallant et al. 1993; Pasupathy & Connor 1999, 2001), which is the derivative or rate of change of orientation with respect to contour length. This finding makes sense because contrast edges in natural scenes (typically produced by object boundaries) are more likely to change orientation within the larger image windows encompassed by V4 receptive fields. Curvature is also a salient quality in human perception (Andrews et al. 1973, Treisman & Gormican 1988, Wilson et al. 1997, Wolfe et al. 1992, Ben-Shahar 2006). Thus, explicit coding of curvature in V4 is an effective way to represent important boundary elements of natural objects (Connor et al. 2007).

Another tuning dimension that appears in intermediate ventral pathway cortex is relative position. Absolute, retinotopic position coding deteriorates as receptive fields grow larger through progressively higher processing stages in the ventral pathway (Felleman & Van Essen 1991). Yet information about the positional arrangement of structural elements is critical for recognizing objects and perceiving their physical structure. Hence, it is not surprising that neurons at the V4 level and higher are acutely sensitive to the position of structural elements relative to each other and to the object as a whole (Connor et al. 2007).

Figure 1*a* exemplifies V4 tuning for curvature and relative position of object boundary fragments. This particular neuron responded to objects with acute convex curvature near the top. This response pattern can be captured with a two-dimensional (2D) Gaussian function on the curvature/angular position domain (**Figure 1***b*). The response pattern remained consistent across changes in absolute, retinotopic position (Pasupathy & Connor, 2001). Also, tuning for convexity near the top remained consistent across wide variations in

Area V4: a major intermediate stage in the primate ventral visual pathway 2D: two dimensional



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global object shape (Figure 1a). This is a critical prediction of structural coding theories that depend on representation by components (Hubel & Wiesel 1959, Selfridge 1959, Sutherland 1968, Barlow 1972, Milner 1974, Marr & Nishihara 1978, Hoffman & Richards 1984, Biederman 1987, Dickinson et al. 1992): Component signals from a given neuron must have the same information value regardless of shape variations elsewhere in the object. In agreement with this prediction, neurons in V4 (Pasupathy & Connor 2001) and higher-level processing stages in inferotemporal (IT) cortex (Brincat & Connor 2004, Yamane et al. 2008) respond at maximal levels to a wide variety of global shapes sharing some spatially localized structural element(s).

The range of different V4 tuning functions is broad and comprehensive enough to serve as a basis set for representing global shape at the population level. This is demonstrated in Figure 1*c*-*e*, where a single shape from the stimulus set (Figure 1c) is reconstructed from the neural population response to that shape. Each neuron's tuning function (e.g., Figure 1b) was weighted by its response to the shape and summed into the overall pattern in Figure 1d. The local maxima in this pattern correspond to the curvatures and positions of the boundary fragments that make up the shape. These local maxima can be used to reconstruct the approximate shape of the original stimulus (Figure 1e). All stimuli were approximately recoverable in this fashion, showing that V4 neurons carry relatively complete information

Figure 1

about the structure of 2D object boundaries at the population level (Pasupathy & Connor 2002). These analyses provide a neural confirmation of the theory of representation by components.

Configural Coding in Higher-Level Cortex

Beyond V4, neurons with larger receptive fields integrate information across entire objects, and as a result the dimensionality of object space becomes much less tractable. Two-dimensional object structure can be parameterized and tested comprehensively at a level of moderate complexity with the use of very large stimulus sets, on the order of 10^3 , which is near the practical limits of neural recording experiments (Brincat & Connor 2004). But this approach becomes unworkable for three-dimensional (3D) object structure, which would require stimulus sets on the order of 10^4 or 10^5 to address object representation at a comparable level of complexity.

Although random and systematic sampling are inadequate at this level of structural complexity, a promising alternative is adaptive sampling, i.e., search through object space guided by neural responses. One version of this idea was pioneered by Tanaka and colleagues (1991). Beginning with a test of IT neural responses to randomly selected objects, the object evoking the strongest response was deconstructed into simpler components. The end point for each neuron was the simplest pattern that still evoked

Representation by components:

a phrase coined by Irving Biederman (1987) to describe representation of objects in terms of their component parts

Inferotemporal (IT)

cortex: a general anatomical label for the more anterior, higher-level stages in the primate ventral visual pathway

