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Coding of visual objects in the ventral stream

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How are objects represented in the brain? Two facets of this question are currently under investigation. First, are objects represented by activity in a relatively small number of neurons that are each selective for the shape or identity of a specific object (a 'sparse code'), or are they represented by a pattern of activity across a large number of less selective neurons (a 'population code')? Second, how are the neurons that code for an object distributed across the cortex: are they clustered together in patches, or are they scattered widely across the cortex? The results from neurophysiology and functional magnetic resonance imaging studies are beginning to provide preliminary answers to both questions.

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Introduction

When a familiar object appears in our field of view, we identify it within a couple hundred milliseconds. Extensive evidence indicates that in primates this feat is accomplished in the ventral visual pathway, which runs along the ventral surface of the brain from the occipital lobe anteriorly into the temporal lobe. What is the nature of the neural representation of object identity in this pathway? Here, we address two aspects of this question. First, how selective are the neurons and regions along this pathway for specific object classes, and hence how many neurons participate in the representation of each object (that is, how sparse is the code)? Second, what is the spatial arrangement of the neurons the activity of which represents a given object?

Note that distinctions between sparse and population codes (see glossary), and between clustered and distributed neural representations are matters of degree. Furthermore, both the sparseness of a neural code and

the clustering of the neurons involved in that code are defined with respect to what is being represented. For example, a face-selective neuron could in principle participate in a sparse code for the presence of a face, but if the same neuron responds to a wide variety of faces, it might participate in a population code for face identity. Finally, although the concepts of sparsity and clustering are not independent at the extremes (a representation carried by a single neuron is necessarily spatially restricted, and a representation that involves all neurons is necessarily spatially distributed), sparseness need not imply clustering. The human hippocampus contains some of the sparsest codes ever reported [1,2••], yet there is no evidence that neurons with similar selectivities are located near each other in the hippocampus.

Sparse codes versus population codes for objects

In a sparse and explicit coding strategy, a small number of neurons could play a decisive role in the representation of each object [3] (Figure 1). In the limit, an individual neuron could signal a particular complex and meaningful stimulus (e.g., one's grandmother), and be activated every time one saw this stimulus. This extreme version of the sparse coding scheme was originally proposed by Konorksi, who called such neurons 'gnostic neurons' [4]. An example of sparse coding is found in the songbird forebrain nucleus HVC (hyperstriatum ventrale pars caudale), where individual neurons selectively code for a temporally precise sequence of specific notes [5]. Another example of such sparseness is observed in the insect olfactory system, where individual odors activate only a small number of neurons that typically respond with only two action potentials [6]. For the representation of a continuous variable (e.g. orientation), a sparse code would mean that each neuron is sharply tuned for a particular value of that variable. Advantages of sparse representations are metabolic efficiency and ease of readout by other areas [7,8].

At the other end of the spectrum are coding strategies in which the relevant information is distributed across a large population of neurons, the concerted activity of which represents the stimulus [9,10] (Figure 1). Evidence for such a population-coding scheme comes from motor cortex, where individual neurons have broad and overlapping tuning curves in three-dimensional space, making it impossible to accurately predict the direction of an arm movement from the activity of any one neuron. However, by combining information across a population of neurons, movement directions can be specified precisely. Other population codes with broad tuning curves have also been

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Glossary
Nonpreferred response: A response in a given neuron that is less than the maximal response.
Nonpreferred stimulus: A stimulus that produces less than the maximal response in a given neuron.
Population codes: A scheme in which a large number of broadly tuned neurons encode each stimulus. (See Figure 1 for an illustration of these ideas.)
Preferred stimulus: A stimulus that elicits the maximal (i.e. strongest observed) response from a given neuron.
**Sparse codes:** A coding scheme in which a small number of highly selective neurons are activated in response to one stimulus.

proposed in sensory systems for encoding continuous stimulus variables such as orientation [11,12]. Population codes are robust to sources of biological noise such as cell death or inherent variability in neuronal responses [11]. However, because the relevant information is distributed across neurons, these codes are more sensitive to the binding problem — the ambiguity arising when more than one stimulus must be encoded simultaneously [13] — because each neuron would be activated by multiple stimuli and, therefore, would not be able to unambiguously report the presence of any one of them.

