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MINIREVIEW

CLASSIFYING SIMPLE AND COMPLEX CELLS ON THE BASIS OF RESPONSE MODULATION

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Abstract—Hubel and Wiesel (1962; *Journal of Physiology, London, 160,* 106–154) introduced the classification of cortical neurons as simple and complex on the basis of four tests of their receptive field structure. These tests are partly subjective and no one of them unequivocally places neurons into distinct classes. A simple, objective classification criterion based on the form of the response to drifting sinusoidal gratings has been used by several laboratories, although it has been criticized by others. We review published and unpublished evidence which indicates that this simple and objective criterion reliability divides neurons of the striate cortex in both cats and monkeys into two groups that correspond closely to the classically-described simple and complex classes.

Simple cells Complex cells Striate cortex Gratings Spatial frequency Response modulation Linear systems

INTRODUCTION

In their early recordings from the striate cortex, Hubel and Wiesel (1962) distinguished two main types of cells: simple and complex. They described four characteristics of simple cells (pp. 109–110).

(1) Spatially separate ON and OFF regions:

> "Like retinal ganglion and geniculate cells, cortical cells with simple fields possessed distinct excitatory and inhibitory subdivisions. Illumination of part or all of an excitatory region increased the maintained firing of the cell, whereas a light shone in the inhibitory region suppressed the firing and evoked a discharge at 'off'."

(2) Summation within each region:

> "A large spot confined to either area produced greater change in rate of firing than a small spot, indicating summation within either region."

(3) Antagonism between ON and OFF subregions:

> "... the two types of region within a receptive field were mutually antagonistic. This was most forcefully shown by the absence or near absence of a response to simultaneous illumination of both regions ..."

(4) Response properties can be predicted from receptive field maps:

> "From the arrangement of excitatory and inhibitory regions it was usually possible to predict in a qualitative way the responses to any shape of stimulus, stationary or moving."

Complex cells were defined by exclusion as cells that failed to display the stated characteristics of simple cells. Hubel and Wiesel (1968) found that the cell classification originally defined in cats could be used equally well to

categorize orientation selective cells in the monkey's striate cortex.

Subsequent investigators have proposed a number of subsidiary or supplementary classifications of cortical cells (e.g. Hubel & Wiesel, 1965; Palmer & Rosenquist, 1974; Gilbert, 1977; Henry, 1977), but these are all based on the concept of simple and complex "families", which remains central to all functionally-based classifications of neurons in the striate cortex.

There are several problems associated with the criteria of Hubel and Wiesel. It has proved difficult to separate cells into distinct classes on the basis of quantitative estimates of ON and OFF region overlap (Sherman, Watkins & Wilson, 1976; Dean & Tolhurst, 1983); investigators have had difficulty predicting orientation and direction selectivity from the receptive field maps of simple cells (Goodwin, Henry & Bishop, 1975; Heggelund & Moors, 1983; but see also Reid, Soodak & Shapley, 1987; McLean & Palmer, 1989); and, using the test proposed by Hubel and Wiesel, it is difficult to distinguish the limit of spatial summation from saturation of the response. Furthermore, the criteria of Hubel and Wiesel are qualitative and their application depends in part on the individual investigator's judgement, thus making it likely that this application varies between individual investigators and laboratories. Finally, the reliance on several criteria leaves it undecided how to classify cells that satify some criteria but not others.

Some investigators have sought to amend the criteria of Hubel and Wiesel by adding or substituting distinguishing characteristics. Among the proposed tests are: spontaneous activity level (Pettigrew, Nikara & Bishop, 1968; Bishop, Coombs & Henry, 1971; Hammond & MacKay, 1977); response amplitude (Pettigrew et al., 1968; Bishop et al., 1971); receptive field size (Bishop et al., 1971; Hammond & MacKay, 1977); length summation (Bishop et al., 1971); "sharpness" of response (Pettigrew et al., 1968); orientation selectivity (Hammond & MacKay, 1977); and response to patterns of random dots (Hammond, Pomfrett & Ahmed, 1989). While simple and complex cells may, on average, differ with respect to most, if not all, of these measures, there is reason to believe that none of them can be used to group cells into distinct classes. Moreover, these measures do not acknowledge the receptive field properties addressed by the criteria of Hubel and Wiesel.