3D: three dimensional

Boundary fragment coding in intermediate ventral pathway cortex. (*a*) Responses of an individual V4 neuron to two-dimensional (2D) silhouette stimuli, recorded from a macaque monkey performing a fixation task. Stimuli were flashed at the cell's receptive field center. Average responses across 5 presentations are represented by gray levels surrounding each stimulus icon (see scale bar). (*b*) Gaussian function describing the response pattern in part *a*. The vertical axis represents boundary curvature (squashed to a scale from -1 to 1), and the horizontal axis represents angular position of boundary fragments with respect to the shape's center of mass. The color scale on the right indicates normalized predicted response. The tuning peak corresponds to sharp convex curvature (1.0) near the top of the shape (84.6°). (*c*) Curvature/angular position function for a single stimulus, plotted in polar coordinates to illustrate correspondence with the stimulus outline. (*d*) Estimated V4 population response across the curvature/angular position domain (colored surface, plotted in Cartesian coordinates) with the veridical curvature function (*white line*) superimposed. A Cartesian plot is used here because a polar plot would distort peak width in the population response. (*e*) Reconstruction of the stimulus shape based on the population response surface in part *d*. Modified from Pasupathy & Connor 2002.

Annu. Rev. Neurosci. 2011.34:45-67. Downloaded from www.annualreviews.org by Medical Research Council (UK) on 10/17/14. For personal use only. near-maximal responses. This approach was a critical tool for demonstrating the columnar organization of IT (Fujita et al. 1992). However, because the method is strictly convergent, the final, simplified structure is limited to whatever existed in the original set of random objects, and the single end point cannot constrain a quantitative model of neural tuning.

A divergent, evolutionary method for adaptively sampling object space was recently tested by Yamane and colleagues (2008). The example experiment on an IT neuron presented in Figure 2 began with two sets of 50 random 3D shapes (Figure 2a, Run 1 and Run 2). Threedimensionality was conveyed by shading cues (visible in **Figure** 2a) and binocular disparity cues. The average responses of the neuron to each stimulus (indicated by background color, according to the scale bar in Figure 2a) were used as feedback to a probabilistic algorithm for defining subsequent generations of stimuli. Subsequent generations emphasized partially morphed versions of high-response stimuli from previous generations, which ensured that structural components eliciting neural responses propagated, evolved, and recombined, producing dense sampling in the most relevant region of object space. For this example neuron, both runs evolved high-response stimuli characterized by a specific configuration of sharp convex projections and concave indentations in the upper right quadrant of the objects (**Figure** *2b,c*).

This configuration of surface fragments was well described with models based on structural tuning for surface curvature, surface orientation, and 3D relative position. The model shown here is based on two Gaussian tuning functions in the curvature/orientation/position domain (Figure 2d). Projection of these tuning functions onto the surface of example high-response stimuli (Figure 2e) shows that the cyan function captured the sharp convexities and the magenta function captured the interleaved concavities. Successful cross-prediction of responses between runs (Figure 2e) demonstrates that the adaptive search algorithm converged on the same result from different starting points.

Across the IT population, neurons exhibit a wide range of tuning for surface fragment configurations (**Figure 3***a*). Tuning for configurations, as opposed to individual structural elements, has been a consistent finding in IT cortex in previous 2D shape experiments as well (Brincat & Connor 2004). Tuning for configurations develops gradually over the course of ~60 ms following initial responses to individual components (Brincat & Connor 2006). Configural tuning may represent a coding optimum between the extremes of componentlevel representation (as in V4, see **Figure 1**)

Figure 2

Adaptive sampling of object structure space. Neural responses were recorded from a single cell in IT of a macaque monkey performing a fixation task. Stimuli were flashed at the center of gaze for 750 ms each. Two independent stimulus lineages (Run 1 and Run 2) are shown in the left and right columns, respectively. Background color (see scale bar) indicates the average response to each stimulus across five presentations. (a) Initial generations of 50 randomly constructed 3D shape stimuli. Stimuli are ordered from top left to bottom right according to average response strength. (b) Partial family trees showing how stimulus shape and response strength evolved across successive generations. (c) Highest-response stimuli across 10 generations (500 stimuli) in each lineage. (d) Response models based on two Gaussian tuning functions. The Gaussian functions describe tuning for surface fragment geometry, defined in terms of curvature (principal, i.e., maximum and minimum, cross-sectional curvatures), orientation (of a surface normal vector, projected onto the x/y and y/z planes), and position (relative to object center of mass in x/y/z coordinates). The curvature scale is squashed to a range between -1 (concave) and 1 (convex). The 1.0 standard deviation boundaries of the two Gaussians (magenta and cyan) are shown projected onto different combinations of these dimensions. The equations show the overall response models, with fitted weights for the two Gaussians, the product or interaction term, and the baseline response. (e) The two Gaussian functions are shown projected onto the surface of a high-response stimulus from each run. The stimulus surface is tinted according to the tuning amplitude in the corresponding region of the model domain. The scatterplots show the relationship between observed responses and responses predicted by the model. In each case, self-prediction by the model is illustrated by the stimulus/scatterplot pair on the left and cross-prediction by the pair on the right. Reproduced from Yamane et al. (2008).



