

---

## CHAPTER 10

---

### **SPARSE CODING OF FACES IN A NEURONAL MODEL: INTERPRETING CELL POPULATION RESPONSE IN OBJECT RECOGNITION**

Arnold Trehub  
Department of Psychology  
Neuroscience and Behavior Program  
University of Massachusetts, Amherst

#### **ABSTRACT**

Response to faces as measured by cell discharge in the temporal cortex of monkeys suggests a sparse cell-population coding of complex visual stimuli. The prevailing view assumes that a sparse population code requires the joint contribution of a relatively small group of cells (a neuronal ensemble) for effective coding and recognition. This assumption is based primarily on the consistent observation that single cells in the temporal cortex are broadly tuned rather than narrowly tuned to individual faces. It has been argued that the joint activity of a relatively small number of broadly tuned cells, each responsive to a different constituent feature of a face, could form an ensemble code selective enough to distinguish individual faces. In the present study, schematic faces were presented as stimuli to a model neuronal system for visual pattern learning and recognition. This model effectively codes individual faces by means of competitive activity among single cells during recognition instead of by ensemble coding. The computer simulation permitted an analysis of the activity profiles of all tuned cells during learning and recognition of the faces. All cells were found to be broadly tuned even though coding was mediated by the discrete output of single cells on a competitive basis in a sparse neuronal population rather than by the joint activity of a group of cells. The results show that the observation of broad tuning of cells in temporal cortex under typical experimental conditions does not warrant the conclusion that neuronal ensembles are required for the coding of individual faces. Suggestions are made for changes in the design of experiments to better test hypotheses about the coding of faces (or any other complex visual patterns).

#### **Introduction**

A central question for our understanding of visual pattern recognition in the brain is how neurons in the visual system code perceived objects. Face recognition is a particularly important aspect of complex pattern recognition and, following the early reports of face-selective cells in the temporal cortex of

monkeys (Gross, Rocha-Miranda, & Bender, 1972; Desimone, Albright, Gross, & Bruce, 1984), there has been a major effort to understand the neuronal coding of faces (see, for example, Kosslyn & Mumford, 1991; Bruce, Cowey, Ellis, & Perrett, 1992).

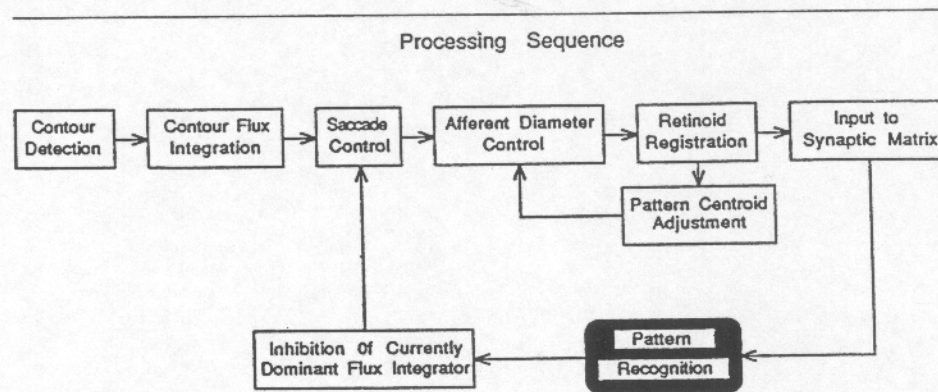
In the typical experimental procedure, the spike discharge of single cells in the inferior temporal cortex of the monkey is recorded while the animal is presented with pictures or drawings of faces. It has been observed that cells which selectively discharge in response to faces as a stimulus class exhibit broad tuning curves in response to the faces of particular individuals. Mainly on the basis of this observation, the prevailing view is that single cells cannot adequately account for selective recognition of individual faces. Instead, it has been proposed that the neuronal processing is in the form of a sparse population code wherein face recognition requires the joint contribution of a small population of cells, each selectively responsive to the presence of a different facial feature (Baylis, Rolls, & Leonard, 1985; Young & Yamane, 1992). In this formulation, it is the *pattern* of activity over an ensemble of cells (a joint activity vector) that constitutes the recognition code (Gross, 1992; Gross & Sargent, 1992).

An unresolved issue is how a neuronal population code, sparse though it may be, can selectively evoke a correct recognition response to a particular member of a stimulus category. This paper examines the activity levels of individual cells in a simulated neuronal model of visual object recognition when the system is required to learn and recognize each face in a group of line-drawn faces. Analysis of cell response profiles suggests an alternative interpretation against the common view that sparse coding of a complex visual pattern such as an individual face implies a neuronal ensemble of separately coded features. The results indicate that instead of a coding scheme based upon an ensemble of separate features, a sparse group of cells where each is holistically tuned to a different exemplar of a particular face provides effective face recognition.

