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Sparse coding of sensory inputs

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Several theoretical, computational, and experimental studies suggest that neurons encode sensory information using a small number of active neurons at any given point in time. This strategy, referred to as 'sparse coding', could possibly confer several advantages. First, it allows for increased storage capacity in associative memories; second, it makes the structure in natural signals explicit; third, it represents complex data in a way that is easier to read out at subsequent levels of processing; and fourth, it saves energy. Recent physiological recordings from sensory neurons have indicated that sparse coding could be a ubiquitous strategy employed in several different modalities across different organisms.

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Abbreviations
V1   primary visual area

Introduction

At any given moment, our senses are receiving vast amounts of information about the environment in the form of light intensities, changes in sound pressure, deformations of the skin, stimulation of taste and olfactory receptors and more. How the brain makes sense of this flood of time-varying information and forms useful internal representations for mediating behavior remains one of the outstanding mysteries in neuroscience. In recent years, a combination of experimental, computational, and theoretical studies have pointed to the existence of a common underlying principle involved in sensory information processing, namely that information is represented by a relatively small number of simultaneously active neurons out of a large population, commonly referred to as 'sparse coding'.

In this review we discuss the theory of sparse coding, methods for measuring sparsity, and the evidence to date

that sparseness constitutes a general principle of sensory coding in the nervous system. We focus here primarily on neural representations in the cortex of mammals, or relatively high levels of processing in other species, but it should be noted that there is substantial evidence for sparse coding occurring at earlier stages of processing across a variety of organisms [1,2].
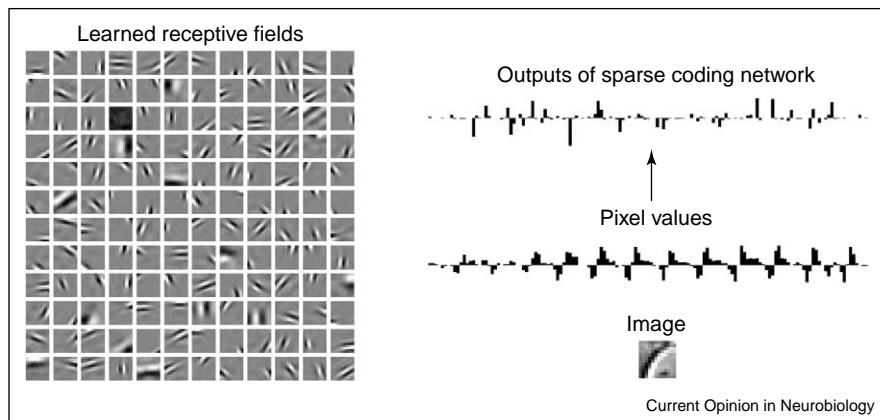
Theory of sparse coding

The principle of sparse coding has been advanced and elaborated on by several different authors, for different reasons. Early work on associative memory models, for example, showed that sparse representations are most effective for storing patterns, as they maximize memory capacity because of the fact that there are fewer collisions (less cross-talk) between patterns [3]. Later work has similarly showed that sparse representations would be advantageous for learning associations in neural networks, as they enable associations to be formed effectively using local (neurobiologically plausible) learning rules, such as Hebbian learning [4–9].

A different line of reasoning was taken by Barlow [10], who observed that in many sensory nervous systems neurons at later stages of processing are generally less active than those at earlier stages. Barlow reasoned that the nervous system was attempting to form neural representations with higher degrees of specificity. For example, a neuron in the retina responds simply to whatever contrast is present at that point in space, whereas a neuron in the cortex would respond only to a specific spatial configuration of light intensities (e.g. an edge of a particular orientation) [11].

Several computational studies conducted since Barlow made this proposal have demonstrated more concretely the relationship between sparsity and the statistics of natural scenes. In the visual system, for example, the images that fall upon the retina when viewing the natural world have a relatively regular statistical structure, which arises from the contiguous structure of objects and surfaces in the environment [12–17,18•]. Field [12] has shown that the receptive field properties of simple-cells in primary visual cortex (V1) are well suited to this structure, in that they produce sparse representations. Our work, and that of others [19–23], has subsequently shown that when the receptive fields of an entire population of neurons are optimized to produce sparse representations, that the set of receptive fields that emerge resemble those of simple-cells (Figure 1). A similar analysis has shown that the spectro-temporal receptive field properties of auditory nerve cells can be accounted for in