APPLICATION OF LINEAR SYSTEMS ANALYSIS TO STRIATE CELLS

In recent years, investigators have applied techniques from linear systems analysis to the study of cortical cells' receptive fields. Hubel and Wiesel's original description of simple cells suggested that they might be well understood as having linear spatial summation, while complex cells have profoundly nonlinear behavior. Quantitative exploration of cortical receptive fields has broadly confirmed this impression (Maffei & Fiorentini, 1973; Movshon, Thompson & Tolhurst, 1978a, b; De Valois, Albrecht & Thorell, 1982), but has also shown clearly that simple cells have a number of important nonlinearities that make it impossible to use linearity *per se* as the basis for classification. The essence of Hubel and Wiesel's description of simple cells has two components: first, the response evoked by a local stimulus (e.g. a bar) preserves the sign of contrast; second, local responses combine roughly linearly, so that it is possible to predict the cell's response by suitably summing local responses. Complex cells, on the other hand, typically gave similar responses to local stimuli of either sign of contrast, thereby losing polarity information. Also, complex cells sum locally evoked responses in a highly nonlinear manner (Hubel & Wiesel, 1962; Movshon et al., 1978b; Spitzer & Hochstein, 1985). Thus the notion of approximate linearity is intimately related to Hubel and Wiesel's original simple-complex classification.

A simple way to determine whether a cell lacks substantial ON/OFF overlap or gross nonlinearity of spatial summation is to examine its response to a sinusoidal input: a cell lacking those nonlinearities responds to a sinusoidally modulated input (e.g. a drifting or counter-phase-modulated sine-wave grating) with a sinusoidal output at the stimulus temporal frequency. (In the case of a spiking neuron, this output is a sinusoidal modulation of the firing frequency.) If a cell were perfectly linear in all respects, the Fourier transform of this response would show all of the energy concentrated at the frequency of stimulation. In reality, even the most linear neurons have nonlinearities that introduce terms into the response at frequencies other than the stimulus frequency, including the zero frequency or d.c. component (e.g. Enroth-Cugell & Robson, 1966). In particular, since most cortical neurons have a maintained activity which is low or absent and cannot fire

at negative rates the response will have a finite d.c. component. This typically yields "half-wave" rectification of the response waveform, but in general this sort of rectification will never cause any response component to exceed the fundamental in amplitude. We might then expect that the *relative modulation* of the response, defined as the ratio of the response at the stimulus frequency to the d.c. response (with baseline activity subtracted), would never fall below 1.0 for the rectified responses of a linear neuron. In the common case of a neuron whose maintained discharge is zero and whose responses are perfectly "half-wave" rectified, the relative modulation would be $\pi/2$ (1.57).

Other nonlinearities commonly shown by simple cells, such as contrast gain control, contrast adaptation, suppressive end- and side-inhibition, have little effect on relative modulation. However, those nonlinearities most characteristic of complex cells, e.g. grossly nonlinear spatial summation, have a major effect on relative modulation in the response to a grating. This reduces the response component at the stimulus temporal frequency and enhances responses at other frequencies, transforming sinusoidally modulated input signals into responses dominated by energy at even multiples of the stimulus temporal frequency (including 0). In particular, these nonlinearities weaken or abolish the response component at the stimulus frequency itself. The value of relative modulation for such neurons would thus tend to be near 0.

A useful test of linearity of summation in cortical cells might be derived from the waveform of the cell's response to a drifting sinusoidal grating, because the temporal luminance variation at each point in such a grating is a sinusoid. Among the many practical advantages of using drifting gratings rather than other potential sinusoidal stimuli are: virtually all striate cells are responsive to moving patterns (whereas many do not respond to flashed or sinusoidally-modulated bars or spots); the test can be carried out in a few seconds and is thus resistant to gradual changes in eye position over time; large and reliable responses can be elicited by stimuli of moderate contrast; the precise location and extent of the receptive field is relatively unimportant; simultaneous stimulation of the entire receptive field elicits responses that depend both on the linearity of local responses and on the way those responses sum spatially. In addition, if suitably validated, this measure would form an objective test not dependent on the experimenter's judgements of responses.