How sparse then are representations of objects in the ventral visual pathway? Since the initial discovery by Gross and co-workers [14,15] of a small group of cells in inferotemporal cortex (IT) that responded with great specificity to images of hands or faces, several groups have reported further evidence for sparse coding for visual information in both monkeys and humans. Cells in anterior IT and prefrontal cortex in monkeys respond selectively to complex, arbitrary visual stimuli, such as 3-D wire-frame objects or computer generated images of cats and dogs [16–20], and cells in the banks of the superior temporal sulcus respond with great specificity to human and monkey faces [21•]. In the human hippocampus, cells have been observed to have sparse and explicit responses to various categories of images [1], in addition to very specific responses to particular individuals, objects or landmarks [2••]. There is now also good evidence that such sparse coding neurons in the human medial temporal lobe can maintain these highly selective responses across markedly different views of the preferred stimulus (see glossary) [2••,22]. Although the specificity of a given neuron or cortical region for a particular stimulus can never be definitively proven (because it is always possible that some untested stimulus would drive that neuron or region more strongly), this problem can be minimized by sampling a very large number of stimuli. For example, by testing each cell on more than 1000 natural images, Foldiak *et al.* [21•] provided some of the strongest evidence to date that (some) face cells are truly selective for faces [23].

Figure 1
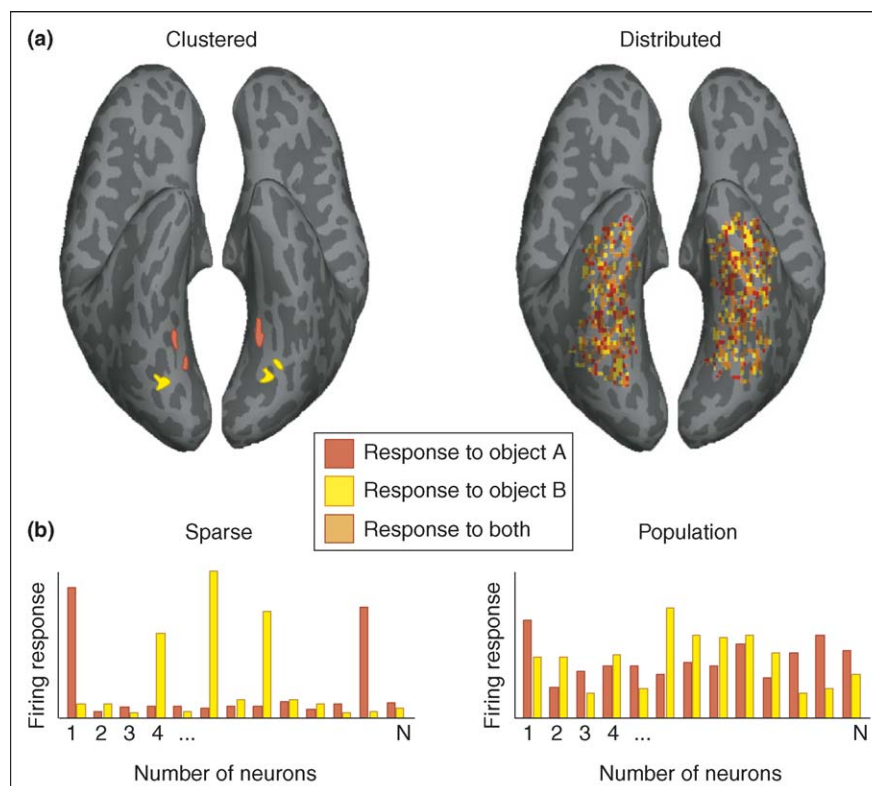
A schematic representation of **(a)** clustered versus distributed representations and **(b)** sparse versus population codes (see glossary).