Figure 1

Sparse coding of natural images. On the left is a set of receptive fields that are learnt by maximizing sparseness in the output of a neural network. Each patch shows the receptive field of a model neuron within a 12 × 12 pixel image patch. The network was trained on approximately half a million image patches (of the same size) extracted from whole images of natural scenes. The receptive fields that emerge from training are spatially localized, oriented, and bandpass (i.e., selective to spatial structure at a particular scale), similar to cortical simple cells. On the right is an example image patch and its encoding by the sparse coding network. The bar chart directly above the image patch shows the 144 pixel values contained in the patch. These input activities are transformed into a much sparser representation in the output of the network, shown in the bar chart at the top. The value of an output unit corresponds (roughly) to the degree of similarity between its receptive field and the input image. As the receptive fields are matched to the structures that typically occur in natural scenes, an image can usually be fully represented using a small number of active units.

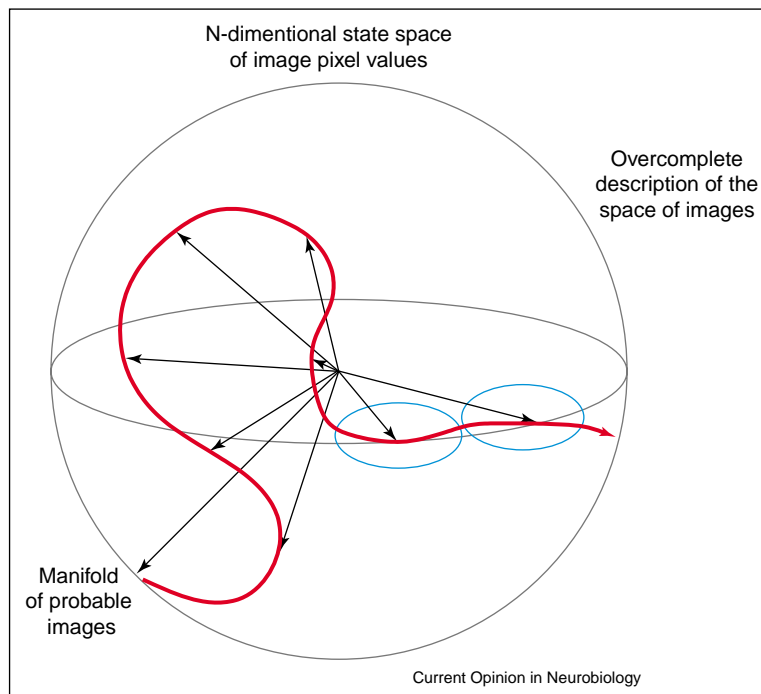terms of a strategy to represent natural sounds as sparse independent events [24••,25].

Several theorists have proposed that natural images (as well as other sensory data) lie along a continuous curved surface or 'manifold' embedded in the high-dimensional state space of images (i.e., where pixel magnitudes form the axes of the space — see figure 2) [26•,27,28•,29]. The surface represents the smooth changes that follow from the transformations that are likely to occur in natural scenes (e.g., translation, scale, rotation, etc.). For example, an object that moves across the pixel array of an image gives rise to a series of different spatial patterns. Each of these spatial patterns corresponds to a point in the state space, and the set of all points resulting from this motion would form a smooth, curved trajectory in the state space (Figure 2). So how can the visual system represent this curved surface of probable images? One possibility is that this is achieved through an overcomplete representation of the state space, in which the number of neurons used to represent the image is potentially much greater than the dimensionality of the input (number of pixels) [30–32]. In this coding scheme, each neuron would have a preferred pattern in the input space (represented by the vectors in figure 2), and a neuron would become active only when the input pattern is sufficiently close to its preferred pattern. We suggest that the advantage of such a coding scheme is that the manifold then becomes flattened out (less curvature) in the higher-dimensional space defined by the neural responses, thus making it easier for higher

areas to learn structure in the data (i.e., the shape of the manifold).

Interestingly, a ubiquitous property of primary sensory cortical areas is that they over-represent their sensory inputs (as relayed from the thalamus) many times over. For example, in cat V1 there is an approximate 25:1 expansion ratio in terms of the number of axons projecting from layers 2/3 on to higher areas relative to the number of inputs from the lateral geniculate nucleus [11]. One possibility, then, is that this over-representation is utilized to produce an even higher degree of sparsity among neurons by making them more selective to specific patterns of input, hence making it possible for higher areas to learn structure in the data. If the idea of sparse overcomplete codes is carried to an extreme, however, it inevitably leads to a 'grandmother cell' type representation, in which a single unique neuron is active for each and every event occurring in the environment [33]. Thus, there is a tradeoff between the gains achieved from overcompleteness and the cost incurred from having to utilize more neurons, and it is possible that the 25:1 expansion in cat V1 is the result of striking the proper balance between these two factors.