DOES CLASSIFICATION BASED ON RESPONSE MODULATION CORRESPOND TO CLASSIFICATION BASED ON HUBEL AND WIESEL'S CRITERIA?

Hubel and Wiesel's classification scheme for simple and complex cells is closely related to a test of summation linearity (Shapley & Lennie, 1985), which should correlate closely with the modulation ratio from drifting sine-wave gratings. Does classification by these two different measures in fact agree?

When cells classified by classical criteria as simple are stimulated with drifting sinusoidal gratings, they respond with a discharge that is modulated in synchrony with the temporal frequency of stimulation, whereas complex cells produce an elevated firing rate that is generally uniform with time (Maffei & Fiorentini, 1973; Movshon & Tolhurst, 1975; Ikeda & Wright, 1975; Schiller, Finlay & Volman, 1976; Movshon et al., 1978a, b; Andrews & Pollen, 1979; Dean, 1981; Holub & Morton-Gibson, 1981; Albrecht & Hamilton, 1982; Pollen & Ronner, 1982; Morrone, Burr & Maffei, 1982; Jones, Stepnoski & Palmer, 1987; Hamilton, Albrecht & Geisler, 1989).

Movshon et al. (1978a, b) showed that the degree of response modulation seemed to distinguish simple and complex cells. They stimulated the cells with drifting sinusoidal gratings and Fourier analyzed the averaged response waveform. As a measure of relative modulation they took the ratio of the amplitude of the first harmonic to the mean response level, after subtraction of the average maintained rate. Movshon et al. (1978a, b) reported that when gratings of optimal spatial frequency were used, simple cells always appeared to have relative modulation values in excess of 1.0, while complex cells' values were less than 1.0. It is important to note that when tested with gratings of lower-than-optimal spatial frequency, they found many complex cells that gave strongly modulated responses.

De Valois et al. (1982) suggested that relative modulation of the response to gratings of optimal spatial frequency could be used in lieu of classical tests to classify neurons: they termed simple those neurons whose relative modulation exceeded 1.0, and complex those

whose values were lower than 1.0. A number of investigators have classified cells as simple and complex using this criterion, either by itself (De Valois & Tootell, 1983; Skottun & Freeman, 1984; Skottun, Grosof & De Valois, 1988; Bonds, 1989) or in conjunction with other tests (Tolhurst & Thompson, 1981; Dean, 1981; Schumer & Movshon, 1984; Ohzawa & Freeman, 1986a, b; Jones & Palmer, 1987; Szulborski & Palmer, 1990).

The use of this criterion has recently been questioned. Hammond et al. (1989) claimed to find many complex cells that showed modulated firing to drifting gratings. This claim was based on observations made in the course of two studies (Hammond, Mouat & Smith, 1985, 1988) in which mainly square-wave gratings were used. As we have noted, it is important to determine the relative modulation using gratings of the optimal spatial frequency, since a lower frequency can elicit a modulated response from many complex cells. The modulated responses described by Hammond et al. (1985, 1988) were likely a result of using too low a spatial frequency. Square-wave gratings contain not just the fundamental frequency but many higher frequency components, which also contribute to the response. As a result, many cells respond optimally to a square-wave grating whose fundamental frequency is lower than the peak spatial frequency as determined by sine-wave gratings (Campbell, Cooper & Enroth-Cugell, 1969; Pollen & Ronner, 1982; Elfar, De Valois & De Valois, 1990). It is therefore inappropriate to use square-wave gratings to determine a cell's optimal spatial frequency.

Several investigators have compared the classification of cells by classical criteria and by the relative modulation, and have generally found the measures to agree in distinguishing simple from complex cells. Dean and Tolhurst (1983) did a substantial evaluation of the two approaches, and found general agreement between relative modulation and classical criteria, with a high correlation between response modulation and a separate measure of the discreteness of ON and OFF regions ($r = 0.87$, $N = 65$, $P < 0.001$). However, they also noted a sufficient number of exceptions to state that supplementary tests were required for unambiguous classification.

