DIRECTIONAL AND ORIENTATIONAL TUNING IN THE STRIATE CORTEX
OF THE CAT FOR CONTRAST AND TEXTURED STIMULI.

TIGWELL, D.A.

University of Keele.

1985

Attention is drawn to the fact that the copyright of this thesis rests with its author.

This copy of the thesis has been supplied on condition that anyone who consults it is understood to recognise that its copyright rests with its author and that no information derived from it may be published without the author's prior written consent.
DIRECTIONAL AND ORIENTATIONAL TUNING IN THE STRIATE CORTEX OF THE CAT FOR CONTRAST AND TEXTURED STIMULI.

This thesis is submitted for the degree of Doctor of Philosophy at the University of Keele.

D.A. TIGWELL
1985.
DEDICATION: TO MY PARENTS.

ACKNOWLEDGEMENTS:

I wish to thank Prof. D.M. MacKay for the opportunity of working in the Department of Communication and Neuroscience. Dr. P. Hammond provided equipment without which this research would not have been possible. I would also like to thank Dr. Hammond for constructive criticism on an earlier draft of this thesis.

The work of Dr. Hammond and Prof. MacKay with visual noise provided a firm foundation of research from which this project developed.

I am grateful to S. Gravano for a computer programme for linear regression analysis and to D.J. Scott for technical assistance with experiments.
ABSTRACT:

1. Striate cortical neurones respond selectively to the orientation of moving contrast bars. The mechanism for that selectivity has alternatively been attributed to the geniculo-cortical synapse or inhibitory intracortical circuitry. Functionally, that selectivity has suggested a role for the single cell in contour analysis in a hierarchical process of feature extraction.

2. Comparison of tuning of complex cells for moving contrast bars and texture-fields has established the mediation of orientation and direction selectivities by separate mechanisms. An unresolved question is the contributions of orientation and direction to the complex cell's response.

3. Tuning for stationary and moving contrast bars, moving spots and fields of visual noise was evaluated. Tuning for a texture-bar moving across a field of visual noise of similar texture and equal mean luminance was compared with tuning for a moving contrast bar and a field of visual noise.

4. Tuning for a stationary contrast bar had poor predictive value for tuning for moving stimuli; tuning for a stationary bar was sharper and more symmetrical than for the same bar in motion and preferred direction for a spot was not orthogonal to preferred orientation. Preferred direction for texture motion could be predicted from preferred direction for a spot. Cells
bimodal in tuning for a moving texture-field were unimodal in tuning for a spot. These findings are reviewed in the context of models for the role of intracortical inhibition.

5. Comparison of tuning for a moving texture-bar with a moving contrast bar and texture-field demonstrated that, in the absence of luminance cues, complex cells are sensitive only to texture motion. A role for direction-selective units in the representation of form is suggested.
CONTENTS

CHAPTER ONE: THE MODEL OF HUBEL AND WIESEL

Introduction .................................................PAGES 1-4.

1.1 An Outline of Hubel and Wiesel's Model. .........................PAGES 4-6

1.2 The Role of the Afferent Input in Hubel and Wiesel's Model. ........PAGES 8-13

1.3 The Classificatory System in Hubel and Wiesel's Model. .........PAGES 13-20

1.4 The Interrelationships of Cells in Hubel and Wiesel's Model. ....PAGES 20-23

1.5 The Columnar Concept and Its Empirical Validity. .................PAGES 23-37

1.6 The Mechanism of Orientation and Direction Selectivity in Hubel and Wiesel's Model. ................PAGES 37-46

1.7 Implications. .............................................PAGES 46-49

CHAPTER TWO: THE ROLE OF INTRACORTICAL CIRCUITRY IN THE
MEDIATION OF ORIENTATION AND DIRECTION SELECTIVITIES

2.1 Models for the Role of Intracortical Inhibition. .................PAGES 50-60

2.2 The Dependence of Orientation and Direction Selectivities on Intracortical Inhibition. ........PAGES 60-66

2.3 The Representation of Inhibition in the Simple Cell Receptive Field. ........PAGES 66-72

2.4 The Mediation of Orientation and Direction Selectivities by Separate Mechanisms. ................PAGES 72-79

2.5 X and Y Cell Input to Simple and Complex Cells. .................PAGES 79-89

2.6 The Role of Dendritic Morphology and Inputs from Inhibitory Interneurones in the Determination of Orientation and Direction Selectivities. ........PAGES 89-104

2.7 The Horizontal Organization of the Striate Cortex. ...............PAGES 104-108
2.8 The Vertical Organization of the Striate Cortex.

................................................PAGES 108-119

2.9 A Synthesis

................................................PAGES 119-122

CHAPTER THREE: THE TUNING OF SIMPLE AND COMPLEX CELLS FOR
CONTRAST AND TEXTURED STIMULI

Introduction

................................................PAGE 123

3.1 The Form of the Tuning Curve for Moving Contrast Bars.

................................................PAGES 124-125

3.2 The Tuning of Simple and Complex Cells for Moving Contrast
Bars.

................................................PAGES 125-130

3.3 Dissociation of the Parameters of Orientation and Direction
with Contrast Stimuli.

................................................PAGES 130-136

3.4 The Tuning of Complex Cells for Contrast and Textured
Stimuli.

................................................PAGES 137-138

3.5 The Tuning for Contrast and Textured Stimuli and Models.

................................................PAGES 138-142

CHAPTER FOUR: THE CONTRIBUTIONS OF ORIENTATION AND DIRECTION
to THE TUNING PROPERTIES OF COMPLEX CELLS

Introduction ......................................PAGES 143-145

4.1 Animal Preparation.

................................................PAGES 145-146

4.2 Recording Sessions.

................................................PAGES 146-149

4.3 Equipment for the Generation of Visual Stimuli.

................................................PAGES 150-151

4.4 Cell Recordings.

................................................PAGES 151-151

4.5 Recording Equipment.

................................................PAGES 151-152

4.6 Determination of Orientation and Direction Tuning Curves.

................................................PAGES 152-154

4.7 Experimental Strategy.

................................................PAGES 155-156
4.8 Results

.................................................................PAGES 156-177

CHAPTER FIVE: IMPLICATIONS OF THE TUNING OF COMPLEX CELLS FOR CONTRAST AND TEXTURED STIMULI FOR MODELS AND THE ROLE OF THE COMPLEX CELL IN VISUAL ANALYSIS

5.1 An Overview.

.................................................................PAGES 178-180

5.2 The Tuning of Complex Cells for Contrast Stimuli.

.................................................................PAGES 180-184

5.3 Implications for Models.

.................................................................PAGES 185-188

5.4 The Tuning of Complex Cells for Textured Stimuli.

.................................................................PAGES 188-193

5.5 Differences in Tuning Between Different Classes of Complex Cells.

.................................................................PAGES 193-198

5.6 The Role of the Complex Cell in Visual Analysis.

.................................................................PAGES 198-210

-oo-

REFERENCES

-oo-
A comprehensive model of the striate cortex was proposed by Hubel and Wiesel (1962, 1963) which incorporated a description of the stimulus selectivity shown at the single cell level and an explanatory mechanism for this selectivity deriving from a comparison of the receptive field organization at the lateral geniculate and cortical levels. The central observation initiating this model was the selectivity shown for the orientation of moving contrast bars. Functionally, that selectivity was interpreted as defining the role of the single cell in perception; specifically, neurones in the visual cortex were conceived as contour detectors. In essence, the model viewed the transformation of the afferent input at the geniculo-cortical synapse as the means by which the striate cortex derived its stimulus selectivity. The function of that mechanism was to ensure the selective response to luminance contours in a hierarchical process of feature analysis within the cortex.

On the basis of receptive field organization, striate cortical cells were classified into three groups, each of which exhibited the property of orientation selectivity but with varying degrees of precision and requirements for restriction in the dimensions of the stimulus. Moreover, the various categories of neurone so defined were viewed as acting in unison; they contributed to the same circuitry and formed a functional unit. The cortical sheet was conceived as being divided into columns each containing the three categories of
neurons, in a serial chain, and in an invariant order. The difference between these units lay in the particular orientation preference shown by each column, the identity of each being the shared common orientation preference. The work of Hubel and Wiesel revised the concept of the visual cortex as a structure with myriads of cells taking part in the formation of every visual image; each cell was found to have specific stimulus requirements and the cortex was divided into functional units with equally clearly defined stimulus requirements.

Both the origin and functional significance of the selectivity for oriented moving contrast bars have been conjectural. The question of mechanism will be raised at this stage. The central role of the afferent input in determining stimulus selectivity at the cortical level has been brought into doubt by empirical tests of the assumption of convergence of afferent fibres (Creutzfeldt and Ito, 1968; Creutzfeldt, Kuhnt and Benevento, 1974; Lee, Cleland and Creutzfeldt, 1977; Sillito, Kemp, Wilson and Berardi, 1980; Berardi, Kemp, Wilson and Sillito, 1980), from consideration of the relationship between the simple cell receptive field plotted with flashed bars and the contribution of the afferent input from the lateral geniculate nucleus (Creutzfeldt, Kuhnt and Benevento, 1974; Sillito, 1975; Berardi, Kemp, Wilson and Sillito, 1980), and the predictability of response from the receptive field plotted in this way (Henry and Bishop, 1972; Bishop, Dreher and Henry, 1972; Henry, Bishop and Dreher, 1974; Henry, Dreher and Bishop, 1974; Watkins and Sherman, 1974; Goodwin, Henry and Bishop, 1975; Notndurft, 1976;
An alternative proposal is that orientational/directional selectivity is mediated by intracortical processes of a predominantly inhibitory nature (Benevento, Creutzfeldt and Kuhnt, 1972, Creutzfeldt, Kuhnt and Benevento, 1974; Sillito, 1976). Evidence will be presented to support this contention.

Orientation selectivity was assessed with moving contrast bars in Hubel and Wiesel's original work and orientation was not dissociated from direction. Whilst subsequent studies have yielded some insight of separate contributions of orientation and direction using this stimulus paradigm, particularly in the context of intracellular recordings (Creutzfeldt, Kuhnt and Benevento, 1974; Innocenti and Fiore, 1974) and blocking of intracortical inhibition (Sillito, 1974, 1973, 1976, 1977; Tsumoto, Eckart, and Creutzfeldt, 1979), the contribution of these two parameters was left unanswered in Hubel and Wiesel's studies. A specific proposal that separate mechanisms operate intracortically to generate orientation and direction selectivities (Schiller, Finlay and Volman, 1976; Hammond, 1978) has considerable support from comparisons of tuning for contrast and textured stimuli (Hammond, 1978; Hammond and Reck, 1980a, b; Hammond, 1981b). This and related evidence will be presented.

A model in which orientational and directional selectivities are determined by separate mechanisms involving intracortical inhibition forms the background to the research to be described. In this theoretical context the question is raised of the contribution of these separate mechanisms to the
cell's response and it is to this question that the research presented here is addressed. Summatory requirements for effective drive for many cortical neurones precludes answering the question with contrast stimuli alone. Moving fields of texture, in particular visual noise (Hammond and Mackay, 1975a and subsequently), provide a stimulus with directional drive free from orientation and at the same time fulfilling summatory requirements. The differential responsiveness of cortical units to visual noise (Hammond and Mackay, 1975a,b; 1976; 1977) restricts the study to one category of neurone, the complex cell of Hubel and Wiesel's classification (Hubel and Wiesel, 1962). A paradigm employing a combination of contrast and visual noise stimuli provides a means of investigating the contributions of orientation and direction mechanisms determining the complex cell's response.

Several stages of discussion precede the presentation of the current research. The first of these centres on the model of Hubel and Wiesel, important not only for the mechanism it proposed for orientational selectivity, but also for its wide-ranging propositions concerning the organization of the striate cortex, the classification of cortical units and their inter-relationships. Subsequent models are derived from consideration of the many aspects of Hubel and Wiesel's model.

1.1 An Outline of Hubel and Wiesel's Model

Hubel and Wiesel's (1962) comparison of response specificities of visual cortical and lateral geniculate neurones revealed that the receptive field of lateral
geniculate neurones, responding to flashed spots with a circular centre-surround organization, gave way to elongated receptive fields responsive to moving oriented lines and borders at the cortical level. In the simple cell, the neurone presumed to occupy the first ordinal position from the geniculate input to the cortex, the receptive field was found to be divided into separate regions, parallel to the orientation axis, responding to opposite polarities of flashed contrast bars. It was argued that orientation and direction selectivity could be understood from the disposition of these regions which in turn reflected the spatial arrangement of the afferent input. Orientational selectivity was derived from the principle of summation within, and antagonism between, these areas. Formation of the simple cell receptive field by convergence of fibres, representing aligned receptive fields of lateral geniculate neurones resulted in the sub-regions of the simple cell receptive field. In illustration, an "on-centre" LGN neurone group would give rise to a simple cell with a central region responding to a bright bar flanked by two regions responding to a dark bar. Such a simple cell became the paradigm for simple cell models (Hubel and Wiesel, 1962, 1963, 1968). The receptive field centres of geniculate neurones were considered to lie in a straight line and extending the length of the stimulus, of appropriate contrast, would cause an increased response as more geniculate field centres were stimulated. Antagonism (or inhibition as Hubel and Wiesel sometimes referred to it) between regions would cause a reduction and eventual elimination of response as the stimulus deviated from the "orientation axis" and encroached into the antagonistic
zones. Such antagonism between zones of LGN cells, it was argued, would result in the withdrawal of excitation to the cortical cells and decreased response. Each simple cell was considered to receive convergent input from either "on"- or "off"-centre fibres. However, Hubel and Wiesel (1962) raised the possibility of enlargement and reinforcement of the inhibitory flanks of the receptive field by "off"-centre geniculate fibres (in the case of "on"-centre simple cells) or "on"-centre geniculate fibres (in the case of "off" centre simple cells).

The lack of a clear division into antagonistic regions within the receptive field and the absence of summation within each region for a second category of cell, the complex cell, implied that these neurones could not receive direct input from the lateral geniculate nucleus. But, the authors argued, the receptive field of this type of neurone is compatible with convergent input from several simple cells stepped in position with the same orientation axis but sequentially different retinal locations. Finally, a third category of neurone, the hypercomplex cell, assumed to be formed by the convergence of several complex cells, exhibits the property of end-inhibition, conferring upon it a selectivity for bars restricted in length.

The three categories of cells were conceived as being linked by excitatory connections in a serial chain from the afferent input; simple, complex, hypercomplex. Such a serial chain comprised an orientation column, tuned by the afferent input and segregated from synaptic contact with members of the
adjacent column. So described, the column forms an anatomical and functional entity. Hubel and Wiesel did not, however, entirely rule out interactions between adjacent columns in the limited case of the formation of the large receptive fields of exceptional complex cells, though such occurrences were considered infrequent and a hierarchical organization of neurones was still complied with.

Economy of wiring required that orientation columns with similar orientations were close together. Such an organization would be discernible through the successive steps in preferred orientation when recorded by an electrode tangentially coursing through the cortex. In some parts of the cortex columns were found to be arranged in a very regular manner. For these cases discrete shifts in orientation would be evident in recordings from a tangentially advanced electrode. In these ordered regions the columns are especially likely to be long and narrow. For other parts of the cortex, Hubel and Wiesel found little order in the arrangement of neighbouring columns. In some cases, "columns" were found to take the form of "slabs" and, in the monkey, the representation was found to be more compatible with a continuous rather than discrete representation of orientation (Hubel and Wiesel, 1974). The columnar organization apparent in physiological recordings was not matched by an anatomical substrate of predictable dimensions and shape.

Specific proposals relate to the various elements of Hubel and Wiesel's model; the role of the afferent input, the classification of cortical neurones in relation to the
afferent input, the relationships between these neurones within the cortex, and the vertical segregation of these types into functional units with common response specificities. Each of these aspects of the model is considered.

1.2 The Role of the Afferent Input in Hubel and Wiesel's Model

The afferent input was assumed to be homogeneous in type, limited in distribution, and untuned in terms of showing no selectivity in response to oriented moving bars. The most important assumption in relation to the geniculate input is that fibres converge onto the simple cell in an aligned manner.

Hubel and Wiesel's (1962) model assumed the predominant site of termination of afferent fibre input to be lamina IV, with a lesser distribution to lamina VI. Such a distribution had been reported by Nauta (1954) and has since been confirmed by numerous studies (e.g. Wilson and Cragg, 1967; Colonnier and Rossignol, 1969; Hubel and Wiesel, 1969; Carey, 1970). However, the distribution of thalamo-cortical fibres has subsequently been found to show a more complex pattern of laminar distribution. This pattern of distribution is not simply numerically greater, in terms of laminae contacted, but represents a pattern of distribution specifically related to different types of afferent fibres. Such fibres represent parallel streams running from retina to cortex (Wilson and Cragg, 1967; Cleland, Dubin and Levick, 1971; Hoffmann, Stone, and Sherman, 1972; Stone and Dreher, 1973; Sherman, Norton and Casagrande, 1975; Tretter, Cynader and Singer,
Three categories of retinal ganglion cell, showing differences in morphology, distribution and conduction velocities have been described (Enroth-Cugell and Robson, 1966; Bishop, Clare and Landau, 1969; Cleland, Dubin and Levick, 1971; Cleland, Levick and Sanderson, 1973; Cleland and Levick, 1974a, b; Stone and Hoffmann, 1972; Fukuda and Stone, 1974, 1975; Stone and Fukuda, 1974a, b; Rowe and Stone, 1976) referred to as X, Y and W cells, or sustained, transient, and sluggish and non-concentric cells. The X cell is characterised by a medium sized soma, small dendritic and receptive fields (Enroth-Cugell and Robson, 1966; Boycott and Wassle, 1974; Cleland and Levick, 1974a, b; Fukuda and Stone 1974, 1975; Hammond, 1974; Stone and Fukuda, 1974a, b; Levick, 1975). This type of cell is concentrated around the area centralis and projects to the cortex via the A laminae of the dorsal lateral geniculate nucleus (Wilson and Cragg, 1967; Cleland, Dubin and Levick, 1971; Hoffmann, Stone and Sherman, 1972; Wilson, Rowe and Stone, 1976; Dreher and Sefton, 1979). In contrast, the Y cells have large soma, large dendritic and receptive fields and thick, fast conducting axons (Enroth-Cugell and Robson, 1966; Bishop, Clare and Landau, 1969; Cleland, Dubin and Levick, 1971; Boycott and Wassle, 1974; Cleland and Levick, 1974; Fukuda and Stone, 1974, 1975; Hammond, 1974; Stone and Fukuda, 1974; Levick, 1975). Compared with X cells they are relatively greater in number in the peripheral retina but as a category congregate in the area centralis and the visual streak (Enroth-Cugell and
Robson, 1966; Cleland, Levick and Sanderson, 1973; Fukuda and Stone, 1974; Rowe and Stone, 1976). These cells project to the cortex via the A and C laminae of the LGNd (dorsal Lateral Geniculate Nucleus) and also the MIN (Medial Interlaminar Nucleus) (Wilson and Cragg, 1967; Cleland, Dubin and Levick, 1971; Hoffmann, Stone and Sherman, 1972; Wilson, Rowe and Stone, 1976; Mason, 1976; Dreher and Sefton, 1979). W cells form a population of small to medium sized ganglion cells with thin, slow conducting axons and large dendritic and receptive fields (Stone and Hoffmann, 1972, Cleland and Levick, 1974a; Stone and Fukuda, 1974; Fukuda and Stone, 1975; Levick, 1975). Concentrated in the visual streak and area centralis (Fukuda and Stone, 1974), they form 50-55% of all ganglion cells. The relay to the cortex of these cells is via the parvocellular C laminae of LGNd (Wilson and Cragg, 1967; Hoffmann, Stone and Sherman, 1972; Cleland, Levick, Morstyn and Wagner, 1976; Wilson, Rowe and Stone, 1976; Dreher and Sefton, 1979) and MIN (Dreher and Sefton, 1979; Mason and Robson, 1979; Guillery, Geisert, Polley and Mason, 1980; Rowe and Dreher, 1982).

The distribution of these three types of fibres differs between cortical areas and in laminar distribution within a specific area. The striate cortex is the site of projection of X fibre input from the LGN (Hoffmann and Stone, 1971; Stone and Dreher, 1973; Singer, Tretter and Cynader, 1975; Dreher, Hale and Leventhal, 1978), but both Y and W cells also provide input to area 17 (Singer, Tretter and Cynader, 1975; Ferster and LeVay, 1978; Leventhal, 1979). In the striate cortex, the three categories show the following pattern of
laminar projection; X cells project to laminae IVc and VI; Y cells project to laminae IVab and VI; W cells project to layers I, III and the layer IV-V border area (Singer, Tretter and Cynader, 1975; Tretter, Cynader and Singer, 1975; Ferster and LeVay, 1978; Leventhal, 1979).

The consequences of this distribution in the present context are: firstly, the distribution of fibres is such that, with the exception of lamina II, each of the laminae of the cortex acts as a recipient site for the afferent fibres; secondly, that such a segregation pattern of fibre terminations may represent separate pathways, certainly at the first synapse, and potentially beyond the first synapse. Recent evidence supports the second possibility (Bullier and Henry, 1979b; Mustari, Bullier and Henry, 1982). The distribution of cells in laminae away from the principal lamina of termination of fibres, lamina IV, does not therefore preclude their occupying the first ordinal position in the cortex as suggested in Hubel and Wiesel's work. To the extent that such parallel streams remain segregated to the point of the geniculo-cortical synapse, the laminar distribution of cell types (Gilbert, 1977; Leventhal and Hirsch, 1978; Bullier and Henry, 1979), raises the possibility that different cell types receive different afferent inputs (Stone and Dreher, 1973; Hoffmann and Stone, 1971; Dreher, Hale and Leventhal, 1978). Even if not segregated in terms of specific correspondence of fibre type and cell type contacted, processing of these separate parallel streams may continue through the cortex, both complicating and contradicting the serial processing envisaged by Hubel and Wiesel.
Several studies have shown that, contrary to the initial report of Hubel and Wiesel (Hubel and Wiesel, 1962), the LGN does show some degree of orientational tuning when tested with moving bars (Daniels, Norman and Pettigrew 1977; Creutzfeldt and Nothdurft, 1978; Lee, Creutzfeldt and Elepfandt, 1979; Vidyasagar and Urbas, 1982). Of the two alternative possibilities for the origins of this bias, namely the geniculate suppressive field (Levick, Cleland and Dubin, 1972) or the asymmetries seen in retinal ganglion cell receptive fields (Hammond, 1974; Levick and Thibos, 1980) the mechanism was attributed by Vidyasagar and Urbas (1982) to the suppressive field but with some retinal contribution. This study revealed strong orientation biases in the LGNd for the vertical and horizontal orientations; oblique orientations are first represented in the cortex. An interesting possibility raised by these authors is the role of the afferent input from the geniculate in forming two principal co-ordinates from which the cortex generates other orientations, a proposition deriving from the theoretical model of Von der Malsberg (1973) and Von der Malsberg and Cowan (1982). Essentially though, this proposition is speculative. The main point raised by this and the preceding studies is that orientation tuning cannot be seen as an exclusively cortical phenomenon though undoubtedly it reaches greater prominence and functional significance at that level (Creutzfeldt and Nothdurft, 1978).

The consideration of the relationship between the afferent input and the simple cell first requires a description and evaluation of Hubel and Wiesel's
1.3 The Classificatory System of Hubel and Wiesel

Three broad questions are raised by Hubel and Wiesel's classificatory system. The first concerns the empirical validity and comprehensiveness of that scheme; can three categories of neurone be distinguished by their criteria and can the system account for all the diverse receptive field types? The second is the extent to which the classificatory system may be used for predicting the ordinal position of neurones in a serial chain. Thirdly, the question is raised of the relationship between the classes of cells defined by receptive field organization and the categories of neurone defined by morphological criteria, and the extent to which a knowledge of this correlation might reveal the functional significance of the various morphological types.

The defining criteria of the various categories of neurone in Hubel and Wiesel's scheme may be summarized as follows. Simple cells exhibit the following properties.

1. The receptive field, plotted with stationary flashed stimuli of appropriate contrast, has separate elongated "on" and "off" regions.
2. In common with retinal ganglion and lateral geniculate receptive fields, simple cell fields show summation of responses within an "on" or "off" region and antagonism between "on" and "off" regions. However, Henry (1977) has pointed out that summation of response was originally reported for circular spot stimuli increasing in size. Since Hubel and
Wiesel later evaluated summation with elongated bars and summation of response along the "orientation axis" is exhibited by both simple and some complex cells, summation of response orthogonal to optimal orientation must be the property exclusive to simple cells.

(3) The orientation selectivity of simple cells, and to a lesser extent the directional selectivity as well, can be explained by and predicted from the layout of the "on" and "off" areas.

Complex cells exhibit the following characteristics:

(1) "On" and "off" areas of the receptive field are often not separate. In most cases flashing stimuli evoke on-off responses or no response.

(2) Where separate "on" and "off" areas can be distinguished in the receptive field, summation within and antagonism between these separate regions is not found.

(3) Complex cells show an orientation selectivity which is position independent; the cells are sensitive to the preferred orientation over a range of positions in the receptive field.

(4) The responses of complex cells to moving objects can neither be predicted nor explained from the maps of the receptive field made with small spots.

(5) Complex cells are only rarely encountered in layer IV of the cortex, the major site of termination of geniculo-cortical axons.

Hypercomplex cells are defined in the following way:

(1) The cells are located in layers of the cortex away from the major termination site of geniculo-cortical afferents.

(2) They exhibit a property of end-inhibition, making them
selective not only for the orientation of the stimulus but also its length. Importantly, the end-inhibition is seen as an all-or-none phenomenon displayed by a distinct group of cells and not a varying property shown by different classes (i.e., simple and complex cells).

1. The end-zone inhibition is orientation sensitive, being generated by a lower level orientation-selective cell, presumed to be the complex cell.

2. The hypercomplex cell is found less frequently in area 17 and increasingly in areas 18 and 19, areas assumed in Hubel and Wiesel's model to be in a hierarchical relationship to area 17, and at a higher step in the hierarchy.

Contrary to the early reports of Hubel and Wiesel, a number of studies have reported hypercomplex cells to be present in striate cortex, distributed in laminae II, III and V. (Camarda and Rizzolatti, 1976; Camisa, Blake and Lana, 1977; Palmer and Rosenquist, 1974; Gilbert, 1977; Rose, 1977; Kato, Bishop and Orban, 1978; Leventhal and Hirsch, 1978). Also, Hubel and Wiesel (1968) reported hypercomplex cells being common in both cat and monkey striate cortex, reversing their earlier view.

The cells in area 17 which exhibit end-inhibition do not constitute a separate group however. There is now substantial evidence that the property of end-inhibition is not the attribute of a separate and distinct group of neurones and, more specifically, it is not an all-or-none phenomenon. Dreher (1972) reported that both simple and complex cells can exhibit end-inhibition and this has subsequently been
confirmed by Carmarda and Rizzolatti (1976), Wilson and Sherman (1976), Hammond and Andrews (1978a, b), Laventhal and Hirsch (1978), and Orban, Kato and Bishop (1979). Though Kato, Bishop and Orban, (1978) reported that they could identify cells which were hypercomplex but not simple or complex in receptive field organization, cells with simple or complex properties with end-inhibition were found. Moreover, Rose (1977) demonstrated that end-inhibition is not an all or none phenomenon. This gradation of inhibition has been reported by Wilson and Sherman (1976) and Gilbert (1977). In summary, end-inhibition is a varied attribute of some simple and complex cells.

The question of two distinct cell types, simple and complex, is more problematical, not least because of the logical grounds for classifying in Hubel and Wiesel's scheme. Simple and hypercomplex cells are defined by attribution, complex cells by exclusion. In other words, both the simple and the hypercomplex cells are defined by possession of certain attributes - in the case of simple cells, separation of the receptive field into zones with properties of summation and antagonism; in the case of hypercomplex cells, the presence of end-inhibition. On purely logical grounds, therefore, such a grouping would most likely be non-homogeneous.

Within the classificatory framework of Hubel and Wiesel, several sub-groups of complex cell have been defined. Henry (1977) has referred to three classes of complex cell. Approximately fifty-five per cent of these comprise cells with
a receptive field of mixed on/off discharge, the remaining forty-five per cent being divided between two sub-classes. The first has a non-uniform receptive field with distinct areas of on and off discharge, being distinct from the simple cell by the failure to show summation of response orthogonal to preferred orientation. The other, and least common complex cell, is unresponsive to flashed light bars or spots but is discharged by exposure to a stationary edge or bar of optimal orientation positioned at any point in the receptive field. Of the three, only the uniform-field complex cell is found in appreciable numbers in the cat striate cortex (Henry, 1977).

Gilbert (1977) has divided complex cells into two groups according to their summatory behaviour along the orientation axis. "Standard" complex cells exhibit summation of response with increased bar length whilst "Special" complex show similar magnitude of response for spot stimuli and for extended bars. Standard complex cells are distributed in laminae II and III (small to intermediate field sizes), lamina V (with intermediate field sizes) and lamina VI (with large receptive field sizes). Special complex cells are reported to be present in lamina V (Palmer and Rosenquist, 1974, Gilbert, 1977) and lamina III (Gilbert, 1977). Special complex cells are absent from and Standard complex cells scarce in lamina IV (Gilbert, 1977).

Henry (1977) and Henry, Lund and Harvey (1978) have identified a complex cell which they refer to as a B cell. In summatory behaviour a "Standard" complex cell, the B cell is distinguished from other complex cells by its generally small
receptive field (less than two degrees in length and width),
preferring slow velocities of stimulus movement and showing
little or no spontaneous activity and a sustained response to
bar flash. Distributed in laminae II and III, including the
III/IV border, and lamina Va, B cells form the predominant
source of projection to the Clare-Bishop area (Henry, Lund and
Harvey, 1978).

Without assuming homogeneity within each group, the
evidence would suggest that a separation between simple and
complex groups can be achieved by the criterion of the
segregation of the receptive field into zones but the picture
relating to summatory behaviour is less clear cut. Many
studies have verified the separation of simple and complex
categories by the presence or absence of divisions within the
receptive field (Maffei and Fiorentini, 1973; Toyama, Mackawa
and Takeda, 1973; Kelly and Van Essen, 1974; Drager, 1975;
Goodwin and Henry, 1975; Ikeda and Wright, 1975; Movshon,
1975; Singer, Tretter and Cynader, 1975; Camarda and
Rizzolatti, 1976; Hammond and Andrews, 1978a, b, c). The
problem of summatory behaviour relates to the conditions under
which the summation is tested and the dimension in which
summation is assessed. Henry (1977) has pointed out not only
that summation orthogonal to the orientation axis is peculiar
to simple cells but that this difference in summatory
behaviour is only evident under threshold conditions. On
grounds of receptive field division but not summatory
behaviour the classificatory system is robust.

An important specification about the type of cell
contacted by the afferent input was made in the model - only simple cells were the recipients of direct afferent input. Because only these cells were recorded from the principal layer of afferent fibre termination, the fourth layer, a unique relationship between afferent fibres and cells of this type was assumed, the basis of the assumption being that geniculate fibres contact cell bodies. Only those cells whose cell bodies are located in lamina IV would therefore be the recipients of direct afferent input. Anatomical studies have demonstrated that afferent fibres make contact with cell dendrites (Garey and Powell, 1971; Winfield and Powell, 1976) and that dendrites of pyramidal cells extend out of layers in which the cell body is located to layers of afferent fibre termination (Cajal, 1911, 1922; O'Leary, 1941; Lorente de No, 1949; Lund, Henry and Harvey, 1979). Therefore, those cells located outside the principal lamina of afferent fibre termination can receive direct monosynaptic input.

The correlation between the laminae of termination of afferent fibres and cell types based on receptive field organization seemed to parallel the distribution of two morphological types; the spiny stellate and pyramidal cells. The main difference between these lies in the possession of a prominent apical dendrite by the pyramidal cell. It had been known that spiny stellate cells are distributed in the major lamina of afferent fibre termination and that pyramidal cells lie outside that lamina (Cajal, 1922; Lorente de No, 1922; O'Leary, 1941). The correlation between spiny stellate cells and simple cells, and complex cells and pyramidal cells reported by Kelly and Van Essen (1974) appeared to provide the
basis for assigning roles to morphologically defined types. That correlation was not however perfect, some pyramidal cells with simple cell receptive fields being amongst their sample. A simple equation of cell types defined by receptive field structure and morphological criteria has not been fulfilled and no single morphological type is seen to be the exclusive recipient of geniculate fibre input. Simple cells are represented by both spiny stellate and pyramidal neurones. Whether a pyramidal cell exhibits simple cell receptive field structure or not appears to depend on the proximity of the basal dendrites to the afferent input (Wiesel and Gilbert, 1981). In contrast to the diverse morphological types having simple cell receptive field structure, the three studies pertinent to the point (Kelly and Van Essen, 1974; Lin, Friendlander and Sherman, 1979; Wiesel and Gilbert, 1981) indicate a high correlation between the complex category and the pyramidal neurone.

1.4. The Interrelationships of Cells in Hubel and Wiesel's Model

The question of the interrelationships between cells in Hubel and Wiesel's model arises in two contexts; the relationships between cell types based on classification by receptive field organization and the interrelationships between cells of the same orientation column. Of course, these are two aspects of the same problem but the special features and importance of the columnar concept in the model warrant separate consideration.
Linkages between cells were considered to be excitatory, one-directional and hierarchical, from simple to complex to hypercomplex. It has already been argued that the hypercomplex category does not represent a separate category of neurone. Evidence will now be presented to counter the suggestion that the complex cell is invariably a second order cortical neurone. The sources of this view are twofold: (1) from latency studies; (2) from evidence that complex cells respond to a range of stimuli to which simple cells are unresponsive.

An early study by Denny, Baumgartner and Adorjani (1968) indicated that all complex cells have latencies reflecting a second order position in relation to the geniculate input to the cortex. Subsequent studies, in which latencies to electrical stimuli were measured for cells identified by their receptive field organization, have established that some proportion of complex cells can be first order cortical neurones (Hoffmann and Stone, 1971; Stone, 1972; Stone and Dreher, 1973; Toyama, Maekawa and Takeda, 1973, 1977; Bullier, Harvey and Henry, 1978). Secondly, comparing the velocity selectivity of simple and complex cells, Movshon (1975) found that some complex cells respond to moving bars at velocities outside the range to which simple cells respond. Thirdly, it was established by Hammond and Mackay (1975a) and confirmed by subsequent studies (e.g. Hammond and Mackay, 1975b, 1976, 1977; Hoffmann and von Seelen, 1978, in the striate cortex and Dinse and von Seelen, 1978 in extrastriate cortex) that complex cells but not simple cells respond to texture motion and that simple cells are therefore not the
sole input to complex cells.