а























and holistic representation. Component-level representation is combinatorial and therefore highly productive, suitable for representing the virtual infinity of potential object shapes. Holistic representation schemes, in which individual neurons signal information about global shape, have more potential for sparse, efficient representation. Configural coding may represent a compromise between productivity and sparseness.

Conceivably, IT neurons tuned for surface fragment configurations serve as basis functions for representing complete 3D object structure. This idea is represented diagrammatically in **Figure 3b**, where a detail from a Henry Moore sculpture is approximated with a computer rendering. Tuning functions from Yamane et al. (2008) are projected onto the surface to suggest how the complete shape could be represented by a neural ensemble signaling its constituent surface fragment configurations. This coding scheme would provide a compact, explicit representation of the kind of 3D object structure we experience perceptually.

Representation of Face Structure

Another way to tackle the enormous dimensionality of object space is to restrict investigation to a well-defined subspace of objects. This approach makes sense for neurons that operate primarily within such a subspace, as with neurons in face-processing regions of the ventral pathway, which show remarkable selectivity for face stimuli over other natural categories of objects (Tsao et al. 2006). Given this restricted coding context, investigators can explore the relevant input space densely and comprehensively. Freiwald and colleagues (2009) did this by parameterizing cartoon faces in terms of size, shape, and relative positions of eyes, brows, nose, and mouth. Neurons in the middle face-processing region of monkey IT exhibited tuning for configurations of parts defined according to these dimensions. The range of tuning patterns suggested that this face patch contains a complete basis function representation of a facial structure space.

Other groups have taken a different theoretical approach inspired by psychophysical results, suggesting that faces are represented in terms of holistic structural similarity and organized with respect to a grand geometric average over all faces encountered through time (Rhodes et al. 1987, Mauro & Kubovy 1992, Leopold et al. 2001, Webster et al. 2004). Loffler and colleagues (2005) provided evidence in favor of this average face principle by showing strong fMRI cross-adaptation in human fusiform face area to stimuli lying along the same morph direction from the average face. Leopold and colleagues (2006) provided parallel evidence for tuning along such morph lines at the level of individual neurons in macaque monkey IT. It would be interesting to see the holistic similarity hypothesis tested directly against the component structure hypothesis with a suitable stimulus set parameterized in both domains simultaneously.

CATEGORICAL CODING

The main alternative to structural object representation is categorical representation. In both words and actions, we group objects into categories on the basis of characteristics

Figure 3

fMRI: functional magnetic resonance imaging

Configural coding in higher-level ventral pathway cortex. (*a*) Surface configuration tuning for 16 example IT neurons. In each case, two high-response stimuli are shown from the first run (*top row*) and the second run (*bottom row*). Models were fit as described in **Figure 2** and the two Gaussian tuning functions were projected onto the surface of the stimuli. (*b*) Hypothetical example of configural coding of 3D object structure. Five 2-Gaussian tuning models (*red, green, blue, cyan, magenta*) from Yamane et al. (2008) are projected onto a 3D rendering (*rigbt*) of the larger figure in Henry Moore's "Sheep Piece" (1971–1972, *left*; reproduced by permission of the Henry Moore Foundation, **http://www.henry-moore-fdn.co.uk**). Reproduced from Yamane et al. (2008).

that are often partially or wholly nonstructural: animacy, behavior, utility, and especially association, either episodic or conceptual. It seems certain that both structure and category must be represented somewhere in the brain and that those representations must interact in some way. But there is potential controversy over which domain provides the most fundamental explanation of object coding in the ventral pathway and, by extension, underlies our perceptual experience of objects.