Dean and Tolhurst classified 391 cells as simple or complex on the basis of a qualitative receptive field map. For the same cells they also measured the relative modulation. The distribution of these values is shown in Fig. 1A. Of 231 cells classified as simple, 27% had a relative modulation of less than 1.0. By contrast, in the case of 160 complex cells all but 5 (97%) had relative modulation of less than 1.0.*

For a subpopulation of 67 cells, they mapped the receptive field quantitatively; Fig. 1B shows the distribution of relative modulation for these cells. In the case of these quantitatively studied cells, there is a much higher agreement between the relative modulation and classical RF mapping. Out of these 67 cells only 3 simple cells and 1 complex cell (less than 6% of the total population) were classified differently by use of relative modulation as opposed to a combination of discreteness and the spatial summation ratio. Furthermore, all four of the cells that were differently classified had relative modulations close to 1.0. In this distribution, all cells with relative modulations well below 1.0 are complex according to their criteria, and cells with relative modulations well above 1.0 are simple.

In addition to these previously published results, we present some new data. Figure 1C shows the distribution of the relative modulation found in 255 cells from the cat's striate cortex recorded according to the procedures of Schumer and Movshon (1984). The cells were independently classified as simple and complex based on the overlap of ON and OFF zones and on qualitative tests of spatial summation. No cell with a relative modulation of less than 1.0 was independently classified as simple, and only five cells with relative modulations larger than 1 were classified as complex based on receptive field mapping, yielding a contradiction in about 2% of the cases.

*About the method of calculating the relative modulation Dean and Tolhurst wrote: "The level of spontaneous activity could be corrected for by subtracting it from the average level of activity in the presence of a grating. This was done for complex cells. . . ." (Dean & Tolhurst, 1983, p. 314). It thus appears that Dean and Tolhurst may have subtracted the spontaneous activity from the d.c. responses of complex cells but not from the d.c. component of the simple cell responses. If this is the case, it would have had the effect of displacing the simple cells toward lower values, i.e. closer to the values of complex cells and thus increasing the degree of overlap between simple and complex cells (in Fig. 1A, B) and reducing the bimodal shape of the distribution (in Fig. 2A). Also, it might be noted that they excluded from their sample nine sample cells with very large modulation because their relative modulation was so large as to be off scale.

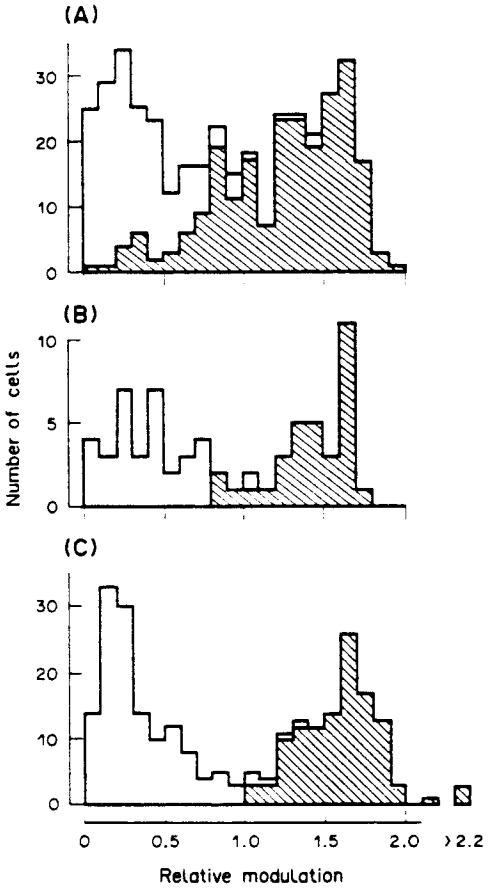

Fig. 1. The distribution of relative modulation for cells from the cat's striate cortex that were independently classified as simple or complex using classical criteria. A and B are combinations of the data in panels B, C and D of Dean and Tolhurst's (1983) Fig. 5 (A) The distribution of 391 cells whose receptive fields were mapped qualitatively. Based on these maps cells were classified as simple or complex according to spatial summation ratio and ON and OFF region overlap. In this way 231 cells were classified as simple (hatched areas) and 160 as complex cells (unhatched areas). (B) The distribution of 67 cells whose fields were mapped with a quantitative technique. Out of 67 cells, 33 were classified as simple (hatched areas) and 34 as complex cells (unhatched areas). (C) The distribution of 255 cells from the striate cortex of the cat, previously unpublished (method of Schumer & Movshon, 1984). The hatched areas represent cells classified as simple according to the separation of the ON and OFF regions.