A situation in which complex cells may be first order cortical neurones, receiving direct afferent input from the LGN, does not lead to a complete refutation of the suggested relationship between simple and complex neurones, particularly in the light of evidence that a proportion of complex cells has been shown to receive an orientationally tuned input (Sillito, 1976), from evidence that some complex cells have latencies to electrical stimulation consistent with their being second order cortical neurones (eg. Denny, Baumgartner and Adorjani, 1968; Bullier, Harvey and Henry, 1978), and that some complex cells receiving direct LGN input receive additional intracortical inputs (Singer, Tretter and Cynader, 1975; Bullier and Henry, 1979a). Clearly, the serial sequence suggested by Hubel and Wiesel can only be part of the story since simple cells may provide only some of the attributed input to some complex cells. Indeed, the picture is further complicated by recent evidence that inhibitory influences - acting in reverse order to the proposed hierarchy - exist, since moving fields of visual noise, to which simple cells are unresponsive, have been found to influence their response to moving contrast bars (Hammond and Mackay, 1978, 1981). The question of the interrelationships of simple and complex cells will be returned to. The conclusion at this stage is that complex cells do not receive an exclusive simple cell input, that within the complex cell group a diversity of connectivity patterns exists, and that all complex cells exhibit properties which cannot be derived from a simple cell input.
The concept of the orientation column is central to Hubel and Wiesel's model in explaining the response specificity of second and third order cortical neurones. Though the concept of the orientation column has subsequently been modified (Hubel and Wiesel, 1962, 1972, 1977), it implies the striate cortex is sub-divided into discrete regions or columns extending from the surface to the white matter in which all cells common to the column have the same "receptive field axis orientation" (Hubel and Wiesel, 1962), i.e. it is defined in terms of common response specificities of a group of neurones in vertical proximity. The question of the shape of such columns or slabs (Hubel and Wiesel, 1977) is secondary to that of an anatomical and functional segregation of cells within a cortical area. Without making presuppositions about the shape of these cell aggregates, two requirements are necessary for the concept to acquire empirical validity; that the column is a discrete entity definable by anatomical criteria, and that vertical interactions within a column can be demonstrated. Though inhibitory connections could play some role in the formation of a column, the specific requirement in the model is that of excitatory connections as described previously. Creutzfeldt, Innocenti and Brooks (1974) have argued against the formation of an orientation column by inhibitory connections on the basis that members of the same column differ in the spatial extents of the inhibitory components of their receptive fields. The equation of the inhibitory zones described in Creutzfeldt, Innocenti and Brooks (1974) with those mediating orientation tuning is not, however,
The evidence brought forward in support of the concept of an orientation column is the following.

1. Penetrations perpendicular to the surface reveal cells whose response retains the same orientation preference (Hubel and Wiesel, 1962, 1972, 1977).

2. In oblique penetrations, graphs of orientation plotted against track distance are straight lines through the cortical thickness (interrupted in part through layer IVc of the monkey in which non-oriented cells are present) (Hubel and Wiesel, 1974).

3. In tangential penetrations abrupt shifts in preferred orientation are encountered (Hubel and Wiesel, 1974).


Though demonstrated by physiological techniques and defined in functional terms, implicit in the concept of the orientation column is an anatomical substrate, and herein lies the difficulty. The problem is summarized by Gould and Ebner (1977).

"It has not been possible, however, to provide a precise anatomical definition of a column boundary in the visual cortex based on the anatomical characteristics of functionally related groups of neurones. The problem lies in the concept
of the 'boundary' itself and in the problem of determining the features of an anatomical boundary. If a boundary for a cortical column is set, it implies a type of anatomical discreteness between adjacent groups of cortical cells or that some different type of cellular organization lies beyond the boundary or set of columns, for example, or the border of a set of columns, or the border between two cytoarchitectural areas. Because columns may overlap and be of variable size and shape, it may prove difficult to demonstrate anatomical discreteness of vertical columns with the usual anatomical techniques.

The pattern of connectivity forming a column, though requiring a discontinuity of intracortical connectivity at the columnar boundary, would only require a partial segregation of the afferent input between columns. Within a column an oriented group of fibres from the LGN confers upon the column a particular orientation. A given system of fibre groups would be appropriate only to cells with a particular receptive field orientation. Therefore, some of the fibres making up a bundle would change at each columnar boundary, this change leading to a progression of preferred orientation. However, Hubel and Wiesel themselves (1974) noted the lack of agreement between columnar width and receptive field dimensions of afferent fibres, Lund (1981b) reported no agreement between columnar and basal dendrite width in any lamina and in a review of the problem Szentagothai (1975) could identify no boundary feature of a column.

In considering the evidence for the discreteness of
orientation columns it becomes important to emphasize the paradigm in which such discreteness was revealed. The experimental approach of Hubel and Wiesel (1962, 1972, 1977) was to make limited measurements of preferred orientation for a moving bar in penetrations perpendicular and tangential to the cortical surface. Such a paradigm confers upon the members of a column a greater specificity for orientation than might be revealed by measurements of the range of orientations to which a cell is responsive and might lead to a picture in which columns respond in an all-or-none manner (i.e. for a particular bar orientation this would lead to either a response of all members in unison, or no response; there is no room in the model for non-optimal orientation resulting in sub-maximal firing).

Two strategies have been adopted to investigate the validity of the concept of the orientation column since the initial studies of Hubel and Wiesel. Firstly, a group of experiments which in outline replicate Hubel and Wiesel's pioneering studies but additionally consider breadth of tuning as well as optimal orientation preference, and a second group of experiments which look at the correlation of activity of cells within a column to investigate directly whether cells within that column interact and determine each others' responses.

Lee, Heggelund, Hulme and Creutzfeldt (1977) investigated the distribution of optimal orientations and range of responses of cells in the postlateral gyrus of the striate cortex and found that, while optimal orientation preferences
Parallel to the radial bundle were similar, there existed considerable variability. Extraneous sources of variability due to electrode drift and sampling from adjacent columns were excluded by this study. In the monkey, recording from foveal striate cortex, Bauer (Bauer, 1982; Bauer, Dow, Snyder and Vautin, 1983) have reported discontinuity in the orientation column between supra- and infra-granular layers with cells exhibiting marked differences in optimal orientation above and below lamina IV.

Further evidence against the discrete representation of orientation across the cortex is provided by the work of Albus (1975) who investigated the spatial arrangement of orientation in long penetrations crossing laminae in tracks oblique and tangential to the cortical surface, again in the postlateral gyrus of the cat. In contrast to the approach of Hubel and Wiesel of recording only the preferred orientation of successively recorded neurones, Albus compared the preferred orientation and tuning width in pairs of cells separated by 200 microns in tangential penetrations. This revealed that, in both the medio/lateral and antero/posterior directions the difference in preferred orientation between the adjacent cells was small and of the order of 30 degrees or less, with a superimposed variation of 5-10 degrees in a typical sequence. In addition, in some penetrations, the preferred orientation did not change over a considerable distance. In a few cases, differences of more than 40 degrees between successive neurones were seen but abrupt changes were limited to cortical regions where two regularly organized areas partially overlapped each other. Considering the overlap in tuning of
adjacent cells in tangential and vertical penetrations and the scatter in preferred orientation in vertical penetrations it is difficult to reconcile these results with a discrete representation. It is interesting to note that a continuous representation of orientation was apparent in Hubel and Wiesel’s study using tangential penetrations in the striate cortex of the monkey (Hubel and Wiesel, 1974) though a discrete representation was considered to exist in the cat (Hubel and Wiesel, 1962). Hubel and Wiesel (1974) were, however, unwilling to accept continuous representation of orientation in monkey striate cortex, arguing that orientation columns were too thin to be resolved in tangential penetrations, that occasional abrupt discontinuities in the representation of orientation in tangential penetrations were seen, and, in perpendicular penetrations, similar preferred orientations were found for successively recorded units.

The de-oxyglucose method for the measurement of local cerebral glucose utilization (Plum, Gjedde and Samson, 1976; Sokoloff, Reivich, Kennedy, Des Rosiers, Patlak, Pettigrew, Sakurada and Shinohara, 1977) has been used as a technique to establish the anatomical basis of the orientation column in a variety of species (Johle and Sokoloff, 1976; Stryker, Hubel and Wiesel, 1977; Lang and Henn, 1980; Hubel, Wiesel and Stryker, 1978; Humphrey, Skeen and Norton, 1980). Carbon 14 labelled de-oxyglucose is incorporated by nerve cells in amounts proportional to their metabolic activity, which in turn is related to their neural activity (Plum, Gjedde and Samson, 1976; Sokoloff, Reivich, Kennedy, Des Rosiers, Patlak, Pettigrew, Sakurada and Shinohara, 1977).
Autoradiographic pictures of de-oxyglucose labelled brain sections do not show neural structures but regional differences in grain density which correspond to differences in glucose uptake between areas of the brain. This method is employed in the present context to map the cortical sites of increased metabolic activity produced by visual stimulation with stripes of a single orientation. These studies produce results consistent with the columnar hypothesis; autoradiographs of striate cortex show vertical bands of label extending through the cortical thickness in the cat (Stryker, Hubel and Wiesel, 1977; Hubel, Wiesel and Stryker, 1978; Humphrey, Skeen and Norton, 1980), tree shrew (Skeen, Humphrey, Norton and Hall, 1978) and, in the monkey, interrupted in lamina IVc, (Hubel, Wiesel and Stryker, 1978). Additionally, Humphrey, Skeen and Norton, (1980) reported that, in the tree shrew, de-oxyglucose labelling confirmed a pattern of anisotropic distribution of orientation selective cells across the cortex previously reported by Humphrey and Norton (1980) from physiological recordings. A test of the assumed correspondence between stripes revealed by the de-oxyglucose method and columns revealed by microelectrode methods was made by Schoppmann and Stryker (1981) in the cat. A first stage in the experiment established preferred orientations of neurones at known positions and then the same animals were stimulated with full-field patterns of stripes of a single orientation and measurements were made of glucose uptake at the sites of the cortical units recorded previously. The centres of densely labelled cortical columns were found to contain cells selective for the stimulus orientation of the stripe pattern. Control experiments revealed no columns after
stimulation with a pattern of changing orientation.

Several results from de-oxyglucose mappings of orientation columns are at variance with the columnar concept. Firstly, for the monkey, labelled columns have been reported in conditions in which stimuli of many orientations are presented (Hendrikson and Wilson, 1979; Horton and Hubel, 1980; Humphrey and Hendrikson 1980; and Hendrikson, Hunt and We, 1980). Secondly, at least two studies have reported marked variation in label density from layer to layer outside lamina IV both in width and density of labelling in autoradiographs after stimulation with a single orientation (Hubel, Wiesel and Stryker, 1978; Albus, 1979). Though laminar differences in width of labelling are clearly incompatible with the columnar hypothesis, laminar differences in label density might be accommodated if these differences correlated with laminar differences in cell density. These two variables are, however, not correlated (Hubel, Wiesel and Stryker, 1978). A further difficulty is raised by studies in which an alternative index of metabolic activity is compared with de-oxyglucose labelling. Horton and Hubel (1981) compared staining for cytochrome oxidase (a mitochondrial enzyme) with de-oxyglucose labelling. Stimuli were monocular presentations of black/white stripes at all orientations or a single orientation. In the former case, the rows of patches with de-oxyglucose autoradiography lay in register with the cytochrome oxidase patches but, for the latter condition, de-oxyglucose label formed a lattice that included the cytochrome oxidase patches but was more extensive. The conclusion was that either de-oxyglucose does not label
orientation columns at all, or that orientation columns coalesce in areas marked by cytochrome oxidase stain. An unresolved complication is the reported species difference in cytochrome oxidase patches, being present in primates (Humphrey and Hendrikson, 1980; Horton and Hubel, 1981) but absent in non-primates (Horton and Hubel, 1981).

The rationale of the de-oxyglucose approach is open to question. It may be argued that the type of experiment described represents no more than a refined version of the type of experiment which initiated the columnar concept. What it re-emphasizes is that if one takes some measure of preferred orientation, be it reflected in the response recorded electrophysiologically from successive units or cells labelled by de-oxyglucose, then the cells within a vertical array share the same mean orientation. Whilst de-oxyglucose studies produce results consistent with a columnar hypothesis they equally produce results in accord with continuous representation of orientation; the method does not overcome the recurring problem for the columnar hypothesis, the provision of evidence of a columnar boundary. The determination of columns by differences in the relative density of labelling between adjacent areas in autoradiographs lacks the degree of resolution required for establishing an anatomical boundary. Furthermore, the method can be used to support continuous representation of orientation (Albus, 1979).

One can consider the column from the viewpoint of an array of cells whose response properties are linked in a
chain, the response of each determined by the preceding member. From this perspective it becomes interesting to evaluate the response identity of members of a column. Creutzfeldt, Innocenti and Brooks (1974) made comparisons between pairs of neurones simultaneously recorded with the same electrode. Contrast bars were used as stimuli and the parameters of the moving bar were optimized for the first encountered cell in the penetration. Cells were classified as being small ERF (small excitatory receptive field) or large ERF (large excitatory receptive field), a categorization closely corresponding to the simple/complex dichotomy. The study revealed that excitatory connections are not a common feature of connectivity within a column. Four features of response led to this conclusion: (1) a comparison of ERFs; (2) a comparison of locations within the receptive field; (3) directional selectivity to forward and backward motion of the bar; (4) amplitude of response. In each case no correspondence of response was found.

In the same context, Towe (1975) has pointed out that whereas a topographic model of the cortex allows considerable variation in the size and shape of receptive fields of neurones of the same column, the columnar model requires that they all be nearly identical. Laminar differences in receptive field geometry (Palmer and Rosenquist, 1974; Singer, Tretter and Cynader, 1975; Sherman, Watkins and Wilson, 1976; Wilson and Sherman, 1976; Gilbert, 1977; Henry, Lund and Harvey, 1978; Leventhal and Miroch, 1978; Gilbert and Wiesel, 1979; Henry, Harvey and Lund, 1979) argue against the columnar principle.
Toyama, K. and Tanaka (1981a, b) have approached the problem of intracolumnar interactions using a cross-correlation technique. Three types of inter-neuronal interaction were revealed in this study:

(1) Joint excitation of two cortical neurones. This was characterized by a positive correlation in response with no delay. Such behaviour was attributed to common excitatory inputs from the lateral geniculate fibres and was typical of half of the neurones studied (105/208).

(2) Delayed excitation, within the monosynaptic range of one cell following the excitation of the other, representing excitatory connections through intracortical routes and typical of approximately one in ten neurones (24/208).

(3) Delayed inhibition of one cell following the excitation of the other, representing inhibitory interactions through intracortical connections and typical of approximately one in ten neurones (26/208).

These patterns of activity had a laminar distribution. Joint excitation was a feature of cells distributed in layers III-IV, i.e. those cells which receive monosynaptic input from the LGN (Toyama, Maekawa and Takada, 1973; Toyama, Matsunami, Ohno and Tokashiki, 1974; Watanabe, Konishi and Creutzfeldt, 1966), and a feature of all cell types except the hypercomplex II category (complex cells with end-inhibition). Delayed excitation was a feature of cells distributed in the border region between granular and supragranular layers in the case of the source cell, and the upper part of the supragranular layer in the case of the target cell. Such interactions were only found from complex to complex cells and
from complex to hypercomplex type II - i.e. no excitatory links were found from simple to complex cells. Intracortical inhibition was confined to four combinations, namely: from $e(on)$, non-oriented cells with excitatory "on" responses, or $e(off)$ non-oriented cells with excitatory "off" responses to simple cells; from simple to complex cells; from $e(on)$ or $e(off)$ to simple cells; from $e(on)$ or $e(off)$ to complex cells or between $e(on)$ and $e(off)$ cells. Only one other study, that of Singer, Tretter and Cynader (1973), has reported the presence of non-oriented cells in cat striate cortex; their monosynaptic type 1 cells included some non-oriented cells. The existence of a class of non-oriented cells is not a commonly accepted feature of cat striate cortex.

In summary, both studies would suggest that excitatory connections are not a common feature of interactions among members of the same column, though Toyama, Kimura and Tanaka's (1981a, b) study does indicate that where excitatory connections do take place, they are between members of the same or adjacent orientation columns. Also, when such links do occur, they are limited in laminar distribution and are not between simple and complex cells, in that order. The demonstration of the second study here, that where such links do exist this kind of linkage does not take place between simple and complex cells, is conjectural since on other grounds it would appear that such links between simple and complex cells (in that order) may exist. This will be returned to in the following chapter. It does not undermine the general point about the lack of excitatory connections.
It has already been argued that the afferent input to the striate cortex is considerably more extensive than would be expected from a columnar organization. The efferent output is likewise extensive, showing a lamellar pattern with specific target sites. Lund (1981) has argued that with the possible exception of laminae I, IVa and IVc in the monkey, every lamina of the striate cortex gives rise to efferent projections and that these efferents are segregated from one another, projecting to different destinations and probably conveying different information. Such a pattern, she has argued, is incompatible with a columnar organization for it implies marked differences in organization at different depths, in contradiction to the columnar principle of a common pattern of organization from the pia to the white matter. With most laminae projecting out of the hypothetical column, a pattern of connections emerges which argues against the intracolumnar pattern of connectivity and against a vertical array of cells so linked to provide a functional entity as implied by the column. Indeed, the point is underscored by anatomical (Szentagothai, 1973; Lund and Booth, 1975; Garey, 1976; Lund, 1976) and physiological evidence (Singer, Tretter and Cynader, 1975; Ito, Sanides and Creutzfeldt, 1977) for monosynaptic termination of geniculate fibres on the apical dendrites of lamina V pyramidal neurones, substantial numbers of which project directly out of the cortex to the tectum (Palmer and Rosenquist, 1974; Gilbert and Kelly, 1975). Such patterns of efferent projections as highlighted by Lund are manifest for both the monkey and cat. Area 17 of the cat and monkey show similarities in the organization of the efferent pathways (Palmer and Rosenquist, 1974; Gilbert and Kelly,
In both species lamina VI pyramidal neurones project to the dorsal lateral geniculate nucleus, lamina V projects to the superior colliculus and pulvinar, laminae IIIa and II of the cat project to area 18 and 19, and lamina IIB provides a projection, together with efferent streams from more superficial laminae, to the Clare-Bishop area.

From the preceding discussion it will be apparent that the proposition that the orientation column exists as an anatomical and functional entity has become untenable. This precludes neither excitatory connections of the type supposed by Hubel and Wiesel, nor vertical interactions within the cortex but it denies the axiom that the presentation of a particular orientation of a moving contrast bar uniquely gives rise to activity in an anatomically segregated array of cells defined by a column. On presentation of such a stimulus, cells vertically (Lee, Heggelund, Hulme and Creutzfeldt, 1977) or horizontally (Albus, 1975) close to a hypothetical column respond to varying extents. Such an aggregation of cells forms an "orientation sub-unit" (Albus, 1975, 1979). This "sub-unit" consists of cells which respond at all to a particular orientation. These cells are vertically aligned through all layers and are on average 200 microns (range 23-450 microns) in the horizontal direction to either side from the centre of an iso-orientation band or spot. Sensitivity to the orientation functionally represented by the sub-unit decreases with increasing distance from the centre band or centre spot respectively. It will be apparent from
the concept of an orientation sub-unit, comprising all those cells which respond at all to a particular orientation that, in contrast to the columnar concept, a small change in stimulus results not in a "switching off" of one column and the "switching on" of the next column but a shift in both the degree of response of those cells previously responding and also in the population of cells responding. The concept of the orientation sub-unit implies that each sub-unit has indeterminate boundaries and that it shares cells with its neighbours. The type of spatial and functional organization of the sub-unit implies by itself that the orientation domain has a continuous representation across the cortex.

1.6 The Mechanism of Orientation and Direction Selectivity in Hubei and Wiesel's Model

The responses of striate cortical cells to moving oriented contrast bars can, according to the model, be predicted and explained from a knowledge of the sub-division of the simple cell receptive field. Partitioning of the receptive field should solely reflect the afferent input and its transformation at the geniculo-cortical synapse. Orientation and direction selectivities are determined by interactions within a unitary input to the simple cell.

The specific requirement of the afferent input for the model to be valid is that the type of receptive field organization shown by the simple cell is determined by the convergence and alignment of the geniculate fibres so as to transform the centre-surround organization into that of
elongated fields with division into on and off regions. Colonnier (1964) provided a model of how that convergence might be brought about. The incoming lateral geniculate axons, presumed to retain the topographical arrangement of the retina, would be grouped upon the cortical cells in relation to the latter's dendritic tree. Since for the majority of stellate cells the dendritic fields are elongated in the tangential plane, (Colonnier, 1964; Seldon and Von Keyserlingk, 1978), the orientation of the elongated dendritic tree would permit a preferential selectivity by the recipient cells for groups of oriented axons; the preferential orientation of axons and dendrites in most layers of the cortex results in a focusing of any one group of specifically oriented axons upon similarly oriented dendrites. The functional significance of dendritic geometry remains conjectural (see chapter two). There is some evidence of preferential elongations being determined by factors of gross anatomy rather than functional considerations at the neuronal level (see Seldon and Keyserlingk, 1978 for discussion). However, substantial physiological and anatomical evidence argues against convergence and therefore whatever functional role may be attributed to dendritic morphology it cannot include one of aligning convergent geniculate fibres.

The majority of evidence against convergence is physiological. Creutzfeldt and Ito (1960), from intracellular recordings, reported that each neurone recorded had 2-4 overlapping areas of off or on excitation or inhibition. Each of these areas had the functional properties of a single geniculo-cortical off or on centre fibre with their receptive
field centres separated by 1-3 degrees. Also, from a knowledge of the average firing frequency of afferent fibres and measurements of post-synaptic potentials an estimate of the number of afferents causing those post-synaptic potentials was made of two to four geniculate fibres.

Wilson and Sherman (1976) reported that the receptive field widths for simple cells closely parallel those for geniculate cells at all eccentricities, being consistent with one or a few geniculate neurones providing the excitatory input to the simple cell. Creutzfeldt, Benevento and Kuhnt (1976), from intracellular recordings, revealed the LGN input to cells to be derived from a small retinal area and of a size comparable to the sizes of central excitatory fields found at lower levels of the visual pathway. Lee, Cleland and Creutzfeldt (1977) were able to make simultaneous recordings from retinal and cortical cells and found that the receptive fields were well superimposed and concentric within 0.5 degrees. In conjunction with the finding of the scatter of the receptive field centres of ganglion cells projecting to a single LGN cell being maximally 0.5 degrees (Levick, Cleland and Dubin, 1972), the result was interpreted as evidence that cortical cells received input from individual axons from the LGN. Sillito et al (Berardi, Kemp, Wilson and Sillito, 1980; Sillito, Kemp, Wilson and Berardi, 1980) found that, following the iontophoretic application of bicuculline, the receptive field dimensions of simple cells judged by moving bar stimuli at optimal and orthogonal orientations corresponded with expectations from a single LGNd cell input. Tsumoto, Eckart and Creutzfeldt (1979) have reported the same result.
Bullier, Mustari and Henry (1982), considering the question of brisk-sustained and brisk-transient fibre convergence, reported differences between the two populations with input to simple cells from 1-2 fibres for brisk transient and 2-20 for brisk sustained. For both populations, mean numbers indicated little convergence.

Those studies which have considered the spatial distribution of the afferent input (Creutzfeldt and Ito, 1968; Schiller, Finlay and Volman, 1976b; Lee, Cleland and Creutzfeldt, 1977; Berardi, Kemp, Wilson and Sillito, 1980; Sillito, Kemp, Wilson and Berardi, 1980; Bullier, Mustari and Henry, 1982) indicate that, in the absence of inhibitory mechanisms, the component of the receptive fields of simple cells attributable to the afferent input displays circular symmetry. It would appear that the division of the simple cell receptive field into regions responding to opposite contrasts is dependent on intracortical inhibition since Sillito (1975) has reported that, following iontophoretic application of bicuculline, simple cells respond to flashed stimuli with mixed on-off responses whether these stimuli are confined to previously determined on or off areas or cover the whole receptive field.

If the organization of the simple cell receptive field into sub-regions, as described by Hubel and Wiesel, is not determined by the afferent input the possibility remains that such an organization, re-attributed to intracortical circuitry, confers upon the simple cell its selectivity for orientation and direction. Indeed, the relatively high degree
of predictability of preferred orientation from the layout of the receptive field is consistent with this.

The relationship between preferred orientation or orientation selectivity and receptive field geometry has been investigated in several studies. Creutzfeldt, Kuhnt and Benevento (1974) found that whilst the excitatory areas of cortical cells were mostly slightly elongated, this elongation was not systematically along the axis of optimal orientation. Plotting the receptive fields of simple cells with flashed spots, Schiller, Finlay and Volman (1976b) reported these to be circular or slightly elliptical, although the long axis did not necessarily fall along the axis of preferred orientation. Watkins and Berkley (1974), though noting that in general orientation selectivity is related to receptive field size, found only a weak correlation between orientation selectivity and receptive field geometry. Schiller, Finlay and Volman (1976b) investigated the predictions: (1) that cells with weak flanks should be more broadly tuned than cells with strong flanks; (2) the orientation specificity of cells with bipartite fields should depend on the spatial separation between the sub-fields and the length of the sub-fields along the axis of orientation; and (3) that cells with tripartite fields might be expected to be sharply tuned since they have two well-defined flanking zones. A comparison of tuning for various classes of simple cells revealed that the tuning specificity of cells with only single receptive field zones was comparable to those in other categories, and cells with multiple receptive field zones were found to be the most poorly tuned (though the sample size was small). Comparing
orientation selectivity with measures of receptive field length, centre-to-centre sub-region separation and centre-to-centre separation divided by receptive field length, yielded low correlations ($r = -0.25$; $r = 0.03$; $r = 0.29$).

Orientation selectivity was thought, by Hubel and Wiesel (1962), to be determined by summation of response within a region and antagonism between sub-regions of the receptive field, the antagonism being presumed to reflect inhibitory interactions at the geniculate level. The increased response associated with increased bar length has been confirmed repeatedly (e.g. Henry, Dreher and Bishop, 1974; Rose and Blakemore, 1974; Schiller, Finlay and Volman, 1976b; Hammond and Andrews, 1978a, b, c). That this does not reflect increased recruitment of afferent fibres will be evident from the preceding discussion of the limited geniculate fibre input to individual simple cells (Creutzfeldt and Ito, 1968; Creutzfeldt, Benevento and Kuhnt, 1974; Creutzfeldt, Innocenti and Brooks, 1974; Wilson and Sherman, 1976; Lee, Cleland and Creutzfeldt, 1977; Sillito, Kemp, Wilson and Sillito, 1980) and its spatial distribution (Creutzfeldt and Ito, 1968; Schiller, Finlay and Volman, 1976b; Lee, Cleland and Creutzfeldt, 1977). Sillito, Kemp, Wilson and Berardi (1980) therefore argue that increased response associated with increased stimulus length is not a product of spatial summation but either increasing disinhibition evoked by the change in stimulus length or subliminal facilitatory effects present at all orientations but normally blanked by the inhibition at non-optimal orientations.
Equally, neither antagonism between centre and surround at the geniculate level, nor interactions between sub-regions of the simple cell receptive field, as plotted with stationary bars, can play any role in orientation tuning. At the geniculate level, Dreher and Sanderson (1973) have reported that moving bars simultaneously covering centre and surround produce only excitatory responses. In the second case, for the proposition to be correct, the inhibitory components of the receptive field of the simple cell would have to be coincident with the borders between sub-regions mapped with flashed bars. Spatially distinct inhibitory sub-regions within the receptive field have been reported by Creutzfeldt and Ito (1968), Henry, Bishop and Coombs (1969), Bishop, Coombs and Henry (1971 a, b), Bishop and Henry (1972) and Bishop, Coombs and Henry (1973), amongst others. When these sub-regions are located using the monocular or binocular conditioning method of Henry, Bishop and Coombs (1969), they are frequently not in register with the regions mapped with stationary or moving stimuli (Henry, Bishop and Coombs, 1969; Bishop, Coombs and Henry, 1971 a, b; Bishop, Coombs and Henry, 1973; Schiller, Finlay and Volman, 1976e). The schematic model of the simple cell incorporating such side-band inhibition is taken up in the context of models invoking intracortical inhibition.

Directional selectivity was viewed also to be the product of the disposition of the receptive field regions, as a product of synergistic action between them. Several predictions follow from the model.

(1) Stimulus movements confined to either discharge region
would not show directional selectivity.

(2) Directional selectivity would not be shown for a moving edge crossing the receptive field.

(3) A directional preference with one sign of contrast would be reversed with contrast reversal.

None of these predictions has been fulfilled. It has been demonstrated that regions smaller than "on" or "off" areas show directional selectivity (Bishop, Dreher and Henry, 1972; Bishop, Goodwin and Henry, 1973; Goodwin, Henry and Bishop, 1975) and that the preferred direction of motion of a contrast bar is not invariably predictable from the spatial layout of the receptive field (Bishop, Dreher and Henry, 1972; Henry and Bishop, 1972; Henry, Dreher and Bishop, 1974; Goodwin, Henry and Bishop, 1975; Nothdurft, 1976; Schiller, Finlay and Volman, 1976a; and Henry, 1977). Directional selectivity has been demonstrated for edges (e.g. Schiller, Finlay and Volman, 1976a). Furthermore, some simple cells show a directional preference independent of contrast reversal (Bishop, Coombs and Henry, 1971a; Emerson and Gerstein, 1977; Albus, 1980). However, the disposition of the regions probably has some bearing on the strength of discharge to moving bars of different widths and contrast polarity (Bishop, Coombs and Henry, 1971b).

A specific addition to the original model was the suggestion of the reinforcement of the "surround zones" by fibres of the opposite type (for a simple cell whose main input is on-centre, the antagonistic region would be reinforced by off-centre fibres, and vice versa). A number of lines of evidence argue against convergence of on- and
off-centre neurones onto individual simple cells. The studies of Dreher and Sanderson (1973) and Bishop, Goodwin and Henry (1973) together indicate that the responses of simple cells to moving contrast bars are consistent with individual simple cells receiving either on- or off-fibre input, but not both. In terms of phase behaviour, simple cells have been reported as falling into two groups (Lee, Elepfandt and Virsu, 1981b) corresponding to on- and off-centre cells at lower levels in the visual pathway (Lee, Elepfandt and Virsu, 1981a). Bullier, Mustari and Henry (1982) established the signature for LGN neurones with moving and stationary bars and identified the signature in the responses of simple cells which indicated that the majority were explicable in terms of a non-mixed input.

However, Lee, Elepfandt and Virsu (1981b) and Bullier, Mustari and Henry (1982) have reported a minority of neurones whose phase or signature behaviour is indicative of a mixed input. It remains conjectural whether those neurones represent higher order simple cells with “mixing” occurring intracortically or cells receiving mixed input at the geniculo-cortical synapse. However, where such mixing occurs it would appear to have no role in determining directional selectivity. Schiller (1982) made use of Slaughter and Miller’s (1981) demonstration that in the isolated eye cup of the mudpuppy and rabbit, DL-2-amino-4-phosphonobutyric acid (APB) reversibly blocks the “on” responses in the retina. The directional selectivity of cortical simple cells was measured before, during and after blocking the retinal “on” system. The directional preferences of the units was unaltered by APB
infusion thus showing directional selectivity not to be dependent on interactions between "on" and "off" channels.

In summary, whilst the subdivision of the simple cell receptive field plotted with flashed bars provides some indication of the preferred orientation for a moving bar, that division neither reflects the distribution of the afferent input nor the mechanism generating that selectivity. Neither can one explain the directional selectivity shown by the simple cell with reference to that scheme.

1.7. Implications.

The primary role of the afferent input in determining the orientation and direction selectivity of cortical neurones is not supported. Since each individual cortical neurone receives, at the most, input from a few geniculate fibres the geometry of the afferent input puts few constraints on the form of the receptive field. The functional properties attributable to the afferent input from the lateral geniculate nucleus are limited to the contributions of individual fibres, from their centre-surround organization and the functional properties of different fibre types. Consideration is given in subsequent discussion to whether some of the functional differences between simple and complex cells are a product of different geniculate fibre inputs. The widespread laminar distribution of afferent fibres means that all cells within a hypothetical column are potential recipients of direct mono-synaptic input. Contact between afferent input and individual cortical neurones is constrained neither by
morphological nor receptive field classes and so no neurone type can occupy a pivotal position in the progression of intracortical circuitry from the afferent input.

The implications of the columnar model with a discrete representation of orientation, that the functional role of striate neurones is defined by their optimal orientation preference and that cells in close vertical proximity with identical optimal orientation preference comprise a functional unit, runs counter to physiological and anatomical evidence. Since striate neurones do not show orientation selectivity but respond with a gradation of response to a range of orientations, their functional properties may only be described by their tuning characteristics. The constraints placed on intracortical organization by the discrete representation of orientation have been contrasted by Towe (1975) with the functional implications of continuous representation of orientation assumed in a topographical model of the cortex.

"The former (a topographic model) views the cerebral cortex as a continuous tissue wherein each individual neurone functions as a fundamental unit, being free to discharge in relation to various subsets of its neighbours. The latter parcels the cerebral cortex into discrete sets of neurones, termed columns, such that each column acts as an elementary functional unit - each neurone within a column can discharge with one and only one set of neurones - those comprising its own column."
As Lund (1976) has pointed out, since the most obvious progression of synaptic relays in area 17 seems to be between laminae, these kinds of connections would underlie the physiological impression of vertically organized columns or slabs - or that the whole set of links would create a unit of function and that all the outputs from such a unit might constitute a set of information common to the unit. There would, however, appear to be neither anatomical evidence for a segregation of columns nor physiological support for the column constituting a functional entity. As suggested by MacKay (1976), there seem to be very few cases in which columnar organization means abrupt functional discontinuity between cells of a given layer. In most cases it means only that cells immediately below one another in a radial penetration have similarly related fields and frequently, but not always, similar stimulus preferences. The column may be fractionated with different patterns of organization linked to lamination. Every lamina of the striate cortex, with the exceptions of laminae I and IV, contains cells projecting extrinsically and it would seem likely, with those outputs projecting to different areas with different functional roles, that each projection out of area 17 carries a particular kind of information or weighting in terms of specific function. Furthermore, each lamina not only projects to different destinations but has a different relationship to the distribution of thalamic afferents and to the patterns of connections intrinsic to the striate cortex. These diverse patterns of connectivity cannot be accounted for by a simple serial chain.
The context set for subsequent discussion is one in which the orientation/direction selectivity of cortical neurones is seen to be a product of intracortical circuitry. Alternative models are presented and evaluated against current knowledge of the pattern of intracortical connections derived from anatomical and physiological studies. Emergent from the discussion is the dependence of orientation/direction selectivity on intracortical inhibition and the need to posit separate mechanisms to explain the orientation and direction selective properties of cortical neurones. The contributions of these separate mechanisms are assessed by determining the tuning curves for stimuli in which the parameters of orientation and direction are dissociated.
CHAPTER TWO: THE ROLE OF INTRACORTICAL CIRCUITRY IN THE
MEDIATION OF ORIENTATION AND DIRECTION SELECTIVE MECHANISMS

2.1 Models for the Role of Intracortical Inhibition

2.1a The Models of the Canberra Group

Bishop and associates (Bishop, Coombs and Henry, 1971b) proposed a model of the simple cell which potentially overcame two shortcomings in Hubel and Wiesel's model: the poor predictive value of a receptive field structure plotted with stationary bars for moving stimuli (Bishop, Coombs and Henry, 1971a; Henry and Bishop, 1972); and the absence of inhibitory interactions between centre and surround at the geniculate level (Dreher and Sanderson, 1973). Receptive field structure was elaborated with moving bars and inhibitory interactions re-attributed to the cortical level. In the absence of a resting discharge for the majority of simple cells, inhibition was measured against a response induced by a conditioning stimulus (Bishop, Coombs and Henry, 1971b). The "dynamic" receptive field was plotted as a peri-stimulus time histogram (PSTH) to a moving bar at the cell's preferred orientation and moving in its preferred direction. In skeleton form, the receptive field determined in this way comprises a central discharge zone flanked by inhibitory side-bands with non-responding end-zones (fig. 2.1).