Categorical representation of objects has long been studied at the qualitative level (Desimone et al. 1984, Vogels 1999). Recently, researchers have begun to use quantitative analyses to study categorical representation in functionally homologous regions of the ventral pathway cortex (Denys et al, 2004). Kiani and colleagues (2007) analyzed categorical representation in a massive data set of 674 neurons recorded from monkey anterior IT, each studied with more than 1000 natural object photographs. Multidimensional scaling (MDS), applied to the distances between objects in neural response space, revealed an overarching division between animate and inanimate objects, with further subdivision of animate objects into subcategories that included human faces, monkey faces, nonprimate faces, hands, human bodies, and quadrupeds. The higherlevel divisions, between animate and inanimate and between faces and bodies, have been replicated for human inferior temporal visual cortex by analyzing fMRI voxel response patterns (Kriegeskorte et al. 2008) (Figure 4). Analyses for reconstruction of natural images from



Figure 4

Categorical coding in higher-level ventral pathway cortex. Ninety-two object photographs were presented to monkeys and humans performing a fixation task. Responses were recorded from 674 IT neurons in two monkeys. Responses of IT cortex in four humans were measured with high-resolution fMRI. For both data sets, multidimensional scaling techniques were used to produce the stimulus arrangements shown here, in which distance between stimuli corresponds approximately to distance in neural (monkey) or voxel (human) response space (i.e., dissimilarity of response patterns). Both stimulus arrangements show that faces, bodies, and other objects fall into separate response clusters. Reproduced from Kriegeskorte et al. (2008).

fMRI voxel response patterns also indicate the existence of category information in anterior human visual cortex (Naselaris et al. 2009).

These findings pose an interesting challenge to structural coding hypotheses. Apparent structural tuning may only be a reflection of selectivity for object categories, which are definable to some extent by their structural characteristics. Conversely, apparent selectivity for an object category could reflect more fundamental tuning for structural characteristics of that category. These alternatives could be differentiated by studies that simultaneously analyze categorical and structural tuning and contrast their explanatory power. Freedman and colleagues (2003) did this for a single, learned categorical distinction (between cat-like and dog-like stimuli) and found that the amount of category information in monkey IT was no greater than that expected on the basis of structural tuning. Similar analyses remain to be done for the naturalistic categories identified in the studies cited above.

ADAPTIVE CODING

In the search for neural codes, we typically measure responses to input alone (e.g., objects, faces) without accounting for context in space (i.e., scene configuration) or time (i.e., previous experiences with a given object). However, accumulating evidence suggests an adaptive neural code that is dynamically shaped by experience. Here, we summarize work showing that experience plays a critical role in shaping structural and categorical coding for object perception. That is, learning optimizes the neural processes that mediate binding of local elements and parts into objects, recognition of objects across image changes that preserve identity (e.g., position, orientation, clutter), and selection of behaviorally relevant features for object categorization. We propose that similar learning mechanisms may mediate long-term optimization through evolution and development, tune the visual system to fundamental principles of feature binding, and shape structure and category representations.

Learning to See Objects

Evolution and development shape the organization of the visual system and facilitate visual recognition in cluttered scenes (Gilbert et al. 2001, Simoncelli & Olshausen 2001). Recent studies suggest that the primate brain is sensitive to regularities that occur frequently in natural scenes (e.g., orientation similarity in neighboring elements) and has developed a network of connections that mediate integration of object features based on these correlations (Sigman et al. 2001, Geisler 2008). However, long-term experience is not the only means by which visual processes become optimized. Learning through everyday experiences in adulthood plays a key role in facilitating the detection and recognition of targets in cluttered scenes (Dosher & Lu 1998, Goldstone 1998, Schyns et al. 1998, Gold et al. 1999, Sigman & Gilbert 2000, Gilbert et al. 2001, Brady & Kersten 2003). Observers are shown to learn distinctive target features by using image regularities to integrate relevant object features and by suppressing background noise (Dosher & Lu 1998, Gold et al. 1999, Brady & Kersten 2003, Li et al. 2004).

Here, we propose that long-term experience and short-term training interact to shape the optimization of visual recognition processes. Whereas long-term experience through evolution and development hones the principles of organization that mediate feature grouping for object recognition, short-term training in adulthood may establish new principles for interpreting natural scenes. For example, long-term experience with the high prevalence of collinear edges in natural environments (Sigman et al. 2001, Geisler 2008) has resulted in enhanced sensitivity for detecting collinear contours in clutter. However, short-term training alters the behavioral relevance of image regularities that violate the typical principles of contour linking (Sigman et al. 2001, Simoncelli & Olshausen 2001, Geisler 2008). Although collinearity is a prevalent principle for perceptual integration in natural scenes, recent evidence (Schwarzkopf & Kourtzi 2008)