We conclude that virtually all cells with relative modulation values above 1.0 are classified as simple by conventional tests, while cells with modulation values below 1.0 are classified as complex. The few discrepant cases involve cells with relative modulations near 1.0, and some of these may represent cells that could not be classified decisively with any test. The introduction by some investigators of intermediate classes (Henry, 1977; Orban, 1984), and our own experience, suggests that there exist cells that cannot be unambiguously classified by any of the conventional criteria.

IS THERE A BIMODAL DISTRIBUTION OF CELLS WITH REGARD TO RELATIVE MODULATION?

We can now address the question of whether there are in fact two distinct classes of cells, corresponding to simple and complex, classifiable on the basis of relative modulation. The first indication that there might be a bimodal distribution of neurons with regard to response modulation came from Schiller et al. (1976), who, working in the monkey, used a measure

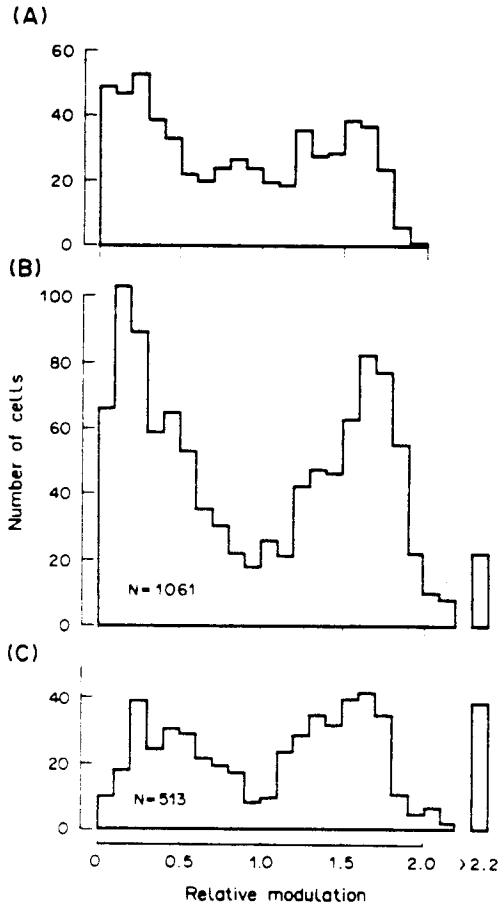

Fig. 2. Distribution of cells with regard to modulation of the response to drifting gratings. (A) Distribution of cells from the cat's striate according to the criterion of relative modulation as used by Dean and Tolhurst (1983) (see text), redrawn from their Fig. 5A. (As to the number of cells in this distribution, Dean and Tolhurst wrote that it contained 563 cells. By our count there are 577 cells.) (B) The distribution of relative modulation found in 1061 cells in cat striate cortex recorded in five laboratories, excluding the data of Dean and Tolhurst shown above. (C) The distribution of relative modulation in 513 cells of monkey VI, recorded in two laboratories.

of modulation that is more accurately characterized as a measure of response variance (and is therefore different from relative modulation as we have defined it) (see Schiller et al., 1976, pp. 1335 and 1341). These authors found a weakly bimodal distribution (see their Figs 8 and 16). On the other hand, using the measure of relative modulation described above De Valois et al. (1982, Fig. 3), Skottun and Freeman (1984, Fig. 2A), and Skottun et al. (1988, Fig. 1) all found pronouncedly bimodal distributions.