In this model, the central discharge zone is formed from aligned receptive fields of converging fibres from the lateral geniculate nucleus and the sidebands arise from inhibitory intracortical circuitry. A reconciliation with Hubel and
The figure illustrates receptive field structure determined in the PSTH to a moving bar in preferred and non-preferred directions for the cell. In the preferred direction, receptive field structure has three components; a central discharge zone (black) formed by converging afferent fibres, inhibitory side-bands flanking the excitatory region and non-responding end-zones. In the non-preferred direction, the non-responding end-zones become part of the inhibitory component of the receptive field.

Filled circles: complete inhibition.
Open circles: partial inhibition.

(after Henry and Bishop, 1972).
INHIBITORY SIDEBANDS

PREFERRED DIRECTION

NON-RESPONDING END-ZONE

1°

NON-PREFERRED DIRECTION
Miesel's model (1962, 1963) was suggested by attributing the structure of the "static" receptive field, plotted with stationary bars, to the excitatory input and the "dynamic" structure to intracortical circuitry. In addition to the assumption contained in Hubel and Wiesel's model of convergence of afferent fibres, a further assumption was introduced; that of a fixed spatial relationship between intracortical inhibition and afferent excitation. This assumption also applied to the model for direction selectivity later developed by Goodwin, Henry and Bishop, (1975) and Goodwin and Henry (1975).

Several variants of the model were elaborated, the end-product of which was a spatial and functional sub-division of the simple cell receptive field (Henry, Dreher and Bishop, 1974; Henry, Bishop and Dreher, 1974; Goodwin and Henry, 1975). In an early version (Bishop, Coombs and Henry, 1971b), both the orientation and direction selective properties of simple cells were attributed to the sidebands. Orientation selectivity was seen as a product of summation of response within the central discharge zone and inhibition mediated by the sidebands.

Since for long bars direction is necessarily orthogonal to orientation (Henry, Dreher and Bishop, 1974), direction selectivity was seen as a parameter limiting response to one of two possible directions set by the cell's preferred orientation. Bishop, Coombs and Henry (1971b) proposed that direction selectivity is a product of events preceding the entry of the stimulus into the central discharge zone.
Direction selectivity would be a consequence of disinhibition to a stimulus starting to move in the preferred direction followed by summation of response in the central discharge zone. In the non-preferred direction, response would be limited or prevented by the non-release of tonic inhibition and by inhibition spreading ahead of stimulus movement. Inhibition of response was considered more localised in action than in the model put forward by Barlow and Levick (1965) to account for the direction selectivity in the rabbit's retina. Inhibition was assumed to be limited to action of those geniculate cells immediately preceding the central discharge zone. Feedforward inhibition was transferred to the discharge centre in Goodwin, Henry and Bishop's (1975) model.

The demonstration of a direction selective response for a stimulus wholly contained within the central discharge zone (Bishop, Goodwin and Henry, 1973) clearly indicated that the directional properties of simple cells are not dependent on side-band inhibition (Bishop, Goodwin and Henry, 1973). The side-bands were retained in the model as a mechanism for generating orientation selectivity. The side-bands were functionally linked with a direction-selective mechanism (Goodwin, Henry and Bishop, 1975) as a barrier to the spread of inhibition generated within the central discharge zone. Orientation selectivity would be generated by convergent afferent fibres conferring on the simple cell a rudimentary orientation bias which would be sharpened by sideband inhibition.
2.1b Direction Selectivity Produced by Feedforward Inhibition: 
The Model of Goodwin, Henry and Bishop

The overall goal of the model was to account for the organization of the discharge zone which prevents response in the non-preferred direction. Barlow and Levick (1965) had earlier shown the direction selectivity of rabbit retinal ganglion cells to be dependent on inhibitory interactions between directionally unselective sub-units within the receptive field. In testing the validity of the model, Goodwin, Henry and Bishop (1975) argued that while the simple cell is not divided into sub-units, direction selectivity can be seen as a product of feedforward inhibition. Evidence against sub-units was that the threshold displacement of a contrast bar is direction selective (Goodwin, Henry and Bishop, 1975). Quantitative analysis of responses in preferred and non-preferred directions implicated suppression of response in the non-preferred direction as the basis of direction selectivity. The major part of the study was therefore addressed to evaluation of the conditions under which direction-specific inhibition is generated.

It was suggested (Goodwin, Henry and Bishop, 1975) that the spread of inhibition mediating direction selectivity depends on two parameters: (1) the spread of inhibition curve - describing the spread of inhibition ahead of a moving stimulus, taking the same form at different locations within the receptive field and decaying in intensity as a function of distance from a moving edge; and (2) location within the receptive field - as reflected in the sensitivity profile to a
stationary flashed bar determined by the profiles of the excitatory and inhibitory inputs across the discharge zone. Goodwin, Henry and Bishop (1975) found inhibition to be distributed over the whole of the discharge area but were unable to assess the contributions of these two parameters. It was however suggested that, at any location, direction-selective inhibition is maintained as long as the edge remains in position.

The model developed by Goodwin, Henry and Bishop (1975) has components from geniculate and cortical levels. Cortical inhibition has a role of limiting the directional bias present at the geniculate level to produce a direction selectivity response. At retinal and geniculate levels, on- and off-centre neurones have a centrifugal or centripetal direction bias (Rodieck and Stone, 1965; Dreher and Sanderson, 1973). As in Bishop, Goodwin and Henry (1973), excitatory input is provided by convergent afferent fibres of either on- or off-centre. Direction selectivity is conferred by blanking out half the receptive field by intracortical inhibition; the direction for which a cell is selective depends on which half of the field is blanked out. Afferent drive to the cortical neurones providing the inhibitory circuitry is suggested to come from mixed on- and off-centre sustained neurones. Input from sustained neurones would ensure that inhibition applied to the simple cell is maintained as long as the edge remains in the field.

Complex cells, in Goodwin and Henry's (1975) scheme, are the recipients of a directionally-tuned input from simple
cells. A similar proposal for complex cells' orientation selectivity was made by Henry, Dreher and Bishop (1974). Both models were elaborated for complex cells of the supragranular layers. Similarities in the directional properties of complex cells with simple cells in the dimension of the smallest displacement giving a direction-selective response and in the role of inhibition in suppressing the response in the non-preferred direction were reported by Goodwin and Henry (1975). The essential difference between simple and complex cells' direction selectivity reported by Goodwin and Henry (1975) was that, whereas for the simple cell inhibition suppresses both driven and spontaneous activity, inhibition suppresses only the driven activity of the complex cell. Earlier, Barlow and Levick (1965) reported that, for on-off direction-selective ganglion cells in rabbit, the suppression of spontaneous activity occurs at the cell where inhibition is active in initiating direction selectivity. If inhibition responsible for the generation of direction selectivity fails to influence the spontaneous activity, complex cells must receive a directionally tuned excitatory input; driven and spontaneous activity are derived from different sources Goodwin and Henry (1975) argued. Complex cells, in Goodwin and Henry's (1975) scheme are the recipients of a directionally tuned input from simple cells. Accepting a parallel model of connectivity between geniculate X and simple cells and geniculate Y cells and complex cells, those complex cells receiving Y input were left unaccounted for in the model.

In a later study, Bishop, Kato and Orban (1980) reported
direction-selective complex cells in cat striate cortex for which suppression of the resting discharge for motion in the non-preferred direction was seen. Such neurones (twelve in total) were located both above and below lamina IV, though two of the four direction-selective cells in laminae II/III had no spontaneous activity and for these, inhibition in the non-preferred direction was only demonstrated against a background discharge to a conditioning stimulus.

It is in establishing the role of feedforward inhibition at the cortical level that the studies of Bishop and associates have made their contribution to the understanding of the stimulus selectivity shown by cortical neurones. The shortcomings of the model of the simple cell developed by Bishop and associates are threefold; in the functional interpretation of inhibition extending outside the central discharge zone, the lack of conceptual development of the relationship between sideband and direction-selective inhibition and leaving unanswered the contribution of stimulus movement to the production of direction-selective inhibition.

2.1c The Mediation of Orientation and Direction Selectivities by Separate Mechanisms: The Model of Schiller, Finlay and Volman

There is a close affinity between the model of the simple cell constructed by Bishop and associates and that put forward by Schiller, Finlay and Volman (1976b, c). The component of the receptive field attributed to intracortical circuitry is virtually identical (fig. 2.2). A primary difference arises...
from the observation of Schiller, Finlay and Volman (1976b) that the excitatory component of the receptive field exhibits circular symmetry. This precludes a role for the afferent input in determining the cell's preferred orientation. Schiller, Finlay and Volman (1976a) gave this role to the geometry of pyramidal cell dendrites, simple cells being represented morphologically by pyramidal cells in the model. Further, on the basis of comparison of the tuning properties of cortical neurones, Schiller, Finlay and Volman (1976a) proposed that orientation and direction selectivities are mediated by separate mechanisms arising from two levels of inhibition.

The simple/pyramidal cell would have its orientation properties mediated by inhibitory circuitry associated with the apical dendrites and its directional properties mediated by inhibitory circuitry associated with the basal dendrites. An immediate attraction of the model was that potentially it could account for the diversity of direction selective properties shown by simple cells, by assuming an unvarying pattern of connectivity for the apical dendrites within the simple cell group, but different basal dendrite patterns. The arguments advanced by Schiller, Finlay and Volman (1976b) provide only partial support for the mediation of orientation and direction selectivities by separate mechanisms. Strong support for the mediation of direction and orientation tuning by separate mechanisms is given by the studies of the tuning of complex cells for bar and texture stimuli (Hammond and Mackay, 1977; Hammond, 1978, 1979; Hammond and Reck, 1980a, b). These studies indicate a functional interdependence of
Fig 2.2

The Model of Schiller, Finlay and Volman.

Orientation and direction selectivities are mediated by separate mechanisms associated with two levels of inhibition.

(A). Orientation selectivity is derived from inhibitory circuitry associated with the apical dendrite. The effective dendritic arborization is bilobed. The axis of orientation is along the perspective line, where inhibition is ineffective. The upper layer of interneurones may receive afferent input directly from the LGN (A), by LGN cells coupled with reciprocal inhibition (B) or by other pyramidal cells (C). The lower level of inhibitory interneurones mediate direction selectivity. Spread of basal dendrites in one direction provides the basis of selectivity for one direction.

(B) Receptive field structure resulting from the spatial organization of dendrites illustrated in fig. A. Excitatory input forms a circular component of the receptive field. Inhibition mediating orientation selectivity is represented as two bands either side of the excitatory centre. Inhibition mediating direction selectivity is distributed to one side of the excitatory centre.

(after Schiller, Finlay and Volman, 1976b, e).
orientation and direction mechanisms. The circuitry mediating these mechanisms, at the single cell level, remains conjectural.

2.1d The Model of Creutzfeldt and Associates

Both Bishop's and Schiller's models assumed that the key to understanding the origin of orientation and direction selectivities lies in the spatial distribution of inhibition within the simple cell receptive field. Each model assumed a hierarchical pattern of intracortical connectivity. A quite different view was taken in the model of Creutzfeldt (Benevento, Creutzfeldt and Kuhnt, 1972; Creutzfeldt, Kuhnt and Benevento, 1974). A strictly parallel model of connectivity was assumed (Hoffmann and Stone, 1971; Stone and Dreher, 1973; Dreher, Hale and Leventhal, 1978). Intracortical connections were proposed to be restricted to inhibitory pathways from complex to simple cells. Excitatory connections were limited to a role in modulating inhibition. Both simple and complex cells, it was suggested, lie in the same inhibitory network with differences in receptive field structure being quantitative not qualitative. An understanding of the functional properties would therefore rest on an understanding of the properties of the neuronal network. Creutzfeldt, Kuhnt and Benevento (1974) further argued that inhibitory circuitry determining cortical cells' trigger features extends beyond the classical orientation column and that the functional properties of cortical neurones is a product of cross-talk between columns (Benevento, Creutzfeldt and Kuhnt, 1972). That pattern of connectivity
would need to be anisotropic in order to generate the cortical cells' anisotropic trigger features (Creutzfeldt, Kuhnt and Benevento, 1974).

The model embodies the following:

(1) The retino-cortical projection preserves a retino-topic gradient, but is essentially random if only small cortical projection points are considered (Hubel and Wiesel, 1963; Creutzfeldt, Kuhnt and Benevento, 1974; Albus, 1975).

(2) Individual cells are mainly excited by a very restricted number of geniculate fibres, often by only one fibre.

(3) Inhibition of cortical neurones extends over distances which are of the same order, or slightly larger than, the diameters of functional orientation columns.

(4) Though an anisotropy is already apparent in the anisotropy of afferent connections (Albus, 1975), the anisotropy on which the tuning properties of cortical neurones depends is more dependent on the pattern of intracortical connections. The possibility was raised by Benevento, Creutzfeldt and Kuhnt, (1972) that such a pattern of connectivity might be arranged in stripes (or bands) as had been described for the basket cells in the motor cortex by Marin-Padilla (1970).

The major contribution of Creutzfeldt's model has been in illuminating the role of the horizontal organization of the striate cortex. The central point of conjecture of the model has been the extent of horizontal inhibitory interactions and the relative contribution of inhibitory input from columns close to or far from the recipient cells (Hess, Negishis and Creutzfeldt, 1975, Hess, Ostendorf, Sanides, Negishi and
2.2 The Dependence of Orientation and Direction Selectivities on Intracortical Inhibition

The geniculo-cortical synapse may be characterized by anatomical and physiological criteria as excitatory. The synapses formed between afferent fibres and both pyramidal and stellate neurones have asymmetrical thickenings (Colonnier and Rossignol, 1969; Garey and Powell, 1971) associated with excitation (Uchizono, 1965). Stimulation of the afferent pathway by an electrical stimulus (Creutzfeldt, Baumgartner and Schoen, 1956; Jung, Creutzfeldt and Baumgartner, 1957; Li, Ortiz-Galvin, Chou and Howard, 1960; Watanabe, Konishi and Creutzfeldt, 1966), diffuse light (Creutzfeldt, Rosina, Ito and Prost, 1969) or a punctiform light stimulus (Creutzfeldt and Ito, 1968) leads to inhibitory postsynaptic potentials (ipsps) as well as excitatory postsynaptic potentials (epsps). The latency of ipsps, compared with epsps, is regularly delayed by 0.8 ms. regardless of whether the site of stimulation is the optic chiasma, lateral geniculate nucleus or optic radiation; the delay is therefore intracortical.

The dependence of orientation/direction selectivities of simple and complex cells on intracortical inhibition has been established from intracellular recordings and by pharmacological studies. Benevento, Creutzfeldt and Kuhnt (1972) reported quantitative changes in inhibition, in intracellular recordings from simple and complex cells, when
the orientation and direction of movement of a contrast bar stimulus was changed. This implies that the inhibition of these cells, as well as the suprathreshold excitatory response, is orientation and direction specific. Other intracellular studies have confirmed the result (Creutzfeldt, Kuhnt and Benevento, 1974; Innocenti and Fiore, 1974).

Pharmacological studies have also revealed the dependence of the tuning of both simple and complex cells for orientation and direction on intracortical inhibition (Sillito, 1974b, 1975b, 1976, 1977, 1979; Tsumoto, Eckart and Creutzfeldt, 1979; Ostendorf and Hess, 1975). Additionally, these studies have indicated a differential dependence between simple and complex cells and within the complex cell group (Sillito 1974b, 1975b, 1976, 1979, 1980; Ostendorf and Hess, 1975; Hess, Ostendorf, Sanides, Negishi and Creutzfeldt, 1976; Tsumoto, Eckart and Creutzfeldt, 1979). The putative inhibitory transmitter in the striate cortex, Gamma Amino Butyric Acid (GABA) (Mitchell and Srinivasan, 1969; Iversen, Mitchell and Srinivasan, 1971), is antagonized by the alkaloid bicuculline (Curtis, Duggan, Felix and Johnston, 1970, 1971; Curtis and Johnston, 1974). Bicuculline blocks the inhibition produced by the iontophoretic application of GABA and visually evoked inhibition (Sillito, 1975a). The intravenous, topical and iontophoretic application has been used to assess the relative contributions of intracortical inhibition and tuned excitatory input to the functional properties of simple and complex cells.

Two studies using intravenous administration of
bicuculline produced contradictory results. Daniels and Pettigrew (1973) reported minimal changes in receptive field structure and tuning properties of simple cells but most complex cells showed a loss of orientation selectivity. Using similar techniques, Rose and Blakemore (1974) found negative results for both simple and complex cells. With topical application of bicuculline to the cortex, these authors found broadening of simple cells' orientation tuning but variable results for complex cells.

Little reliance can be placed on the two studies. Sillito (1975b) has pointed out that intravenously injected bicuculline produces changes in excitability of many parts of the nervous system including possible actions on the retina and lateral geniculate body (Straschill and Perwein, 1969; Curtis and Tebaca, 1972). Topical application may produce changes in the overall excitability and hence possible modifications of receptive field properties. These problems are not associated with the iontophoretic application of bicuculline.

Sillito (1974b), in addition to reporting changes in the partitioning of the simple cell receptive field, found cells' orientation and direction selectivities to moving contrast bars reduced following bicuculline application. Often, but not always, this was accompanied by a large increase in magnitude of the evoked response. Confirming the reduction of orientation selectivity, Sillito (1975b) saw elimination of direction selectivity for a few cells after bicuculline application. Tsumoto, Eckart and Creutzfeldt (1979) reported
that while, for a majority of simple cells, direction selectivity was abolished or reduced, orientation selectivity was abolished in no case and reduced in only two of eight cells. For complex cells, these authors found direction selectivity to be abolished or reduced in half the sample of six cells. The resistance of orientation tuning of both simple and complex cells has been reported in the studies of Ostendorf and Hess (1975) and Hess, Negishi and Creutzfeldt, (1975). The possibility of an orientationally tuned input to simple cells or incomplete synaptic blockade by bicuculline was therefore raised.

A resolution of the question came from the work of Tsumoto, Eckart and Creutzfeldt, (1979) and Sillito, Kemp, Wilson and Berardi (1980). Tsumoto, Eckart and Creutzfeldt (1979) used the inhibitor of GABA synthesis 3-mercaptoproprionic acid (MP) (Lamar, 1970; Rodriguez, Alberici, De Robertis, 1972; Rodriguez, Alberici, Robiolo and Mistrorigo, 1973; Karlsson, Fonum, Malthe-Sorensen and Storm-Mathisen, 1974; Wu, 1975) in combination with bicuculline or given alone. Bicuculline application alone was never found to produce complete elimination of orientation selectivity but combined administration of MP (intravenous) with iontophoretic bicuculline abolished orientation tuning in one third of simple cells. For two out of six complex cells tested, orientation selectivity was abolished under combined application; the sample size was too small to suggest a differential effect of MP on simple and complex cells. In a re-evaluation of simple cell orientation selectivity, Sillito, Kemp, Wilson and Berardi (1980) found that, following
lontophoretic application of the GABA antagonist N-methyl bicuculline, previously sharply tuned simple cells responded equally well to all orientations/directions. The result supported the conclusion that the orientation bias remaining after bicuculline application in previous studies was a consequence of inadequate blockade of synapses.

A differential dependence of the orientation and direction selective properties within the complex cell group has been indicated by the extensive studies of Sillito (1975b, 1976a, b, 1977, 1979). Sillito (1975b) found that the orientation selectivity of complex cells, following the lontophoretic application of bicuculline, was reduced. In many cases, cells subsequently responded to an orientation orthogonal to the optimal with equal magnitude of response. The same study indicated that the direction selectivity of complex cells was less affected than that of simple cells. In addition, when large changes in orientation tuning were seen, the direction selectivity was relatively unaltered. Sillito (1976) found that, for those cells most closely resembling simple cells, bicuculline eliminated or reduced these cells' direction selectivity. However, for all other complex cells, bicuculline had much less effect on direction selectivity, particularly in the case of lamina V complex cells identified with the cortico-tectal neurones in Palmer and Rosenquist's study (1974). For such neurones, a transmitter other than GABA mediating direction selectivity was suggested.

The differences in origin of complex cells' direction selectivity was highlighted in a further study. Sillito
(1977) grouped complex cells into three categories in terms of the origin of their direction selectivity. Type 1 complex cells' direction selectivity was eliminated during bicuculline application. These cells were located in the supragranular layers. The direction selectivity of type 2 complex cells was unaffected by bicuculline despite increases in response magnitude, a block of the action of iontophoretically applied GABA and, in some cases, changes in receptive field properties. Type 2 cells were located both superficial and deep to lamina IV with the majority in lamina V. The type 3 complex cell, whose receptive field properties were seen to be similar to cortico-tectal neurones, showed no elimination of direction selectivity on application of bicuculline, but exhibited a powerful suppression of the resting discharge in response to stimulus motion in the non-preferred direction. For those lamina V neurones, iontophoretic application of ammonium ions revealed a small excitatory response in place of suppression.

These results may be summarized by saying that type 1 cells receive a directionally non-specific excitatory input and that, as for simple cells, the direction selectivity derives from the action of GABA-mediated post-synaptic inhibitory input. Type 2 receive a direction specific excitatory input. For type 3 neurones, the direction selectivity could be dependent, at least in part, on inhibitory processes which are not GABA-mediated.

Within the "standard" complex cell group (Gilbert, 1977) a differential dependence of orientation tuning on
intracortical inhibition has been revealed (Sillito, 1979). For one group, the orientation tuning was eliminated during bicuculline application, indicating the excitatory input to these cells to be non-orientation specific. The other group of "standard" complex cells, although showing a decrease in orientation tuning, retained a preference for a range of orientations that was generally centred around the optimal orientation. For these cells, it was suggested that the inhibitory input enhances the orientation tuning of an excitatory input that is already broadly orientation tuned. The laminar distribution of the two groups was left unanswered as was the origin of the orientation selectivity of "special" complex cells.

2.3 The Representation of Inhibition in the Simple Cell Receptive Field

Inhibitory side-bands were viewed as a feature of the receptive field present in simple but absent in complex cells (Henry, Bishop and Coombs, 1969; Bishop, Coombs and Henry, 1971b; Bishop and Henry, 1972; Henry, Drahel and Bishop, 1974). Though the possibility of side-band inhibition in complex cells was raised by Goodwin and Henry (1975), Glezer, Ivanov and Tsherbach, (1973) and Heggelund and Moors (1978), the majority of studies have reported their absence in the complex cell receptive field (Wilson and Sherman, 1976; Schiller, Finlay and Volman, 1976b; Sherman, Watkins and Wilson, 1976; Leventhal and Hirsch, 1978). Albus and Fries (1980), in an analysis of data from Fries and Albus (1976) and Fries, Albus and Creutzfeldt (1977), confirmed the presence of
sidebands in simple cells but also observed them in a minority of complex cells (3 out of 18) when tested with the monocular conditioning technique. These sidebands were non-orientation specific.

Asymmetries in the spatial arrangement of the inhibitory flanks of the simple cell have been reported by Bishop, Goodwin and Henry (1973), Creutzfeldt, Innocenti and Brooks (1974) and Innocenti and Fiore (1974). This suggests that the response to a moving stimulus reflects temporal factors as well as a fixed, spatial receptive field pattern (c.f. Rodieck and Stone, 1965; Bishop, Coombs and Henry, 1971a). Fries and Albus (1976) reported that the majority of simple cells show an asymmetrical zone for one direction of stimulus movement and a symmetrical one for the opposite direction. The dependence of activity profiles on temporal factors and on the contrast of the stimulus was evaluated by these authors. Comparisons were made of response to stationary and moving bars for cells with asymmetrical flanks. Receptive field structure determined with stationary bars was compared with the response to moving bars in the peri-stimulus time histogram (PSTH) and in the activity profile (Bishop, Coombs and Henry, 1971b). The receptive field structure seen in activity profiles was only loosely related to stationary maps of the receptive field. In illustration, for a cell showing an off-centre flanked by two on regions, the activity profile indicated that the inhibitory peaks preceding the discharge coincided with the off region. In the PSTH to a moving bar, the bar was seen to elicit, in the same region, an excitatory response. For this unit, light bar discharges were found to
occur after the dark discharge for both directions of movement. Discharge peaks to light stimuli seem to occur in different retinal locations according to the direction of movement. Moving the stimulus over an on zone lying before the off zone produced only a subliminal response. Thus, the retinal locus where excitation is evoked depends on the contrast and on the direction of movement of the stimulus. A further mismatch between receptive field structure determined with the PSTH and a stationary bar RF plot was noted for the optimal movement direction; in the activity profile a further inhibitory region followed the discharge peak. Fries and Albus commented that similar inhibitory zones, revealed only with moving stimuli, can be seen in the PSTHs of responses of retinal ganglion cells (Rodieck and Stone, 1965) and of LGN neurones (Dreher and Sanderson, 1973). Fries and Albus also found in their study that, while "off" zones always corresponded to inhibitory troughs in the activity profile, extra inhibitory responses were seen in the profile which were not related to an area excitable by stationary bars. This inhibition appears to arise from temporal factors, i.e. effects associated with stimulus movement.

The weak association between afferent excitation and inhibitory zones in the receptive field is further demonstrated in intracellular recordings. Benevento, Creutzfeldt and Kuhnt (1972) and Creutzfeldt, Kuhnt and Benevento (1974) both reported little correlation between the spatial distribution of intracortical inhibition and afferent excitation. Intracellular recordings have also been used to assess the relationship between inhibition measured by the
conditioning technique and intracortical inhibition. Innocenti and Fiore (1974) raised the question of whether the suppression of response revealed on an artificially enhanced background activity is due to post-synaptic inhibition or reflects a disfacilitation induced by intrathalamic mechanisms. In support of the latter possibility are the observations of similar patterns of excitation-inhibition seen in the response of geniculate neurones to moving stimuli (Dreher and Sanderson, 1973; Singer and Creutzfeldt, 1970). Innocenti and Fiore (1974) compared responses obtained with the conditioning technique with those seen in intracellular recordings. Extracellularly recorded responses to moving bars at the cell's preferred orientation were classified into four groups according to the sequential order in which excitatory and inhibitory components appeared in the PSTH:
(A) Excitation followed by inhibition (B) Excitatory responses preceded by inhibitory responses (C) Symmetrical inhibitory-excitatory-inhibitory responses (CI = inhibitory-excitatory-inhibitory; CII = excitatory-inhibitory-inhibitory-excitatory) (D) Purely excitatory responses.
Recordings were also made from the lateral geniculate nucleus. These responses were very similar to type A (on-centre neurones), type B (off-centre neurones) or the types CI and CII.

From a comparison of intracellular with extracellular recordings at the cortical level differences were noted in the responses of directionally selective neurones to movement in the null direction. In extracellular recordings these were essentially inhibitory. In intracellular recordings only one
case of a purely hyperpolarizing response was seen in the null direction; sub-threshold epsps could usually be seen and these were clearly antagonized by concomitant ipsps. Innocenti and Fiore (1974) concluded that inhibitory responses revealed by monocular conditioning, though already present in the LGN, do reflect intracortical inhibition. However, they argued that the inhibitory components of the receptive field of geniculate cells are reconstructed at the cortical level by a local mechanism (Watanabe, Konishi and Creutzfeldt, 1966). Innocenti and Fiore (1974) qualified this statement by saying that it is difficult to assess quantitatively the contribution of intracortical inhibition and of thalamic disfacilitation to the discharge suppression around the excitatory centre of the cortical cell.

The role of the inhibitory sidebands in mediating orientation tuning would suggest that cells lacking this feature would lack orientation tuning. Bishop and Henry (1972) themselves described simple cells with a single side-band located to one side of the central discharge zone and others with no sidebands yet showing orientation tuning. One would predict, as Henry, Dreher and Bishop, (1974) and Rose noted (Rose, 1977), that if sidebands were responsible for the cell's orientation properties inhibition would be shown for a stationary flashed bar as well as for a moving bar. However, Bishop, Dreher and Henry (1972) and Bishop, Goodwin and Henry (1973) found, when the inhibitory sidebands were stimulated with stationary stimuli, excitatory responses were frequently obtained at "on" or "off" at different sites in the sidebands.
There is no evidence for a spatial division of the simple cell receptive field such that the extension of inhibition outside the central discharge zone constitutes a separate intracortical input mediating tonic inhibition and conferring on the cell its orientation properties. The dynamic properties of that inhibitory zone suggest a functional continuity with inhibition distributed within the central discharge zone. There is therefore a possibility that the tuning properties of the simple cell can be accounted for by the mechanism proposed for direction selectivity (Goodwin and Henry, 1975).

Goodwin and Henry (1975) argued for inhibition preceding stimulus motion on the basis of the absence of response in the non-preferred direction and of the absence of reduction in direction selectivity when stimulus speed is reduced. Though many neurones show direction selectivity (Schiller, Finlay and Volman, 1976a; Hammond, 1978) a large number show varied degrees of response in the non-preferred direction; they are direction biased (e.g. Hammond, 1978). Contrary to Goodwin et al's studies (Goodwin, Henry and Bishop, 1975; Goodwin and Henry, 1975) later studies have indicated that reduction in stimulus velocity is accompanied by reduced direction selectivity (Orban, Kennedy and Maes, 1981; Nothdurft, 1983). There is, however, evidence that direction-selective inhibition may be initiated by a stationary edge. Ganz and Felder (1984) investigated the direction selective properties within excitatory "on" or "excitatory "off" components of the receptive fields of direction-selective simple cells (a sub-group of simple cells whose direction selectivity is not a
product of synergistic action between "on" and "off" areas). The direction-selective inhibition produced by pairs of flashed bars with zero or small (0-25 milliseconds) temporal asynchronies was equivalent to that for a bar moving across the same receptive field positions.

2.4 The Mediation of Orientation and Direction Selectivities by Separate Mechanisms.

Schiller, Finlay and Volman (1976b, e) advanced four arguments for the mediation of orientation and direction selectivities by separate mechanisms.
(1) In the monkey, orientation preference is organized in a columnar manner (Hubel and Wiesel, 1972, 1974) but cells of the same orientation column may differ in their preferred direction, with cells successively recorded showing opposite preferred directions.
(2) Cells which show orientation selectivity with oriented moving contrast bars show orientation selectivity when the same stimulus is held stationary and flashed; orientation tuning is not therefore contingent on stimulus motion.
(3) From their comparison of orientation and direction tuning for moving bar and spot stimuli, Schiller, Finlay and Volman (1976b) inferred that orientation tuning is critically dependent on, and direction selectivity independent of, stimulus length.
(4) If there is a dependent relationship between direction selectivity and orientation selectivity it would be expected that selectivity for orientation of directional cells (Schiller's term) would be different from those of
non-directional ones. An evaluation was made for simple and complex cells separately. Schiller, Finlay and Volman (1976b) interpreted their data to show that the two groups, directional and non-directional cells, did not differ in terms of their orientation tuning, though the data were more complete for complex than simple cells, reflecting the predominantly unidirectional population in the simple cell group.

Schiller, Finlay and Volman (1976b) suggested that orientation and direction selectivities are accomplished by relatively independent mechanisms which appear to be linked since "directionality", by which is presumably meant preferred direction, is typically at right angles to the axis of orientation. Subsequent studies have yielded only partial support for Schiller's evidence.

The cortical organization of direction selectivity has received little attention. Payne, Berman and Murphy (1980) assessed the differences in preferred directions of cells within 200 microns of each other during tangential penetrations. They concluded that, compared with a random population, a significantly higher number of pairs had similar preferred direction preferences than opposite direction preferences. Tolhurst, Dean and Thompson, (1981) evaluated both the vertical and tangential organization of direction preferences, again with contrast bars. It was suggested that preferred direction is organized in an identical columnar fashion to orientation. In oblique penetrations, the correlation between preferred orientation and preferred
direction of pairs of neurones declined with increasing distance and was hardly evident at 300 microns. In normal penetrations, the measures declined together but a statistically significant correlation was retained up to 600 microns.

This study may be criticized on two counts. The preferred direction for a moving contrast bar is necessarily orthogonal to orientation (Henry, Dreher and Bishop, 1974). That the correlation between direction and orientation declines at a faster rate in the horizontal than the vertical dimension can be seen as a consequence of the cortical organization of orientation. Secondly, if direction and orientation are organized on an identical columnar basis neither the absolute decline in correlation of preferred orientation with depth nor the relative decline in correlation between orientation and direction with increasing distance would be expected. Tolhurst, Dean and Thompson (1981) themselves observed a minority of neurones within the same orientation column which exhibited differences in preferred direction.

Schiller's observation that successively recorded neurones in vertical penetrations may show opposite preferred directions had previously been noted by Creutzfeldt, Innocenti and Brooks (1974) and confirmed by Hammond (1978). In this context Hammond’s (1978) consideration of the columnar organization of bar and texture tuning is interesting. This clearly indicated that the direction and orientation mechanisms are not in register for all cells, especially those
of the infragranular layers. Differences in directional tuning for bar and noise stimuli tended to be reflected in sequences of consecutively recorded cells in a single penetration, often over several hundred micra of electrode advance. In that study, three neurones, presumed to be cortico-tectal neurones, were recorded successively in a single penetration and, although the preferred direction for the first recorded cell was exactly the opposite to that for the remaining two, the cell showed similar differences between preferred directions for bar and noise. In addition, abrupt changes in texture tuning, even between neighbouring cells with similar preferred orientations for a bar, were seen. There is therefore confirmation that cells which show similar preferred orientations may have different directional tuning properties.