Statistical learning: learning of regularities by mere exposure

Recurrent processing:

processing based on horizontal and feedback connections

suggests that the brain can learn to exploit other image regularities (i.e., orthogonal alignments) that typically signify discontinuities for contour linking. Furthermore, both infants and adults learn fast and without explicit feedback to extract and exploit novel spatial and temporal regularities that appear frequently in visual scenes. Examples of this type of statistical learning comprise parsing speech into meaningful language streams (Saffran et al. 1996, Pena et al. 2002), integrating shapes across space (Fiser & Aslin 2001, Baker et al. 2004, Turk-Browne et al. 2009), combining object views across time (Kourtzi & Shiffrar 1997, Wallis & Bulthoff 2001), grouping objects into spatial configurations and visual scenes (Fiser & Aslin 2005, Orban et al. 2008), and abstracting visual categories (Brady & Oliva 2008).

Which are the neural mechanisms that mediate our ability to extract statistical regularities and learn novel principles of perceptual organization for object detection and recognition? Recent neurophysiology and imaging studies implicate recurrent processing between local integration mechanisms that tune image statistics in visual cortex and top-down fronto-parietal mechanisms that mediate the formation and flexible selection of behaviorally relevant rules and features. Consistent with a theoretical model of attention-gated reinforcement learning (Roelfsema & van Ooyen 2005), learning enhances responses in fronto-parietal circuits (Schwarzkopf & Kourtzi 2008). These gain effects may relate to a global reinforcement mechanism that is important for identifying salient image regions and detecting objects in clutter. Goal-directed attentional mechanisms may then optimize visual processing within these salient regions and change the neural sensitivity to the relevant object features rather than spurious image correlations. Thus, learning may support efficient target detection by enhancing the salience of targets through increased correlation of neuronal signals related to the target features and decorrelation of signals related to target and background features (Jagadeesh et al. 2001, Li et al. 2008). That is, feedback from higher fronto-parietal regions may change neural processing (i.e., neural selectivity or local correlations) in higher occipitotemporal circuits that support shape integration and recognition (Kourtzi et al. 2005, Sigman et al. 2005, Schwarzkopf et al. 2009).

Recent studies combining behavioral and brain-imaging measurements (Zhang & Kourtzi 2010) propose two routes to visual learning in clutter (**Figure 5**). These studies show that long-term experience with statistical regularities (i.e., collinearity)

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Learning statistical regularities. (a) Examples of stimuli: Collinear contours in which elements are aligned along the contour path and orthogonal contours in which elements are oriented at 90° to the contour path. For demonstration purposes only, two rectangles illustrate the position of the two contour paths in each stimulus. (b) Average behavioral performance across subjects (percent correct) before and after supervised training (i.e., observers received feedback on a contour detection task) or exposure (i.e., observers performed an irrelevant contrast discrimination task) to collinear or orthogonal contours. Before training, detection was difficult for both collinear and orthogonal contours. After training, the observers' performance in detecting orthogonal contours improved significantly following supervised training but not following mere exposure. In contrast, for collinear contours, observers showed similar improvement in detection performance following supervised training or exposure. These learning effects were specific to the trained contour orientation for orthogonal contours, whereas they generalized to untrained orientations for collinear contours. (c) fMRI responses for observers trained with orthogonal versus collinear contours. fMRI data (percent signal change for contour minus random stimuli) are shown for trained contour orientations before and after supervised training on orthogonal (upper panel) versus collinear (lower panel) contours. Training enhanced responses in intraparietal regions for orthogonal contours while in higher occipitotemporal regions for collinear contours. Taken together, the behavioral and fMRI findings demonstrate that opportunistic learning of statistical regularities (i.e., collinear contours) may occur by frequent exposure and is mediated by occipitotemporal areas, whereas bootstrap-based learning of discontinuities (i.e., orthogonal contours) requires extensive training and is mediated by intraparietal regions. Adapted from Zhang & Kourtzi (2010).

may facilitate opportunistic learning (i.e., learning to exploit image cues), whereas learning to integrate discontinuities (i.e., elements orthogonal to contour paths) entails bootstrap-based training (i.e., learning new features) for detecting contours in clutter. Learning to integrate collinear contours occurs simply through frequent exposure, generalizes across untrained stimulus features, and shapes processing in higher occipitotemporal regions implicated in the representation of global forms. In contrast, learning to integrate discontinuities (i.e., elements orthogonal to contour paths) required task-specific training





(bootstrap-based learning), was stimulus dependent, and enhanced processing in intraparietal regions implicated in attention-gated learning. Similarly, recent neuroimaging studies suggest that a ventral cortex region becomes specialized through experience and development for letter integration and word recognition (Dehaene et al. 2005), whereas parietal regions are recruited for recognizing words presented in unfamiliar formats (Cohen et al. 2008). Taken together, these findings propose that opportunistic learning of statistical regularities shapes bottom-up object processing in occipitotemporal areas, whereas learning new features and rules for perceptual integration recruits parietal regions involved in the attentional gating of recognition processes.