#### **Brief Description of Model**

The neuronal model simulated here (Trehub, 1991, chapters 2, 3, 4, 5, and 7) consisted of five key integrated mechanisms: (1) a 16x16-cell foveal retina; (2) a mechanism for triggering saccadic excursions to regions of high edge density in the visual field; (3) a putative post-retinal mechanism for positioning the centroids of retinotopic excitation patterns close to a standard internal axis (stimulus capture); (4) a learning mechanism for tuning synaptic transfer weights on individual adaptive cells (filter cells) in a detection set to patterns of retinal stimulation; (5) a competitive (winner-take-all) mechanism that selects a recognition response contingent on the relative activation levels of cells in the detection set in the context of each stimulus. The spike frequency of each cell can be considered as a positive monotonic function of its activation level.





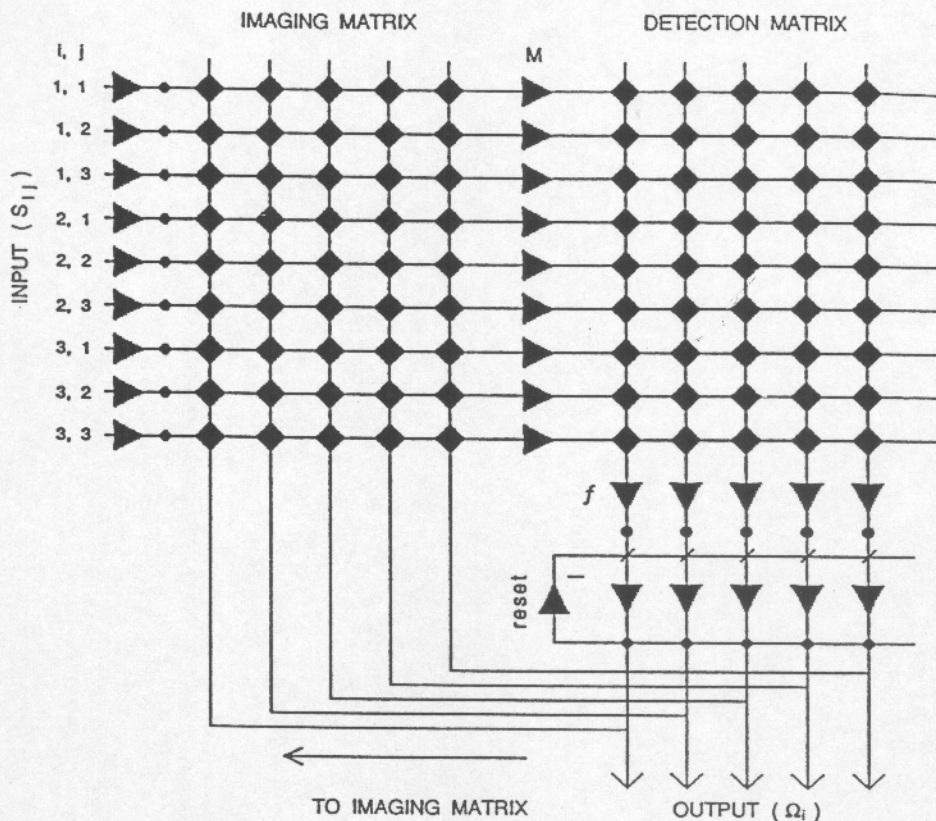
**FIGURE 1.** Processing sequence for parsing an object in a complex visual environment.

Figure 1 illustrates the processing sequence for parsing an individual face out of the set of 10 faces presented in the model's visual field. The total field is analyzed by an array of retinotopically indexed cells (flux detectors), each of which receives input from a relatively small region of the complete retinal field. Each flux detector integrates the amount of visual contour excitation in its particular retinal region and discharges with a frequency proportional to its total excitation. The contour flux detectors feed a matched array of cells that control visual saccades. The flux detector with the highest discharge frequency captures control of the saccadic apparatus and directs a saccade to the circumscribed visual region that provides its input. Thus, the region of visual space with the highest contour density will be fixated first.

There is a field constriction mechanism that limits the fovea-centered aperture of retinotopic input to a short-term memory module called a retinoid (Treuhub, 1977). The retinoid can translate retinotopic excitation patterns over cells in an egocentric coordinate space. It is quadrantally organized, and automatically locates and positions pattern centroids on a standard reference axis within the visual system by shifting its visual pattern so that excitation is balanced within a threshold of tolerance over all quadrants. At the start of the parsing process, the visual field aperture is constricted to a small window on the stimulus field and an initial tolerance level is set for hemifield mismatch in the retinoid system. The centroid of the current effective visual pattern is then shifted to the standard egocentric reference axis. The visual aperture is progressively enlarged in a stepwise fashion and, at the same time, the system relaxes its tolerance for quadrant-excitation imbalances. At each step, the

system seeks to adjust the current centroid of the stimulus component within the afferent aperture so that it lies approximately on the reference axis. When the visual aperture reaches a limiting size, the pattern of retinoid excitation in its standardized position within the aperture is projected to a neuronal mechanism for learning and recognition called a synaptic matrix (Trehub, 1991).