Another reason for favoring sparse codes is that they are energy efficient [34]. Attwell and Laughlin [35] have recently produced an estimate of the energy required for signaling in cortical neurons, and they conclude that average firing rates must be rather low, that is, less than

Figure 2

State-space of natural scenes and overcomplete codes. The sphere represents the N-dimensional state-space of natural scenes — that is, the space of all possible images composed of N pixels. The axes of this space (not shown) are simply the pixel values of the image. Natural images are thought to lie along a low-dimensional manifold embedded in this space. The red curve represents the hypothetical trajectory of an image feature (such as an edge) as it would appear in this space as a result of translating over the pixel array. Each black arrow corresponds to the preferred feature of a neuron. The blue ellipses denote the response zone of the neuron — that is, an image falling within this zone would cause the neuron to fire. The representation is 'overcomplete' when there are more pattern vectors than input dimensions (image pixels). N pattern vectors would be sufficient to represent the manifold, but a sufficiently dense (highly overcomplete) tiling allows for a piecewise representation of a highly curved manifold, thus simplifying its representation for higher stages of analysis.

1 Hz. On the basis of their findings, Lennie [36•] estimates that at any given moment only 1/50th of the population of cortical neurons could afford to be significantly active. Thus, given the actual energy constraints of the mammalian cortex, sparse coding would seem to be a necessity.

To summarize, there are at least four reasons for favoring sparse representations as a model of sensory signaling. First, they are useful for forming associations or storing patterns in memory using local learning rules, second, they make the structure occurring in natural sensory input explicit, third, they produce a more simple flattened representation of the curved manifold structure of data (when combined with overcompleteness), and fourth, they are energy efficient.

How to measure sparseness?
To assess whether or not neurons are utilizing a sparse code, there must be a method for measuring sparseness. Many of the coding models described above employ analog-valued units that could take on both positive and negative values, with responses symmetrically dis-
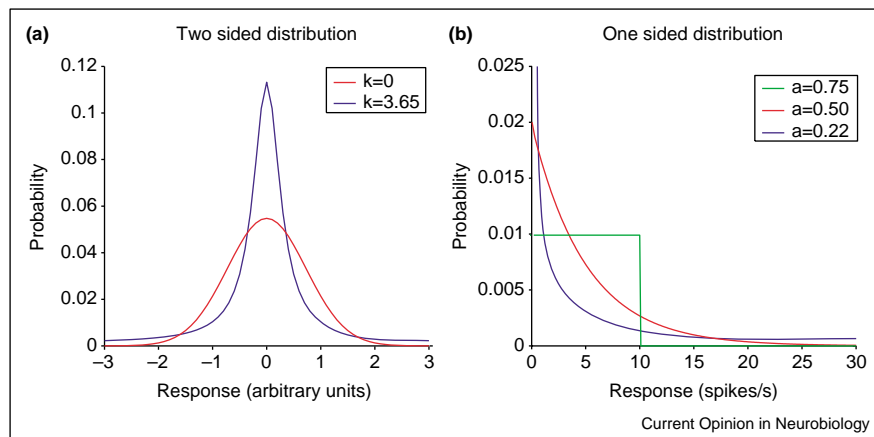
tributed around zero (Figure 3). A standard measure of sparseness for such artificial units is the kurtosis, which measures the 4th moment relative to the variance squared:

$$k = \frac{1}{n}\sum_{i=1}^{n}\frac{(r_i - \overline{r})^4}{\sigma^4} - 3$$

where r is the response of the neuron, $\overline{r}$ is the mean response and σ is its standard deviation. For a Gaussian (non-sparse) distribution $k=0$, whereas for a heavy-tailed (sparse) distribution $k>0$. However, in reality a neuron cannot produce a response that is symmetric about zero, or even symmetric about the mean firing rate. Thus, its firing rate distribution will necessarily be one-sided. In addition, measures such as kurtosis are extremely sensitive to outliers — that is, a small number of data points far from the mean can have a significant impact on kurtosis.