A supporter of Bishop's model might raise the objection to Schiller, Finlay and Volman's (1976b, c) second argument that if tuning for stationary and moving bars were seen to be identical this would show that inhibition mediating the response to a moving bar could be identical to that producing the stationary bar response.

Schiller's model, like Bishop's, assumes that the preferred direction for a spot is identical to that for a moving bar. Equally it would require that the bar is a linear sum of spots with each position within the bar given an equal weighting function. There is evidence that the latter assumption is not valid (Bodis-Wollner, Pollen and Ronner, 1976; Rose, 1977; Hammond and Andrews, 1978a, c) as is
discussed further (chapter three). Indeed, there is some
evidence that preferred orientations/directions for forward
and backward motion of contrast bars are not identical (Albus,
1975; Haamond, 1978c). Many neurones are unresponsive to
spots (Henry, Bishop and Dreher, 1974; Rose, 1977).

Comparing orientation tuning for direction selective and
non-selective neurones, Schiller, Finlay and Volman (1976b)
found no dependent relationship between orientation tuning and
the degree of direction selectivity. Evidence to the contrary
for complex cells has been given by Harvey (1980). A
population of 18 cortico-tectal, special and standard complex
cells was compared. Of the ten complex cells which showed
little or no length summation, all were highly selective for
direction of stimulus motion. But, of the eight cells which
responded optimally to long edges, four showed no direction
selectivity and two were weakly direction selective, direction
selectivity being defined in relation to preferred and
non-preferred directions.

Results from pharmacological and deprivation studies are
compatible with the mediation of orientation and direction
selectivities by separate mechanisms. For example, Sillito
(1975b, 1977) found that, for complex cells of the
infragranular layers, orientation selectivity but not
direction selectivity was considerably reduced following the
lontophoretic application of bicuculline. Several studies
have shown that selective exposure, during the critical
period, to a stroboscopically illuminated environment - which
deprees the kittens of real visual movement - results in
cortical neurones which display orientation selectivity but whose direction selectivity is lost (Cynader, Berman and Hein, 1973; Olson and Pettigrew, 1974; Cynader, Berman and Hein, 1975).

The most direct evidence for the mediation of orientation and direction selectivity by separate mechanisms comes from the extensive studies of the tuning properties of complex cells for moving contrast bars and texture fields (Groos, Hammond and Mackay, 1976; Hammond and Mackay, 1977; Hammond 1978; Hammond 1979b, c; Hammond and Reck, 1980a, b). Comparisons of tuning for fields of moving visual noise and contrast bars against the same stationary noise field as background reveal a separation of peak positions of the tuning curves for the two stimuli which, in the case of cells showing a unimodal peak in the texture tuning curve, averages 30-40 deg. (Groos, Hammond and Mackay, 1976; Hammond and Mackay, 1977; Hammond, 1978). The difference is greatest for cells of the infragranular layers (Hammond, 1978) which show greater responsiveness to texture motion than those of the supragranular layers (Hammond and Mackay, 1977; Hammond, 1978).

Tuning for bar and texture motion differs in other respects. Optimal velocity and bandwidth are invariably higher for texture than bar motion (Hammond, 1978; Hammond and Reck, 1980a, b). Texture tuning is dependent on and bar tuning independent of velocity. At low velocities, texture tuning is unimodal but, at higher velocities, the tuning curve becomes bimodal with depression of response for directions
optimal for bar motion (Hammond and Reck, 1980a, b). However, some cells retain a unimodal response as stimulus velocity increases (Hammond and Reck, 1980a, b; Hammond and Smith, 1983).

Several lines of evidence indicate separate inputs mediating bar and texture sensitivity, in particular, interocular comparisons of tuning for these stimuli (Hammond and MacKay, 1977; Hammond, 1978; 1979b, c). At the cell's optimal velocity for a moving bar, ocular dominance for bar and texture may be similar or differ significantly for the two stimuli (Hammond, 1979; 1981b). Differences of up to three ocular dominance groups, with reversal of eye preference have been reported (Hammond, 1979b, c; 1981b). Binocular comparisons further indicate that velocity characteristics are not invariably identical for the two eyes (Hammond, 1981b). This study indicated that preferred direction for bars is velocity invariant through each eye although differences in width of bar tuning were sometimes seen. Only when preferred velocity and velocity bandpass differed between the two eyes did measured ocular dominance vary significantly with velocity. As with bar tuning, interocular differences in texture responsiveness and tuning at different velocities were also found to influence ocular dominance.

Collectively, the evidence from comparisons of tuning for moving bar and texture fields establishes that orientation and direction tuning are mediated by separate mechanisms associated with distinct inputs mediating bar and texture sensitivity. In one variant of Schiller's model (Schiller,
Finlay and Volman, 1976) separate inputs were served by parallel afferent fibre streams from the LGN to sites associated with separate levels of inhibition. An immediate question is raised of whether inputs mediating the orientation and direction properties of cortical cells arise from parallel streams from the lateral geniculate nucleus. A further consideration is the role of the afferent input in determining the temporal properties of tuning; Schiller’s model suggested the simple cell to be the recipient of both X and Y cell input while in Bishop’s model the simple cell receives only X fibre input. As raised by Mason (1976), Ahmed (1981) and Ahmed and Hammond (1984), the differential responsiveness of simple and complex cells to visual noise could reflect differential input from the LGN. The afferent input to simple and complex cells is considered in these contexts.

2.3 X and Y Cell Input to Simple and Complex Cells

At lower levels in the retino-striate pathway, a number of tests have been used to distinguish between X and Y cells. A primary difference lies in linearity of summation; X and Y cells differ in response to contrast reversal of a stationary, sinusoidal grating. For X cells, a null position is seen where no response is elicited but, for Y cells, contrast reversal produces excitation at all parts of the receptive field (Enroth-Cugell and Robson, 1966; Hamasaki and Sukee, 1979). X and Y cells differ in the time course of their responses to a standing contrast, with X cells producing a sustained response and Y cells a transient response (Cleland, Dubin and Levick, 1971; Fukada, 1971). To a moving grating,
X cells show modulated responses for the full range of spatial frequencies to which they respond whereas Y cells no modulation at higher spatial frequencies (Cleland, Dubin and Levick, 1971).

X and Y cells can be distinguished by other properties. Receptive field sizes of X and Y cells are significantly different (Hoffmann, Stone and Sherman, 1972; Cleland and Levick, 1974; Hammond, 1974). Within the central 15 degrees of the visual field, receptive field diameters of X cells range from 0.5 to 1.5 degrees while those of Y cells range between 1 and 4 degrees (Hoffmann, Stone and Sherman, 1972). Cleland and Levick (1974) reported brisk-sustained units had smaller receptive field centres than brisk-transient units over the first 12 degrees from the area centralis. Hammond (1974) documented differences between sustained on- and off-centre and transient on- and off-centre cells in the dimensions of the major axis of their receptive field centres, the means being: sustained on-centre 1.30 degrees; sustained off-centre 1.95; transient on-centre 2.30 degrees; and transient off-centre 2.90 degrees, for units within seventeen degrees of the area centralis.

X and Y cells differ in flicker sensitivity. Fukada and Saito (1971) have reported differences in the responses of Type I (Y cells) and Type II (X cells) ganglion cells to small spots flickering in the receptive field centre. For Type I cells, average impulse frequency was found to vary as a function of flicker frequency, whereas the responses of Type II cells were independent of flicker frequency. For Type I
calls, impulse frequency increased to a maximum and decreased as the flicker frequency was further increased but for Type II cells, this was essentially constant as the flicker frequency was further increased. Also, with flicker stimulation near the point at which the maximum impulse frequency occurred, Type I cells were seen to discharge periodically at about 200 impulses/sec., this firing superimposing on the response to individual flashes of flicker.

X and Y cells differ in their responses to movement of stimuli outside the classical receptive field. A 'periphery effect' has been described by McIlwain (1964). A small spot of light was flashed continuously within the receptive field centre of a retinal ganglion cell and the intensity of the spot was reduced until it was subthreshold. A disc was then moved in the periphery and was found to bring the field centre above threshold for response to the flashing spot (McIlwain, 1964). The periphery effect is absent or weak in X cells, but seen for nearly all Y cells (Barlow, Derrington, Harris and Lennie, 1977; Derrington, Lennie and Wright, 1979).

The complexity of cortical neurones' receptive fields, arising from intracortical circuitry, means that criteria for distinguishing between X and Y cells at the geniculate level can only be applied with caution when inferring afferent input to simple and complex cells. For example, cortical neurones, especially simple cells, may have little or no maintained discharge (Pettigrew, Mikara and Bishop, 1968; Rose and Blakemore, 1974) and their responses are more transient than those of the LGN (Ikeda and Wright, 1975). Cortical cells do,
however, differ in their summation properties and linearity or non-linearity of summation may be an indication of input from X or Y cells. Potentially, afferent input can be inferred from receptive field properties, e.g. velocity selectivity or size, or from conduction velocities of afferents, from correlations between fibre termination and stratification of neurones and, most directly from simultaneous recordings from fibres and recipient cells.

For simple cells, Movshon, Thompson and Tolhurst (1978a) found that, in the responses to stationary gratings flickering in different parts of the receptive field, most simple cells showed linear spatial summation and gave modulated responses to gratings moved steadily across the receptive field. Andrews and Pollen (1979) also reported similar linear summation for a majority of simple cells but noted a minority showing non-linear summation and which gave an unmodulated response to moving gratings. However, the non-linear cells were not distinguished from linear cells by preferred spatial frequency. Preferred spatial frequency would be expected to be lower if the the non-linear cells were driven by Y cells. Movshon, Thompson and Tolhurst (1978c) attributed the responses of non-linear simple cells to intracortical circuitry.

Ikeda and Wright (1975) distinguished two classes of simple cells on the basis of the time courses of their responses to the step onset of a stimulus. Transient units were found to be insensitive to gratings moving slowly across the receptive field and preferred gratings of lower spatial
frequency whereas sustained units were found to be quite sensitive to low temporal frequencies. From latency measurements to a visual stimulus, sustained units were found to have longer latencies than the transient units from which it was inferred that sustained simple cells receive an X input and transient simple cells a Y input. In the same study it was reported that among complex cells were cells receiving an X input or a Y input. The overall conclusion was that cells receive sustained or transient input independent of the simple/complex division.

Movshon, Thompson and Tolhurst (1978c) found cells resembling Ikeda and Wright's transient cells only in area 18 thereby questioning the existence of a transient simple cell population in area 17. Both Ikeda and Wright (1975) and Movshon, Thompson and Tolhurst (1978c) made measurements of spatial frequency tuning of simple cells from which estimates of sub-regions were made. Ikeda and Wright (1975a) reported the smallest regions to be smaller than those found for Y cells in the LGN but both Ikeda and Wright (1975) and Movshon, Thompson and Tolhurst (1978c) reported many simple cells having spatial frequency selectivities within the range of geniculate Y cells.

For complex cells, Movshon, Thompson and Tolhurst (1978b) reported pronounced non-linearities of spatial summation which were more marked than their non-linear simple cell population (Movshon, Thompson and Tolhurst, 1978a). Complex cells were seen to respond to gratings of low spatial frequency with modulated discharge but at higher spatial frequencies an
unmodulated elevation of discharge was found (see also Maffei and Fiorentini, 1973; Ikeda and Wright, 1975). Comparisons of spatial frequency tuning indicated no difference separating simple and complex cells (Movshon, Thompson and Tolhurst, 1978b). Hubel and Wiesel (1962) found that the most effective stimulus for some complex cells was as narrow as for some simple cells. This has also been reported by Ikeda and Wright (1975) and Movshon, Thompson and Tolhurst (1978c). The result would indicate that some complex cells are the recipients of X cell input.

Circumstantial evidence that simple and complex cells receive different inputs is apparent in the correlation between receptive field size and preferred stimulus velocity. Cortical cells with small receptive fields prefer slow moving stimuli, whereas cells with large receptive fields prefer faster moving stimuli (Pettigrew, Nikara and Bishop, 1968; Dreher, Hoffmann and Stone, 1971; Sherman, Watkins and Wilson, 1976; Wilson and Sherman, 1976; Leventhal and Hirsch, 1978). However, there is no support for a bimodal distribution between simple and complex cells and it would be reasonable to conclude that within both the simple and complex cell groups receptive field size and velocity preference are related to X and Y cell input.

Two early studies of latencies to electrical stimulation indicated a separation of afferent input between simple and complex cells. Hoffmann and Stone (1971) made measurements of latency after electrical stimulation to optic chiasa or optic radiation and reported that none of the simple cells had
latencies consistent with $Y$ input though some had latencies consistent with $X$ input. Stone and Dreher (1973) confirmed the result. In their study, Hoffmann and Stone (1971) reported 30% of their complex cell sample could be activated with latencies consistent with a mono-synaptic $Y$ input and Stone and Dreher (1973) reported a proportion of their complex cell sample receiving $Y$ input but others had latencies indicating $X$ input.

Subsequently, Singer, Tretter and Cynader (1975) reported 40% of their simple cell sample to be driven by fast i.e. $Y$ cells. Bullier and Henry (1979a) found the bulk of their simple cell sample to be mono-synaptically activated, with half of them activated by $Y$ fibres and half by $X$ fibres (Bullier and Henry, 1979b). Also, Singer, Tretter and Cynader (1975) reported that although some 40% of their complex cell sample were activated by fast conducting afferents, units were found that had latencies consistent with activation by slow afferents (or fast afferents over more than one synapse). Bullier and Henry (1979b) found that although many complex cells appeared to be activated mono-synaptically by fast afferents, a large proportion of the same units received inputs routed through additional synapses (c.f. Singer, Tretter and Cynader, 1975).

The approach from latency studies is not without difficulties of interpretation. Many cortical cells project back to the LGN (Gilbert and Kelly, 1975; Gilbert, 1977) and can therefore be activated antidromically by electrical stimulation of the optic radiation. Antidromic activation
could be the cause of the short latency shown by some cells (Stone and Dreher, 1973; Bullier and Henry, 1979a). Also, there is a difficulty in interpreting whether a unit with long latency to electrical stimulation is activated via fast afferents through several synapses or via slow afferents through one or a few synapses.

While no conclusions can be made from direct comparisons of the laminae of termination of geniculate fibres and the distribution of cell bodies of simple and complex cells, indirect evidence from lamination has shed light on the question of connectivity of X and Y with simple and complex cells. Simple cells are not confined in layer IV to lamina IVc as would be expected if simple cells are only driven by X cells (Gilbert and Wiesel, 1979; Bullier and Henry, 1979c). Comparing receptive field sizes, Gilbert (1977) and Leventhal and Hirsch (1978) found simple cells in lamina VI had the largest fields and lamina IV the smallest. Simple cells in lamina IV ab have larger fields than those in IV c (Gilbert and Wiesel, 1979; Bullier and Henry, 1979c). Leventhal and Hirsch (1978) found simple cells in lamina VI were sensitive to higher stimulus velocities than their counterparts in lamina IV. These results could be interpreted to be consistent with Y input to simple cells in laminae IV ab and VI and X input to those in lamina IV c.

Direct evaluation of afferent input by simultaneous recording from cortical neurones and their afferent input has been attempted in three studies. Lee, Cleland and Creutzfeldt (1977) found that, for a sample of six simple cells, three
were each excited by an X fibre, two from a Y fibre and one was the recipient of both X and Y input. Tanaka (1983) reported that simple cells receive mostly X cell input with "special" complex cells receiving only Y input but "standard" complex cells receiving both X and Y fibre input. Henry, Mustari and Bullier (1983) have reported that B cells receive inputs from slowly conducting axons.

From this review the following conclusions can be drawn. Firstly, there is no evidence that X and Y cells provide independent, parallel streams to simple and complex cells respectively, but there is strong evidence that within both classes of cortical cells there are members which receive input from either type of fibre. Evidence for both X and Y cell input to the simple cell, suggested in the first variant of Schiller, Finlay and Volman's (1976b, e) model, is limited to one cell in Lee, Cleland and Creutzfeldt's (1977) study.

If simple and complex cells do not receive differential inputs from the lateral geniculate nucleus, it is unlikely that the differential sensitivity of simple and complex cells to moving visual noise arises from differences in thalamic input. Several studies suggest, more directly, that the differential sensitivity of simple and complex cells to texture motion must arise from intracortical circuitry.

At the retinal level, Ahmed (1981) and Ahmed and Hammond (1984) reported that responses of both brisk sustained and brisk transient cells are modulated by moving fields of visual noise, with response modulation dependent on receptive field
size and the configuration of the texture elements determining the temporal properties of response. Mason (1976) found no differential sensitivity to visual noise between brisk sustained and brisk transient neurones of laminated lateral geniculate nucleus and between these cells and brisk transient neurones of the MIN. The texture sensitivity of W cells is unknown.

There is further evidence that the differential sensitivity to visual noise between simple and complex cells must arise from intracortical circuitry. X and Y cells convey the same information about deterministic (bar) and texture stimuli (Hoffmann, Morrone and Reuter, 1980). If a bar is moved in phase with a field of visual noise, simple cells have thresholds 2-4 times lower than LGN neurones (thresholds being defined by the signal to noise ratio when amplitude of response to bar was equal to the peak response to noise in a PSTH). When the bar is moved across the stationary noise field, the thresholds of the simple cells are still a further two times lower than the thresholds of X and Y cells, indicating a mechanism, in addition to averaging, is required (Hoffmann, Morrone and Reuter, 1980). Hoffmann, Morrone and Reuter (1980) suggested the hypothesis of an unselective suppression of response to noise present in the LGN input. They further suggested that this inhibitory input is mediated by infragranular complex cells. In the case of lamina IV simple cells, inhibition may arise from lamina VI. There is anatomical (Gilbert and Wiesel, 1979, 1981) and physiological (Ferster and Lindstrom, 1983) evidence of a pathway from lamina VI to IV contacting inhibitory interneurones (Hornung,
2.6 The Role of Dendritic Morphology and Inputs from Inhibitory Interneurones in the Construction of the Receptive Field

Schiller, Finlay and Volman (1976e) suggested three possibilities for the neural substrate of receptive field organization mediating orientation and direction selectivities. The first alternative was that of an isomorphism between the spatial organization of the receptive field (see fig. 2.1) and the spatial distribution of the apical and basal dendrites; the apical dendrite would show a bilobed distribution and the basal dendrites would be skewed relative to the cell body. As a second alternative, Schiller, Finlay and Volman (1976e) suggested that the inhibitory components of the receptive field would be reflected in the distribution of inhibitory connections on the dendritic fields, with dense connections to some sites and few connections with others. Thirdly, it was suggested by Schiller, Finlay and Volman (1976e) that the geometry of the interneurones’ axons might determine the organization of the receptive field.

Those studies which have considered the relationship between dendritic morphology and receptive field structure have been limited to assessing if there is a correlation between dendritic orientation and the cell’s stimulus orientation preference. This relationship has been considered in the studies of Coleman, Flood and Emerson (1981), Tieman and Hirsch (1982) and Martin and Whitteridge (1984). Coleman
et al (1981) investigated the effect of selective exposure to striped cylinders with vertical or horizontal stripes and Tieman and Hirsch (1982) the effect of selective exposure to vertical or horizontal lines on the shape of dendritic fields as seen in Golgi preparations.

Coleman et al (1981) were unable to find a relationship between the spatial arrangement of dendrites and stimulus orientation during the exposure period for spiny and non-spiny stellate neurones in lamina IV of kittens when only measures of dendritic macrostructure (the general orientation of an entire dendritic tree and the relative elongation of the dendritic tree) were considered. By contrast, measuring the Dendritic Angular Distribution (DAD - the angular location of dendritic segments relative to the major brain axes as a function of distance from the cell body) provided evidence of a correlation between dendritic distribution and stimulus orientation during exposure. In the tangential plane, for control kittens (experiencing no exposure) there was a peak in the number of intersections at 90 deg; this peak remaining for up to 80-90 microns from the cell body. Those kittens reared viewing vertically oriented stripes produced two peaks in the DAD, one prominent at 270 deg. and a smaller one at 90 deg. i.e. in the dorso-ventral axis, approximating the cortical representation of the horizontal visual axis. For kittens reared viewing horizontal stripes, no clear peaks were seen in the DAD but distributions of angular positions at 30-40 microns appeared to be quite different from the distributions seen closer to the cell body. Thus, overall, for control cats the distribution appeared to correlate with
the distribution closer to the cell body, for kittens raised viewing horizontal or vertical stripes dendritic orientation distant from the cell body was affected by selective exposure, but only for kittens reared viewing vertical stripes was dendritic orientation clearly related to stimulus orientation during selective exposure.

Tienman and Hirsch (1982) reported that, for kittens in a control group not experiencing selective exposure, dendritic fields of lamina III pyramidal cells were uniform in distribution while the distributions for lamina III pyramidal cells, of kittens experiencing selective exposure, were shifted, the shift in distributions being related to conditions of viewing. Dendritic orientation was measured by two indices following the plotting of dendritic orientations of cells with the aid of Sholl diagrams and converting the x, y co-ordinates of each intersection of a dendrite with a circle into polar co-ordinates, each intersection being represented by a vector with an angle and a radius. The two indices were; the proportion of vectors within 45 deg. of vertical in the visual field and the mean angle for each cell using vector addition.

For kittens raised viewing only vertical lines, the dendritic fields were oriented orthogonal to the representation of the vertical meridian and, for kittens raised viewing only horizontal lines, the dendritic fields were oriented parallel to the representation of the vertical meridian. The distribution of dendrites of lamina IV spiny stellate neurones were found to be unaffected by selective
exposure in Tieman and Hirsch's (1982) study. To account for this, these authors argued that while some neurones in striate cortex require early visual experience for the development of orientation, others do not, the studies of Leventhal and Hirsch (1977, 1980), Fregnac and Imbert (1978) and McCall, Leventhal, Tieman and Hirsch (1981) being cited in support of this view.

The support given by the studies of Coleman, Flood, Whitehead and Emerson (1981) and Tieman and Hirsch (1982) for an association between dendritic morphology and a cell's preferred orientation is weak. The studies disagree on the effect of selective exposure on lamina IV spiny stellate cells and, indeed, on the magnitude and direction of dendritic orientation of pyramidal neurones following selective exposure. Schiller, Finlay and Volman's (1976e) model required that the orientation of the dendritic field to be perpendicular to the cell's preferred orientation (c.f. Colonnier's model, described earlier, which required the orientation of the dendritic field to match the cell's preferred orientation). Tieman and Hirsch's (1982) data are in accord with Schiller, Finlay and Volman's (1976e) model. However, as Tieman and Hirsch (1982) themselves have pointed out, the orientation of dendrites orthogonal to stimulus orientation might not necessarily be a reflection of a relationship between dendritic orientation and a cell's preferred stimulus orientation but a byproduct of a cell's direction-selective properties with the relationship to preferred orientation incidental and arising as a consequence of orientation being orthogonal to the direction of motion of
Martin and Whitteridge (1984) have raised a number of objections to both studies: a selective sampling of cells was undertaken; with the Golgi method there is no certainty that similar populations of cells in normal and selectively reared animals are similar; differences in morphology of cells sampled between control and selectively reared animals were apparent. A major weakness of both Coleman, Whitehead and Emerson (1981) and Tieman and Hirsch (1982) studies is that, in neither study, were the neurones' preferred orientations, assessed in tuning curves from single cell recordings, determined. In Martin and Whitteridge's (1984) study, the preferred orientations of single cells were obtained in unit cell recordings and then the cells were injected with horseradish peroxidase. Cells from all laminae in cat striate cortex, with the morphology of pyramidal, spiny and non-spiny stellate neurones were included. In the tangential plane, no correlation was found between the cells' preferred orientations and orientations of their dendritic trees. In sum, there is no convincing evidence for a dependence of a cell's orientation preference, defined in terms of stimulus selectivity, and a neurone's dendritic orientation. Additionally, one might add, given that cells with similar morphology may differ in synaptic connectivity (Davis and Sterling, 1979), an undue emphasis on dendritic morphology is unwarranted.

The dependence of the orientational and directional tuning properties of cortical neurones on GABA-mediated
inhibition (Sillito, 1975, 1977, 1979; Berardi, Kemp, Wilson and Sillito, 1980) requires a role for inhibitory interneurons in the formation of the receptive field structure mediating these properties. Identification of GABA as the synaptic transmitter of a specific class of neurone or with a particular synaptic site potentially would yield insight into the formation of receptive field structure determining orientational and directional tuning.


From Golgi studies, several distinct morphological types of non-spiny stellate neurones have been described in close association with pyramidal cells: the basket cell (Cajal,

Distributed in laminae II through V, basket cells have an axon which forms horizontally extended branches or archades, the branches giving off short twigs and tufts which pass round the cell bodies of adjacent neurones to contribute to pericellular baskets (Cajal, 1911; Marin-Padilla, 1969, 1974; Hollander and Vanegas, 1981). The formation of pericellular baskets around the cell body, as seen in Golgi pictures, has suggested basket cells selectively contact the perikarya of pyramidal neurones (Cajal, 1911; Marin-Padilla, 1969, 1974; Marin-Padilla and Stibitz, 1974; Szentagothai and Arbib, 1974; Szentagothai, 1975, 1978; Jones, 1975; Tombol, 1978; Peters and Regidor, 1981).
In studies using the combined Golgi/EM method, synaptic contact of basket cells with pyramidal cell bodies has been confirmed. Peters and Proskauer (1980) reported a close association between a multipolar smooth stellate cell and a laminar III pyramidal cell in rat striate cortex. Electron microscopy showed the axon terminal to form symmetric synapses with the cell body of the pyramidal cell. The equivalence of this neurone with the basket cell of cat and monkey striate cortex has been made by Peters and Regidor (1981). DeFelipe and Fairén (1982) reported basket cells in the superficial layers of the cat visual cortex forming symmetric synapses with the perikarya of pyramidal neurones. Somogyi, Kisvarday, Martin and Whitteridge (1983), using an HRP/EM preparation, described three large basket cells in cat striate cortex forming symmetric synapses with pyramidal cell perikarya. Martin, Somogyi and Whitteridge (1983), using an HRP/EM preparation, reported two basket cells contacting the cell bodies of pyramidal neurones via symmetric synapses in cat striate cortex.

Several studies have provided evidence for the formation of pericellular baskets by convergence of an indeterminate number of basket cells (Cajal, 1911; Marin-Padilla, 1969, 1974; Hollander and Vanegas, 1981). At the same time, there is evidence that individual basket cells may contribute to the pericellular basket through multiple synaptic contacts with the cell body. In their study, Peters and Proskauer (1980) reported, for one multipolar smooth stellate cell and a laminar III pyramidal cell in rat striate cortex, the axon terminal formed five symmetric synapses with the cell body.
Hollander and Vanegas (1981) described axons, thought to derive from basket cells, which made a large number of synaptic contacts on the soma of a pyramidal cell. DeFelipe and Fairen (1982) also reported that multiple synaptic contacts were made on the cell bodies of pyramidal cells by basket cells in laminae II and III of cat striate cortex. Martin, Somogyi and Whitteridge (1983) described four basket cells forming multiple synaptic contacts with cell bodies of pyramidal neurones in cat striate cortex.

A reconsideration of the specificity of connectivity of basket cells with the pyramidal cell body has been necessary in the light of several studies. Peters and Proskauer (1980) reported their smooth stellate cell to form symmetric contacts not only with the pyramidal cell body, but also one symmetric contact with the apical dendritic shaft and three with basal dendrites. The study confirmed an earlier demonstration that multipolar neurones form synapses with a variety of post-synaptic processes of pyramidal neurones, including dendritic shafts and perikarya (Peters and Fairen, 1978). DeFelipe and Fairen (1982) reported basket cells in the superficial layers of cat striate cortex make symmetric synapses with the perikarya, but also the proximal dendrites of pyramidal cells. Somogyi, Kisvarday, Martin and Whitteridge (1983) reported that while approximately one third of basket-pyramidal neurone contacts were on the soma, 20% of synapses were located on spines and the remainder on apical and basal dendrites. In their study, Martin, Somogyi and Whitteridge (1983) reported that 90% of axon terminals of large basket cells synapse with pyramidal cells; 40%
involving the cell bodies and 50% with apical and basal dendrites, the remaining 10% of boutons encountered synapsing with dendrites which could not be identified.

Double-bouquet cells, first described by Cajal (1911), have axons which emerge from the main shaft of a descending dendrite, or from the cell body, to form thin main collaterals which descend in a radial direction and so traverse layers II through V in a bundle 20 to 150 microns in diameter (Somogyi and Cowey, 1981). A number of studies have described the vertical axon bundles of double-bouquet cells as following the apical dendrite of pyramidal cells (Cajal, 1911; Colonnier, 1966; Szentagothai, 1973, 1975, 1978; Jones, 1975) suggesting these neurones provide synapses on the apical dendritic spines, though, even on the basis of Golgi preparations, this assumption was questioned (Valverde, 1978). Using the Golgi/EM method, Somogyi and Cowey (1981) reported that, for double-bouquet cells of lamina III of cat striate cortex, 86.4% of boutons (from a total of 66) formed synapses with dendritic shafts, many of them belonging to non-pyramidal cells, 9% with perikarya of non-pyramidal cells and only 4.6% with spines. Somogyi and Cowey (1981) reported that no pyramidal cell body or axon initial segment was among the postsynaptic structures.

The chandelier cell was first described by Szentagothai and Arbib (1974). These cells are found from lamina II through V in cat striate cortex (Peters and Regidor, 1981). The axon is distinctive, branching a short distance from its origin to produce a plexus characterized by vertically
oriented branches composed of strings of bouton-like swellings (Peters and Regidor, 1981). On the basis of the Golgi picture, several authors suggested the apical dendrite of pyramidal neurones to be the site of synaptic contact of chandelier cells (Szentagothai and Arbib, 1974; Jones, 1975; Szentagothai, 1975, 1978; Tombol, 1978). This suggestion has been denied on the basis of combined Golgi/EM studies. Somogyi (1977) described a type of interneurone in rat visual cortex showing vertically arranged threaded boutons that synapse specifically with the axon initial segment of pyramidal cells. This axo-axonal neurone has been equated with the chandelier neurone (Somogyi, 1979; Somogyi, Hodgson and Smith, 1979). Subsequently, Fairen and Valverde (1980) showed that the terminal formations of chandelier cells make symmetric synapses upon the initial segments of pyramidal neurones in cat striate cortex.

To understand the contribution of GABA-mediated inputs to the formation of receptive field structure, a primary question is whether GABA can be identified as the transmitter of a specific class of non-spiny stellate neurone. There is emerging evidence that the non-spiny neurones using GABA are non-homogeneous.

Somogyi, Kisverday, Martin and Whitteridge (1983) advanced three lines of indirect evidence that basket cells use GABA as a transmitter. Firstly, these authors noted that the types of synaptic contacts formed by their sample of basket cells, and the types of synaptic vesicles of boutons seen in their study were the same as those of GAD
immunoreactive terminals in rat (Ribak, 1978), monkey (Ribak, Harris, Vaughn and Roberts, 1979) and cat (Freund, Martin, Smith and Somogyi, 1983). Secondly, Freund, Martin, Smith and Somogyi's (1983) study of boutons on lamina III pyramidal cells in cat striate cortex demonstrated that nearly all boutons on the perikarya and proximal dendrites are GAD positive therefore, they argued, the boutons of large basket cells in their study (Somogyi, Kisvarday, Martin and Whitteridge, 1983) provide inputs at sites which are very likely to be among the GAD-positive terminals. Thirdly, they argued, on the basis of the similarity in morphology between Martin, Somogyi and Whitteridge's (1983) basket cells and cells in Freund, Martin, Smith and Somogyi's (1983) study, which were shown to contain GAD, for an identity of these neurones with basket cells.

Ribak (1978) has characterized the axo-axonic synapse as using GABA since GAD-positive terminals make symmetric contacts on initial segments. The axo-axonic synapse is specific to the chandelier cell (Somogyi, 1977; Fairén and Valverde, 1980), thereby implicating the transmitter for the chandelier cell as GABA. Additionally, Somogyi and associates (Somogyi, Cowey, Halasz and Freund, 1981; Somogyi, Freund, Halasz and Zoltan, 1981) have provided evidence that the transmitter of the double-bouquet cell is GABA; 3H-GABA, injected into laminae V and VI of the primate visual cortex labelled, by selective retrograde transport, neurones within lamina II. The neurones were identified as double-bouquet cells which are known to have radially arranged axons travelling in bundles and terminating within lamina V.
It follows from the preceding review that GABA cannot be identified as the synaptic transmitter of a single class of non-spiny stellate neurone nor, given the diversity of sites of synaptic contact of basket, chandelier and double-bouquet cells, with a specific synaptic site on the pyramidal neurone. On the basis of connectivity patterns revealed in Golgi/EM and HRP/EM studies of basket, double-bouquet and chandelier cells (Somogyi, 1977; Fairen and Valverde, 1980; Somogyi and Cowey, 1981; DeFelipe and Fairen, 1982; Martin, Somogyi and Whitteridge, 1983; Somogyi, Martin, Kisvarday and Whitteridge, 1983), there is no support for Schiller, Finlay and Volman's (1976a) suggestion of two separate levels of inhibitory interneurones associated with apical and basal dendrites.

Schiller, Finlay and Volman's (1976a) model assumed representation of the simple cell by the pyramidal neurone. Lamina IV is a primary site in which simple cells are distributed (Kelly and Van Essen, 1974; Wilson and Sherman, 1976; Gilbert, 1977; Leventhal and Misch, 1978) in which simple cells may be represented by spiny stellate neurones (Gilbert and Wiesel, 1979; 1981). The division of inhibitory synapses into two levels for the spiny stellate neurone would be unrealistic. If applicable, the model would be more appropriate for the complex cell, for which there is a good correlation with the pyramidal neurone (Kelly and Van Essen, 1974; Lin, Friedlander and Sherman, 1979). However, from the preceding discussion, it has been argued that Schiller, Finlay
and Volman's (1976a) assumptions about inhibitory inputs to
the pyramidal neurone are invalid.

The diversity of sites of different inhibitory
interneurones associated with the pyramidal neurone is
problematical in understanding which inhibitory input is
responsible for individual components of receptive field
structure and attributes of the cell's tuning properties.
Differences within the non-spiny stellate group, in terms of
specificity of site of synaptic contact, type of neurone
contacted and spatial extent of axonal arborization do suggest
diverse roles and, on the basis of connectivity and
morphology, one may ask how these differences are related to
function.