A schematic of the synaptic matrix is shown in **Figure 2**. Its structural properties and the learning rule can be briefly summarized as follows. Retinotopic afferents  $S_{ij}$  are in discrete point-to-point synapse with a following set of



**FIGURE 2.** Schematic of a synaptic matrix. Afferent inputs are designated  $S_{ij}$ . Mosaic cells are designated  $M$ . Dots represent fixed excitatory synapses; short oblique slashes represent fixed inhibitory synapses; filled lozenges represent adaptive excitatory synapses. Reset neuron (-) generates an inhibitory postsynaptic potential to reset all class cells when discharged. Given any arbitrary input to the synaptic matrix, the class cell coupled with the filter cell having the highest product sum of afferent axon activity and corresponding transfer weights will fire first and inhibit all competing class cells.



neurons, called mosaic cells ( $M$ ). The axon of each mosaic cell is in parallel adaptive synapse with all members of a set of cells in the detection matrix, which are called filter cells ( $f$ ). Each filter cell is in discrete synapse with an output neuron called a class cell ( $\Omega$ ). Each class cell integrates the activation input from its coupled filter cell. The axon of each class cell bifurcates and sends a collateral back in adaptive synapse with the dendrites of all mosaic cells ( $M$ ) in the imaging matrix. Finally, a reset neuron (marked  $-$ ) receives excitatory input from the axons of all class cells ( $\Omega$ ) and sends its own inhibitory input back in parallel synapse with all class cells. Integration of filter-cell input to paired class cells, together with the reset mechanism, ensures that the class cell that receives the highest activation from its coupled filter cell will fire first and inhibit all competing class cells.

One-trial learning of a visual stimulus pattern takes place by modification of adaptive synapses on filter cells in the detection matrix and mosaic cells in the imaging matrix. (In this simulation, processes taking place in the imaging matrix will not be discussed.) The magnitude of learning-related changes in synaptic transfer weight ( $\phi$ ) are determined according to the following expression:

$$\phi_{im} = b + S_{im} (c + kN^{-1}) \quad (1)$$

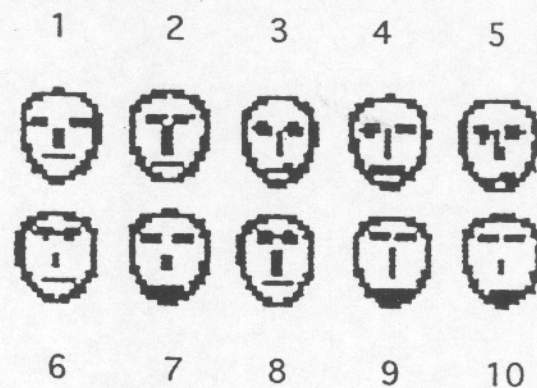
$b \rightarrow Lim$

where  $\phi_{im}$  is the transfer weight of synapse  $\phi_{im}$ , from the basal value ( $b$ ) to the saturation limit ( $Lim$ ), on an adaptive filter cell  $m$ ;  $b$  is the initial transfer weight of the unmodified synapse;  $c$  is a fixed synaptic contribution from the active axonal contact on  $\phi_{im}$ ;  $kN^{-1}$  is a proportional synaptic contribution taking account of  $N$  coactive axons on the cell  $m$  at the time of learning, and a synaptic modification constant  $k$ ; and  $S_{im}$  is the activity level of axonal input at  $\phi_{im}$ . The product sum of afferent axon activity over the mosaic cell array ( $M$ ) and the corresponding synaptic transfer weights ( $\phi$ ) on each filter cell determine its activation level.

The parameter values used in the present study for stimulus capture, learning, and recognition of faces were the same as used in a previous simulation of self-directed learning in a complex environment (Trehub, 1991, chapter 12).

### Procedure

The stimuli that were presented to the model consisted of schematic faces (in pixel display) that had been used in previous experiments to explore perceptual classification in humans. A subset of 10 faces taken from the original line-drawn stimuli used in studies by Reed & Friedman (1973) and Nosofsky (1991) were digitally scanned and reduced in size so that each face was approximately 18 pixels in height. All 10 faces were presented together throughout the simulation.