Dean and Tolhurst (1983) examined the distribution of cells with regard to the relative modulation of response, and their data are reproduced in Fig. 2A. About this distribution Dean and Tolhurst wrote:

> "The degree of modulation in the response was continuously distributed between low values typical of complex cells and high values typical of simple cells; the distribution was not bimodal" (Dean & Tolhurst, 1983, p. 305).

Our own view of these data is that the distribution at least shows a bimodal tendency, since the density distribution of cells is higher below 0.5 and near 1.5 than around 1.0.

To examine this issue with a large cell sample and to observe the consistency of the result across a wide variety of measuring conditions, we have pooled distributions from the cat from five laboratories and from the monkey from two laboratories. Figure 2B is a compendium of both previously published and unpublished measurements of the modulation index in 1061 cells from the cat striate cortex. Included are cells recorded under conditions described in the following papers: Skottun and Freeman (1984), 157 cells; Skottun et al. (1988), 201 cells; Hamilton et al. (1989), 301 cells; Bonds (1989), 143 cells; and Schumer and Movshon (1984), 255 cells (also shown in Fig. 1C). In Fig. 2C is shown the distribution of a total of 513 cells from V1 of the monkey with regard to modulation index. Included are 343 cells from De Valois et al. (1982), and 170 cells recorded under the conditions described by Hamilton et al. (1989).

The distributions from both cat and monkey are clearly bimodal. Hammond et al. (1989) suggested that relative modulation might be used to classify cells in the monkey but not in the cat; the similarity of these distributions fails to lend any support to this contention. If anything, the cat data are more clearly bimodal than those from the monkey.

To summarize, we have examined the distribution with regard to the relative modulation of several independent samples from the striate cortex of both the cat and the monkey. Notwithstanding the statements by Dean and Tolhurst (1983), all samples show bimodal distributions both individually and in combination. While a small number of cells have ratios in the area of 1.0, it is unclear whether this is a consequence of the method or whether these cells are not readily classifiable with any approach. We conclude, therefore, that on the whole the relative modulation of the response to drifting sinusoidal gratings from neurons in the striate cortex of both cats and monkeys falls into two distinct distributions, and that these correspond to the classical categories of simple and complex.

CONCLUSIONS

The data presented above indicate that in striate cortex two different types of cells can be distinguished on the basis of the relative modulation of their responses to drifting sinusoidal gratings. Although relative modulation is a measure of linearity and has historically been associated with linear systems theory, adoption of this criterion does not involve commitment to any particular theory of cortical function or neural circuitry. The criterion might therefore be applicable, with due caution, to other species or other brain areas.

Using a relative modulation of 1.0, cells are divided into classes that correspond closely to the classes of simple and complex as defined by Hubel and Wiesel (1962). There are several reasons for believing that classifying cells according to this criterion is more useful than any previous classification: (1) this single criterion places the great majority of cortical cells into distinct classes; (2) the degree of modulation is objective and easily quantifiable; (3) the relative modulation is determined with stimuli which stimulate the whole receptive field and typically generate substantial responses; (4) the relative modulation is determined with moving stimuli, and is therefore not limited to cells that can be activated with stationary patterns; (5) the degree of response modulation can be determined quickly—often drifting a few cycles across the receptive field is sufficient to determine the cell class, once the optimal frequency and orientation are known; (6) because

the method is fast, it is relatively resistant to contamination of data by eye movements.

Thus the use of relative modulation to classify cells has much to recommend it, and we would commend its use to those who seek a rapid and reliable way to categorize neurons in the striate cortex.

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REFERENCES

Albrecht, D. G. & Hamilton, D. B. (1982). Striate cortex of monkey and cat: Contrast response function. *Journal of Neurophysiology 48*, 217–237.

Andrews, B. W. & Pollen, D. A. (1979). Relationship between spatial frequency selectivity and receptive field profile of simple cells. *Journal of Physiology, London, 287*, 163–176.

Bishop, P. O., Coombs, J. S. & Henry, G. H. (1971). Responses to visual contours: Spatio-temporal aspects of excitation in the receptive fields of simple striate neurones. *Journal of Physiology, London, 219*, 625–657.

Bonds, A. B. (1989). Role of inhibition in the specification of orientation selectivity of cells in the cat striate cortex. *Visual Neuroscience, 2*, 41–55.