However, in some cases precise information about the stimulus is only obtained by pooling the output of a large population of neurons. For instance, shape information in visual areas V4 and posterior IT is encoded by an ensemble of neurons that each carry information about simpler features of the shape [24,25]. In anterior IT, population codes can distinguish among the shapes of objects [26], and provide accurate information over short timescales about the category and identity of more complex objects [27•]. Indeed, the number of objects that can be discriminated at a fixed accuracy has been found in anterior IT to increase almost exponentially with the number of neurons [27•], a relationship that is indicative of a population based code [28]. (By contrast, decoding accuracy for sparse codes is a linear function of the number of neurons, although possibly with a shallow slope [29].) As noted previously, a given set of neurons can participate in both sparse and population codes for different information. For example, although face-selective cells can be said to form a sparse code for the presence of a face, some such cells have been found to be broadly tuned to various facial dimensions, and hence to participate in a population code for face shape [30]. Conversely, simple object features could be represented sparsely, whereas at the level of entire objects representations might be coded by populations of sparse neurons [31]. In such a population-coding scheme, the representation of an entire object could arise from spike correlations among individual neurons, each coding for different parts of the object [32].

Thus, the ventral visual pathway contains representations varying in their degree of sparsity, with some neurons coding shape features that will be found in many objects, and others responding only to specific object categories or even only to specific people or places.

Clustered versus distributed representations of objects

How are neural representations of objects arranged spatially in the cortex? Are the neurons that are active in response to a given object clustered together, or are they spread across centimeters of the ventral visual pathway (Figure 1)? Clustering of functional properties in the cortex has been described on many scales, from columns to 'patches' to topographic maps and cortical areas. It has been argued that such functional clustering arises because wiring (i.e., axons and dendrites) costs can be minimized by placing functionally related neurons near each other in the cortex [33•]. Thus to the extent that functional clustering is found within the ventral visual pathway this may indicate an important role for local computations in these regions. One such possibility is that clustering enables sharpening of within-class selectivities through lateral cortical connections [34,35]; an hypothesis that would imply a causal link between sparsity and clustering. Another speculative possibility is that clustering

minimizes the risk that the responses of different neural populations contributing to the representation of a given object will be temporally out-of-phase with each other because of conduction delays along the ventral visual pathway. However, it should be noted that just because clustering of selectivities is a prominent feature of the cortex need not imply that such clustering has any important functional significance. Indeed, it has recently been argued that even the very well established and much studied ocular dominance columns do not serve any purpose [36].

In the case of object representation, physiological investigations in monkeys have found quasi-columnar clustering of object selectivity on the scale of 400 to 800 microns [18,37] as measured by spiking activity, and on a substantially larger scale (5 mm) as measured by local field potentials (LFPs) and optical imaging studies [38]. Furthermore, results from functional magnetic resonance imaging (fMRI) studies showing selective responses to specific object classes also imply some clustering, at least within the span of a single voxel (1–3 mm); without such clustering, selectivity would be invisible in the pooled response of the hundreds of thousands of neurons in each voxel. FMRI studies in humans have shown localized regions of cortex that respond selectively to specific image categories: faces produce selective activations in the fusiform face area (FFA) [39–43], places and scenes in the parahippocampal place area (PPA) [44,45], bodies in the extrastriate body area (EBA) [46] and fusiform body area [47,48], and letter strings and words in a region of the left fusiform gyrus [49,50]. These highly specific regions, each of which can be identified in approximately the same location in any normal subject, are defined by fairly sharp peaks in spatial activation profiles [51]. Face- and body-selective regions have also been found in macaques using fMRI [52,53], and face-selective regions have been identified at single-cell resolution in marmosets using immediate-early gene expression [54••]. However, category-selective regions might, in general, be rare in the ventral pathway; for the most part, clusters of category selectivity for other stimulus classes in humans have not been observed reliably, at least at the standard resolutions used in fMRI studies [47].

These considerations suggest that at least for some categories, object representations are localized to focal regions of cortex. In an important challenge to this idea, Haxby and co-workers [55,56] argued that weak or 'non-selective' responses to objects across the ventral visual pathway could carry information about object category. According to this view, each object category would be represented not merely by a strong response in a small region of cortex but by the entire distributed, graded and overlapping pattern of activation across the ventral visual pathway [55,56]. Indeed, mathematical analyses indicate that optimal estimations can be attained not by focusing

exclusively on the most informative signals but instead by summing evidence from multiple sources, each weighted by its reliability [57]. Evidence that information is in fact contained within 'non-selective' responses comes from demonstrations that activation patterns for many object classes are different enough from each other to enable discrimination of object categories based only on regions with relatively low responses to the objects in question [55,56,58–60]. However, not all regions in the ventral temporal cortex appear to be equally involved in representing diverse object categories. In particular, clusters such as the FFA and PPA, which can easily discriminate between preferred and nonpreferred image categories, perform significantly worse at classifying nonpreferred objects, suggesting that at least some regions are primarily involved in the processing of a single stimulus class [58,61•].