Baddeley and co-workers [37] have shown that when an animal views movies of natural scenes, the response distributions of many visual cortical neurons display a

Figure 3

Response distributions and sparseness. **(a)** Examples of two-sided response distributions for a unit that takes on both positive and negative values. A sparse representation would be consistent with a response distribution that is highly peaked at zero and with heavy tails (blue) compared to a Gaussian of the same variance (red). The former has positive kurtosis (k). **(b)** Examples of one-sided response distributions for a unit that takes on positive values only (e.g., firing rate). All distributions shown have the same mean firing rate. When plotted in this manner, a response distribution that is peaked at zero with heavy tails (blue) would be considered sparse, whereas a uniform response distribution (green) would not. The former has a low activity ratio (a) whereas the latter has a high activity ratio. The exponential distribution (red) lies somewhere in between. Note that measures of kurtosis (k) and activity ratio (a) are dimensionless.

heavy-tailed distribution that can be described by an exponential function, $P(r) \propto e^{-\alpha r}$. Although such a distribution would be consistent with the sparse coding hypothesis, they argue instead that such distributions support the notion that neurons are trying to maximize entropy, subject to a constraint on mean firing rate (energy consumption).

Rolls and Tovee [38] developed a sparseness measure for one-sided distributions, and their approach has been applied to a number of neuronal populations and stimulus sets [39,40•]. Their method provides a means of describing a distribution with heavy tails by computing the activity ratio:

$$a = \frac{\left(\frac{1}{n} \sum_i r_i \right)^2}{\frac{1}{n} \sum_i r_i^2}$$

where r_i is the response to the ith stimulus averaged across trials (e.g. the ith frame of a movie) and n is the number of stimuli. This ratio has a maximum value of 1.0 when each stimulus or frame receives equal numbers of spikes, and is near zero when one stimulus from the set of stimuli, or one frame, contains all the spikes (maximum sparsity). Vinje and Gallant [39] have transformed this ratio to obtain a convenient sparseness scale, 'S', that ranges from 0 to 1: $S = (1 - a)/(1 - a_{\min})$. Thus, S measures how selective the neuron is to the population of stimuli presented to it. The result can be dependent on the size of the temporal window used to compute the firing rate, but
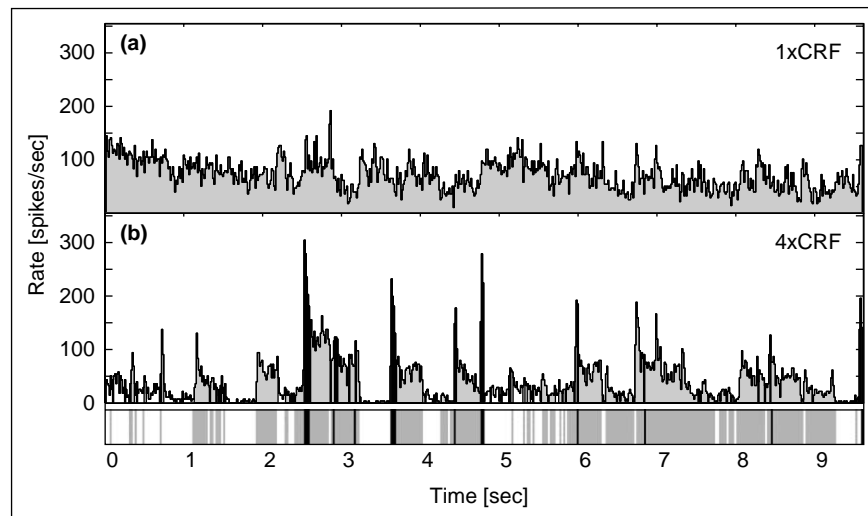
provides a good measure of the relative sparseness of responses under different conditions.

However, measuring the response of a neuron over time does not provide a complete account of how the population behaves with regards to sparsity. A population of neurons could appear sparse according to the above measures even though all of them are firing together. For example, neurons involved in driving eye movements or responding to a stimulus after a saccade would show significant correlations to each other. Willmore and Tolhurst [41] use the term 'lifetime sparseness' to describe the activity of a single neuron over time, and 'population sparseness' to describe the activity of a population of neurons for a given time window. One form of sparsity does not necessarily imply the other. Most investigators have measured lifetime sparseness using single-unit recording, but there have been recent attempts at measuring population sparseness by using multiple electrode arrays to monitor activity at several recording sites simultaneously [40].