Campbell, F. W., Cooper, G. F. & Enroth-Cugell, C. (1969). The spatial selectivity of the visual cells of the cat. *Journal of Physiology, London, 203*, 223–235.

Dean, A. F. (1981). The relationship between response amplitude and contrast for cat striate cortical neurones. *Journal of Physiology, London, 318*, 413–427.

Dean, A. F. & Tolhurst, D. J. (1983). On the distinctness of simple and complex cells in the visual cortex of the cat. *Journal of Physiology, London, 344*, 305–325.

De Valois, K. K. & Tootell, R. B. H. (1983). Spatial-frequency-specific inhibition in cat striate cortex cells. *Journal of Physiology, London, 336*, 359–376.

De Valois, R. L., Albrecht, D. G. & Thorell, L. G. (1982). Spatial frequency selectivity of cells in macaque visual cortex. *Vision Research, 22*, 545–559.

Elfar, S., De Valois, K. K. & De Valois, R. L. (1990). Sine waves, square waves. *Investigative Ophthalmology and Visual Science (Suppl.) 31*, 397.

Enroth-Cugell, C. & Robson, J. G. (1966). The contrast sensitivity of retinal ganglion cells of the cat. *Journal of Physiology, London, 187*, 517–552.

Gilbert, C. D. (1977). Laminar differences in receptive field properties of cells in cat primary visual cortex. *Journal of Physiology, London, 268*, 391–421.

Goodwin, A. W., Henry, G. H. & Bishop, P. O. (1976). Direction selectivity of simple striate cells: Properties and mechanism. *Journal of Neurophysiology, 38*, 1500–1523.

Hamilton, D. B., Albrecht, D. G. & Geisler, W. S. (1989). Visual cortical receptive fields in monkey and cat: Spatial and temporal phase transfer function. *Vision Research, 29*, 1285–1308.

Hammond, P. & MacKay, D. M. (1977). Differential responsiveness of simple and complex cells in cat striate cortex to visual texture. *Experimental Brain Research, 30*, 275–296.

Hammond, P., Mouat, G. S. V. & Smith, A. T. (1985). Motion after-effects in cat striate cortex elicited by moving gratings. *Experimental Brain Research, 60*, 411–416.

Hammond, P., Mouat, G. S. V. & Smith, A. T. (1988). Neural correlates of motion after-effects in cat striate cortical neurones: Monocular adaptation. *Experimental Brain Research, 72*, 1–20.

Hammond, P., Pomfrett, C. J. D. & Ahmed, B. (1989). Neural motion after-effects in the cat's striate cortex: Orientation selectivity. *Vision Research, 29*, 1671–1683.

Heggelund, P. & Moors, J. (1983). Orientation selectivity and the spatial distribution of enhancement and suppression in receptive fields of cat striate cortex cells. *Experimental Brain Research, 52*, 235–247.

Henry, G. H. (1977). Receptive field classes of cells in the striate cortex of the cat. *Brain Research, 133*, 1–28.

Holub, R. A. & Morton-Gibson, M. (1981). Response of visual cortical neurons of the cat to moving sinusoidal gratings: Response-contrast functions and spatiotemporal interactions. *Journal of Neurophysiology, 46*, 1244–1259.

Hubel, D. H. & Wiesel, T. N. (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology, London, 160*, 106–154.

Hubel, D. H. & Wiesel, T. N. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *Journal of Neurophysiology, 28*, 229–289.

Hubel, D. H. & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology, London, 195*, 215–243.

Ikeda, H. & Wright, M. J. (1975). Spatial and temporal properties of "sustained" and "transient" neurones in area 17 of the cat's visual cortex. *Experimental Brain Research, 22*, 363–383.

Jones, J. P. & Palmer, L. A. (1987). The two-dimensional spatial structure of simple receptive fields in cat striate cortex. *Journal of Neurophysiology, 58*, 1187–1211.

Jones, J. P., Stepnoski, A. & Palmer, L. A. (1987). The two-dimensional spectral structure of simple receptive fields in cat striate cortex. *Journal of Neurophysiology, 58*, 1212–1232.