The selective and exclusive formation of an axo-axonic
synapse by the chandelier cell with the pyramidal neurone
(Somogyi, 1977; Fairen and Valverde, 1980) would suggest the
role of a gating neurone, specific to the pyramidal cell,
acting at the output stage (Colonnier, 1981). The
double-bouquet cell, contacting both non-pyramidal as well as
pyramidal cells shows a lower specificity compared with the
chandelier cell reflected in the synaptic contact with
dendritic shafts on non-pyramidal and pyramidal cells,
perikarya of non-pyramidal cells and spines (Somogyi and
Cowey, 1981). The axonal spread of the double-bouquet cells,
with axons arising from the main shaft of a descending
dendrite or cell body, to form collaterals which pass through
layers II to V in a bundle 20 to 150 microns in diameter
(Somogyi and Cowey, 1981) is relatively narrow. Thus, the
Axonal spread is considerably more localized than the basket cell which may reach 700 microns (Gilbert and Wiesel, 1979, 1981). Inhibitory action would therefore be sharp, due to the limited axonal spread, but diverse in the synaptic location at which inhibition is effected.

The pyramidal cell, as Somogyi, Kisvarday, Martin and Whitteridge (1983) have argued, may receive inputs at three levels from basket cells: a generalized inhibition, via input to the soma, of excitation coming to the soma via the neurone's dendrites; selective inhibition of particular dendrites, mainly the apical dendrite; selective inhibition of excitatory input to particular parts of the dendrite. If the cell body provides the optimal site for an inhibitory input to the cell body (Jack, Noble and Tsien, 1975), but individual basket cells make relatively few contacts with the cell body (Somogyi, Kisvarday, Martin and Whitteridge, 1983), an important contribution to receptive field structure may arise from convergence of basket cells on the cell body (Somogyi, Kisvarday, Martin and Whitteridge, 1983). Thus, a complication to the understanding of the role of the basket cell arises from the multiple sites of contact with the pyramidal neurone and from the contribution of convergent inputs to the pericellular basket.

In considering the functional role of the basket cell, an important consideration has been the pattern of arborization seen in Golgi preparations. The view, based on the Golgi picture, that the basket cell might fulfil a role in the construction of orientation columns (Colonnier, 1966;
Marin-Padilla and Stibitz, 1974; Jones, 1975, 1981; Szentagothai, 1973, 1975, 1978; Peters and Regidor, 1981) is undermined by the absence of a correspondence between the spatial distribution of axons with the shape or repetition rate (Martin, Somogyi and Whitteridge, 1983) with the dimensions suggested for orientation columns (Hubel and Wiesel, 1963, 1974; Shatz, Lindstrom and Wiesel, 1977). The slab-like appearance of the axonal arborization of the basket cell in Golgi preparations (Marin-Padilla and Stibitz, 1974; Jones, 1975; Peters and Regidor, 1981) would appear, on the basis of Martin, Somogyi and Whitteridge’s (1983) study, using HRP-injected material, to underrepresent the axon arborization of the basket cell.

The wide extent of the axonal arborization of the basket cell could, potentially, mediate inhibitory interactions across columns with dissimilar tuning properties. If orientation-selective inhibition is generated by columns with preferred orientations distant from that of the recipient cell (Sillito, 1976, 1979), the basket cell would be a more plausible candidate for mediating orientation-selective inhibition than the double-bouquet cell with its more limited horizontal axonal spread.

2.7 The Horizontal Organization of the Striate Cortex

Creutzfeldt, Kuhnt and Benavento (1974) held the view that the lateral connections in striate cortex are inhibitory and emphasised the functional role of inhibition at orientations near the cell’s preferred orientation.
Inhibition in Creutzfeldt's model is centered around the optimal orientation and arises from horizontal interactions extending little more than one orientation column. Creutzfeldt, Kuhnt and Benevento (1974) suggested inhibitory interactions between adjacent columns on the basis of intracellular recordings. Thus, these authors noted (Creutzfeldt, Kuhnt and Benevento, 1974) that;

"It is important to emphasize that inhibition within the excitatory region appears also during the response to the optimal stimulus, it is often better recognized under these optimal stimulus conditions than when the stimulus is oriented non-optimally. This may be partly due to the fact that IPSPs are relatively larger when the cell is depolarized but also indicates a true difference of inhibition at or near the optimal orientation."

The model was in line with psychophysical experiments in man showing mutual inhibition between detectors with slightly different orientations (Andrews, 1965; Blakemore, Carpenter and Georgeson, 1970). Also, Blakemore and Tobin (1972) demonstrated, in cat striate cortex, inhibition centered around the same orientation as the peak in the tuning curve for a moving contrast bar. Blakemore and Tobin (1972) established the preferred orientation for a cell and, while repeatedly stimulating the cell with that stimulus, moved a high contrast grating, covering the whole of the stimulus screen except for a circular area slightly larger than the cell's receptive field, at a range of orientations. Blakemore and Tobin (1972) reported the grating inhibited the cell's response over a broad range of orientations (-60 deg. to +60 deg. relative
to the cell's preferred orientation) centred at the same orientation as the peak of the bar tuning curve. Inhibition, in this context, was suppression of response below the cell's resting discharge seen in extracellular recordings.

Axonal degeneration studies in monkey (Fisken, Garey and Powell, 1973, 1975) and cat (Creutzfeldt, Garey, Kuroda and Wolff, 1977) indicate extensive spread of horizontal fibres (up to 4 mm in monkey and 1.5 mm in cat) compatible with horizontal interactions extending between columns representing all orientations (Hubel and Wiesel, 1974; Albus, 1973) and encompassing receptive field centres of neurones over a visual field area of 2-4 deg. depending on eccentricity (Creutzfeldt, Innocenti and Brooks, 1974; Albus, 1975). The rate of fall-off in the relative numbers of asymmetrical terminals is much more rapid than that of symmetrical ones; connections over long distances are inhibitory (Fisken, Garey and Powell, 1973) with the exception of interactions between columns representing the same orientation (Mitchison and Crick, 1982). For the monkey (Fiskin, Garey and Powell, 1973, 1975) and the cat (Creutzfeldt, Garey, Kuroda and Wolff, 1977), an asymmetry in the spread of horizontal connections is seen, as suggested by intracellular recordings (Benevento, Creutzfeldt and Kuhnt, 1972; Creutzfeldt, Kuhnt and Benevento, 1974) and required by Creutzfeldt's model (Benevento, Creutzfeldt and Kuhnt, 1972; Creutzfeldt, Kuhnt and Benevento, 1974). The asymmetry is more conspicuous for the oblique than the short horizontal fibres in the cat (Creutzfeldt, Garey, Kuroda and Wolff, 1977).
Pharmacological studies have confirmed inhibitory interactions from columns representing orientations distant from that of the recipient column (Hess, Nagishi and Creutzfeldt, 1975; Hess, Ostendorf, Sanides, Nagishi and Creutzfeldt, 1976) and have revealed the relative contributions of inhibition from columns far and close to the recipient column (Sillito, 1976, 1978). In the two studies by Hess and co-workers, inhibitory interactions were seen to extend laterally 400 microns, with a maximal effect between 100 and 200 microns. Inhibitory interactions between adjacent neurones cannot be ruled out (Hess, Nagishi and Creutzfeldt, 1975) and are suggested by results of double recordings from a single electrode (Creutzfeldt, Kuhnt and Benevento, 1974; Hess and Murata, 1974) and the cross-correlation study of Toyama, Kimura and Tanaka, 1981a, b).

Sillito (1976), commenting on the broadening of the complex cell orientation tuning curve following iontophoretic application of bicuculline, inferred that inhibition acting in the orientation domain would be generated by orientations up to 90 deg. from the cell's optimum. Later, in a quantitative evaluation of GABA-mediated inhibition, Sillito (1978) compared normal orientation tuning curves for moving contrast bars with those observed during the iontophoretic application of bicuculline, thereby providing a basis for estimating the orientation tuning of GABA-mediated inhibition. It was concluded that, at normal resting discharges, orientations to either side of the optimal orientation, rather than those centred at the optimum, generate the most powerful inhibitory input. Thus, neurones in the striate cortex receive
inhibitory inputs via intracortical pathways which are
anisotropically organized with maximal inhibition provided by
neurones with preferred orientations distant from that of the
recipient cell.

2.8 The Vertical Organization of the Striate Cortex

In the models of Bishop, Coombs and Henry (1971b),
Goodwin and Henry (1975) and Schiller, Finlay and Volman
(1976a), complex cells were assumed to derive their
orientation and/or direction selectivities from simple cells.
Pharmacological studies have shown that some complex cells
derive their orientation or direction selectivities from a
These studies do not, however, identify the receptive field
class of the cells providing that tuned input. In the
following section, consideration is given to the patterns of
intracortical pathways, demonstrated by anatomical and
physiological methods, through which excitatory connections
are formed.

By reference to physiological studies, the questions of
whether and how simple and complex cells are functionally
linked by excitatory connections is discussed. Additionally,
the possibility that some complex cells may derive some of
their properties from other complex cells is considered. In
providing the bridge between anatomical and physiological
studies, it is assumed that complex cells are represented
morphologically by pyramidal neurones (Kelly and Van Essen,
1974; Lin, Friedlander and Sherman, 1979; Gilbert and Wiesel
1979, 1981) though, since some complex cells may be represented morphologically by non-spiny or partially spiny stellate neurones (Martin, Somogyi and Whitteridge, 1983), this is an oversimplification.

2.8a Intracortical Circuitry Revealed by Anatomical Methods

Excitatory connections are formed by pyramidal and spiny stellate neurones (LeVay, 1973; Peters and Fairen, 1978; Somogyi, 1978; White, 1981; Peters and Kimurer, 1981; Peters and Proskauer, 1980a, b, 1981). Spiny stellate neurones show localised dendritic and axonal spread, suggesting they receive afferent input and form localised connections in the lamina in which the cell bodies are distributed (Cajal, 1922; O'Leary, 1941; Lorente de No, 1949; LeVay, 1973; Szentagothai, 1973; Fairen and Valverde, 1979; Lund, Henry and Harvey, 1979). From the distribution of apical and basal dendrites, pyramidal cells are functionally linked to laminae outside the layer in which the cell body is located (Lund and Boothe, 1975; Lund, Henry and Harvey, 1979). Axons of pyramidal cells in laminae II to VI project extrinsically with supragranular layer pyramidal cells sending axon collaterals to lamina V (O'Leary, 1949; Lund, Henry and Harvey, 1979).

Spiny stellate neurones are prominently distributed in lamina IV (Cajal, 1922; O'Leary, 1941; LeVay, 1973; Szentagothai, 1973; Lund, Henry and Harvey, 1979; Fairen and Valverde, 1979). Axons spread locally, those of lower lamina IV spread laterally in the upper part of lamina IV and those
of the upper part of lamina IV have long horizontal branches which give off vertically oriented collaterals extending into lamina II and III (Lund, Henry and Harvey, 1979; Gilbert and Wiesel, 1979; Peters and Regidor, 1981). LeVay (1973), using the Golgi/EM method, reported the recipient cell post-synaptic to spiny stellate cells of lamina IV to be pyramidal cells. The distribution, synaptology and connectivity of spiny stellate cells suggests they form the source of excitatory pathways arising from lamina IV.

Pyramidal neurones occupying the middle to lower regions of lamina IV are few (Lund, Henry and Harvey, 1979) but the border of lamina IVa/III is populated by large pyramidal neurones (O'Leary, 1941; Lund, Henry and Harvey, 1979) those of upper lamina IV resembling adjacent stellate cells except for the possession of an apical dendrite. The border pyramids (O'Leary, 1941) of lamina IVa/III have an apical dendrite which branches just superficially to the cell body and extends to reach lamina II or I with occasional branches in lamina III or II (Lund, Henry and Harvey, 1979; Lorente de No, 1949). The axons of these neurones have collaterals rising obliquely to lamina III and II and others that run laterally within lamina IV and the descending trunk contributes to lamina V and continues out of the cortex.

Pyramidal cells of the infragranular layers differ in the extent of arborization of the apical dendrite (Cajal, 1911, 1922; Lorente de No, 1949; O'Leary, 1941; Lund, Henry and Harvey, 1979). Apical dendrites of lamina V pyramidal cells show side branching of the apical dendrite close to the soma.
then the dendrite ascends with few or no side branches frequently reaching lamina I (Lund, Henry and Harvey, 1979). Basal dendrites arborize mainly within lamina Vb though Lund, Henry and Harvey (1979) reported some spread to lamina Vb and the lowest part of lamina IV. The axon largely parallels that of the basal dendrites (Lund, Henry and Harvey, 1979). Apical dendrites of lamina Vb traverse the superficial laminae reaching lamina I and their axons give off collaterals in lamina Vb before projecting out of the cortex. The majority of lamina VI pyramids have apical dendrites which arborize in laminae VI and V then ascend to lamina I with minimal branching in laminae IV, III and II (Lund, Henry and Harvey, 1979). The specific arborization of lamina VI pyramidal apical dendrites found in the monkey (Lund and Boothe, 1975) is absent in the cat (Lund, Henry and Harvey, 1979).

Axonal degeneration complements the Golgi method but overcomes two limitations of the latter; that it is difficult to make generalizations from individual neurones and axons cannot easily be traced over long distances. Axonal degeneration has been used in the striate cortex of the cat by Creutzfeldt, Garey, Kuroda and Wolff (1977) and in the monkey by Spatz, Tigges and Tigges (1970), Fiskern, Garey and Powell (1973, 1975) and Tigges, Spatz and Tigges (1973). Each study used intact cortex but the study of Creutzfeldt, Garey, Kuroda and Wolff (1977) additionally used chronically isolated cortex, thereby enabling them to distinguish between degenerating fibres of extrinsic and intrinsic origin. The distribution of fibres seen in chronically isolated and intact cortex were similar.
Creutzfeldt, Garey, Kuroda and Wolff (1977) identified four fibre systems following intracortical lesions: (a) vertically descending; (b) obliquely descending; (c) obliquely ascending; and (d) horizontal fibres. No significant vertically upwards coursing group of fibres was seen. Horizontal fibres were found in considerable numbers for approximately 500 microns from lesions mainly in laminae I, III, IV and V, a few reaching 2-3 mm. Oblique axons were seen to run downwards from the middle layers into laminae V and VI or upwards into laminae I and II. Axons arising from laminae II to V were seen to descend vertically into the white matter. Additionally, Creutzfeldt, Garey, Kuroda and Wolff (1977) found degeneration in lamina V, following superficial lesions, as had Fisken, Garey and Powell (1973, 1975) but their presence was described as moderate, contrasting with the massive degeneration in lamina V reported in the monkey by Spatz, Tigges and Tigges (1970) and Nauta, Butler and Jones (1973). In other respects, the pattern seen in cat is similar to that in cat (Spatz, Tigges and Tigges, 1970; Fisken, Garey and Powell, 1973, 1975; Tigges, Spatz and Tigges, 1973) though differences are seen in the extent of the axonal spread (Fisken, Garey and Powell 1973; Creutzfeldt, Garey, Kuroda and Wolff, 1977). Degeneration studies are therefore in agreement with Golgi studies in suggesting efferent pathways from laminae II to VI, intrinsic pathways arising from laminae IV, vertically ascending or descending, and an intracortical pathway from the supra- to the infragranular laminae.
2.8b Intracortical Connectivity Revealed by Physiological Techniques

Early intracellular studies indicated three patterns of connectivity to and within the striate cortex of the cat: monosynaptic excitation and disynaptic inhibition upon cortical cells of laminae III-V; disynaptic excitation and trisynaptic inhibition of cells of laminae III-V; and disynaptic excitation and trisynaptic inhibition on cells of laminae II and VI (Creutzfeldt and Ito, 1968; Ohno, Kiyohara and Simpson, 1970; Toyama, Matsunami, Ohno and Takashiki, 1974). The more recent study of Ferster and Lindstrom (1983) confirmed and extended these results. Laminae III, IV, upper V and VI were seen to be monosynaptically excited by geniculate afferents, while cells in laminae II and lower V were seen to receive only indirect excitation via other cortical neurones. Lamina III neurones were distinct in that they were found to receive a prominent excitatory input over two synapses in addition to direct excitation from the LGN. Identifying the receptive field structure of cells intracellularly recorded, Ferster and Lindstrom (1983) reported simple cells of lamina IV and VI to be monosynaptically innervated, while complex cells of laminae II, III, V and VI showed connectivity patterns related to their laminar patterns. Those in laminae VI and upper V received direct excitation, those in lamina III received direct plus indirect excitation and those in laminae II and lower V only indirect excitation from the LGN. For cells identified by their efferent projections, a pattern of connectivity was revealed in which cortico-geniculate neurones
are monosynaptically excited and cortico-collricular neurones di- and trisynaptically excited by geniculate afferents. Cortico-cortical neurones in laminae II and III were found to receive excitation over two synapses, or over one synapse plus excitation over two synapses, depending on laminar position (Ferster and Lindstrom, 1983). Ferster and Lindstrom (1983) also identified an excitatory pathway from lamina V to VI. Intracellular studies therefore indicate a diversity of connectivity patterns amongst complex cells with intracortical excitatory pathways contributing inputs to cells of both the supra- and infragranular layers.

Results from current-source-density analysis are in accord with anatomical studies in suggesting lamina IV to be the principal site for the origin of intracortical excitatory pathways (Mitzdorf and Singer, 1978). Three prominent excitatory pathways in cat striate cortex, each starting from lamina IV, were identified by these authors. The first would form an excitatory pathway to supragranular pyramidal cells via local connections to lamina III and from there, via long distance connections, to lamina II. A second pathway would link lamina IV to V, contacting the apical dendrites of lamina VI pyramidal neurones. The third pathway, with one synaptic delay in lamina IV, would provide an excitatory connections from lamina IV to III. In addition, current-source-density analysis (Mitzdorf and Singer, 1978) also indicated convergence of excitatory input from the supragranular layers to lamina V.

Consistent with simple cells forming the first link in
the excitatory pathways arising from lamina IV, it is known that simple cells are the predominant receptive field class in lamina IV (Hubel and Wiesel, 1962; Kelly and Van Essen, 1974; Wilson and Sherman, 1976; Gilbert, 1977; Leventhal and Hirsch, 1978). By contrast, cross-correlation studies provide weak support for a functional link between simple and complex cells. Michalski, Gerstein, Czarkowski and Tarnecki (1983) made comparisons of response planes (Palmer and Davis, 1981) to determine whether the type of interaction between neurones depends on receptive field class. Response planes were analysed for twenty-four neurones; six pairs were recorded (at different times) with one bundle of electrodes and in four cases three neurone groups were studied, consisting of two neurones from one bundle and a third from the other bundle. The population consisted of seven simple cells and seventeen complex cells with interactions between complex cells reported for ten pairs; three pairs where both were simple and five cases where one cell was simple and the other complex. Eight out of ten interactions between complex cells revealed shared input and two were stimulus dependent. For the three pairs of simple cells, one pair shared input co-ordination, one was stimulus dependent and one did not show any co-ordination. The simple/complex pairs had shared interactions in three out of five cases, stimulus-dependent in one case and both stimulus dependent and direct excitation in only one case.

Toyama, Kimura and Tanaka's (1981a, b) study, described earlier, provided data on a much larger sample of neurones. That study and Michalski, Gerstein, Czarkowska and Tarnecki's (1983) are in agreement in reporting that shared input is the
most common form of co-ordination and includes a broad range
of receptive field types. However, Toyama, Kimura and Tanaka
(1981a, b) had reported direct connections only between
complex cells or from complex cells to hypercomplex cells.
Michalski, Gerstein, Czarkowska and Tarnecki's (1983)
demonstration of a direct connection, simple to complex, needs
to be treated with caution since this was shown for only one
cell and for that example it was combined with a large
stimulus peak making the correlogram difficult to interpret.

Even if simple cells provide an input to complex cells,
there is evidence against the view (Henry, Dreher and Bishop,
1974; Goodwin and Henry, 1975 and Schiller, Finlay and
Volman, 1976e) that the orientation and direction tuning of
complex cells in the supragranular layers derives from an
input from lamina IV. Malpeli (1983) has studied the effect
of functionally inactivating cortical laminae by selective
injection of 4mM cobaltous chloride into lamina A of the
lateral geniculate nucleus. Following the injection, visual
activity in laminae IVab, IVc and VI was virtually abolished.
However, the orientation and direction selectivity of cells in
laminae II and III was unaffected. In contrast, more variable
effects were seen for cells in lamina V; special complex
cells were least affected and simple cells the most.

Several studies, in addition to the cross-correlation
study of Toyama, Kimura and Tanaka (1981a, b) suggest that
some properties of complex cells may arise from an input from
other complex cells, though the contributions of such inputs
to receptive field structure remains to be established.
Laamina II cells receive only indirect excitation from the LGN (Toyama, Mackawa and Takada, 1977; Toyama, Kimura, Shida and Takada, 1977; Ferster and Lindstrom, 1983). Toyama et al (Toyama, Mackawa and Takada, 1977; Toyama, Kimura, Shida and Takada, 1977) reported that lamina II complex cells shared temporal features of response with cells of the middle layers and, in terms of spatial features of their responses along the direction perpendicular to the preferred orientation, resembled complex cells of the middle layers. Gilbert and Wiesel's (1979, 1981) studies reported complex cells, pyramidal in morphology and located in the upper part of laminae II and III, the descending axons of which project extensively in lamina V in which simple cells are few (Kelly and Van Essen, 1974; Wilson and Sherman, 1976; Gilbert, 1977; Leventhal and Hirsch, 1978). Also, Gilbert and Wiesel (1979, 1981) have reported specific patterns of connectivity of lamina V 'standard' and 'special' complex cells, a characteristic feature of standard complex cells being an extensive projection to lamina VI, in which complex cells are invariably 'standard' (Gilbert, 1977; Gilbert and Wiesel, 1979, 1981) while 'special' complex cells send a large trunk out of the cortex to the superior colliculus (Gilbert and Wiesel, 1979, 1981). The laminar V to VI pathway, apparent also in the study of Ferster and Lindstrom (1983), would therefore appear to link complex cells with similar summatory behaviour.

The following conclusions may be drawn from this review of intracortical circuitry. Anatomical and physiological studies are in accord in suggesting multiple inputs to complex
cells some of which are of intracortical origin. The diversity of connectivity patterns of complex cells seen in anatomical and physiological studies is supportive of evidence from pharmacological studies (Sillito, 1975, 1976a, b, 1977, 1979) of differences in the origin of tuning properties between complex cells with some complex cells deriving their orientation or direction tuning properties from an intracortical excitatory input.

The contribution of intracortical excitatory pathways to the receptive field structure of complex cells remains, at best, poorly understood. A discrepancy exists between cross-correlation studies, which provide little evidence of excitatory connections between simple and complex cells, and evidence that lamina IV, in which the simple cell predominates, is a primary source of intracortical excitatory pathways. The discrepancy may, in part, reflect the technical difficulties of the cross-correlation technique.

If simple cells provide an excitatory input to complex cells, the contribution of such inputs to the receptive field structure of complex cells remains unclear. Malpeli's (1983) study casts doubt on the assumption that lamina IV simple cells provide the source of orientation and direction tuning of supragranular complex cells or, indeed, lamina V 'special' complex cells. Emerging evidence suggests a role for excitatory connections between complex cells in the formation of complex cell receptive field structure; pathways from laminae III to II, from V to VI and III to V are suggested as mediating such links. The latter pathway, as suggested by
Hammont and Reck (1980b), may provide the basis for the greater sensitivity to texture motion of infragranular, compared with supragranular, complex cells.

2.9 SYNTHESIS.

The primary objective of the preceding discussion has been to establish the dependence of striate cortical neurones' orientation and direction selectivities on intracortical inhibition and the mediation of orientation and direction selectivities by separate mechanisms. Consideration has been given to the receptive field structure from which cortical neurones' orientation and direction selectivities derive and the underlying patterns of connectivity from which that receptive field structure is built up.

The dependence of orientation and direction selectivities on intracortical inhibition has been shown from the effects of blockade of GABA-mediated inhibition and in the orientation/direction dependence of intracortical inhibition seen in intracellular recordings. Between simple and complex cells, there is a differential dependence of orientation and direction selectivities on intracortical inhibition with simple cells showing a complete dependence on intracortical inhibition.

Three models for the role of intracortical inhibition in generating orientation and direction selectivities have been reviewed. Bishop's model (Bishop, Coombs and Henry, 1971b) assumed the key to understanding the tuning properties of
cortical cells to lie in the receptive field organization of the simple cell; specifically in the spatial relationship between intracortical inhibition and afferent excitation from the lateral geniculate nucleus. It has been argued that there is no separate component of the simple cell receptive field arising from tonic inhibition and conferring on the simple cell its orientation tuning; inhibition outside the central discharge zone shows a spatial and functional continuity with that within. From intracellular recordings, it has been demonstrated that the distribution of inhibition within the simple cell receptive field is not constrained by the spatial organization of excitatory input from the lateral geniculate nucleus. Inhibition throughout the receptive field has dynamic properties.

Afferent input from the lateral geniculate nucleus to the striate cortex is provided by parallel streams of X, Y and W fibres showing a laminar-specific pattern of projection. These parallel streams are not segregated at the geniculo-cortical synapse to produce parallel X fibre to simple cell and Y fibre to complex cell streams. Inhibitory input to the single cell comes from columns differing in preferred orientation with maximal contribution from columns distant from the recipient cell. As required by Creutzfeldt's model (Benevento, Creutzfeldt and Kuhnt, 1972; Creutzfeldt, Kuhnt and Benevento, 1974), the pattern of fibres assumed to mediate inhibitory intercolumnar interactions is anisotropically organized.

Schiller, Finlay and Volman (1976e) suggested the
mediation of orientation and direction selectivities by separate mechanisms. Strong support for separate mechanisms mediating orientation and direction selectivities is given by studies showing dissimilar tuning for bar and texture motion. Comparisons of ocular dominance for moving contrast bars and fields of texture and velocity tuning for bar and texture motion have indicated bar and texture tuning to be associated with distinct inputs. Within the complex cell group, there are differences in the origin of bar tuning, some deriving their tuning properties from intracortical inhibition and others from a tuned excitatory input. At present, there is no strong evidence that simple cells provide the orientationally or directionally tuned input to these complex cells. Complex cells with similar summatory behaviour may differ in the origin of their orientation and direction tuning properties.

Current understanding of connectivity, at the single cell level, subserving these separate mechanisms is at a very early stage. A pre-condition for formulation of models for the neural substrate of these mechanisms is an appropriate model of receptive field structure. The model of Schiller, Finlay and Volman (1976b, e) incorporated an element of Bishop, Coombs and Henry's (1971b) model of simple cell receptive field structure; specifically, side-band inhibition. Therefore, the design was partly built on a false template. The models of Bishop, Coombs and Henry (1971b), Goodwin and Henry (1975) and Schiller, Finlay and Volman (1976b, e) made assumptions about the tuning properties of cortical neurones, and, by implication, receptive field structure, which were untested in the original formulations of the models; the
predictability of response to a moving bar from tuning for a stationary bar and linearity of summation.

The responsiveness of complex cells to texture motion imply a greater complexity of receptive field structure and connectivity than is required to explain bar tuning. The absence of a differential sensitivity to texture motion between the various classes of LGN cells requires an intracortical origin for the differential sensitivity to texture motion between complex and simple cells. Intracortical connectivity may also account for the greater texture sensitivity of complex cells in the infragranular layers compared with those in the supragranular layers.

Consideration is now turned to the tuning properties of simple and complex cells for contrast and textured stimuli. Studies which have evaluated tuning of simple and complex cells for contrast stimuli are reported and reviewed in the context of models for the role of intracortical inhibition in determining tuning characteristics. The tuning of complex cells for texture field motion is described to highlight differences in tuning properties and receptive field structure between complex and simple cells. Differences in tuning for contrast and textured stimuli between complex and simple cells are also considered as a background to a later discussion of how such differences suggest a distinct role for the complex cell in visual analysis.
CHAPTER THREE: THE TUNING OF SIMPLE AND COMPLEX CELLS FOR
CONTRAST AND TEXTURED STIMULI

INTRODUCTION

Campbell, Cleland, Cooper and Enroth-Cugell (1968) provided the first quantitative study of orientation tuning properties of cortical neurones. Moving rectangular wave-form gratings were used to determine the relationship between response amplitude and orientation of the stimulus. A linear relationship between spike frequency and the angle on either side of the optimal or preferred orientation was reported, with linearity being maintained up to a point where response fell to zero or a base line frequency. The term angular selectivity was introduced and defined as the half-width at half-height of the tuning-curve. Angular selectivity of thirty-five neurones was determined and more than half of these fell within the range of 14-26 deg. Campbell et al noted that fourteen neurones were directionally selective, with twenty-one neurones producing a bi-directional response, though not of equal magnitude for opposite directions of motion. No significant correlation between response amplitude at optimal orientation and angular selectivity was found and the distribution of preferred orientation showed no bias for vertical/horizontal against oblique. In this study no distinction between cell types was made and data were combined from striate and extrastriate cortex.
3.1 The Form of the Tuning Curve for Moving Contrast Bars

The linear relationship found with gratings has also been reported for the tuning curve determined with moving contrast bars (Henry, Dreher and Bishop, 1974; Rose and Blakemore, 1974; Watkins and Berkey, 1974; Ikeda and Wright, 1975; Hammond and Andrews, 1978a, b, c; Heggelund and Albus, 1978) and holds for simple, complex and hypercomplex cells (Henry, Dreher and Bishop, 1974; Rose and Blakemore, 1974; Hammond and Andrews, 1978a, b) in cat striate cortex. Deviation from linearity has only been found at the extreme flanks of the tuning curve (Heggelund and Albus, 1978; Scobey and Gabor, 1979) with deviations from linearity significant only for broadly tuned units (DeValois, Yund and Hepler, 1982). There is some evidence that, for the monkey, the tuning curve follows an exponential function similar to the psychophysical curve for man (Campbell and Kulikowski, 1966; Campbell, Cleland, Cooper and Enroth-Cugell, 1968; Hubel and Wiesel, 1968). The shape of the tuning curve is invariant for a range of contrast values from three times threshold to threshold, though response amplitude is seen to decline with declining mean luminance (Bisti, Clement, Maffei and Meccacci, 1977). Constancy of tuning with changing mean luminance was also reported by Hoepfner (1974).

Though there has been some controversy over the question of time-dependent changes in orientation tuning, variability of tuning being reported by Horn and Hill (1969), Horn, Stechler and Hill (1972) and Donaldson and Nash (1973, 1975), the weight of evidence would indicate that though marked
spontaneous fluctuations in cells' responsiveness may occur (e.g. Bishop, Coombs and Henry, 1971b; Lee, Cleland and Creutzfeldt, 1977) orientation tuning assessed with moving contrast bars remains constant (Hubel and Wiesel, 1962, 1963; Barlow, Blakemore and Pettigrew, 1967; Pettigrew, Nikara and Bishop, 1968; Hoffmann and Stone, 1971; Dreher, 1972; Henry, Dreher and Bishop, 1974; Ikeda and Wright, 1974, 1975; Andrews, Hammond and James, 1975; Hammond, Andrews and James, 1975).

3.2 The Tuning of Simple and Complex Cells for Moving Contrast Bars

For both simple and complex cells the tuning curves for contrast bars of opposite polarity are identical (Henry, Dreher and Bishop, 1974). Several studies have suggested that, as a group, simple cells are more sharply tuned than complex cells (Henry, Dreher and Bishop, 1974; Watkins and Berkley, 1974; Albus, 1975; Hammond and Andrews, 1978b; Leventhal and Hirsch, 1978; DeValois, Yund and Hepler, 1982). Henry, Dreher and Bishop (1974) reported the mean half-widths for simple cells to be 17 deg. (range 8-31 deg.) compared with 27.5 deg. (range 20.5-40 deg.) for complex cells. Insufficient data were available for hypercomplex cells. Rose and Blakemore (1974), though presenting no quantitative analysis, observed sharper tuning for simple than complex cells but no difference between these two groups and hypercomplex cells. Heggelund and Albus (1978) found differences in the mean orientation discrimination (MOD) - the change in orientation angle away from the optimal which would
produce a response statistically different at the 1% level from that at the optimum orientation - to be higher in simple than complex cells. Sharper tuning for simple cells was reported by Watkins and Berkley (1974) who, though finding orientation tuning to be weakly related to receptive field geometry, noted that cells with large fields are less sensitive to stimulus orientation than those with small fields. Hammond and Andrews (1978c) further confirmed differences in tuning between simple and complex cells and reported the relatively sharper tuning of simple cells in area 17 than in 18. In this study, average half-widths of tuning in area 17 were reported to range from 7-30.5 deg. with a mean of 18.3 deg. and a modal value between 10 and 15 deg. Hammond and Andrews (1978b) found area 17 simple cells half-width values to range from 7-26.5 deg. with a mean of 15.3 deg. and a modal value of 10-15 deg. Corresponding values for complex cells were range 16.5-30.5 deg., mean 26.6 deg. and modal value 15-20 deg.

Comparison of tuning between simple and complex cells as a function of eccentricity (Wilson and Sherman, 1976) and laminar position (Gilbert, 1977; Leventhal and Hirsch, 1978) have indicated class differences with relative constancy of tuning for simple cells for each parameter. Wilson and Sherman (1976) reported that the breadth of the orientation tuning curve increased with eccentricity with a greater eccentricity-related change in the orientation tuning of complex than simple cells. These authors found the change in receptive field size as a function of eccentricity to be more evident for complex than simple cells. An increase in the
proportion of complex cells as a function of eccentricity was reported by Wilson and Sherman (1976). Payne and Berman (1983) found that at all eccentricities the tuning width of simple cells was smaller than complex cells but no systematic change in tuning width for either group was apparent. Kennedy and Orban's study (1979) supported Wilson and Sherman's results.

Gilbert (1977) observed a similarity in tuning for standard complex cells and simple cells with differences between complex and simple cells being most noticeable when infragranular layer complex cells were compared with the simple cell group. Simple cells were similar in tuning for all laminae. Leventhal and Hirsch (1978) reported data in agreement with Gilbert's observations.

The possibility has been raised of an anisotropy in the proportion of cells representing the vertical and horizontal meridians compared with oblique orientations (Rose and Blakemore, 1974). It has been further suggested that the anisotropy is class-dependent with differences in tuning properties of simple and complex cells related to their orientation preference (Rose and Blakemore, 1974). Psychophysical experiments in man have suggested that the thresholds for detection of stimuli near the principal vertical and horizontal meridians are lower than for the oblique (Campbell and Kulikowski, 1966; Andrews, 1967; Mitchell, Freeman and Westheimer, 1967; Campbell and Maffei, 1971). The oblique effect has been demonstrated behaviourally for the monkey (Boltz, Harwerth and Smith, 1979; Williams,
Boothe, Kiorpes and Teller, 1981) and for the cat (Orban and Vandenbusche, 1979).