Learning Object Structure

How does the brain construct structural object representations that are sensitive to subtle differences in object identity so we can discriminate between similar objects while being

ADAPTIVE CODING ACROSS TEMPORAL SCALES

A range of fMRI studies using learning or repetition suppression paradigms (i.e., when a stimulus is presented repeatedly) show similar effects for long-term training, rapid learning, and priming, which depend on the nature of the stimulus representation. In particular, enhanced responses have been observed when learning engages processes necessary for new representations to form, as in the case of unfamiliar (Schacter et al. 1995, Gauthier et al. 1999, Henson et al. 2000), degraded (Tovee et al. 1996, Dolan et al. 1997, George et al. 1999), masked unrecognizable (Grill-Spector et al. 2000, James et al. 2000), or noise-embedded (Kourtzi et al. 2005) targets. In contrast, when the stimulus perception is unambiguous (e.g., familiar, undegraded, recognizable targets presented in isolation), training results in more efficient processing of the stimulus features indicated by attenuated neural responses (Henson et al. 2000, James et al. 2000, Jiang et al. 2000, van Turennout et al. 2000, Koutstaal et al. 2001, Chao et al. 2002, Kourtzi et al. 2005).

tolerant of image changes that preserve object identity, enabling us to recognize different presentations of the same object? Recent neurophysiological studies propose that although individual neurons contain highly selective information for image features, connections across neural populations may support object recognition across image changes. In particular, neural populations in higher temporal areas may contain information about object identity that may generalize across image changes (e.g., Rolls 2000, Grill-Spector & Malach 2004, Hung et al. 2005, Quiroga et al. 2005). Computational models (Fukushima 1980, Riesenhuber & Poggio 1999, Ullman & Soloviev 1999) propose that the brain builds these robust object representations using neuronal connections that group together similar image features across image transformations. Furthermore, recent neurophysiological studies (Zoccolan et al. 2007) show that temporal cortex neurons with high object selectivity have low invariance. These studies suggest that connections between neurons selective for similar features are critical for the binding of feature configurations and the robust representation of object identity.

But how does the brain know which neurons to connect or which connections across neural populations to strengthen to build robust object representations? Experience and training may be a solution to this problem (Foldiak 1991, Wallis & Rolls 1997, Ullman & Soloviev 1999, Wallis & Bulthoff 2001) by enhancing the sparseness and clustering of the neural code. fMRI studies show that at the level of large neural populations training results in differential responses to trained compared with untrained object categories (see sidebar, Adaptive Coding Across Temporal Scales). In particular, learning changes the distribution of voxel preferences for the trained stimuli, suggesting altered sensitivity to stimulus features rather than simply gain modulations that would preserve the spatial distribution of activity (Op de Beeck et al. 2006, Schwarzkopf et al. 2009).

At the single-neuron level, training with novel object configurations and combinations of object parts or mere experience with novel objects in the animals' living environment tunes temporal cortex neurons to novel objects and supports some generalization to neighboring object views (Miyashita & Chang 1988, Logothetis et al. 1995, Rolls 1995, Kobatake et al. 1998, Baker et al. 2002). Furthermore, training enhances not only the selectivity but also the clustering of IT neurons, with similar object selectivity enabling stronger local interactions (Erickson et al. 2000). Temporal continuity enhances the binding of disparate images into the same object representation (Kourtzi & Shiffrar 1997, Wallis & Bulthoff 2001, Cox et al. 2005). For example, recent work (Li & DiCarlo 2008) has shown that IT neurons learn to bind into the same object features that are presented at different retinal locations but in temporal correlation, supporting position-invariant object representations.