**FIGURE 3.** Bit-mapped face stimuli. Faces 1-5 are in category A; faces 6-10 are in category B.

The 10 faces could be separated into 2 different categories with 5 faces in each category on the basis of a multidimensional (MDS) analysis of eye height, eye separation, nose length, and mouth height (Figure 3; Reed & Friedman, 1973; Nosofsky, 1991). In the current study, each of the faces was assigned an identifying name and a letter designation indicating that it belonged to category A or B (e.g., Tim-A, Ned-B). Before the start of the recognition procedure, synaptic transfer weights on one filter cell ( $f_1$ ) in the detection set were tuned (weights selectively increased by the learning mechanism) to a random pattern of retinal excitation. This cell evoked the response "RANDOM" whenever it was the most active filter cell in the detection set. On all subsequent trials the neuronal model was presented with all 10 faces in a single display. On each trial, the model retina automatically fixated on an individual face in a quasi-random fashion. The task was to capture a face, report its name (face recognition), and give its category designation. If the response was correct, the operator typed in "yes" and another face was captured and the procedure repeated. If the response was wrong, the operator typed in "no" and a previously unmodified filter cell (e.g.,  $f_2$ ) in the detection set was synaptically tuned to the retinal pattern of the captured face (the current exemplar) by the intrinsic properties of the learning mechanism. Then the operator typed in the appropriate name and category designation which would be evoked by the model whenever  $f_2$  was the most active filter cell. Again, the system captured another face and the same procedure was repeated. Notice that on the first recognition trial, the only possible response that the system could make was "RANDOM", since it had nothing else in its response repertoire. Each response to a captured



face was counted as a trial whether the response was correct and followed immediately by a new capture, or whether it was incorrect and resulted in the exemplar-tuned synaptic modification of another filter cell in the detection set (learning). The simulation proceeded until 400 trials were completed. Performance was examined for face recognition and category designation in each of 16 sequential blocks of 25 trials for each block.

## Results

### *Face recognition and categorization*

Figure 4 shows the learning curves over all blocks. The percentage of correct responses for both face recognition and categorization was characterized by a curve with an initial rapid rise over the first 50 trials followed by deceleration of improvement. The categorization response improved more rapidly than did the recognition of individual faces. At the end of the 400 trials, correct performance for both recognition and categorization was at the 96% level. The conclusion that categorization of faces improved more rapidly than the recognition of individual faces was based on the following considerations. In the simulation, a correct identification of a face also evokes its correct

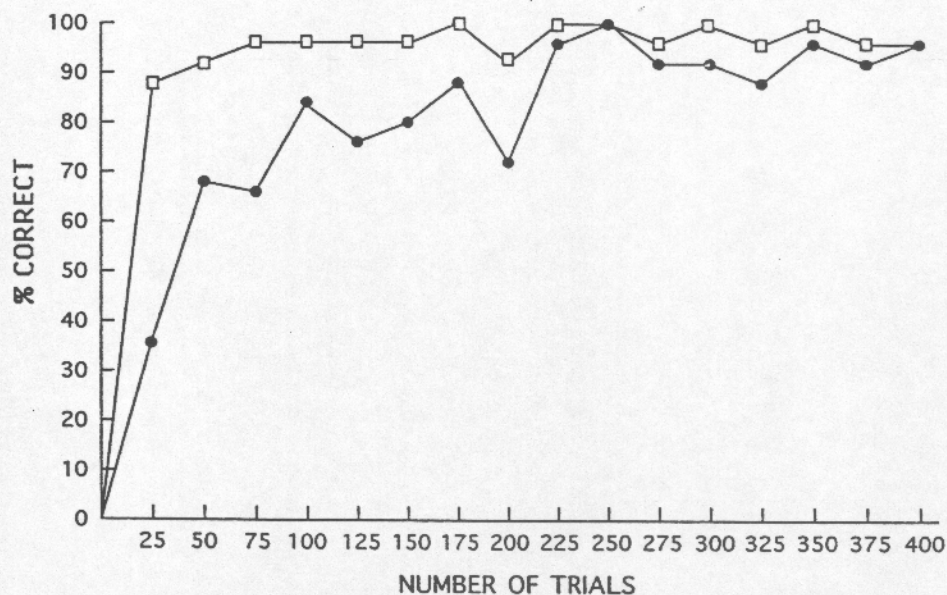
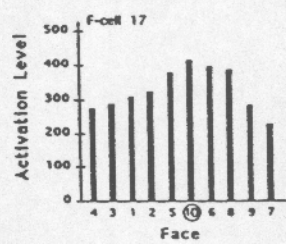
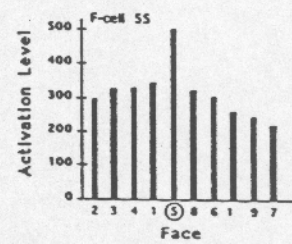
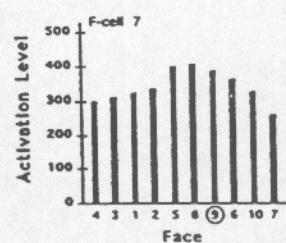
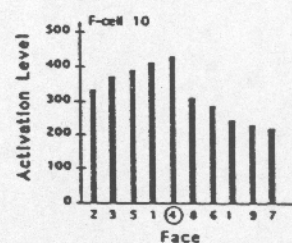
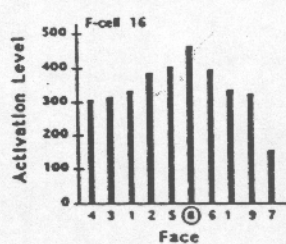
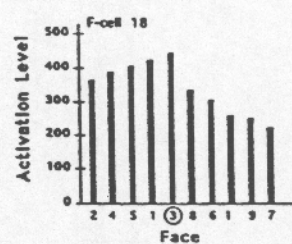
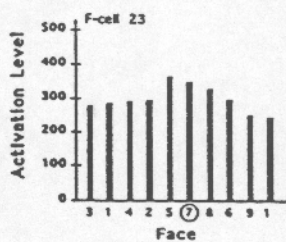
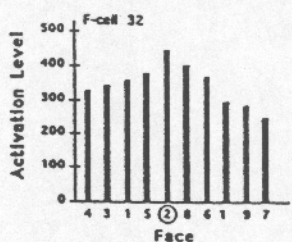
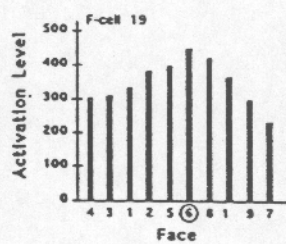
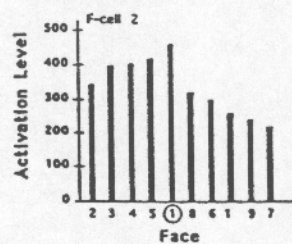