Rose and Blakemore (1974) reported a correlation for the oblique effect; orientation selectivity of simple cells was found to be inversely related to the angular distance of the preferred orientation from the principal meridians. No such correlation was found for complex cells. Wilson and Sherman (1976) could not confirm this result. Gilbert (1977) reported that no lamina was selective for a given orientation nor did any lamina have cells that were more sharply tuned than those in another lamina as would be anticipated from laminar differences in simple and complex cell distributions.

A possible substrate for the oblique effect might be an over-representation of neurones tuned to the horizontal and vertical. This has little support. Kalla and Whitteridge's (1973) claim that more than half of neurones in the cat's monocular segment of striate cortex prefer horizontally oriented stimuli was not supported in Wilson and Sherman's (1976) investigation. Similarly, Rose and Blakemore (1974) in cat, and Finlay, Schiller and Volman (1976) and Poggio, Doty and Talbot (1977) in monkey, found no differences in the number of cells tuned to the horizontal/vertical versus oblique. Mansfield (1974) and Mansfield and Ronner (1978) provided evidence that, for the macaque, cells tuned to horizontal and vertical are more numerous than those tuned to oblique orientations in the foveal projection region, but that various optimal orientations are seen in equal numbers in the parafoveal region. The conclusion was not supported in the
studies of Finlay, Schiller and Volman, (1976) and Poggio, Doty and Talbot (1977). DeValois, Yund and Hepler (1982) compared tuning of foveal and parafoveal simple and complex cells and concluded that, for the macaque, tuning width between the four groups was not significantly different. However, they reported that their foveal, but not parafoveal sample showed a meridional anisotropy with more cells tuned to horizontal/vertical. The statistical significance of the result was low (Chi-squared, P=0.07) thereby weakening their conclusion. In summary, there is no evidence that simple and complex cells differ in tuning properties as a function of meridional anisotropy.

Asymmetries in the tuning curve of simple and complex cells for moving contrast bars are evident in several studies (Rose and Blakemore, 1974; Henry, Dreher, and Bishop, 1974; Schiller, Finlay and Volman, 1976b; Hammond and Andrews, 1978b; Leventhal and Hirsch, 1978) though quantitative analysis was made in only two studies (Henry, Dreher and Bishop, 1974; Hammond and Andrews, 1978b). Henry, Dreher and Bishop introduced the measure of the ratio of the greater to the lesser half-width at half-height of the tuning curve as an index of symmetry. For a sample of forty simple cells, combining data for both light and dark bars for some cells, the mean asymmetry was 1.26 (range 1-2). The corresponding figure for complex cells was 1.62 (range 1-2.8). Hammond and Andrews (1978b) reported 60% of cells recorded in area 17 and 18 to be asymmetrically tuned in excess of 20% with ratios of half-widths ranging from 1.0-3.0, exceptionally 5.8. These authors found asymmetries to be more marked in area 18, than
17, except that area 18 hyper-complex type 2 cells (complex cells with end-inhibition), as a group, were relatively symmetrically tuned for orientation.

3.3 Dissociation of the Parameters of Orientation and Direction with Contrast Stimuli

Henry, Bishop and Dreher (1974) drew attention to the fact that the preferred direction of motion for a contrast bar is necessarily orthogonal to the preferred orientation. Many studies have used moving bars for determining orientation tuning. In such studies, the contributions of orientation and direction could not be assessed. These contributions have been assessed with contrast stimuli by making comparisons of tuning for moving and stationary bars (Henry, Dreher and Bishop, 1974), moving spots and bars (Henry, Dreher and Bishop, 1974) or by varying stimulus length symmetrically (Bodis-Wollner, Pollen and Ronner, 1976) or non-symmetrically (Rose, 1977; Hammond and Andrews, 1978 a, c) over the geometric centre of the receptive field. Those studies varying length symmetrically across the receptive field centre have assumed linearity of summation.

Henry, Bishop and Dreher (1974) compared tuning for stationary and moving bars, the stationary bar being aligned with the midpoint of the discharge centre. It was concluded that simple cells show identical tuning for a stationary bar and the same bar in motion. No detailed quantitative evaluation was made. Rose, in his doctoral thesis (Rose, 1978, p.28) noted from his data and from those of Blakemore
and Tobin (1972) that almost identical curves were obtained in some cases but, in others, breadth of tuning differed by 50%. Hammond and Andrews (1978, and unpublished observations) observed tuning of some striate cortex neurones to be more sharply and symmetrically tuned for a stationary bar than a moving bar. There has been no quantitative comparison of tuning for stationary and moving bars for complex cells.

Henry, Bishop and Dreher (1974) evaluated tuning for a bar and spot moving through the geometric centre of the receptive field. As in the evaluation for stationary and moving bars no systematic quantitative consideration of data was undertaken. For the unit illustrated, the preferred direction (or axis in Henry et al's terminology) was orthogonal to the cell's preferred orientation. For one hypercomplex I cell (simple with end-inhibition) comparisons were made for a spot with both a moving and stationary bar. In each case, reduction in stimulus length brought about no change in preferred direction but decreased response and broadening of tuning; preferred direction therefore appeared to be predictable from the response to a stationary flashed bar.

From responses to moving spot and bar stimuli, Henry, Bishop and Dreher (1974) identified two classes of complex cells. For the first category, as for the simple cell, decrease in bar length produced a reduced response with broadening of tuning but no change in the cell's preferred direction. For the second category, reducing stimulus length similarly produced no change in preferred direction, a smaller
change in response but no change in tuning width. The existence of the second type of complex cell is doubtful. The tuning curves were derived from a limited range of directions and extension of the range could have revealed differences in breadth of tuning for the two stimuli. Summatory behaviour of the neurones would identify the group as the "special" complex category of Gilbert's (1977) classification, of which the cortico-tectal neurones of Palmer and Rosenquist's (1974) study are members. For a cortico-tectal neurone illustrated by Palmer and Rosenquist (1974), a broadening of tuning is apparent in the tuning curve for a spot compared with that for a bar.

Length-response curves for a bar moving at the cell's preferred orientation and moving in its preferred direction have indicated non-linearities of summation (Bodis-Wollner, Pollen and Ronner, 1976; Rose, 1977). Bodis-Wollner, Pollen and Ronner (1976), though finding a general tendency for the length-response function to be linear over a considerable range, and in some cases the complete range, reported that, for most cells, non-linearities were evident before the optimal length was reached. Three factors contributed to the non-linearity.

1. receptive field shape; some cells were found to have round or ovoid receptive fields and the summation of responses from excitatory zones of varying optimal lengths was seen to result in a non-linear length response curve.

2. the central regions could contribute more to cell response than the lateral regions.

3. a non-linearity arising from saturation of response at the
upper range of slit lengths.

In Rose's study (1977), cells were classified into three types according to the effects on the cells' responses of extending bar length beyond the central region of the receptive field. The cells were further divided into three groups depending on their responsiveness to very short bars crossing the receptive field centre. By the first classificatory system, cells were divided into facilitatory flanks (FF), no flanks (NF) and inhibitory flanks (IF). On the basis of their spot responses, cells were grouped into US (unresponsive), PS (cells whose length-response is linear up to a limit) and RS (cells responding very well to small spots). A cell would therefore be placed in one of nine groups. No significant differences in the distributions of the nine groups between simple and complex cells was found. The functional properties of the nine groups could be summarized as follows:

(1) cells with inhibitory flanks respond well to spots whereas cells with facilitatory flanks require summation within the field centre before they fire;
(2) the more responsive a cell is to spots, the shorter is its receptive field centre, with centre length increasing with distance of the field from the area centralis;
(3) field size is positively correlated with field centre size, both for FF and IF cells. Type FF cells have stronger flanks than IF cells. The stronger the flanks of type IF cells the shorter the flanks are and cells responsive to spots also have short flanks.
(4) length response behaviour is related to orientation
selectivity; cells with strong facilitatory flanks tend to be narrowly tuned for orientation while cells with strong inhibitory flanks respond over a wide range of orientations.

Rose used the conditions to establish how the component parts of the receptive field interact. In the first condition, a short bar was moved through the receptive field but its axis of movement was displaced laterally after eight to ten presentations to stimulate different parallel strips of the receptive field. A second condition used a very short bar with one end always moving along the line bisecting the minimum response field which after 8-10 presentations, was extended by a small amount at its peripheral end only; one half of the receptive field was not stimulated at all and the other half was stimulated more and more from the centre outwards. For the third condition, an initially short bar passing well to one side of the field centre, was extended gradually to form a very long bar crossing the whole receptive field. For each condition the bar was presented at the optimal orientation and the total number of spikes as the bar traversed the field was counted.

No obvious asymmetries in the strengths or the sizes of the flanks on each side were apparent (c.f. Hammond and Andrews, 1978b). Although the initial segment of the length response tuning curve often rose linearly up to the boundary of the receptive field centre, summation was strictly linear only if the cell was type PS. For type RS cells, the responses to a stimulus covering the whole central region were less, and for the type US cells greater, than the sum of
responses to shorter bars. Summation of the centre and flank components must also be non-linear because facilitatory flanks do not (by definition) drive the cell when stimulated alone nor do inhibiting flanks suppress firing when they are stimulated in isolation.

Hammond and Andrews, in a series of papers (Hammond and Andrews, 1978a, b, c) produced an extensive study of the effect of stimulus length on response magnitude and tuning. Though their data were drawn from recordings in area 18, their results provide interesting observations on how the component parts of a receptive field may interact. The extent to which these authors' observations are specific to that area or whether the properties reported are descriptive of simple and/or complex cells of striate cortex requires a replication of their experiments in area 17. With these considerations in mind, their studies are described with an emphasis on the possibilities they raise for complexities of receptive field organization.

Hammond and Andrews (1978c) found that, for area 18 cells, interaction within receptive field halves could be facilitatory, additive, partially additive, or subtractive and that the organization within one half was not predictable from that in the other. Moreover, interactions between halves could be facilitatory, additive, partially additive, or subtractive and could not be predicted from interaction within halves. Hammond and Andrews argued for a (minimal) division of the receptive field into halves, with summation between halves differing from that within each half-field.
Hammond and Andreas (1978a) considered the half-field in terms of its orientation tuning properties. Some area 18 cells were found to have dissimilar preferred orientations for each receptive field half. In cells whose receptive field halves were similarly tuned, broadly tuned, or apparently untuned for orientation, simultaneous stimulation of both halves of the receptive field led to substantial sharpening of tuning.

Collating the data from length-response, orientation and symmetry of tuning studies, Hammond and Andrews (1978c) observed that the zones which make up the receptive field interact in a complex way. To produce the length summation data it is necessary to involve summation of signals within each half field (partial, complete, or subtractive if inhibition is present, and with differences between each half-field) and, secondly, there is an interaction between the two half-field signals (summative, partially summative, facilitatory or inhibitory). To account for the orientation tuning results, a third summative principle would be required and it was suggested that different inhibitory bands facilitate one another, the degree of facilitation varying between cells. In addition, Hammond and Andrews commented that the zones of the half-fields must differ in some way, causing asymmetrical tuning and dissimilar tuning for the two halves, though they pointed out these differences may be of geometry rather than summative principle.
3.4 The Tuning of Complex Cells for Contrast and Textured Stimuli

For the majority of complex cells, the preferred directions for moving contrast bars and fields of visual noise are different (Hammond and MacKay, 1977; Hammond, 1978; Hammond and Reck, 1980a, b). Hammond (1978) found that the majority (fifty-two) of his sample of sixty-two neurones showed significant differences in preferred directions for bar and noise. The average difference in tuning peaks for bar and texture reported by Hammond (1978) was 30-40 deg. Greater peak separation was reported for complex cells of the infragranular layers (Hammond and MacKay, 1977; Hammond, 1978), that is those more responsive to visual noise (Hammond and MacKay, 1977; Hammond, 1978; Hammond and Reck, 1980a, b). Tuning for bars was found to be sharper than for noise, as would be expected, since orientation tuning is well known to depend on contour length (Henry, Bishop and Dreher, 1974; Gilbert, 1977; Hammond and Andrews, 1978b). For cells asymmetrically tuned for bar stimuli, tuning has been reported to be broader on the flank of the tuning curve closest to the preferred direction for noise (Hammond, 1978).

According to Hammond (1978), compared with a moving bar stimulus, moving noise fields enhance complex cell directional bias; cells directionally biased for a bar may be directionally selective for noise. Two thirds of a sample of forty-nine neurones directionally biased for bars were directionally selective for noise, ten of these showing suppression of firing to noise moving in the null direction.
A further twenty-three cells were directionally selective for bar stimuli and noise, nine with suppression of firing in the null direction.

The tuning curve for texture takes two forms; a single peak in the tuning curve (unimodal cells) or a bimodal tuning with depression of response around the peak in the bar tuning curve (bimodal cells) (Hammond, 1978; Hammond and Reck, 1980a, b). Peaks of the noise tuning curve for bimodal cells may be symmetrically or asymmetrically located about the peak for bar tuning (Hammond, 1978). Preferred velocity and velocity bandpass are invariably higher for texture motion than bar motion. Texture tuning profiles are typically unimodal at low velocities and increasingly bimodal at higher velocities (Hammond and Reck, 1980a, b), whereas bar tuning is essentially velocity invariant (Hammond, 1978; Hammond and Reck, 1980b).

3.5 Tuning for Contrast and Textured Stimuli and Models

In response to moving contrast bars, the tuning curve of simple cells is generally sharper than that of complex cells. The length-response function is essentially non-linear, reflecting complex interactions within and between half-fields. The assumptions of Bishop's group (Bishop, Coombs and Henry, 1971b; Goodwin and Henry, 1975) and Schiller, Finlay and Volman (1976b, e), that a bar is a linear sum of component spots is unsupported (Bodis-Wollner, Pollen and Ronner, 1976; Rose, 1977; Hammond and Andrews, 1978c).
Tuning shown by simple cells for stationary and moving bars is identical. Moreover, the preferred direction for a moving spot is orthogonal to the cell's preferred orientation. These findings are in accord with Bishop's model. Since, however, the data were based on cells showing symmetrical tuning for moving bars the support given by the data to the model is limited. Asymmetrically tuned units are problematical for Bishop's model. Given the primary role of the inhibitory sidebands in determining orientation tuning (Henry and Bishop, 1972; Henry, Dreher and Bishop, 1974), asymmetric tuning would reflect the asymmetric location of one sideband in relation to the central discharge zone. The principle of a fixed spatial relationship between intracortical inhibition and afferent excitation would therefore be denied. It has previously been argued both that inhibition outside the discharge zone has no separate role in orientation tuning and that intracortical inhibition has no fixed spatial relationship to the afferent input.

It was suggested that the tuning properties of simple cells might be accounted for by reference to the model of Goodwin, Henry and Bishop (1975) for direction selectivity. This would also predict that tuning for moving and stationary bars would be identical. For a cell asymmetrically tuned for a moving bar, this would imply that the spatial organization of the receptive field, determined when the sensitivity profile is mapped with a stationary flashed bar, would show an asymmetry. Preferred direction for a spot would also be predictable from the response to a stationary edge. The data from Henry, Bishop and Dreher's study (1974) and Goodwin and
Henry's (1975) paper are inadequate to test these predictions.

Complications arise when the complex cell is considered. The direction-selective response produced by a moving field of noise demonstrates that the luminance increment caused by a stationary edge is neither the sufficient nor the necessary condition for a direction selective response for that cell type. To date no study has been made of the parameters contributing to direction-specific inhibition for contrast and textured stimuli.

The origin of the bimodal tuning for moving noise fields has provoked much discussion (Hammond, 1978; Hammond and Reck, 1980b; Hammond and Smith, 1983). The possibility that it is artefactual has been raised by Movshon (cited by Hammond and Smith, 1983), who suggests that the bimodality represents the response to the vector of velocity in the cell's preferred direction. Several arguments weigh against this possibility. Some cells remain unimodal at velocities of motion beyond the high velocity cut-off point for an oriented stimulus (Hammond and Smith, 1983) and other cells are bimodal at velocities beyond that producing response to a moving bar and at velocities below that optimal for texture (Hammond and Smith, 1983). The two lobes for texture tuning at higher velocities of motion are often asymmetrical and differ in width and strength (Hammond, 1978; Hammond and Reck, 1980b; Hammond and Smith, 1983). The trough in the texture field tuning curve corresponds to the bar tuning peak, but can persist at velocities beyond the cut-off point for producing a bar response (Hammond and Smith, 1983). Depression of texture
sensitivity is greatest at high velocities when response is driven below the cell's resting discharge level (Hammond and Rock, 1980b).

Hammond (Hammond, 1978; Hammond and Rock, 1980b; Hammond and Smith, 1983) sought to explain the bimodality in the texture field tuning curve as a product of the directional mechanism alone or from an interaction between orientation and direction mechanisms. Two possibilities for the direction mechanism alone were suggested: that the depression of response might arise as a result of self-inhibitory feedback preventing cell overload, or through inhibitory convergence from neighbouring cells. In the latter case, inhibitory input from cells in the same or different laminae, with similar preferred directions would cause depression of response. Excitation would be maximal for directions to either side of that preferred by the cell. The suggestion is similar to that proposed by Sillito (1979) for the orientation domain with inhibitory contributions to orientation selectivity being greatest not at the preferred orientation but to either side of the preferred orientation.

Hammond (1978) has noted that it would be difficult to account for the depressed sensitivity in texture tuning of bimodally-tuned cells in the vicinity of the peak in bar tuning without invoking some interaction between direction and orientation mechanisms. There is direct evidence of such an interaction. Hammond (1981a) and Hammond and Smith (1983) reported the response of complex cells to in-phase motion of bar and texture over a range of velocities of stimulus
movement. At higher velocities the directional tuning profile for bar and texture was found to be comparable to the addition of the direction tuning profiles for each stimulus alone. As stimulus velocity was reduced, however, the tuning profile for simultaneous motion of bar and texture was found to increasingly resemble that for the bar alone. The interpretation was that a cell's responsiveness to texture backgrounds is vetoed by a simultaneous signal arriving at its bar-sensitive input. A problem for the interpretation that depression of texture tuning reflects an interaction between orientation and direction mechanisms is that, as reported by Hammond and Reck (1980b), the trough may be more pronounced above the optimal velocity for bar and broader than the total width of the bar tuning curve.

To date, little quantitative data have been available to assess the contributions of orientation and direction to the tuning properties of complex cells for contrast stimuli. Furthermore, complexities indicated by studies of tuning for textured stimuli suggest differences of receptive field structure which cannot be accounted for by models developed to explain the simple cell's response to contrast stimuli. A combination of contrast and textured stimuli has therefore been used to assess the tuning properties and receptive field structure of complex cells in cat striate cortex.
Introduction

Orientation selectivity has classically been assessed with moving contrast bars (Hubel and Wiesel, 1962, 1963; Henry, Dreher and Bishop, 1974) and orientation has not been dissociated from direction. For a moving bar, direction is necessarily orthogonal to orientation (Henry, Bishop and Dreher, 1974). Comparisons of tuning for bars and moving fields of visual noise indicate the mediation of orientation and direction by separate mechanisms (Hammond, 1978 and subsequently). Though some consideration has been given to the contributions of orientation and direction to the simple cell's response, using contrast stimuli (Henry, Bishop and Dreher, 1974), corresponding data for the complex cell are scant. Moving fields of visual noise overcome the summatory requirements for effective drive of many cortical neurones and at the same time provide a stimulus free from inherent orientation. A combination of contrast and textured stimuli have therefore been used to assess the contributions of orientation and direction to the complex cell's response.

It is of interest, not only from the perspective of receptive field organization, but also for an understanding of their functional role in visual analysis, to investigate complex cells' tuning properties. In Hubel and Wiesel's model, the single cell was given a role in contour analysis in a hierarchical process of feature extraction. Representation
of form at the level of the single cell has been questioned (see chapter 5 for discussion). To fulfil a universal role in contour analysis cortical cells should respond selectively not only to contours of luminance but also, for example, contours of colour or texture. Discontinuities of texture density, as Hammond and MacKay (1977) have pointed out, even without any change in mean luminance, can outline a contour as unmistakably as those of colour or luminance. Even with uniform texture, discontinuities of texture velocity, such as "texture contours" produced when a camouflaged animal moves against a stationary background, can reveal the outline of an otherwise undetectable object. The stimulus provided by a bar of texture moving across a field of similar texture and equal mean luminance is of interest in this context since, though camouflaged when at rest, in motion both its form and motion are perceived. A comparison of tuning for this stimulus with stimuli in which the attributes of either form or motion are present would contribute to the understanding of the role of the single cell in perception.

Consideration was therefore given to the tuning properties of complex cells to contrast and textured stimuli in which the parameters of orientation and direction were dissociated. Three specific objectives were set.

(1) To evaluate tuning for a stationary flashed contrast bar and the same bar in motion.

(2) To compare these results with tuning for a spot moving through the geometric centre of the receptive field and tuning for a moving field of visual noise, to assess the contributions from orientation and direction selective
mechanisms.

(3) To evaluate tuning for a texture bar moving across a field of visual noise of similar texture and equal mean luminance, to determine whether tuning is biased towards tuning for a contrast bar or whether, in the absence of luminance cues, cells are sensitive only to texture bar motion.

4.1 Animal Preparation

The semi-chronic preparation (Hammond, 1979) was used for the experiments. Attached to the skull were a stainless-steel peg and a perspex chamber, the former providing an atraumatic head restraint during recording sessions and the latter a means of access to the visual cortex. Figure 4.1 shows the semi-chronic preparation used for the experiments (after Hammond, 1979). To ensure accurate stereotaxis, an individually adjusted bridge retained the animal’s head in standard stereotaxic co-ordinates by anchoring the peg. The perspex chamber was centred over the sagittal suture with anterior/posterior co-ordinates for the mid-point of the chamber close to P5. The chamber was marked during implantation with four grooves, the stereotaxic co-ordinates of which were established in order to provide reference points for the location of electrodes during recording sessions.

Implantation of peg and chamber was carried out under surgical anaesthesia provided by a mixture of 2% halothane with 72.5% nitrous oxide : 27.5% oxygen. A midline incision of the scalp was made and, following disinsertion and retraction of the temporalis muscles, the chamber and peg were
A Semi-chronic Preparation for Cortical Recording

The figure illustrates the preparation used for recordings from the striate cortex. Attached to the skull are a stainless-steel peg and a perspex chamber. By means of the peg, in conjunction with an individually adjusted bridge, the animal's head is held atraumatically with accurate stereotaxis. The perspex chamber provides access to the striate cortex and additionally serves to provide reference points for stereotaxic location of electrodes. (Reference points are grooves on the top of the chamber). Fixed in the wall of the chamber are sockets for terminals for connection of leads for monitoring the EEG. The insert shows the location of the peg and chamber.
fixed to the skull with dental acrylic and anchored to the skull by means of six stainless steel screws. Two of these screws additionally functioned as terminals for EEG monitoring: one located over the primary auditory cortex and the other over extra-striate visual cortex. Teflon-insulated wires lead from these terminals to gold-plated pins, fixed in the chamber wall, to which wires were connected during recording sessions for EEG monitoring. Following implantation, the scalp was sutured around the implant with Michel clips and the wound margins protected by overlapping flanges on the peg and chamber. Topical application of Xylocaine spray (Astra) provided local anaesthesia of the wound during the recovery period and localised application of Cicatrin powder (Wellcome), together with intramuscular procaine penicillin (30 mg/kg), before and after implantation, and during the recovery period, ensured infection-free recovery. Suture clips were removed 10-14 days after implantation.

4.2 Recording Sessions

Animals were used for recording sessions of approximately nine hours including preparation and reversal periods. A minimum space of two clear days between recording sessions was standard practice, with an individual animal being used no more than three times in any two week period. Anaesthesia was induced with a mixture of halothane (Fluothane, ICI) initially 3% rising to 5%, with 72.5% nitrous oxide: 27.5% oxygen. Single-cell recordings were made under light anaesthesia maintained with the same composition of nitrous oxide/ oxygen
supplemented with 0.3-0.7% halothane. Ventilation was via a
McGill cuffed endotracheal tube (3.0-4.5mm) inserted after
coating with the local anaesthetic gel Xylocaine (Astra).
Ventilation rate and stroke volume were under the control of a
Palmer ("Ideal") pump. Ventilation rate was set at 28
strokes/min. The stroke volume was adjusted to maintain an
end-tidal carbon dioxide percentage of between 3.8-4.0%.
End-tidal carbon dioxide was monitored, breath by breath, by
an infrared medical gas analyser (Beckman, LB2) and registered
for the duration of the experiments on a Washington 400 MD/2
pen recorder.

Care was taken with this lightly anaesthetized
preparation to maintain an adequate level of anaesthesia by
constant reference to the various indices of anaesthetic
level, principally the EEG but additionally the ECG, pulse
rate, end-tidal carbon dioxide, temperature, and firing rate
of recorded units. The EEG was constantly monitored and an
adequate depth of anaesthesia ensured by reference to the
presence of spindles in the EEG and amplitude of the EEG.
Heart rate was observed to maintain a norm of three beats per
second. Permanent records were kept of the carbon dioxide
levels, EEG, heart rate and spike firing rates. The
temperature of the animal was maintained by a homoeothermic
blanket control (type 8185, CF Palmer) with body temperature
monitored by a rectal thermistor introduced with a lubricant
gel. Body temperature was maintained at 38.75 deg.
centigrade.

Eye preparation and paralysis were conventional.
Phenylephrine hydrochloride (10%) and atropine methanitrite (1%) (Minims, Smith and Nephew) were used to retract the lids and nictitating membranes and to dilate the pupils. The corneas were protected with neutral contact lenses (two-curve lenses, Hamblin). The contact lenses were applied with sulphacetamide (10%) (Minims, Smith and Nephew Ltd.) and the wetting agent Transol (Smith and Nephew, Ltd.) was applied to the exposed surfaces of the eyes not covered by the lenses. The lenses had base/peripheral curves of either 8.0/8.5 or 8.5/9.0 mm., both with base/peripheral diameter 8.0/12.0 mm. according to the relation:

\[ Y = 7.28 + 0.34X \]

derived by Andrews and Hammond (1970), relating the corneal radius of curvature (Y mm) and body weight (X kg), and based on the data of Bishop, Kozak and Vakkur (1962) and Vakkur, Bishop and Kozak (1969). Artificial pupils, 5mm. in diameter, were mounted in front of the contact lenses by flexible frames attached to the bridge.

The refractive correction required to focus the eyes at a distance of 57 cm. on the screen of a Hewlett-Packard display, on which stimuli were presented, was determined by slit-rinoscopy. At that distance, one centimetre on the screen was equivalent to one degree of visual angle. Supplementary lenses (range -3.0 to +4.5 dioptres) in steps of 0.25 dioptres were used to provide the appropriate optical correction where required. Using the back projection method of Fernald and Chase (1971), the position of the area
centrales of each eye was marked on a perspex screen in front of the Hewlett-Packard display unit. Receptive field positions were located with reference to these positions. Paralysis of the eyes was achieved by an initial dose of 0.5ml gallamine triethiodide (Flaxedil, May and Baker, 40 mg/ml) with a subsequent infusion of 7-10 mg/kg/hr via a Butterfly cannula (23G or 25G, Abbott) inserted in the left cephalic vein.

A standard procedure for recovery from paralysis and anaesthesia was followed. Infusion of Flaxedil was terminated approximately one and a half hours before the end of the recording session and excess remaining in the cannula was flushed through with sterile saline. On completion of the recording session, procaine penicillin (30 mg/kg) was administered intramuscularly. Atropine sulphate (0.1 ml at 0.06 mg/ml), to prevent spasm, and neostigmine methylsulphate (typically 0.2 mg. at 0.5 mg/ml) to antagonize any residual non-metabolised Flaxedil were given via the cannula. The exact amount of neostigmine administered was titrated against the animal's recovery of spontaneous breathing which was frequently tested during the recovery period. The craniotomy was cleaned, treated with Cicatrin powder and capped. After removal of the contact lenses, the eyes were irrigated with sulphacetamide (10%) (Minims, Smith and Nephew Ltd) and wetting agent (Transol, Smith and Nephew) was applied.
4.3 Equipment for the Generation of Visual Stimuli

The apparatus described in MacKay and Yates (1975) and Hammond and MacKay (1977) was used to generate visual stimuli. A square raster of 256 lines, each of 256 elements was modulated by a special purpose generator using digital integrated circuits to present up to 50 picture frames per second. Two independent 16-stage fed back shift registers made available two pseudorandom pulse trains NA and NB each of which could be reset and locked in phase from one frame to the next so as to give a static noise texture. The noise field subtended a ten by ten degree square. The phases of NA and NB could also be manually adjusted to control against the possibility that accidental features of a particular noise field might be responsible for specific response peaks. Grain sizes of the noise fields averaged 4 min of arc. An electronic changeover switch, driven by a gating circuit, defined a moveable rectangular window of the raster which could be painted by NA, NB or a steady black or white signal at will. Where contrast stimuli formed the window - spots or bars of various dimensions - relative luminance levels were set at 0.6 log units below noise background (black bar) or 0.25 log units above the noise background (white). Mid-mesopic levels of illumination were used with average screen luminance of around 0.9 log cd/m sq. in conjunction with 5mm diameter artificial pupils (Ahmed, Hammond and Nothdurft, 1977). A conventional sine-cosine potentiometer circuit (MacKay and Fisher, 1962) allowed calibrated rotation of the XY plane. Contrast stimuli could be moved relative to a stationary background of static noise or flashed with the
noise as background, the contrast bar replacing the noise field in that rectangle. Alternatively, a noise bar could be moved relative to the noise background or the noise field could be moved in isolation.

### 4.4 Cell Recordings

Extracellular recordings were made with glass pipettes filled with 4M sodium chloride with tip sizes averaging 2 microns with impedance values of between 0.65 and 1.3 Meg Ohms at calibration and up to 2 Meg Ohms in the cortex. Electrodes were introduced into the cortex via a dural puncture made with a sterile syringe needle (no. 12; 0.7 x 32mm) fixed by an adaptor to a microdrive mounted on a micro-manipulator. Stereotaxic positioning of the electrode was achieved by reference to the marks made on the chamber as previously described. Electrodes were located at stereotaxic co-ordinates between 1.5 and 1.7mm of the midline and between 4.0 and 6.0 mm behind the interaural plane. On insertion of the electrode, the cortex was stabilized by sealing in the electrode with warm 2% sterile agar in 0.9% saline, filling the chamber with solution. Cell search was accomplished by fine vertical movements under the control of an hydraulic microdrive.

### 4.5 Recording Equipment

Spike amplification and discrimination were conventional with raw spikes displayed on a dual-beam oscilloscope (Tektronix RM 565) and monitored by an audio-monitor.
Fig 4.2

Dot display for registering spikes during recording of tuning curves (after Hammond 1981a, Fig. 2).

The response to a forward and backward sweep of each pair of stimuli is represented by a single row of the display. Between each row, direction has been stepped by 10 deg. Direction of motion is specified from 0 to 350 deg. measured clockwise from vertically upward motion. The complete display is made up from four round-the-clock sequences. Each of these sequences consists of data from eighteen pairs of directions; two blocks of nine followed by two complete cycles with only the stationary noise background present. The stimulus cycle at the foot of the diagram allows it to be related to fig. 4.3.
Discrimination was provided by a level and window discriminator. Discriminated spikes were displayed as:
1. spike rate on a linearized pen recorder (Washington, 400 MD/2);
2. a dot display on a single beam storage oscilloscope (Tektronix, 3111) with each dot representing a discriminated spike (see fig 4.2 and accompanying explanation);
3. an averaged response histogram by means of a Biomac 1000 data retrieval computer (Data Labs);
4. individual counts by electronic counters (Advance, TC 11A) for gated periods of the stimulus cycle. The counters could be reset between cycles or could be used to provide cumulative counts.

Data were stored for off-line analysis on cassette tapes used in conjunction with a Bell and Howell (CR 3000) four-channel, AM/FM tape-recorder. Dot displays were stored on polaroid photographs. Tuning curves, obtained by the method of Hammond (1978) and Hammond and Reck (1980a, b), described below, were produced on an analogue (Bryans, 29000) XY plotter from the output of the Biomac in the four-channel mode.

4.6 Determination of Direction and Orientation Tuning-Curves

A modified version of the multihistogram method of Henry, Tupper and Dreher (1973) was used. The method was developed by Hammond (Hammond, 1978, 1981a; Hammond and Reck 1980a, b). The stimulus cycle was of six seconds duration and initiated by a synchronization pulse. In the first two seconds the
field of texture moved in one direction followed by its opposite. During the third second of the cycle, the texture-field remained stationary and a stationary contrast bar was presented with the noise field as background. The bar replaced the noise as a moveable rectangular window and was defined by a changeover switch driven by a gating circuit. Alternation between the noise and bar was provided by a reed relay. During the fourth and fifth seconds the bar was moved in the directions previously traversed by the noise field. During the sixth second, the direction/orientation of the stimulus was stepped by ten degrees i.e. during the one second pause before the onset of texture-field motion. Direction was stepped clockwise.

For the generation of tuning curves for stationary, flashed contrast bars, the texture-field remained stationary for the complete six-second cycle. In the early experiments, a black or white bar was flashed for a period of one second during the fourth second of the stimulus cycle. When stationary bars were presented under conditions of contrast reversal, a white bar was presented during the first to third seconds of the cycle. For the duration of the fourth second, contrast was reversed, the white bar becoming a black bar. For the fifth second, contrast was reversed again and a white bar presented.

A total of eighteen sweeps provided the data for tuning curves in paired comparisons between texture-field motion and a contrast stimulus or texture bar. Two additional cycles, during which only a stationary texture-field was presented,
provided a measure of the cell's resting discharge level. The sequence of eighteen sweeps was taken in two blocks of nine for reasons of convenience. Tuning curves were produced on an analogue XY plotter (Bryans, 29000) in conjunction with a Biomac 1000 (Data Labs). The discriminated pulses were fed into the Biomac for accumulation in sequential bins, in a single channel mode, during the first, second, fourth and fifth seconds. Bin advance was controlled externally by pulses arriving 1, 2, 4 and 5 seconds after the start of each cycle. Data for the first stimulus were thus entered into bins 1, 5, 9 ... 77 (forward texture motion) and 2, 6, 10 ... 78 (backward texture motion); those for the second stimulus into bins 3, 7, 11 ... 79 (forward bar motion) and 4, 8, 12 ... 80 (backward bar motion) respectively. Four round-the-clock sequences formed the total data collection cycle. Tuning curves were derived by outputting the single-channel stored data through four channels, each channel containing half a tuning curve for a particular stimulus. In addition to the sets of tuning curves with simultaneously recorded measures of resting discharge, a calibration signal (200 Hz) was added after the final round-the-clock sequence, providing a standard for evaluation of spike firing in the tuning curves (bins 81-88, i.e. 2 bins per channel, corresponding to an impulse firing rate of 50/sec. in the case of 4 complete sequences). The method is illustrated in fig 4.3.
Fig 4.3  
Illustrating data accumulation for determination of tuning curves (after Hammond, 1981a).