Taken together, neurophysiology and imaging studies provide evidence for learningdependent plasticity mechanisms in the temporal cortex that mediate robust representations of object structure. However, whether learning results in long-term changes in neural properties or optimizes the readout signals in IT remains an open question. Recent neurophysiology studies showing that learning enhances the selectivity of the most informative neurons for a feature discrimination task (Raiguel et al. 2006) suggest that learning optimizes the readout of IT neurons. In particular, learning is thought to operate via top-down mechanisms that originate at decision stages, determine the relevance of object features, and reweight neural selectivity in sensory areas in a task-dependent manner (Dosher & Lu 1998, Ahissar & Hochstein 2004, Roelfsema & van Ooyen 2005, Law & Gold 2008). Accumulating evidence for such mechanisms comes from studies showing task-dependent learning effects in visual cortex (Gilbert et al. 2001, Kourtzi et al. 2005, Sigman et al. 2005). Thus, learning shapes robust object representations by enhancing the processing of feature detectors in local circuits using top-down knowledge about the relevant task dimensions and demands.

Learning Object Category

Extensive behavioral work on visual categorization (e.g., Goldstone et al. 2001) suggests that the brain learns the relevance of visual features for categorical decisions rather than simply representing physical similarity. That is, learning may reduce object space dimensionality by reweighting feature representations on the basis of their behavioral relevance in the context of a task.

Although a large network of brain areas has been implicated in visual category learning (see sidebar, Brain Networks for Category Learning), the role of temporal cortex in the learning and representation of visual categories remains controversial. Recent imaging studies have revealed a distributed pattern of activations for object categories in the temporal cortex (Haxby et al. 2001), including regions specialized for categories of biological importance (e.g., faces, bodies, places) (Reddy & Kanwisher 2006). However, some neurophysiological studies propose that the temporal cortex represents primarily the visual similarity between stimuli (Op de Beeck et al. 2001,

BRAIN NETWORKS FOR CATEGORY LEARNING

A large network of cortical and subcortical areas has been implicated in visual category learning (e.g. Vogels et al 2002; for reviews, see Keri 2003, Ashby & Maddox 2005). In particular, areas in the prefrontal cortex have been implicated in rule-based tasks in which the category structure is determined by a single stimulus dimension. This is consistent with the role of the prefrontal cortex in guiding visual attention to select behaviorally relevant information (for reviews, see Miller 2000, Duncan 2001). In contrast, the basal ganglia have been implicated primarily in information-integration tasks that require combining information from different stimulus dimensions for making categorical decisions. Furthermore, the medial temporal cortex has been implicated in category-learning tasks that rely on memorization. Finally, prototype-distortion tasks during which participants compare category exemplars to prototypical visual stimuli engage occipitotemporal regions.

Thomas et al. 2001, Freedman et al. 2003, Jiang et al. 2007, Op de Beeck et al. 2008), whereas others suggest that it represents learned stimulus categories (Meyers et al. 2008) and diagnostic stimulus dimensions for categorization (Sigala & Logothetis 2002, Mirabella et al. 2007). Furthermore, recent work suggests that the representations of object categories in the temporal cortex are modulated by task demands (Koida & Komatsu 2007) and experience (e.g., Op de Beeck et al. 2006, Gillebert et al. 2009).

Understanding the mechanisms that mediate adaptive coding of object categories is critical to understanding our ability to make flexible perceptual decisions. Here, we propose that adaptive categorical coding is implemented by interactions between top-down mechanisms related to the formation of rules and local processing of task-relevant object features. For example, recent neuroimaging studies (Li et al. 2007) using multivariate analysis methods provide evidence that learning shapes feature and object representations in a network of areas with dissociable roles in visual categorization (Figure 6). In particular, observers were trained to categorize dynamic shape configurations on the basis of single stimulus dimension

(form versus motion) or feature conjunctions. Temporal and parietal areas encode the perceived similarity in form and motion features, respectively. In contrast, frontal areas and the striatum represent task-relevant conjunctions of spatio-temporal features critical for forming more complex categorization rules. These findings suggest that neural representations in these areas are shaped by the behavioral relevance of sensory features and by previous experience to reflect the perceptual (categorical) rather than the physical similarities between stimuli. This notion is consistent with neurophysiological evidence for recurrent processes that modulate selectivity for perceptual categories along the behaviorally relevant stimulus dimensions in a top-down manner (Freedman et al. 2003, Smith et al. 2004, Mirabella et al. 2007) resulting in enhanced selectivity for the relevant stimulus features in visual areas.

Further evidence for recurrent processing for flexible categorical representations comes from recent work (Li et al. 2009) showing that category learning shapes decision-related processes in frontal and higher occipitotemporal regions rather than signal detection or response execution in primary visual or motor areas.