FIGURE 4. Plot of performance. Points plotted show the percent of correct responses over 16 blocks of 25 trials each. Filled circles indicate level of performance for face recognition in each of the successive trial blocks. Open squares indicate level of performance for category designation on corresponding blocks.





category. Only those trials where the identification response was wrong could provide information about the rate of category learning (cat) relative to the rate of recognition learning (rec). Since two categories of faces (A and B) were presented, there was a 50% chance that a wrong identification response would nevertheless name a face in the correct category. Hence on each block of trials we would expect a relative advantage for category performance on the basis of chance alone. Only if the magnitude of the advantage were greater than expected by chance could we conclude that categorization improved more rapidly than recognition. Thus in order to determine if the rate advantage for categorization was significantly greater than chance expectation, the following formula was applied on each block of trials:

$$\text{Exp Adv [cat]} = \% \text{ Correct [rec]} + (100 - \% \text{ Correct [rec]})/2 \quad (2)$$

The differences between the observed percentage of correct categorization and the Expected Advantage [cat] over all 16 blocks of 25 trials provided the data on which to assess the rate of improvement in categorization. There was an unbiased advantage for categorization ranging from +20% on block 1 to +6% on block 8. Over the last eight blocks, the categorization advantage ranged from +4% to 0%. A total of 70 filter cells in the detection set had been synaptically tuned by the learning mechanism to exemplars of the captured faces. All filter cells exhibited broad tuning curves over the faces that were captured. This is illustrated in **Figures 5** and **6** where the activation levels of 10 different filter cells are shown in response to each of the 10 faces. These were randomly selected from the cells that signaled the correct response in a sample drawn from the last 50 trials in which 10 different faces were captured.