Experimental evidence
Experimental evidence for sparse coding has been found in several different sensory modalities in a variety of animals. In the visual system of primates, Vinje and Gallant [39,42••] have demonstrated that neurons in V1 produce sparse punctate responses when stimulated with image sequences resembling those that occur during natural vision (Figure 4). Interestingly, when the same neurons are stimulated only within their classical receptive fields (the region of space within which a stimulus

Figure 4

Responses to natural scenes. Context in natural scenes sparsifies responses of V1 neurons. Shown is the average response of a neuron to multiple repetitions of a natural vision movie played just within the receptive field of the neuron (top) or the same movie but with additional spatial context extending into the receptive field surround (bottom). Context appears to make the neuron more selective to certain episodes within the movie sequence. Taken from [42••], with permission. Copyright 2002 by the Society for Neuroscience.

presented in isolation can evoke a response from the neuron), the responses are much more dense or evenly distributed over time. Thus, it would appear that context sparsifies the responses of V1 neurons. These effects could possibly be mediated either by recurrent horizontal connections within V1 or by top-down feedback from higher areas. In higher visual areas (inferotemporal cortex), it has been suggested that the population code response to faces is sparse [43], but others claim that the activity ratio favors more of a dense code [38].

In the auditory system of rats, DeWeese and co-workers [44••] have demonstrated that neurons in primary auditory cortex can produce a single spike in response to a sound, and that this response is highly reliable across trials. They refer to this behavior as 'binary coding', as the neuron appears to produce either a 0 or a 1 in response to a stimulus. The probability of spiking overall appears to be very low, consistent with the sparse coding hypothesis, although it remains to be seen whether or not this effect can be attributed to anesthesia. Very low firing rates have also been reported for neurons in layer 4 of somatosensory (barrel) cortex in the rat, where it is hypothesized that relatively few (in the order of tens) unitary inputs locked precisely to whisker deflection are sufficient to produce a response in a neuron [45•]. Sparse coding has also been observed in the olfactory system of insects, where neurons in the mushroom body typically issue on the order of two spikes in response to an odor stimulus [46•,47••,48••].

It has been known for some time that neurons in the hippocampus can exhibit extremely sparse responses.

One experiment showed that nearly two-thirds of all hippocampal neurons that exhibited activity under anesthesia became silent in the awake behaving rat [49], which suggests that these neurons are so rarely active that it can be difficult to observe them firing during natural behavior. This overall pattern appears to be upheld in the macaque hippocampus, where overall firing rates below 0.1 Hz are routinely observed [50].

Although this review is focused on sensory coding, it should be mentioned that the principle of sparse coding extends to motor systems as well. For example, certain classes of neuron in layer 6 in the motor cortex of rabbits issue one spike or less during certain phases of locomotion [51], and in rats, single neuron stimulation can be sufficient to elicit whisker movement [52•]. In the zebra finch, neurons in nucleus HVC (higher vocal center) can issue one spike with high reliability at a precise moment in time within the production of a song sequence [53], and it has been demonstrated that this scheme makes it easier to learn song production [54].

Extreme sparseness appears to present a quandary for attempting to characterize the response properties of neurons. Traditional methods using single acute electrodes rely on the ability of the investigator to elicit a response from a neuron. But if some neurons fire so rarely that they do not spike within the time the investigator is searching for a neuron, they are likely to be missed. Reports routinely appear in the literature of neurons in both sensory cortex and hippocampus with spontaneous rates of 5 Hz and above, whereas Attwell and Laughlin's

analysis states that the average should be much lower [35], which suggests that there has been a routine sampling bias in many studies. By contrast, recording techniques that utilize chronic implants, which yield a less biased sample (B Skaggs, pers comm), or antidromic stimulation to identify neurons [51,53$^{\bullet\bullet}$], report much lower firing rates on average.

Conclusions

Although the principle of sparse coding has been discussed and elaborated for nearly three decades now, serious empirical investigation of its use in the nervous system has begun only recently. Investigating whether sparse coding is employed in a certain region, however, will require using ecologically valid stimuli (i.e. natural scenes). The studies reviewed here suggest that sparse coding provides an efficient means of representing data found in the natural world. Moreover, it provides a means of efficiently forming associations and storing memories, and it achieves all of this using relatively small amounts of energy. Future work might point to new explanations for these sparse patterns of activity. In any case, it appears that sparse representations constitute an important processing strategy of the nervous system.

Acknowledgements

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