The stimulus cycle was initiated by a synchronization pulse. Discriminated spikes were fed into the Biomac for accumulation in sequential bins in a single channel mode. Data for texture motion were entered into bins 1, 5, 9 .. 77 (forward motion) and 2, 6, 10 .. 78 (backward motion) and those for the second stimulus into bins 3, 7, 11 .. 79 (forward motion) and 4, 8, 12 .. 80 (backward motion). Data were collected from four round-the-clock sequences. Tuning curves were derived by outputting the single-channel stored data through four channels, each channel containing half a tuning curve for a particular stimulus.
4.7 Experimental Strategy

Cell search was carried out using combined presentation of bar and texture-field moving in phase. Cells were classified as complex by the absence of a division of the receptive field into discrete on and off areas (Hubel and Wiesel, 1962, 1963), into "Standard" and "Special" complex by the criteria of Gilbert (1977) and "Standard" complex cells were further classified as B cells by the criteria of Henry, Lund and Harvey (1978). Ocular dominance was assessed and the non-dominant eye occluded. Receptive fields were plotted as "minimum response fields" (Barlow, Blakemore and Pettigrew, 1967). Stimulus parameters were then optimized for the dominant eye. End-inhibition was tested by reference to the length-response curve; cells showing a significant reduction of response when length was increased beyond an optimal value were classified as showing end-inhibition. Quantitative descriptions are made for cells which did not exhibit end-inhibition so-defined. Three cells with end-inhibition were recorded for which qualitative observations are made.

Paired comparisons of tuning were made for the following stimulus combinations:

1. Moving field of visual noise versus moving contrast bar;
2. Moving field of visual noise versus moving contrast spot;
3. Moving field of visual noise versus moving texture bar;
4. Stationary noise field with black and white bars flashed.

Tuning for the moving spot was made with the spot moving through the geometric centre of the minimum response field.
In the stationary bar condition, the bar was rotated symmetrically about the geometric centre of the field and the moving bar was moved symmetrically through the receptive field, taking the geometric centre as reference point. Tuning curves were obtained in pairs with the stimuli being interleaved during recording of responses for each direction of motion in round-the-clock sequences. One member of the pair, a moving texture-field, remained constant. Keeping one member of the pair of stimuli constant, when a complete range of stimuli was used, allowed any time-dependent changes in responsiveness to be monitored. In order to prevent differences in responsiveness during the course of the experiment biasing results, stimulus order was randomized and repeated measures were made from time to time during the course of experiments. The texture sample was routinely changed and for evaluation of tuning for texture bars, tuning curves for each cell were obtained for two samples of visual noise.

4.8 RESULTS

Data were obtained from eighty well-discriminated units from a total of 9 cats. Of these, three units showed end-inhibition and are not included in the quantitative description of data. The remaining seventy-seven units included twenty-six standard complex and twenty special complex cells; thirteen standard complex cells showing a single peak for texture field tuning (unimodal standard cells) and thirteen standard complex cells showing a double peak for texture tuning (bimodal standard complex cells), thirteen
unimodal special complex cells and seven bimodal special complex cells. One B cell was recorded and found to show tuning properties identical to other standard complex cells with which it is included. An additional thirty-one complex cells, not classified into standard and special complex cells, provided data for some of the stimulus conditions; moving contrast bar or spot, moving texture-bar or stationary bar. Twenty-nine of these units were unimodal and two bimodal in their texture-field response. All units had receptive fields within ten degrees of the area centralis.

The original observations of Hammond and MacKay, (1977), Hammond, (1978) and Hammond and Rack, (1980a, b) were confirmed. Only complex cells showed a response to moving texture fields and texture bars; seven simple cells tested with these stimuli showed no significant response. The texture field response was velocity-dependent and took unimodal or bimodal forms. Ocular dominance differences between bar and texture were frequently observed, though ocular dominance differences were not pursued in the present study. Comparison of tuning for bar and texture fields in motion revealed differences in peak position for the two stimuli with depression of texture sensitivity associated with the peak in bar tuning. For units showing a unimodal texture-field response, mean peak separation was found to be 32.9 degrees. By reference to lamina IV small field, monocular simple cells, the distribution of complex cells between the supragranular and infragranular layers was assessed. Of the 77 cells, 21 (27%) were located in the supragranular layers and 56 (73%) in the infragranular layers.
4.8(a) Comparison of Tuning for Moving and Stationary Bars

Measurements were made of peak, tuning width and symmetry of tuning for moving and stationary bars and determined with linear regression lines fitted to the two flanks of the tuning curve. The peak was defined by the intersection of the regression lines, and breadth of tuning by the full and half-width at half height, allowing for resting discharge. Symmetry was defined by the ratio of the greater to the lesser half-width.

Following the convention of Hammond (1978), the term direction replaces the term axis used in Henry, Dreher and Bishop’s (1974) study. Direction sensitivity is a vector of response magnitude in any specified direction between 0 deg to 360 deg (measured clockwise from vertically upward motion and, for convenience, a bar stimulus is specified by its direction of motion, orientation orthogonal to direction, rather than its orientation per se). For easy comparison of tuning for a stationary with a moving contrast bar, stationary bars are defined with reference to the direction taken for the same bar in motion. For example, a vertically oriented bar has the value 90 deg, corresponding to the direction in which bar movement would take place.

Data for assessment of symmetry of tuning were available for a total of 77 units. Fifty-five were unimodally tuned for texture of which the majority were asymmetrically tuned for bar motion, the wider flank adjacent to the tuning curve for texture field motion (c.f. Hammond, 1978). One unit,
unimodal in texture-field tuning, had the broader flank not adjacent to the texture-field tuning curve and, to maintain overall consistency in the presentation of data, this unit's symmetry of tuning is defined by the ratio of the half-widths with the flank adjacent to the texture-field as the numerator. This unit (176/2) therefore is identified by a symmetry ratio of less than one (0.9). This unit was unresponsive to a flashed bar. Excluding this unit, asymmetry ranged from 1.1 to 2.9, exceptionally 3.2 with a mean value of 1.6 (data summary table 1). Units bimodally-tuned for texture (twenty-two) were either symmetrically or asymmetrically tuned for moving bar, as Hammond (1978) has also reported. Those units asymmetrically tuned for bar motion were characterized by one peak of the texture tuning curve being more prominent. Conversely, cells symmetrically tuned had texture-field tuning with the two peaks equally prominent. The values for symmetry of tuning for the bimodal cells ranged from 1.0 to 1.6, exceptionally 2.6 with a mean of 1.3 (data summary table 2).

4.8(b) Tuning for Moving Contrast Bars as a Function of Deviation of a Cell's Preferred Orientation from the Principal Meridians

In order to assess whether, in the population of cells sampled, there was a non-uniformity in the proportion of complex cells representing horizontal/vertical or oblique orientations and whether tuning for a moving bar is related to the deviation of a cell's preferred orientation from the principal meridians, breadth and symmetry of tuning as a function of preferred orientation was evaluated. In figure
4.4, the distribution of preferred orientations, as a function of deviation from the principal meridians, for the population of seventy-seven cells, is shown. Whilst there is not an exact equivalence in numbers of cells representing each range of orientations, there is no evidence from the histogram of an overrepresentation of cells tuned to the principal meridians or oblique orientations.

In figures 4.5 and 4.6, breadth and symmetry of tuning for a moving bar are plotted as a function of deviation of a cell's preferred orientation from the principal meridians. As can be seen from fig. 4.5, there is a wide scatter in breadth of tuning for most orientations. Though the two most broadly-tuned units have preferred orientations which are oblique, and cells with preferred orientations close to the principal meridians are amongst the most sharply tuned, there is no indication that breadth of tuning shows a linear increase as a function of deviation of a cell's preferred orientation from the principal meridians. Examples can be found, at most orientations, of cells whose breadth of tuning is within the range shown for cells close to the principal meridians.

Fig. 4.6 shows symmetry of tuning as a function of the deviation of a cell's preferred orientation from the principal meridians. For the great majority of cells, the ratio of half-widths, at all orientations, falls within the range of 1.0 to 2.0 and the distribution of symmetry values, at all orientations, is similar.
Fig. 4.4

Distribution of Cells' Preferred Orientations in Relation to the Principal Meridians.

The histogram shows the distribution of cells' preferred orientations. The cells' preferred orientations have been calculated by fitting two regression lines to the flanks of the cells' tuning curves and determining the intercept values. The deviation of the preferred orientations from the vertical and horizontal meridians has then been calculated and the distribution for the total population of cells has been constructed.
DEVIATION OF CELL'S PREFERRED ORIENTATION FROM
THE PRINCIPAL MERIDIANS [DEG.]
The graph has been constructed to assess whether breadth of tuning for a moving contrast bar is related to a cell's preferred orientation. Breadth of tuning is defined by the total width of the tuning curve at half-height. Breadth of tuning has then been plotted as a function of the deviation of the cell's preferred orientation from the principal meridians.
TOTAL TUNING WIDTH AT HALF HEIGHT [DEG]

DEVIATION OF CELL'S PREFERRED ORIENTATION FROM THE PRINCIPAL MERIDIANS [DEG]
Fig. 4.6

Graph of Symmetry of Tuning for a Moving Contrast Bar as a Function of a Cell's Preferred Orientation in Relation to the Principal Meridians.

The graph has been constructed to assess whether symmetry of tuning for a moving contrast bar is related to a cell's preferred orientation. Symmetry of tuning is defined by the ratio of the half-widths at half-height of the tuning curves following the fitting of regression lines to the flanks. Symmetry of tuning has then been plotted as a function of the deviation of the cell's preferred orientation from the vertical and horizontal meridians.
DEVIATION OF CELL'S PREFERRED ORIENTATION FROM THE PRINCIPAL MERIDIANS [deg.]

RATIO OF HALF-HEIGHTS AT HALF-HEIGHT
In summary, for the population of complex cells sampled, there is no evidence of an overrepresentation of cells with oblique or horizontal/vertical preferred orientations, nor is there a trend for breadth or asymmetry of tuning for a moving bar to increase as a function of the deviation of a cell's preferred orientation from the principal meridians.

A.8(c) A Comparison of Tuning for Stationary and Moving Contrast Bars

Assessment of tuning for stationary and moving contrast bars was made on a total of 36 cells. Of the thirty-six units 27 gave adequate responses to allow comparison of response for the two stimuli: 17 unimodal units (9 standard, 8 special complex), and 10 bimodal units (9 standard, one special). Units unresponsive to bar flash were distributed amongst both standard and special complex cell groups (4 standard, 5 special). In agreement with previous studies of the simple cell (Henry, Dreher and Bishop, 1974), peak positions in tuning for stationary and moving contrast bars for the majority of complex cells were found to coincide (23/27 units). Similarity of tuning for opposite contrasts of polarity of moving bars was also found for 4 cells tested.

Comparison of breadth of tuning for cells responsive or unresponsive to a stationary flashed bar revealed the former to be more sharply tuned for a moving bar. For the units responsive to a bar flash, the mean breadth of tuning (total width of the tuning curve at half-height) was 49.4 deg. with a range of 26 to 96 deg. The corresponding values for the
cells unresponsive to bar flash were; mean 75.1 deg. with a range of 54 to 113 deg. Comparing the two groups in terms of symmetry of tuning, cells unresponsive to bar flash had a mean symmetry of 1.6 with a range of 1.0 to 2.3. The unit with the broader flank not adjacent to the texture-field tuning curve (176/2), with a symmetry ratio of 0.9, was also a cell unresponsive to bar flash. Cells responding to bar flash had a mean symmetry of 1.5 with a range of 1.0 to 3.2.

Tuning for stationary bars for cells unimodal in their tuning for texture field motion, was consistently sharper than for the same bar in motion (data summary table 3) with a mean difference in total tuning width of 21.4 deg. with a range of 1 to 37. Similarly, for cells showing a bimodal texture response and with asymmetrical bar tuning curves, the same bar presented stationary and flashed produced a sharper and more symmetrical tuning curve. For those cells symmetrical in their tuning for moving bars the corresponding tuning curve for the stationary bar was very similar to that for the moving bar. For the eight standard complex cells with bimodal texture-field tuning showing a response to a stationary flashed bar, the mean difference in the total tuning width between the tuning curves for stationary and moving bars was 9.6, with a range from 0 to 14 deg. The difference in tuning width for the special complex cell showing a bimodal texture-field response was 9 deg. The results for the population of bimodal cells is given in table 4. Expressed as ratios of half-widths, the mean value for symmetry of tuning for stationary bars for the total population of unimodal and bimodal cells was 1.1 (27 units). Comparisons of tuning for
stationary and moving bars for cells unimodal or bimodal in texture-field tuning are illustrated in figs. 4.7-4.10.

4.6(d) Invariance of Tuning for Moving Contrast Bars

Interactions between figure (bar) and ground (texture-field) would clearly bias results. To reduce the possibility of interactions between bar and texture-field, the sample of texture was frequently changed during all experiments and repeated measures of bar tuning against different samples of texture made. Invariance of bar tuning against different samples of texture and over time is illustrated in fig. 4.11. Moving texture-field responses are illustrated in the left-hand figures of the diagram and moving bar responses in the right-hand figures. Between recording of the upper and lower sets of tuning curves, the sample of texture was changed and an interval of one and a half hours elapsed. Though some variability in the texture-field response is apparent, the tuning for the moving bar is constant, despite the different samples of background texture used.

Interesting, in this context, is the cell illustrated in fig. 4.12. The cell was studied over some time, with intervals between the recording of pairs of tuning curves of 30 minutes between the first and second pairs and 1 hr. 30 mins. between the second and third pairs. The texture sample was changed between recording each pair of tuning curves. The feature of response which is of particular interest is that a bimodality is present in the tuning for the moving contrast
bar. Separation of the two peaks in the contrast bar tuning curves is approximately 40 degrees. Tuning for a moving texture-field, illustrated in the right-hand tuning curves, is unimodal.

To summarize the main points of the preceding data analysis, the results of comparison of tuning for stationary and moving bars would suggest that the asymmetry seen in the moving bar tuning curve arises from stimulus motion. Identical tuning for stationary and moving bars, reported by Henry, Bishop and Dreher, (1974) for simple cells, is only seen in the limited case of cells which show symmetrical tuning for a moving bar. These cells are found amongst both cells bimodally and unimodally tuned for texture. Cells unresponsive to stationary bars, and whose orientation response is clearly contingent on stimulus motion, are distributed amongst both standard and special complex cells. With reference to lamina IV simple cells, units could be characterized as supra- or infragranular. For the nine cells unresponsive to bar flash, seven were located in the infragranular layers and two in the supragranular layers. The majority were therefore located deep to layer IV. To relate these numbers to the distribution of cells in the total population, 27% (21 cells) of the complex cells recorded were from the supragranular layers and 73% (56) from the infragranular layers.
<table>
<thead>
<tr>
<th>UNIT NUMBER</th>
<th>178/3</th>
<th>178/4</th>
<th>178/6</th>
<th>176/2</th>
<th>178/7</th>
<th>177/8</th>
<th>177/9</th>
<th>177/11</th>
<th>178/24</th>
<th>178/25</th>
<th>178/26</th>
</tr>
</thead>
<tbody>
<tr>
<td>TEXTURE PEAK</td>
<td>237</td>
<td>236</td>
<td>182</td>
<td>243</td>
<td>72</td>
<td>254</td>
<td>253</td>
<td>23</td>
<td>261</td>
<td>55</td>
<td>8</td>
</tr>
<tr>
<td>BAR PEAK</td>
<td>291</td>
<td>268</td>
<td>216</td>
<td>283</td>
<td>90</td>
<td>310</td>
<td>291</td>
<td>30</td>
<td>279</td>
<td>91</td>
<td>21</td>
</tr>
<tr>
<td>&quot;A&quot; FLANK 1/2</td>
<td>45</td>
<td>24</td>
<td>49</td>
<td>24</td>
<td>22</td>
<td>53</td>
<td>51</td>
<td>22</td>
<td>45</td>
<td>33</td>
<td>57</td>
</tr>
<tr>
<td>&quot;B&quot; FLANK 1/2</td>
<td>23</td>
<td>24</td>
<td>22</td>
<td>27</td>
<td>11</td>
<td>26</td>
<td>26</td>
<td>15</td>
<td>31</td>
<td>21</td>
<td>40</td>
</tr>
<tr>
<td>RATIO A:B</td>
<td>2.0</td>
<td>1.0</td>
<td>2.3</td>
<td>0.9</td>
<td>2.0</td>
<td>2.0</td>
<td>2.0</td>
<td>1.5</td>
<td>1.5</td>
<td>1.6</td>
<td>1.4</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>UNIT NUMBER</th>
<th>177/12</th>
<th>177/13</th>
<th>178/28</th>
<th>178/32</th>
<th>178/33</th>
<th>169/59</th>
<th>177/61</th>
<th>178/65</th>
<th>177/67</th>
<th>178/71</th>
<th>178/73</th>
</tr>
</thead>
<tbody>
<tr>
<td>TEXTURE PEAK</td>
<td>63</td>
<td>255</td>
<td>260</td>
<td>119</td>
<td>187</td>
<td>189</td>
<td>200</td>
<td>334</td>
<td>272</td>
<td>108</td>
<td>220</td>
</tr>
<tr>
<td>BAR PEAK</td>
<td>58</td>
<td>276</td>
<td>316</td>
<td>126</td>
<td>217</td>
<td>220</td>
<td>205</td>
<td>371</td>
<td>325</td>
<td>120</td>
<td>247</td>
</tr>
<tr>
<td>&quot;A&quot; FLANK 1/2</td>
<td>28</td>
<td>22</td>
<td>81</td>
<td>54</td>
<td>49</td>
<td>28</td>
<td>55</td>
<td>29</td>
<td>31</td>
<td>27</td>
<td>36</td>
</tr>
<tr>
<td>&quot;B&quot; FLANK 1/2</td>
<td>18</td>
<td>19</td>
<td>32</td>
<td>26</td>
<td>21</td>
<td>26</td>
<td>35</td>
<td>16</td>
<td>16</td>
<td>17</td>
<td>19</td>
</tr>
<tr>
<td>RATIO A:B</td>
<td>1.5</td>
<td>1.2</td>
<td>2.5</td>
<td>2.1</td>
<td>2.3</td>
<td>1.1</td>
<td>1.6</td>
<td>1.8</td>
<td>1.9</td>
<td>1.5</td>
<td>1.9</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>UNIT NUMBER</th>
<th>169/49</th>
<th>175/5</th>
<th>178/27</th>
<th>169/1</th>
<th>177/10</th>
<th>176/21</th>
<th>177/22</th>
<th>175/23</th>
<th>177/63</th>
<th>182/64</th>
<th>169/45</th>
</tr>
</thead>
<tbody>
<tr>
<td>TEXTURE PEAK</td>
<td>120</td>
<td>253</td>
<td>22</td>
<td>114</td>
<td>183</td>
<td>380</td>
<td>326</td>
<td>146</td>
<td>80</td>
<td>365</td>
<td>260</td>
</tr>
<tr>
<td>BAR PEAK</td>
<td>153</td>
<td>4</td>
<td>22</td>
<td>68</td>
<td>154</td>
<td>327</td>
<td>259</td>
<td>94</td>
<td>44</td>
<td>340</td>
<td>229</td>
</tr>
<tr>
<td>&quot;A&quot; FLANK 1/2</td>
<td>21</td>
<td>29</td>
<td>49</td>
<td>27</td>
<td>35</td>
<td>54</td>
<td>40</td>
<td>31</td>
<td>31</td>
<td>40</td>
<td>70</td>
</tr>
<tr>
<td>&quot;B&quot; FLANK 1/2</td>
<td>21</td>
<td>23</td>
<td>48</td>
<td>23</td>
<td>21</td>
<td>17</td>
<td>42</td>
<td>17</td>
<td>21</td>
<td>18</td>
<td>35</td>
</tr>
<tr>
<td>RATIO A:B</td>
<td>1.0</td>
<td>1.3</td>
<td>1.0</td>
<td>1.2</td>
<td>1.7</td>
<td>3.2</td>
<td>1.0</td>
<td>1.8</td>
<td>1.5</td>
<td>2.2</td>
<td>2.0</td>
</tr>
<tr>
<td>UNIT NUMBER</td>
<td>169/46</td>
<td>177/76</td>
<td>177/77</td>
<td>178/29</td>
<td>177/31</td>
<td>177/32</td>
<td>177/66</td>
<td>177/68</td>
<td>177/70</td>
<td>177/70</td>
<td></td>
</tr>
<tr>
<td>-------------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
<td></td>
</tr>
<tr>
<td><strong>TEXTURE PEAK</strong></td>
<td>254</td>
<td>222</td>
<td>216</td>
<td>14</td>
<td>22</td>
<td>172</td>
<td>222</td>
<td>13</td>
<td>44</td>
<td>177</td>
<td>159</td>
</tr>
<tr>
<td><strong>BAR PEAK</strong></td>
<td>248</td>
<td>209</td>
<td>156</td>
<td>16</td>
<td>30</td>
<td>122</td>
<td>209</td>
<td>335</td>
<td>47</td>
<td>163</td>
<td>151</td>
</tr>
<tr>
<td>&quot;A&quot; FLANK 1/2</td>
<td>54</td>
<td>24</td>
<td>32</td>
<td>24</td>
<td>39</td>
<td>24</td>
<td>25</td>
<td>25</td>
<td>26</td>
<td>46</td>
<td>50</td>
</tr>
<tr>
<td>&quot;B&quot; FLANK 1/2</td>
<td>31</td>
<td>13</td>
<td>28</td>
<td>17</td>
<td>28</td>
<td>20</td>
<td>13</td>
<td>20</td>
<td>18</td>
<td>46</td>
<td>48</td>
</tr>
<tr>
<td><strong>RATIO A:B</strong></td>
<td>1.7</td>
<td>1.9</td>
<td>1.1</td>
<td>1.4</td>
<td>1.3</td>
<td>1.2</td>
<td>1.6</td>
<td>1.3</td>
<td>1.4</td>
<td>1.0</td>
<td>1.1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>UNIT NUMBER</th>
<th>178/72</th>
<th>178/74</th>
<th>178/54</th>
<th>175/44</th>
<th>169/46</th>
<th>169/47</th>
<th>175/51</th>
<th>176/52</th>
<th>169/55</th>
<th>181/56</th>
<th>178/57</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>TEXTURE PEAK</strong></td>
<td>295</td>
<td>129</td>
<td>41</td>
<td>318</td>
<td>245</td>
<td>96</td>
<td>249</td>
<td>96</td>
<td>238</td>
<td>236</td>
<td>194</td>
</tr>
<tr>
<td><strong>BAR PEAK</strong></td>
<td>324</td>
<td>153</td>
<td>33</td>
<td>165</td>
<td>263</td>
<td>86</td>
<td>326</td>
<td>96</td>
<td>223</td>
<td>290</td>
<td>210</td>
</tr>
<tr>
<td>&quot;A&quot; FLANK 1/2</td>
<td>28</td>
<td>24</td>
<td>12</td>
<td>22</td>
<td>35</td>
<td>33</td>
<td>31</td>
<td>25</td>
<td>34</td>
<td>21</td>
<td>46</td>
</tr>
<tr>
<td>&quot;B&quot; FLANK 1/2</td>
<td>18</td>
<td>24</td>
<td>9</td>
<td>12</td>
<td>34</td>
<td>23</td>
<td>31</td>
<td>23</td>
<td>22</td>
<td>15</td>
<td>27</td>
</tr>
<tr>
<td><strong>RATIO A:B</strong></td>
<td>1.6</td>
<td>1.0</td>
<td>1.3</td>
<td>1.8</td>
<td>1.0</td>
<td>1.4</td>
<td>1.0</td>
<td>1.1</td>
<td>1.6</td>
<td>1.4</td>
<td>1.7</td>
</tr>
</tbody>
</table>
TABLE TWO - SYMMETRY OF TUNING FOR MOVING CONTRAST BARS RELATED TO TUNING FOR MOVING FIELDS OF TEXTURE FOR COMPLEX CELLS SHOWING A BIMODAL RESPONSE TO A MOVING FIELD OF TEXTURE. (UNITS: DEGREES)

(A FLANK refers to the greater and B FLANK the lesser of the two sides of the bar tuning curve).

<table>
<thead>
<tr>
<th>UNIT NUMBER</th>
<th>175/14</th>
<th>175/15</th>
<th>169/16</th>
<th>169/17</th>
<th>169/18</th>
<th>176/19</th>
<th>177/20</th>
<th>169/60</th>
<th>176/34</th>
<th>175/35</th>
<th>169/36</th>
</tr>
</thead>
<tbody>
<tr>
<td>TEXTURE PEAK 1</td>
<td>100</td>
<td>207</td>
<td>4</td>
<td>144</td>
<td>28</td>
<td>204</td>
<td>227</td>
<td>143</td>
<td>103</td>
<td>124</td>
<td>302</td>
</tr>
<tr>
<td>TEXTURE PEAK 2</td>
<td>170</td>
<td>302</td>
<td>94</td>
<td>248</td>
<td>90</td>
<td>332</td>
<td>319</td>
<td>233</td>
<td>158</td>
<td>153</td>
<td>38</td>
</tr>
<tr>
<td>BAR PEAK</td>
<td>137</td>
<td>255</td>
<td>42</td>
<td>203</td>
<td>53</td>
<td>308</td>
<td>270</td>
<td>188</td>
<td>103</td>
<td>176</td>
<td>347</td>
</tr>
<tr>
<td>&quot;A&quot; FLANK 1/2</td>
<td>22</td>
<td>24</td>
<td>42</td>
<td>19</td>
<td>27</td>
<td>25</td>
<td>22</td>
<td>17</td>
<td>20</td>
<td>18</td>
<td>17</td>
</tr>
<tr>
<td>&quot;B&quot; FLANK 1/2</td>
<td>17</td>
<td>15</td>
<td>16</td>
<td>15</td>
<td>20</td>
<td>22</td>
<td>20</td>
<td>13</td>
<td>13</td>
<td>12</td>
<td>13</td>
</tr>
<tr>
<td>RATIO A:B</td>
<td>1.3</td>
<td>1.6</td>
<td>2.6</td>
<td>1.3</td>
<td>1.3</td>
<td>1.1</td>
<td>1.1</td>
<td>1.3</td>
<td>1.5</td>
<td>1.5</td>
<td>1.3</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>UNIT NUMBER</th>
<th>175/38</th>
<th>176/39</th>
<th>175/40</th>
<th>175/41</th>
<th>176/42</th>
<th>175/43</th>
<th>175/53</th>
<th>175/50</th>
<th>176/58</th>
<th>178/75</th>
<th>175/37</th>
</tr>
</thead>
<tbody>
<tr>
<td>TEXTURE PEAK 1</td>
<td>53</td>
<td>99</td>
<td>100</td>
<td>212</td>
<td>255</td>
<td>26</td>
<td>342</td>
<td>321</td>
<td>143</td>
<td>114</td>
<td>38</td>
</tr>
<tr>
<td>TEXTURE PEAK 2</td>
<td>128</td>
<td>192</td>
<td>174</td>
<td>314</td>
<td>323</td>
<td>99</td>
<td>56</td>
<td>43</td>
<td>216</td>
<td>233</td>
<td>147</td>
</tr>
<tr>
<td>BAR PEAK</td>
<td>91</td>
<td>140</td>
<td>137</td>
<td>263</td>
<td>289</td>
<td>53</td>
<td>13</td>
<td>362</td>
<td>156</td>
<td>179</td>
<td>93</td>
</tr>
<tr>
<td>&quot;A&quot; FLANK 1/2</td>
<td>24</td>
<td>28</td>
<td>22</td>
<td>13</td>
<td>23</td>
<td>27</td>
<td>24</td>
<td>24</td>
<td>32</td>
<td>22</td>
<td>25</td>
</tr>
<tr>
<td>&quot;B&quot; FLANK 1/2</td>
<td>18</td>
<td>27</td>
<td>17</td>
<td>13</td>
<td>23</td>
<td>20</td>
<td>20</td>
<td>24</td>
<td>28</td>
<td>10</td>
<td>18</td>
</tr>
<tr>
<td>RATIO A:B</td>
<td>1.3</td>
<td>1.3</td>
<td>1.3</td>
<td>1.1</td>
<td>1.0</td>
<td>1.3</td>
<td>1.2</td>
<td>1.0</td>
<td>1.1</td>
<td>2.2</td>
<td>1.4</td>
</tr>
</tbody>
</table>
TABLE THREE - COMPARISON OF BREADTH OF TUNING FOR MOVING AND STATIONARY CONTRAST BARS.

(Tuning breadth expressed as total width at half-height of the tuning curve fitted with linear regression lines) P=Peak in the tuning curve, W=Width of the tuning curve at half-height. UNITS : DEGREES.

<table>
<thead>
<tr>
<th>UNIT NUMBER</th>
<th>169/1</th>
<th>176/2</th>
<th>178/3</th>
<th>178/4</th>
<th>175/5</th>
<th>178/6</th>
<th>178/7</th>
<th>177/9</th>
<th>177/10</th>
<th>177/11</th>
<th>177/12</th>
<th>177/13</th>
</tr>
</thead>
<tbody>
<tr>
<td>MOVING BAR P</td>
<td>68</td>
<td>283</td>
<td>291</td>
<td>268</td>
<td>364</td>
<td>215</td>
<td>90</td>
<td>291</td>
<td>154</td>
<td>390</td>
<td>58</td>
<td>275</td>
</tr>
<tr>
<td>STATIONARY BAR P</td>
<td>68</td>
<td>NR</td>
<td>297</td>
<td>265</td>
<td>380</td>
<td>NR</td>
<td>96</td>
<td>NR</td>
<td>150</td>
<td>396</td>
<td>NR</td>
<td>55</td>
</tr>
<tr>
<td>MOVING BAR W</td>
<td>50</td>
<td>51</td>
<td>68</td>
<td>48</td>
<td>53</td>
<td>71</td>
<td>33</td>
<td>76</td>
<td>56</td>
<td>37</td>
<td>47</td>
<td>42</td>
</tr>
<tr>
<td>STATIONARY BAR W</td>
<td>31</td>
<td>NR</td>
<td>31</td>
<td>26</td>
<td>39</td>
<td>NR</td>
<td>24</td>
<td>NR</td>
<td>34</td>
<td>26</td>
<td>42</td>
<td>40</td>
</tr>
</tbody>
</table>

SPECIAL UNIMODAL CELLS.

<table>
<thead>
<tr>
<th>UNIT NUMBER</th>
<th>176/21</th>
<th>177/22</th>
<th>175/23</th>
<th>178/24</th>
<th>178/25</th>
<th>178/26</th>
<th>178/27</th>
<th>178/28</th>
<th>178/29</th>
<th>177/30</th>
<th>177/31</th>
<th>178/32</th>
<th>178/33</th>
</tr>
</thead>
<tbody>
<tr>
<td>MOVING BAR P</td>
<td>327</td>
<td>259</td>
<td>91</td>
<td>279</td>
<td>91</td>
<td>23</td>
<td>22</td>
<td>316</td>
<td>16</td>
<td>30</td>
<td>122</td>
<td>126</td>
<td>217</td>
</tr>
<tr>
<td>STATIONARY BAR P</td>
<td>326</td>
<td>NR</td>
<td>91</td>
<td>NR</td>
<td>NR</td>
<td>28</td>
<td>NR</td>
<td>NR</td>
<td>10</td>
<td>42</td>
<td>121</td>
<td>134</td>
<td>229</td>
</tr>
<tr>
<td>MOVING BAR W</td>
<td>71</td>
<td>83</td>
<td>48</td>
<td>76</td>
<td>54</td>
<td>96</td>
<td>96</td>
<td>113</td>
<td>41</td>
<td>67</td>
<td>44</td>
<td>81</td>
<td>70</td>
</tr>
<tr>
<td>STATIONARY BAR W</td>
<td>44</td>
<td>NR</td>
<td>39</td>
<td>NR</td>
<td>NR</td>
<td>40</td>
<td>NR</td>
<td>NR</td>
<td>38</td>
<td>27</td>
<td>38</td>
<td>36</td>
<td>32</td>
</tr>
</tbody>
</table>

STANDARD BIMODAL CELLS.

<table>
<thead>
<tr>
<th>UNIT NUMBER</th>
<th>176/34</th>
<th>175/35</th>
<th>169/36</th>
<th>175/37</th>
<th>175/38</th>
<th>176/39</th>
<th>175/40</th>
<th>175/41</th>
<th>176/42</th>
<th>175/43</th>
</tr>
</thead>
<tbody>
<tr>
<td>MOVING BAR P</td>
<td>103</td>
<td>175</td>
<td>347</td>
<td>93</td>
<td>91</td>
<td>140</td>
<td>137</td>
<td>263</td>
<td>289</td>
<td>53</td>
</tr>
<tr>
<td>STATIONARY BAR P</td>
<td>104</td>
<td>179</td>
<td>345</td>
<td>93</td>
<td>81</td>
<td>NR</td>
<td>139</td>
<td>263</td>
<td>289</td>
<td>58</td>
</tr>
<tr>
<td>MOVING BAR W</td>
<td>33</td>
<td>30</td>
<td>31</td>
<td>43</td>
<td>42</td>
<td>55</td>
<td>39</td>
<td>26</td>
<td>46</td>
<td>47</td>
</tr>
<tr>
<td>STATIONARY BAR W</td>
<td>25</td>
<td>26</td>
<td>19</td>
<td>34</td>
<td>30</td>
<td>NR</td>
<td>30</td>
<td>26</td>
<td>32</td>
<td>38</td>
</tr>
</tbody>
</table>

Only one "Special" complex cell with a bimodal texture response responded to a flashed bar.

The corresponding figures for that unit were:

UNIT NUMBER 175/14 Total tuning width for moving contrast bar : 39 deg. Peak : 137 deg.
Total tuning width for stationary contrast bar : 30 deg. Peak : 140 deg.

(Units marked NR for the stationary bar condition were unresponsive to a flashed bar)
Description of Tuning Curves.

The following convention is followed for this and subsequent diagrams. Tuning curves represent the response for a particular stimulus, for movement in a round-the-clock sequence. Vertically upward motion is specified as 0 deg. Each bin shows the response for each direction of stimulus movement with binwidth set at ten degrees. Direction was stepped clockwise. The right-most pair of bins is a calibration signal of 50 spikes/sec. The horizontal dotted line represents the cell’s resting discharge.