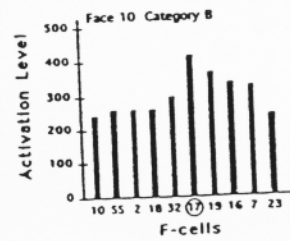
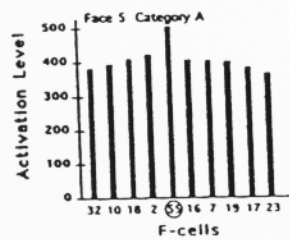
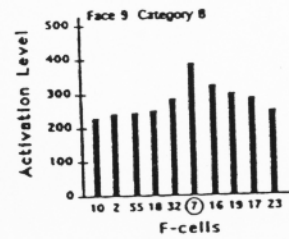
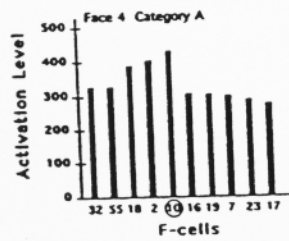
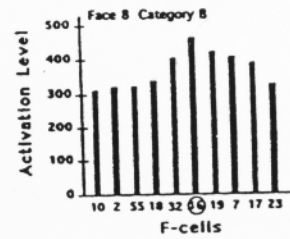
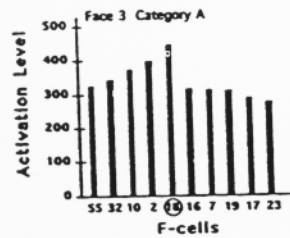
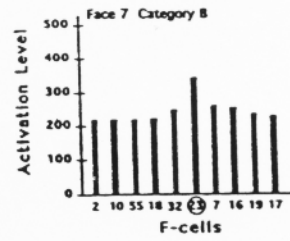
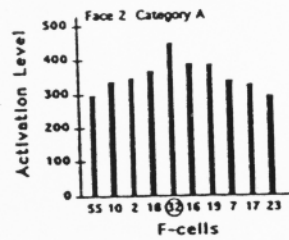
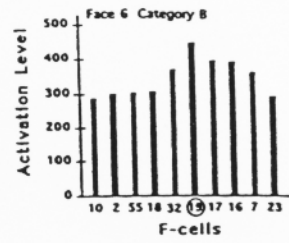
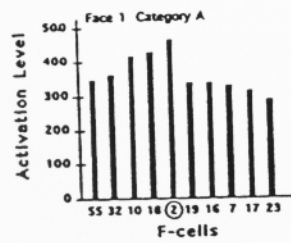
#### *Cell response profiles*

On each trial, the neuronal model selects a discrete recognition response on the basis of competitive activity among cells. The filter cell with the highest activation level evokes its associated name for the face that has been captured while inhibiting the output effects of all other cells. It is important to notice that a filter cell that has been selectively tuned to a particular face can exhibit a stronger response to other faces. This will not degrade the effectiveness of the

---

**FIGURE 5 (left).** Activation levels of each of 10 sampled filter cells (F-cells) in response to exemplars of each of the 10 face stimuli. Activation response of each F-cell plotted against each face. Each F-cell in the left column had been synaptically tuned during learning to one of the 5 faces in category A. Each F-cell in the right column had been tuned to one of the 5 faces in category B. For each cell, the face that it had learned is indicated by being circled. In each of the 10 plots, faces in category A are ordered so that the level of F-cell activation evoked by each face grades down to the left of the distribution; faces in category B are ordered so that the activation they evoked grades down to the right of the distribution.

---





recognition system as long as the response of the correct cell is higher than any other cell in the detection set at the time that its learned exemplar or a pattern most similar to it is captured. For example, it can be seen in **Figure 5** that F-cell 7 gives a stronger response on the trials in which faces 5 and 8 were captured than on the trial in which face 9 (the face it had learned) was captured. Yet, as **Figure 6** shows, the response of F-cell 7 to the capture of face 9 is stronger than any of its competing filter cells when face 9 is the effective stimulus.

The overall selectivity of the recognition system can be characterized by the number of competing filter cells which approach the peak activation level on each trial in which there is a correct response. This is illustrated in **Figure 7** which shows the distribution of the number of competing cells with activation levels within 10% of the peak on all correct trials. It was found that on 31% of the trials there was no competing cellular activity within 10% of the peak response. On 41% of the trials there was only one competing cell within this range. The general shape of the selectivity distribution is similar to the reported distribution of discrepancies between population vectors (ensembles) of unit responses in cells of the macaque inferotemporal cortex and corresponding stimulus (face) vectors (Young & Yamane, 1992).