Maffei, L. & Fiorentini, A. (1973). The visual cortex as a spatial frequency analyser. *Vision Research, 13*, 1255–1267.

McLean, J. & Palmer, L. A. (1989). Contribution of linear spatiotemporal receptive field structure to velocity selectivity of simple cells in area 17 of cat. *Vision Research, 29*, 675–679.

Morrone, M. C., Burr, D. C. & Maffei, L. (1982). Functional implications of cross-orientation inhibition of cortical visual cells. I. Neurophysiological evidence. *Proceedings of the Royal Society of London B, 216*, 335–354.

Movshon, J. A. & Tolhurst, D. J. (1975). On the response linearity of neurones in cat visual cortex. *Journal of Physiology, London, 249*, 56–57P.

Movshon, J. A., Thompson, I. D. & Tolhurst, D. J. (1978a). Spatial summation in the receptive fields of simple cells in the cat's striate cortex. *Journal of Physiology, London, 283*, 53–77.

Movshon, J. A., Thompson, I. D. & Tolhurst, D. J. (1978b). Receptive field organization of complex cells in the cat's striate cortex. *Journal of Physiology, London, 283*, 79–99.

Ohzawa, I. & Freeman, R. D. (1986a). The binocular organization of simple cells in the cat's visual cortex. *Journal of Neurophysiology, 56,* 221–242.

Ohzawa, I. & Freeman, R. D. (1986b). The binocular organization of complex cells in the cat's visual cortex. *Journal of Neurophysiology, 56,* 243–259.

Orban, G. A. (1984). *Neuronal operations in the visual cortex.* Berlin: Springer.

Palmer, L. A. & Rosenquist, A. C. (1974). Visual receptive fields of single striate cortical units projecting to the superior colliculus in the cat. *Brain Research, 67,* 27–42.

Pettigrew, J. D., Nikara, T. & Bishop, P. O. (1968). Responses to moving slits by single units in cat striate cortex. *Experimental Brain Research, 6,* 373–390.

Pollen, D. A. & Ronner, S. F. (1982). Spatial computation performed by simple and complex cells in the visual cortex of the cat. *Vision Research, 22,* 101–118.

Reid, R. C., Soodak, R. E. & Shapley, R. M. (1987). Linear mechanisms of directional selectivity in simple cells of cat striate cortex. *Proceedings of the National Academy of Science, 84,* 8740–8744.

Schiller, P. H., Finlay, B. L. & Volman, S. F. (1976). Quantitative studies of single-cell properties in monkey striate cortex. III. Spatial frequency. *Journal of Neurophysiology, 39,* 1334–1351.

Schumer, R. A. & Movshon, J. A. (1984). Length summation in simple cells of cat striate cortex. *Vision Research, 24,* 565–571.

Shapley, R. & Lennie, P. (1985). Spatial frequency analysis in the visual system. *Annual Review of Neuroscience, 8,* 547–583.

Sherman, S. M., Watkins, D. W. & Wilson, J. R. (1976). Further differences in receptive field properties of simple and complex cells in cat striate cortex. *Vision Research, 16,* 919–927.

Skottun, B. C. & Freeman, R. D. (1984). Stimulus specificity of binocular cells in the cat's visual cortex: Ocular dominance and the matching of left and right eyes. *Experimental Brain Research, 56,* 206–216.

Skottun, B. C., Grosof, D. H. & De Valois, R. L. (1988). Responses of simple and complex cells to random dot patterns: A quantitative comparison. *Journal of Neurophysiology, 59,* 1719–1735.

Spitzer, H. & Hochstein, S. (1985). A complex-cell receptive-field model. *Journal of Neurophysiology, 53,* 1266–1286.

Szulborski, R. G. & Palmer, L. A. (1990). The two-dimensional spatial structure of nonlinear subunits in the receptive fields of complex cells. *Vision Research, 30,* 249–254.

Tolhurst, D. J. & Thompson, I. D. (1981). On the variety of spatial frequency selectivities shown by neurons in area 17 of the cat. *Proceedings of the Royal Society of London, B, 213,* 183–199.