FMRI, of course, has limited spatial resolution, with each voxel comprising millions of neurons at standard resolution, and tens or hundreds of thousands of neurons at 'high resolution'. Both the selectivity and the clustering in any region of cortex will look quite different at higher resolution. Recent studies that are pushing the resolution of fMRI are finding increased patchiness [62] and functional heterogeneity [63] in face-selective regions. At the same time, increased spatial resolution can reveal new and sharper selectivities that were not apparent at lower resolution [48,64].

Despite the recent improvements in the resolution of fMRI, any fMRI evidence that discriminative information is not contained in the profile of nonpreferred responses (see glossary) will be weak, because such results can always be trumped by higher resolution methods that reveal that such information is present after all. Thus, ultimately the question of whether neural responses can distinguish between nonpreferred stimuli (see glossary) can only be resolved by the gold standard in neuroscience of single-unit recording. Two recent studies provide crucial new insights on just this question. Using fMRI in macaques to locate face-selective patches, Tsao et al. [65••] then directed electrodes into a patch to record from the neurons that comprise it. A staggering 97% of the neurons in this region responded selectively to faces, and indeed nearly exclusively so. This study provides the strongest evidence to date for both selectivity and clustering of visual object representations in the ventral visual pathway. And the nearly exclusive response of this region to faces leaves little room for this patch of cortex to play an important role in the representation of nonface stimuli. Furthermore, Afraz et al. have recently demonstrated that microstimulation of a cortical region with a high concentration of face-selective cells increased the monkey's bias to report that a stimulus was a face, thus demonstrating the causal role in face perception of this region of IT [66••].

Nonetheless, even if face-selective patches are exclusively involved in representing faces, it is still possible that the rest of the ventral pathway might also participate in the representation of faces. However, evidence that such broader regions are not sufficient for face perception comes from a case of selective loss of face recognition (prosopagnosia) resulting from a very small lesion in just this region [67], and from electrical microstimulation studies that target small regions of cortex and produce selective disruptions of face perception [68,69]. Similarly, recognition of body parts was selectively disrupted by transcranial magnetic stimulation (TMS) to the EBA [70•], indicating that this region is necessary for normal recognition of body parts. Finally, a new study shows that surgical removal of a very small region of cortex just posterior to (and hence presumably deafferenting) the letter-string selective region in the left fusiform gyrus leads to a selective deficit in visual word recognition [71•]. Thus even if discriminative information about a given category exists outside the cortical regions that respond maximally to that category, that information is not sufficient for normal perceptual performance, at least for object classes such as faces, bodies and words. These findings are thus consistent with our conjecture that representations of some visual categories (including faces, bodies, and words) are largely concentrated within focal regions of cortex that respond very selectively to that category.

Concluding remarks

We have argued that visual objects are often represented in the ventral visual pathway by groups of very selective neurons (thus comprising relatively sparse representations), and that these neurons are often clustered near each other in the cortex. Note, however, that the sparse and clustered representations for faces and some other categories described here may be atypical; for most other object categories (aside from bodies, letter strings, and places) such sparse and clustered representations have not yet been reported [47].

What then are the crucial factors that determine when sparse and clustered codes are used in the nervous system? One possibility is that familiarity with the objects being represented might influence their representations. FMRI studies have shown that both specificity and clustering can increase with stimulus familiarity [72], for example in the case of the letter-string-selective region in the left fusiform gyrus [50,73]. At the neuronal level, training enhances selectivity [74,75,76•], thus resulting in sparser representations. Training also appears to make neighboring neurons more likely to respond to similar features, making representations more clustered [77]. Thus, increased familiarity with a stimulus class might make the corresponding representations first, more sparse, and therefore less susceptible to the binding problem and less reliant on attention [13], and second,

more clustered, and therefore better suited for rapid local computation and efficient readout.

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