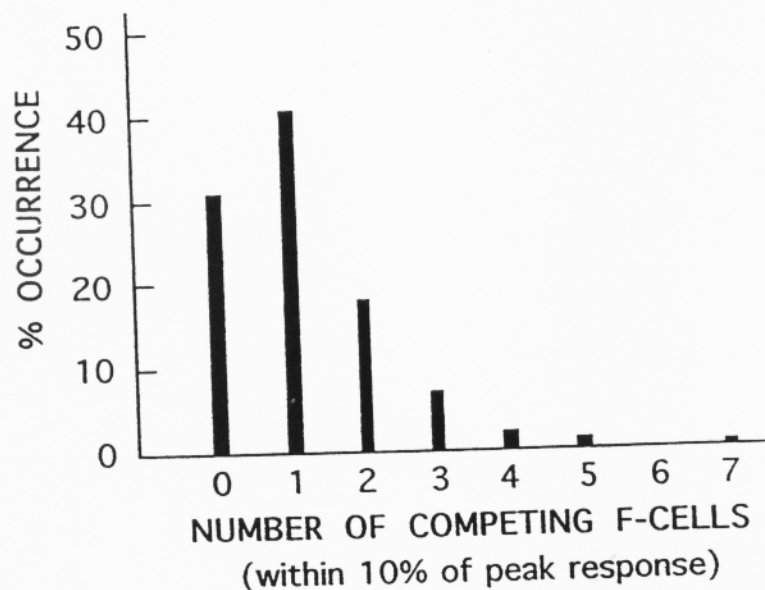
### Implications

It is clear from these results that filter cells exhibit a graded response to all faces and therefore do not exhibit a punctate code. This finding is consistent with some kind of sparse coding mechanism for face recognition. However, the question of how sparse coding is used to ensure reliable recognition is more problematic. It is commonly proposed that a sparse population code entails the *joint* activity of a relatively small number of cells (an ensemble), each making its own necessary contribution to the set of encoded features which, taken together, characterize an individual face (Baylis, Rolls, & Leonard, 1985; Gross, 1992; Gross & Sergent, 1992; Young & Yamane, 1992). Similarly, in the more general context of object recognition, it has been suggested that objects are coded by sparse combinations of active cells where each cell represents the presence of a particular complex partial feature of the object (Tanaka, 1993; Tanaka, Saito, Fukada, & Moriya, 1991). Let us call this kind of code *sparse-code 1*. This approach to the problem of object recognition postulates a structure of overlapping feature detectors (mini-templates) in the visual system

---

**FIGURE 6 (left).** Activation evoked by each face plotted against each F-cell. For each face, the cell that had learned it is indicated by being circled. Cells that had learned faces in category A are ordered so that their response levels grade down to the left; cells that had learned faces in category B are ordered so that their response levels grade down to the right.

---



**FIGURE 7.** Bar graph showing the percent of trials in which differing numbers of competing F-cells had an activation response within 10% of the observed peak response.

that are assumed to be distributed in replicated fashion over the visual field. The critical notion is that each stack of feature detectors (putatively in columnar organization) is tagged by its retinotopic location so that a complete object can be uniquely defined by the whole concurrent activation pattern of a *set* of particular detectors at their particular locations.

However, a caution must be raised here. If, at any given moment, there is only one object in the visual field, then an activated set of spatially indexed features might provide a unique definition of that single object. But what if there is more than one object in the visual field, as is normally the case in the natural world? Under the normal circumstance, we would need a biologically plausible mechanism that is able to map our complex retinal activation patterns onto just those discrete groups of spatially-indexed feature detectors that correspond to each of the separate objects in view (the binding problem). This is not a trivial problem. Indeed, it remains one of the serious obstacles for the general class of pattern recognizers based upon the principle of detecting and combining partial features.

An alternative interpretation of sparse coding is suggested by the operating characteristics of the neuronal model (Trehub, 1991) that generated the results



obtained in the present simulation study. In this model, when a face is captured within the visual afferent aperture, all filter cells show increased activation, but the cell with the highest activation level in response to the current retinal (proximal) stimulus evokes the appropriate discrete output. Hence, for each proximal stimulus a single cell can generate a code precise enough for effective recognition (Barlow, 1972, 1985; Konorski, 1967; see also Konishi, 1991). The joint contribution of other coding cells is not required.

If this is the case, why did effective performance in the present simulation require that more than 10 filter cells be synaptically tuned to learn 10 faces? The answer is revealed in the difference between the distal (environmental) and the proximal (retinal) stimulus. When a face is in the visual field, we do not know exactly where its features will be registered on the retina. At one time, fixation might be centered on the upper part of a given face; at another time on a lower part of the same face. The features of a constant distal stimulus may excite differing proximal patterns on the retina at different times. Variations in fixation of no more than 1 degree in visual angle can result in significant changes in the distribution of foveal excitation. Each retinal pattern represents only an exemplar of a given stimulus. Some exemplars may vary from previously learned patterns to the extent that they exceed the capacity of the recognition system to generalize correctly. Thus effective recognition of a face (or any other complex pattern) requires that different cells be tuned to at least a few different exemplars of the face in order to facilitate proper generalization and compensate for fortuitous shifts in exemplar capture (Trehub, 1991). In this sense, the sub-population of exemplar-tuned cells that *individually* signal a particular face also constitute a sparse code for that face. Notice, however, that this code is significantly different from sparse-code 1 in that it does not require the *joint* activation of an ensemble of exemplar-tuned cells to achieve effective recognition. Let us call this kind of neuronal code *sparse-code 2*.