Figure 6

Learning rules for categorical decisions. (a) Five sample frames of a prototypical stimulus depicting a dynamic figure. Each stimulus comprised ten dots that were configured in a skeleton arrangement and moved in a biologically plausible manner (i.e., sinusoidal motion trajectories). (b) Stimuli were generated by applying spatial morphing (steps of percent stimulus B) between prototypical trajectories (e.g., A-B) and temporal warping (steps of time warping constant). Stimuli were assigned to one of four groups: A fast-slow (AFS), A slow-fast (ASF), B fast-slow (BFS), and B slow-fast (BSF). For the simple categorization task (left panel), the stimuli were categorized according to their spatial similarity: Category 1 (red dots) consisted of AFS, ASF, and Category 2 (blue dots) of BFS, BSF. For the complex task (right panel), the stimuli were categorized on the basis of their spatial and temporal similarity: Category 1 (red dots) consisted of ASF, BFS, and Category 2 (blue dots) of AFS, BSF. (c) Multivariate pattern analysis (MVPA) of fMRI data: Prediction accuracy (i.e., probability with which the presented and perceived stimuli are correctly predicted from brain activation patterns using a linear support vector machine classifier (SVM) for the spatial similarity (blue line) and complex (green line) classification schemes across categorization tasks (simple, complex task). Prediction accuracies for these MVPA rules are compared with accuracy for the shuffling rule (baseline prediction accuracy, dotted line). Interactions of prediction accuracy across tasks in dorsolateral prefrontal cortex (DLPFC) and lateral occipital (LO) regions indicate that the categories perceived by the observers are reliably decoded from fMRI responses in these areas. In contrast, the lack of a significant interaction in V1 shows that the stimuli are represented on the basis of their physical similarity rather than on the rule used by the observers for categorization. Adapted from Li et al. (2007).

In particular, in prefrontal circuits, learning shapes the estimation of the decision criterion only in the context of the categorization task. In contrast, in higher occipitotemporal regions, the representations of perceived categories are sustained after training independent of the task and may serve as selective readout signals for optimal decisions (**Figure 7**).





Figure 7

Learning shapes behavioral choice. (*a*) Observers were trained to categorize global form patterns as radial or concentric. Four example Glass pattern stimuli (100% signal) are shown at spiral angles of 0°, 30°, 60°, and 90°. Before training (pretraining test), the mean categorization boundary (50% point on the psychometric function) was close to the mean of the physical stimulus space (45° spiral angle). Observers were then trained with feedback to assign stimuli into categories on the basis of two different category boundaries: 30°, 60° spiral angle. The two tested boundaries and spiral angles that indicate the categorical membership of the stimuli for each boundary are shown (*blue bar: stimuli that resemble radial; red bar: stimuli that resemble concentric*). Observers were first trained on one of the two boundaries and then retrained on the other. (*b*) Testing the observers without feedback after training demonstrated that training had shifted the observers' criteria for categorization to the trained boundary (i.e., criterion of psychometric functions). (*c*) A linear support vector machine classifier (SVM) was trained to classify fMRI signals on the basis of the observer's behavioral choice (radial versus concentric) on each trial and tested for accuracy in predicting the observers' choice on an independent data set. For each observer, the mean performance of the classifier (proportion of trials classified as concentric for each stimulus condition) was calculated across cross-validations (fMR-metric functions). Comparing the classifier's choices with the observer's choices showed that fMR-metric functions in frontal and higher occipitotemporal areas resemble psychometric functions, suggesting a link between behavioral and neural responses. Adapted from Li et al. (2009).

CONCLUSION

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Object vision is a remarkable perceptual capacity that has remained largely unexplained at the level of neural coding mechanisms. A primary obstacle has been the high, unknown dimensionality of objects, which precludes comprehensive sampling of the relevant input space. We have reviewed recent approaches to this problem: quantitative modeling of structural coding, adaptive sampling of object space, quantitative evaluation of categorical representation, and measurement of adaptive changes in object coding. Results from these different approaches are compelling, but they do not obviously cohere within a single framework. Structure is a conceptually different domain from category, and it is not clear which domain provides more fundamental explanations or how the two might interrelate. Both structural and categorical coding require some level of stability, a principle that is challenged by the strong adaptability of object responses. Future progress will depend in part on addressing these different themes within the same experimental contexts. The high dimensionality of object space will remain an enormous challenge, demanding further innovation in experimental and analytical design.

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