The characteristic strategy for investigating selective coding of faces (or other objects) in neurophysiological experiments has depended on finding cells in which the peak spike rate is systematically evoked by the presentation of particular faces in an arbitrary set of stimuli (Desimone et al, 1984; Perrett, Mistlin, & Chitty, 1987; Young & Yamane, 1992; see also Tanaka et al, 1991; Gallant, Braun, & Van Essen, 1993). Implicit in this strategy is the general assumption that if the output of a cell is to be a reliable indicator of a particular object, the cell must respond more vigorously when that object is seen than when any other object is seen. This investigatory approach precludes the possibility of uncovering a neuronal recognition mechanism based upon competitive discrimination by sparse-code 2. For example, under the usual paradigm, F-cell 7 in the present simulation (Figures 5 and 6) would be thought to more likely code for face 5 or face 8 than for face 9, which it actually learned and correctly recognized within the competitive recall model (Trehub, 1977, 1991).

If the neuronal brain mechanism for face recognition in the monkey is organized on the principle of sparse-code 2 then several implications for the interpretation of single-cell recordings follow: (1) broad tuning of many cells in response to a particular face (or any other complex pattern) does not straightforwardly imply an ensemble code; (2) discovering a set of exemplar-tuned cells requires that we record the *concurrent* responses of a large number of cells to many presentations of each face (the distal stimulus) in the stimulus set because the retinal pattern (the proximal stimulus) that is captured is likely to vary over time even for identical faces as a result of shifts in fixation; (3) given the effect of variation in fixation, it would be helpful for the interpretation of results to monitor fixation throughout an experiment; (4) the critical indicator of selective coding is not the relative spike rate of a cell in response to different stimuli, but rather the rate of its output relative to other cells responding at the same time.



## REFERENCES

Barlow, H. B. (1972). Single units and sensation: A neuron doctrine for perceptual psychology? *Perception*, 1, 371-394.

Barlow, H. B. (1985). The twelfth Bartlett memorial lecture: The role of single neurons in the psychology of perception. *Quarterly Journal of Experimental Psychology*, 37A, 121-145.

Baylis, G. C., Rolls, E. T., & Leonard, C. M. (1985). Selectivity between faces in the responses of a population of neurons in the cortex in the superior temporal sulcus of the monkey. *Brain Research*, 342, 91-102.

Bruce, V., Cowey, A., Ellis, A. W., & Perrett, D. I., Eds. (1992). Processing the facial image. *Philosophical Transactions of the Royal Society of London. B*, 335, 1-128.

Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience*, 4, 2051-2062.

Gallant, J. L., Braun, J., & Van Essen, D. C. (1993). Selectivity for polar, hyperbolic, and cartesian gratings in macaque visual cortex. *Science*, 259, 100-103.

Gross, C. G. (1992). Representation of visual stimuli in inferior temporal cortex. *Philosophical Transactions of the Royal Society of London. B*, 335, 3-10.

Gross, C. G., Rocha-Miranda, C. E., & Bender, D. B. (1972). Visual properties of neurons in inferotemporal cortex of the macaque. *Journal of Neurophysiology*, 35, 96-111.

Gross, C. G. & Sergent, J. (1992). Face recognition. *Current Opinion in Neurobiology*, 2, 156-161.

Konishi, M. (1991). Deciphering the brain's codes. *Neural Computation*, 3, 1-18.

Konorski, J. (1967). *Integrative activity of the brain*. University of Chicago Press.

Kosslyn, S. M. & Mumford, D., Eds. (1991). Special issue on face perception. *Journal of Cognitive Neuroscience*, 3, 1-88.

Nosofsky, R. M. (1991). Tests of an exemplar model for relating perceptual classification and recognition memory. *Journal of Experimental Psychology: Human Perception and Performance*, 17, 3-27.

Perrett, D. I., Mistlin, A. J., & Chitty, A. J. (1987). Visual cells responsive to faces. *Trends in Neuroscience*, 10, 358-364.



Reed, S. K. & Friedman, M. P. (1973). Perceptual vs. conceptual categorization. *Memory & Cognition* , 1, 157-163.

Tanaka, K. (1993). Neuronal mechanisms of object recognition. *Science* , 262, 685-688.

Tanaka, K., Saito, H., Fukada, Y., & Moriya, M. (1991). Coding visual images of objects in the inferotemporal cortex of the macaque monkey. *Journal of Neurophysiology* , 66, 170-189.

Trehub, A. (1977). Neuronal models for cognitive processes: Networks for learning, perception and imagination. *Journal of Theoretical Biology* , 65, 141-169.

Trehub, A. (1991). *The Cognitive Brain* . Cambridge: MIT Press.

Young, M. P. & Yamane, S. (1992). Sparse population coding of faces in the inferotemporal cortex. *Science* , 256, 1327-1331.