FIG 4.7

Comparison of Tuning for Stationary and Moving Contrast Bars for a Cell Bimodally Tuned for Moving Texture-field with Unequal Peaks in the Texture-Field Tuning Curve.

Tuning for bar motion is asymmetrical with the broader flank in bar tuning facing the more prominent peak in the texture-field tuning curve. Compared with tuning for a moving bar, tuning for a stationary, flashed bar is sharper and more symmetrical though peaks are identical for both bar stimuli. For each pair of responses to a moving contrast bar, i.e. for each of two opposite directions of motion, there is one common value for bar orientation. Therefore, whilst the responses to a moving bar are registered in the two halves of the tuning curve, the responses to the corresponding stationary bar are contained within one half. To indicate this equivalence, the stationary bar responses are replicated over the two halves of the tuning curve in this and the following three diagrams.

Unit number: 169/36 Standard complex cell from the supragranular layers.
Receptive field size: 1.8 deg. sq.

Bar dimensions: 8.7 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar and texture-field 1.5 deg./sec.

Calibration Signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
X AXIS OF TUNING CURVES: DIRECTION OF MOTION [DEG.]
Comparison of Tuning for Stationary and Moving Contrast Bars for a Cell Unimodally Tuned for Texture Motion

Tuning for moving bar is asymmetrical with the broader flank in the tuning curve adjacent to the texture-field tuning curve. Compared with tuning for moving bar, tuning for a stationary flashed bar is sharper and more symmetrical. Peak positions for stationary and moving bars are dissimilar.

Unit number: 178/33 Special complex cell of the infragranular layers.
Receptive field size: 9.3 deg. sq.
Bar dimensions: 8.3 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar and texture-field 3 deg./sec.
Calibration signal: 30 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
STATIONARY CONTRAST BAR

X AXIS OF TUNING CURVES: DIRECTION OF MOTION [DEG.]

MOVING TEXTURE FIELD

MOVING CONTRAST BAR

STATIONARY CONTRAST BAR
Comparison of Tuning for Stationary and Moving Contrast Bars for a Complex Cell Showing Bimodal Texture-Field Tuning with Equally Prominent Peaks in the Texture-Field Tuning Curve.

The tuning of this cell for contrast bars is typical of complex cells with bimodal texture-field tuning with equally prominent peaks in texture-field tuning. Tuning for a moving contrast bar is symmetrical. Tuning for the same bar presented stationary and flashed is identical in breadth and symmetry. As for most cells showing a response to a stationary bar, peak positions for stationary and moving bar are identical.

Unit number: 175/41 Standard complex cell of the infragranular layers.
Receptive field size: 6.7 deg. sq.

Bar dimensions: 9 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar and texture-field 1.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge is indicated by the dotted line.
X AXIS OF TUNING CURVES: DIRECTION OF MOTION [DEG.]
Comparison of Tuning for Stationary and Moving Contrast Bars for a Complex Cell Showing Unimodal Texture-Field Tuning Curve with Moving Contrast Bar and Texture-Field Tuning Curve Peaks in Register

The symmetrical tuning curve for a moving bar is typical for units with peaks in tuning curves for moving bar and texture-field in register. Peaks in the tuning curves for stationary and moving bars are identical and tuning for the stationary bar is symmetrical. In comparison to the same bar in motion, tuning for a stationary bar is sharper.

Unit number: 178/4 Standard complex cell of the infragranular layers.
Receptive field size: 7.0 deg. sq.
Bar dimensions: 8.9 x 0.5 deg.
Contrast: 0.25 log units above noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar and texture-field 5.5 deg./sec.
Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
X AXIS OF TUNING CURVES: DIRECTION OF MOTION (DEG.)
Comparison of Tuning for a Contrast Bar Moving Against Different Samples of Visual Noise

The figure illustrates invariance of tuning for a contrast bar moving against different samples of stationary visual noise. Between the recording of the upper and lower pairs of tuning curves, the sample of texture was changed. An interval of one and a half hours elapsed between the recording of the two pairs of tuning curves. Though some variability is seen in the texture-field response for the two samples of texture, tuning for the moving contrast bar is invariant despite the changed background.

Unit number 178/7 Standard complex cell of the supragranular layers.
Receptive field size: 6 deg. sq.
Bar dimensions: 85 x 4 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar and texture-field 2.5 deg./sec.
Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
TEXTURE SAMPLE 1: TIME 2:55 P.M.

TEXTURE SAMPLE 2: TIME 4:25 P.M.
Fig. 4.12 Bimodality of Tuning for a Moving Contrast Bar

The figure illustrates a cell for which a bimodality in tuning for a moving contrast bar is evident. Each row illustrates tuning for a moving contrast bar (left-hand side) and the corresponding tuning curve for moving texture-field (right-hand side). Between the recording of each pair of tuning curves (A, B, C) the sample of texture was changed. A bimodality is evident in tuning for the moving contrast bar with a peak separation of about 40 degrees. By contrast, the tuning curve for the moving texture-field is unimodal. These recordings were made over a period of two hours, with an interval between the recording of each pair of tuning curves of thirty minutes, between the first and second pairs, and one and a half hours between the second and third pairs.

Interval between recordings A and B: 30 mins.
Interval between recordings B and C: 1 hr. 30 mins.

Unit number: 176/21 Special complex cell of the infragranular layers.
Receptive field size: 1.9 deg. sq.

Bar dimensions: 8.5 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Velocity of moving contrast bar and texture-field 4 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG]
4.8(e) Tuning of Spots in Comparison with Moving Contrast Bars and Fields of Moving Visual Noise

Tuning for moving contrast spots and contrast bars was compared for 38 cells. In each case, the dimensions of the spots were set at the width of the contrast bar with which tuning was compared and the spot moved through the geometric centre of the receptive field. Spot sizes ranged from 0.3 to 0.5 deg. of visual angle.

Of the 38 cells, 23 were unimodal in their texture response (12 standard and 11 special complex) and 15 were bimodal in their texture field response (8 standard, 7 special complex). The tuning of 3 of the 23 unimodal cells showed identical tuning peak positions for bar and texture. For these cells, the spot peak coincided with that of the contrast bar and texture-field tuning curves. For the other 20, differences in peak position for spot and bar tuning were evident. The mean difference in peak position between the tuning curves for bar and spot was 23.8 deg. with a range of 0 to 65 deg., when all 23 units were included. Data for the bimodally tuned units indicated that, for those units classified as standard complex, 4 out of 8 cells exhibited identical peak positions for bar and spot tuning curves with the other 4 showing differences in peak position of 7, 7, 10 and 14 deg. Two of the special complex cells cells showed co-incidence of spot and bar peaks in the tuning curves the remainder showing a difference in peak position from 11 to 46 degs. with a mean of 26.7 deg.
Collating the results for cells showing symmetrical or asymmetrical bar tuning curves, the following pattern emerged. The results are related to tuning for moving fields of texture. For those cells which were symmetrical in tuning for a moving bar, peaks in the tuning curves for spot and bar coincided. In their texture-field response, these neurones were either unimodal with bar and texture field tuning peaks in register, or bimodal cells with equal peaks. Cells asymmetrical in tuning for a moving bar showed a peak shift in the tuning curve for a moving spot. For those cells asymmetrical in their tuning for bar motion, and unimodal in their texture field tuning, the peak shift was in the preferred direction of motion for the texture field. One exception to the rule was found for a cell for which the tuning peaks for bar and texture field were clearly separated but peaks for bar and spots coincided. For cells bimodally tuned for texture motion, with one peak in texture tuning more prominent, a peak shift in the peak of the tuning curve for a spot compared to that for bar motion was seen. The peak shift was in the direction of the prominent peak of the texture-field tuning curve. As would be anticipated from the greater breadth and asymmetry in bar tuning of units of the infragranular layers (Hammond, 1978) peak shift in spot tuning was greater for these cells than their counterparts in the supragranular layers.

Each of these patterns of response is illustrated. Figures 4.13 and 4.14 illustrate units which, asymmetrical in bar tuning, show a peak shift for spot tuning. Cells symmetrical in bar tuning, with no peak shift, or a weak peak
shift in the spot tuning curve, are illustrated in figs. 4.15 and 4.16. Data for the whole population of cells studied are summarized in table 4. As shown by this table, the patterns of behaviour described were independent of the standard/special complex cell classification. As is apparent from the definition of standard and special complex cells (Gilbert, 1977), the former were less responsive to spots. For the majority of neurones, tuning for spot was narrower than tuning for moving texture-field. Comparing tuning for spot and texture-field, greater similarity in breadth of tuning for these two stimuli was found for standard than for special complex cells. The difference in tuning between spot and texture-field was, for standard unimodal cells, 13.7 deg. with a range of 3 to 30 deg. and, for standard bimodal cells, 12.6 deg. with a range of 6 to 21 deg. For special complex cells the figures were: special unimodal mean 17.3 deg. with a range of 0 to 40 deg. and special bimodal cells with a mean of 49.6 deg. with a range of 10 to 81 deg.

Of the three additional units recorded which showed significant end-inhibition, two were bimodal in texture-field tuning and one was unimodal in texture-field tuning. Though distinguished from the other units in the reduction of response magnitude, at lengths beyond an optimal value, the tuning of these units for moving spot, bar and texture-field did not differ from the pattern seen for the larger population. The tuning of the two cells, bimodal in texture-field tuning, for a moving spot, was unimodal.

Henry, Dreher and Bishop (1974) reported that, for all
simple cells and the majority of complex cells, the effect of reducing bar length was to produce no change in the peak of the tuning curve but a broadening of tuning width. A second group of complex cells from the same study, resembling Gilbert's (1977) special complex cells in summatory behaviour, were reported to show similar tuning widths for bars and spots. In this context, breadth of tuning of standard and special complex cells was evaluated. Tuning for standard complex cells exhibited the pattern reported by Henry, Dreher and Bishop (1974) for their majority of complex cells. For the sample of special complex cells investigated in the present study, tuning was invariably broader for spot than for bar. The mean difference was 42.5 deg. with a range of 14 deg. to 109 deg. The existence of Henry, Dreher and Bishop's (1974) second group of complex cells was not confirmed.

4.8(f) Direction Bias and Direction Selectivity for Contrast and Textured Stimuli

"Direction" was distinguished from "axis" in Henry, Dreher and Bishop's (1974) analysis. In the preceding description, little consideration was given to "direction selectivity" or "direction bias" as defined by Henry, Dreher and Bishop (1974). Responses to opposite directions of motion for spot, bar and texture are described in the following analysis.

Of 38 units from which data were recorded for spot, bar and texture motion, 33 were direction-selective in their response to bar, spot and texture motion. The large number of
direction-selective units may reflect a bias in recording from the infragranular layers. The remaining five units showed some degree of bias in response for opposite directions of motion for at least one of the three stimuli.

Two of the units were unimodal in their texture-field response. One unit was direction-selective for bar and spot motion but directionally biased for texture motion at the cell's preferred velocity for bar motion (unit 178/57). The other unit was, at the cell's preferred velocity for bar motion, directionally selective for texture and bar motion but direction biased for spot motion (unit 175/3; fig. 4.17).

From the three units showing a bimodal texture-field response, two units (175/35; 175/50) were direction biased for bar but selective for moving texture-field and spot. The third unit (176/42) was extensively studied and is illustrated in fig 4.18. At lower velocities, the cell was direction biased for bar motion, and direction selective for texture-field and spot motion. The response to texture-field motion was unimodal at 3 deg./sec. As stimulus velocity increased, direction bias in the bar response increased, with only a small response response in the non-preferred direction at a stimulus velocity of 5 deg./sec. The spot response remained unimodal as velocity was increased. Tuning for texture-field motion became increasingly bimodal while remaining direction selective as velocity was increased. For clarity of exposition, and to emphasise the differences in spot and texture-field tuning, spot tuning at one velocity is shown.
TABLE FOUR - COMPARISON OF TUNING CURVE PEAK POSITIONS FOR MOVING CONTRAST BAR, MOVING SPOT AND MOVING TEXTURE FIELDS (PEAKS DETERMINED FROM THE INTERCEPTS OF LINEAR REGRESSION LINES).

(UNITS: DEGREES).

STANDARD COMPLEX CELLS SHOWING A UNIMODAL TEXTURE FIELD RESPONSE.

<table>
<thead>
<tr>
<th>UNIT NUMBER</th>
<th>169/1</th>
<th>176/2</th>
<th>178/3</th>
<th>178/4</th>
<th>178/6</th>
<th>178/7</th>
<th>177/8</th>
<th>177/9</th>
<th>177/10</th>
<th>177/11</th>
<th>177/12</th>
<th>177/13</th>
</tr>
</thead>
<tbody>
<tr>
<td>BAR PEAK</td>
<td>68</td>
<td>283</td>
<td>291</td>
<td>268</td>
<td>216</td>
<td>90</td>
<td>310</td>
<td>291</td>
<td>154</td>
<td>30</td>
<td>58</td>
<td>276</td>
</tr>
<tr>
<td>SPOT PEAK</td>
<td>63</td>
<td>263</td>
<td>258</td>
<td>252</td>
<td>207</td>
<td>83</td>
<td>257</td>
<td>269</td>
<td>177</td>
<td>31</td>
<td>60</td>
<td>268</td>
</tr>
<tr>
<td>TEXTURE FIELD PEAK</td>
<td>114</td>
<td>243</td>
<td>237</td>
<td>236</td>
<td>182</td>
<td>72</td>
<td>254</td>
<td>253</td>
<td>183</td>
<td>23</td>
<td>63</td>
<td>255</td>
</tr>
</tbody>
</table>

SPECIAL COMPLEX CELLS SHOWING A UNIMODAL TEXTURE FIELD RESPONSE.

<table>
<thead>
<tr>
<th>UNIT NUMBER</th>
<th>176/21</th>
<th>177/22</th>
<th>175/23</th>
<th>178/24</th>
<th>178/25</th>
<th>178/26</th>
<th>178/29</th>
<th>178/30</th>
<th>177/31</th>
<th>177/32</th>
<th>178/33</th>
</tr>
</thead>
<tbody>
<tr>
<td>BAR PEAK</td>
<td>327</td>
<td>259</td>
<td>94</td>
<td>279</td>
<td>91</td>
<td>21</td>
<td>16</td>
<td>30</td>
<td>122</td>
<td>126</td>
<td>217</td>
</tr>
<tr>
<td>SPOT PEAK</td>
<td>356</td>
<td>325</td>
<td>103</td>
<td>270</td>
<td>79</td>
<td>1</td>
<td>24</td>
<td>17</td>
<td>150</td>
<td>116</td>
<td>207</td>
</tr>
<tr>
<td>TEXTURE FIELD PEAK</td>
<td>380</td>
<td>326</td>
<td>146</td>
<td>261</td>
<td>55</td>
<td>8</td>
<td>14</td>
<td>22</td>
<td>172</td>
<td>119</td>
<td>187</td>
</tr>
</tbody>
</table>
TABLE FIVE - COMPARISON OF TUNING CURVE PEAK POSITIONS FOR MOVING BAR, MOVING SPOT AND MOVING TEXTURE
FIELDS. (PEAKS ARE DERIVED FROM THE INTERSECTION OF REGRESSION LINES FITTED TO THE TUNING
CURVES). (UNITS : DEGREES).

STANDARD COMPLEX CELLS SHOWING A BIMODAL TEXTURE FIELD RESPONSE.

<table>
<thead>
<tr>
<th>UNIT NUMBER</th>
<th>176/34</th>
<th>169/36</th>
<th>175/37</th>
<th>175/38</th>
<th>176/39</th>
<th>175/40</th>
<th>175/41</th>
<th>176/42</th>
</tr>
</thead>
<tbody>
<tr>
<td>BAR PEAK</td>
<td>103</td>
<td>347</td>
<td>93</td>
<td>91</td>
<td>140</td>
<td>137</td>
<td>263</td>
<td>289</td>
</tr>
<tr>
<td>SPOT PEAK</td>
<td>97</td>
<td>350</td>
<td>91</td>
<td>101</td>
<td>147</td>
<td>139</td>
<td>267</td>
<td>303</td>
</tr>
<tr>
<td>TEXTURE PEAK ONE</td>
<td>103</td>
<td>302</td>
<td>38</td>
<td>53</td>
<td>99</td>
<td>100</td>
<td>212</td>
<td>255</td>
</tr>
<tr>
<td>TEXTURE PEAK TWO</td>
<td>158</td>
<td>38</td>
<td>147</td>
<td>128</td>
<td>192</td>
<td>174</td>
<td>314</td>
<td>323</td>
</tr>
</tbody>
</table>

SPECIAL COMPLEX CELLS SHOWING A BIMODAL TEXTURE FIELD RESPONSE.

<table>
<thead>
<tr>
<th>UNIT NUMBER</th>
<th>175/14</th>
<th>175/15</th>
<th>169/16</th>
<th>169/17</th>
<th>169/18</th>
<th>176/19</th>
<th>177/20</th>
</tr>
</thead>
<tbody>
<tr>
<td>BAR PEAK</td>
<td>137</td>
<td>255</td>
<td>42</td>
<td>203</td>
<td>53</td>
<td>308</td>
<td>270</td>
</tr>
<tr>
<td>SPOT PEAK</td>
<td>99</td>
<td>244</td>
<td>47</td>
<td>179</td>
<td>98</td>
<td>316</td>
<td>255</td>
</tr>
<tr>
<td>TEXTURE PEAK ONE</td>
<td>100</td>
<td>207</td>
<td>4</td>
<td>144</td>
<td>28</td>
<td>204</td>
<td>227</td>
</tr>
<tr>
<td>TEXTURE PEAK TWO</td>
<td>170</td>
<td>302</td>
<td>94</td>
<td>248</td>
<td>90</td>
<td>332</td>
<td>319</td>
</tr>
</tbody>
</table>
Comparison of Tuning for a Moving Contrast Spot with Moving Contrast Bar and Texture-field for a Cell Bimodal in Its Texture-field Response

Responses to the three stimuli were recorded at the same velocity, intermediate in the cell's response range. Tuning for texture-field motion shows one prominent peak. The broader flank in the contrast bar tuning curve is on the side adjacent to the more prominent peak in texture-field tuning. The response to a moving spot is typical for a cell bimodal in its texture-field response with unequal peaks in texture-field tuning. The reduced stimulus length results in a peak shift from that in bar tuning to the prominent peak in texture-field tuning.

Unit number: 175/15 Special complex cell of the infragranular layers.
Receptive field size: 8.5 deg. sq.

Bar dimensions: 9 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Spot dimensions: 0.4 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar, spot and texture-field 3.5 deg/sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
X AXIS OF TUNING CURVES: DIRECTION OF MOTION (DEG)
Comparison of Tuning for a Moving Contrast Spot with a Moving Contrast Bar and Texture-field for a Cell Unimodal in Its Texture-field Response

Tuning for a moving contrast spot is related to tuning for a moving contrast bar and texture-field. The responses were recorded at the same velocity which was intermediate in the cell’s response range. With reduced length, a peak shift is seen with the peak in the spot tuning curve shifted from the peak in bar tuning to the peak in texture-field tuning.

Unit number: 177/31 Special complex cell of the infragranular layers.
Receptive field size: 9 deg. sq.

Bar dimensions: 8.4 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Spot dimensions: 0.4 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar, spot and texture-field 7 deg/sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
X AXIS OF TUNING CURVES: DIRECTION OF MOTION (DEG.)
Comparison of Tuning for a Moving Contrast Spot with Moving Contrast Bar and Texture-field for a Cell Bimodal in Texture-field for a Cell Bimodal in Texture-field Response with Equally Prominent Peaks in the Texture-field Tuning Curve

Tuning for a moving contrast spot is related to tuning for a moving contrast bar and texture-field. For this cell, symmetrical in tuning for a moving bar, the peak in tuning for a spot is close to the peak in the tuning curve for the moving bar. Though tuning for texture-field motion is bimodal, the spot tuning curve is unimodal.

Unit number: 175/41 Standard complex cell of the infragranular layers.  
Receptive field size: 6.7 deg. sq.

Bar dimensions: 9 x 0.5 deg.  
Contrast: 0.6 log units below noise background.  
Spot dimensions: 0.5 x 0.5 deg.  
Contrast: 0.6 log units below noise background.  
Texture-field dimensions: 10 x 10 deg.  
Stimulus velocity for moving bar, spot and texture-field 3 deg./sec.

Calibration signal: 50 spikes/sec.  
Binwidth: 10 deg.  
Resting discharge indicated by the dotted line.
MOVING CONTRAST BAR

MOVING CONTRAST SPOT

X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]
Comparison of Tuning for a Moving Contrast Spot with Tuning for a Moving Texture-field and Contrast for a Cell Unimodal in Texture-field Tuning with Bar and Texture-field Tuning Curve Peaks in Register

Tuning for a moving contrast spot is related to tuning for a moving contrast bar and texture-field. Responses were recorded at the same velocity, intermediate in the cell's response range. For this unit, as for others with bar and texture-field tuning curve peaks in register, the peak in the spot tuning curve is identical to that for bar and texture-field.

Unit number: 177/12. Standard complex cell of the supragranular layers.
Receptive field size: 4.8 deg. sq.

Bar dimensions: 9.5 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar, spot and texture-field 2.5 deg./sec.

Calibration signal: 50 spikes/sec.
Resting discharge indicated by the dotted line.
X AXIS OF TUNING CURVES: DIRECTION OF MOTION [DEG.]
The response to opposite directions of motion is illustrated in the tuning curves for moving texture-field, contrast bar and spot. In response to moving texture-field and contrast bar, the cell is direction-selective. By contrast, the response to the contrast spot is direction biased. The tuning curves were obtained at the same velocity, intermediate in the cell's response range.

Unit number: 175/5. A complex cell of the supragranular layers intermediate between classical standard and special complex cells, but with the response to a moving spot clearly less than that to the moving contrast bar.

Receptive field size: 2.1 deg. sq.

Bar dimensions: 8.5 x 0.5 deg. Contrast: 0.6 log units below noise background.
Spot dimensions: 0.5 x 0.5 deg. Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving bar, spot and texture-field 1.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
MOVING TEXTURE FIELD

MOVING CONTRAST BAR

MOVING CONTRAST SPOT

X AXIS OF TUNING CURVES: DIRECTION OF MOTION [DEG.]
The Dependence of Direction Bias and Tuning on Stimulus Velocity

The tuning for contrast and textured stimuli at a range of velocities is illustrated. At low velocities (3-4 deg./sec.), the cell was direction-biased for bar motion but direction-selective for moving texture-field and spot. As velocity increased, the direction bias for bar tuning increased with reduced response to bar motion in the non-preferred direction at 5 deg./sec. At low velocities, response to texture-field motion was unimodal. Increasing the velocity of texture-field motion produced a bimodal texture-field tuning curve. The response to the moving contrast spot remained unimodal and direction-selective at all velocities. For clarity and to emphasize the differences in spot and texture-field tuning, spot tuning is illustrated at a high velocity.

Unit number: 176/2. Standard complex cell of the infragranular layers.
Receptive field size: 6.9 deg. sq.
Bar dimensions: 8 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Spot dimensions: 0.4 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by dotted the line.
VELOCITY 3 deg/sec

MOVING TEXTURE FIELD

MOVING CONTRAST BAR

VELOCITY 4 deg/sec

MOVING TEXTURE FIELD

MOVING CONTRAST BAR

VELOCITY 5 deg/sec

MOVING TEXTURE FIELD

MOVING CONTRAST BAR

VELOCITY 5 deg/sec

MOVING TEXTURE FIELD

MOVING CONTRAST SPOT

X AXIS OF TUNING CURVES: DIRECTION OF MOTION (DEG
4.8(g) Tuning for Moving Spot and Texture Fields as a Function of Velocity

Differences in tuning properties for moving spot and texture-fields were evident when stimulus velocity was varied. For the unit illustrated in fig 4.19, bar tuning was velocity invariant. At a low velocity, (1 deg./sec.), tuning for texture-field motion was weakly bimodal. Comparisons of the spot tuning curve with that for moving texture-field and moving contrast bar, show that the peak in the moving spot tuning curve is shifted from that for the contrast bar towards the prominent peak in the texture-field tuning curve at all velocities used. As velocity was increased to 3 deg./sec. and 5 deg./sec., sensitivity to texture-field motion was depressed in directions optimal for bar motion; with increasing velocity the texture-field tuning curve became progressively bimodal. By contrast, the tuning curve for a moving spot remained unimodal at all velocities.

A cell retaining a unimodal texture-field response at all velocities of texture-field motion is illustrated in fig. 4.20. Comparisons of the peak positions for bar, spot and texture-field tuning curves, at the same velocity, illustrates a common feature of unimodal units with separated peaks for bar and texture-field motion; the peak for spot tuning is shifted from the bar tuning curve peak towards that for texture motion. The feature highlighted in this figure is that, at all velocities, the peak position for the moving spot is shifted from the peak in bar tuning to that of the texture-field.
Comparison of Tuning for a Moving Contrast Spot and Texture-field at Different Velocities for Complex Cell Typically Bimodal in Its Texture-field Tuning Curve

The responses to moving texture-field and a contrast spot at a range of velocities is illustrated. At a velocity of 1 deg./sec., response to a moving texture-field is weakly bimodal. As velocity is increased to 3 deg./sec. and then to 5 deg./sec., the response to texture-field motion is increasingly bimodal. At the lowest velocity tested, response to texture-field motion is predictable from tuning for spot. At higher velocities, when texture-field tuning is bimodal, tuning for moving spot remains unimodal. Bar tuning was velocity invariant.

Unit number: 177/20. Special complex cell of the supragranular layers.
Receptive field size: 5.8 deg. sq.
Bar dimensions: 8.5 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Spot dimensions: 0.5 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
VELOCITY 1 deg/sec

VELOCITY 3 deg/sec

VELOCITY 5 deg/sec

X AXIS OF TUNING CURVES: DIRECTION OF MOTION (DEG.)
FIG 4.20

Comparison of Tuning for a Moving Contrast Spot and Texture-field at a Range of Velocities for a Complex Cell Unimodal in its Texture-field Responses

The responses to a moving texture-field and a contrast spot are illustrated at three velocities. At all velocities tested, the cell's response to a moving texture-field remained unimodal. In comparison with tuning for a moving contrast bar, the peak in the tuning curve for a moving spot is shifted towards the peak in the tuning curve for the moving texture-field.

Unit number: 177/9 Standard complex cell of the supragranular layers.
Receptive field size: 9 deg. sq.

Bar dimensions: 8.4 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Spot dimensions: 0.4 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocities are indicated in the diagram.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
VELOCITY 4 deg/sec

VELOCITY 6 deg/sec

VELOCITY 8 deg/sec

MOVING TEXTURE FIELD

MOVING TEXTURE FIELD

MOVING TEXTURE FIELD

MOVING CONTRAST SPOT

MOVING CONTRAST SPOT

MOVING CONTRAST SPOT

MOVING CONTRAST BAR

MOVING CONTRAST BAR

MOVING CONTRAST BAR

X AXIS OF TUNING CURVES  DIRECTION OF MOTION [DEG.]
An important question is whether changing velocity would alter the shift in peak position in the tuning curve for spot motion. For unit 177/20 the peaks were 259 deg. (at 1 deg./sec.), 256 deg. (at 3 deg./sec.) and 249 deg. (at 5 deg./sec.). Corresponding figures for the other unit 177/9 were 269 deg. (at 4 deg./sec.), 267 deg. (at 6 deg./sec.) and 253 deg. (at 8 deg./sec.). For the third unit 177/31, not illustrated, the figures were 142 deg. (at 4.0 deg./sec.), 150 deg. (at 7 deg./sec.) and 164 deg. (at 8 deg.). For this unit, peak positions for bar and texture respectively were 122 deg. and 172 deg. (at 7 deg./sec.). In summary, increasing velocity produces a shift in the peak position of the spot tuning curve in the direction of the texture-field tuning curve peak.

4.8(h) Tuning for Texture Bars in Comparison with Contrast Bars and Texture Fields

Tuning curves for a texture bar moving across a field of identical texture and equal mean luminance were compared with those for a moving contrast bar and a whole field of texture for 56 units. In every case, a comparison was made of the tuning curve with the texture bar of the same dimensions as a contrast bar optimal for the cell. Additionally, for some units, an extension in the width of the noise bar was made to increase summatory drive or the width of the bar was set at dimensions which appeared to provide an optimal response. For two cells, the contour of the texture bar alone, without the accompanying body of texture was moved across the background texture. This condition is described as a "ghost bar" (see
Hammond and MacKay, 1977). Tuning at different velocities was assessed for three units.

(1) Differences in Sensitivity to Texture Bar Motion

As illustrated for unit 177/12 (fig. 4.21), a cell of the supragranular layers, all cells were sensitive to the phase of the visual noise sample. Those of the supragranular layers were particularly sensitive to the clustering of elements in the noise sample, as previously reported by Hammond and MacKay (1977) for responsiveness to fields of visual noise. Taking more than one sample of visual noise allowed an estimate of sensitivity to texture bar motion to be made.

Invariably, response to a texture bar was less than that of the cell's responses to a moving contrast bar or moving texture field. Differences in sensitivity to a moving texture bar between complex cells were seen. Several factors contributed to these differences. A primary determinant of responsiveness was receptive field size. As a measure of sensitivity, mean frequency of firing at the preferred direction for texture bar motion was compared with receptive field size (minimum response field). The dimensions of the texture bar were set at those optimal for a contrast bar. For receptive fields of more than 10.5 deg. sq., little modulation of response by the texture bar was seen (bar dimensions ranged from 8 x 0.4 deg. to 9.5 x 0.8 deg.). Below that receptive field size, in general, there was a trend for responsiveness to texture bar motion to increase with
decreasing receptive field size (receptive field size ranging from 10.5 to 1.7 deg. sq.). At the extreme ends of the receptive field size range, special and standard complex cells differed in frequency distribution; the larger receptive field sizes being associated with special complex and the lower end with standard complex cells. There was, however, no clear difference in sensitivity between standard and special complex cells, reflecting the considerable overlap at intermediate receptive field sizes.

Responsiveness was clearly influenced by the tuning properties of the cell. For example, unit 177/10 and unit 169/55 had receptive field sizes of 6.5 and 6.1 deg. sq. respectively, but the response of the second unit was three times that of the first (27 spikes/sec. : 9 spikes/sec.). Comparison of tuning for moving contrast bar and texture field indicated that those neurones most sensitive to texture bar motion were those whose tuning curves for contrast bar and texture-field motion were most similar, typically those neurones of the supragranular layers (e.g. see fig. 4.23) with identical peaks in bar and texture-field tuning curves. Conversely, at the other extreme, one infragranular neurone with well separated peaks for bar and texture tuning showed little sensitivity to texture bar motion. (fig. 4.24). The range of texture-bar responses is illustrated in figs. 4.23-4.27.

Of the fifty-six units only one cell showed an identical tuning curve to the corresponding contrast bar; for this cell tuning remained invariant for two noise bars from different
Occasionally, a cell was encountered which at first appeared to exhibit identity of tuning for these stimuli but changing the sample of texture brought about a change in the tuning curve i.e. the response was phase-dependent. Some cells were unresponsive to texture bars of the same dimensions as an optimal contrast bar (8 unimodal, 8 bimodal cells). A number of units produced a response to clusters of elements within the texture bar while showing little degree of tuning (14 unimodal and 4 bimodal cells).

Some units responded well to texture bars of the same dimensions of the contrast bar chosen as optimal for the cell. Characteristically, these were units with a unimodal texture response with texture field and contrast bar tuning curve peaks in register (7 units). Four units, unimodal in their texture field tuning and with dissimilar tuning for bar and texture field tuning were seen whose responses to texture bars (of the same dimensions as the corresponding contrast bar) matched closely the texture-field response, in both peak position and width of tuning.

For cells showing a bimodal texture field response, two types of response were seen. Some units, five in total, gave texture bar responses identical in form to the cell's texture field response but reduced in strength. Six units showed a texture bar response similar to that for the texture-field but with a plateau in the tuning curve. Whilst there was some impression that cells with smaller receptive field sizes were more likely to produce a bimodal response to a moving texture-bar, it is important to note that no evaluation of
tuning for texture-bar motion, as a function of velocity, for cells with bimodal texture-field tuning was undertaken. Differences between cells showing a bimodal texture-field tuning curve may, therefore, be attributable to differences in velocity tuning characteristics. Four cells, bimodally tuned for texture-field motion, showed response to elements within the texture-bar but produced no clear tuning curve.

(ii) Response to a Dynamic Texture Contour

Response to a dynamic contour was tested on two cells. The dynamic contour was produced by a bar shaped "window" through which a second, stationary noise field was visible as the window was swept to and fro. As the foreground was also stationary, a stimulus was produced that provided the dynamic contour of the noise bar moving across the receptive field (for further details see Hammond and Mackey, 1977). For both neurones, motion of the dynamic contour produced a small modulation of response about the resting discharge level. In neither case did the response to the dynamic contour match the tuning curve for a moving contrast bar. The tuning of both units for texture bar motion was similar to the corresponding moving texture-field tuning curve, though reduced in amplitude. An example is illustrated in fig. 4.28.

4.8(iii) Temporal Summation with a Moving Texture Bar

Three cells, unimodal in their texture field response, were tested with a texture bar whose dimensions were set for a contrast bar optimal for the cell but whose velocity was
varied. A qualitative assessment was first made of the velocity range to which each cell responded to texture-field motion. Within that range, velocity was varied and response to texture field and texture bar was recorded. The data for one cell, in the form of tuning curves for texture-field and texture bar motion are illustrated in Fig. 4.29. At the lowest velocity tested, there was a weak excitatory response to the moving texture-bar. As velocity increased, there was a small excitatory response at 2 deg./sec., with reduction of response below the level of the resting discharge for the non-preferred directions. When the velocity was increased to 3.5 deg./sec., there was no evidence of an excitatory response but very clear suppression of response below the resting discharge level for a range of directions over which there was a suppression of response to a moving texture-field. The two other units, for which the effect of texture bar velocity was tested, showed similar patterns of behaviour. No data were obtained for response to texture bar motion at different velocities for cells showing a bimodal response to texture field motion.

(iv) Spatial Summation with a Moving Texture Bar

In early experiments, units were encountered giving weak or negligible responses to texture bars of dimensions of a contrast bar optimal for the cell. The increased summatory drive provided by wider texture bars was used to investigate the tuning properties of these cells.

For those cells which were unresponsive to texture bars of dimensions optimal for a contrast bar, the summatory drive
given by increasing the stimulus width was seen to produce an increased amplitude of response. There was, however, no evidence that changing the width of the noise bar changed the range of directions to which the cell responded. An example is illustrated in fig 4.30.
The tuning curves illustrate the dependence of texture-bar responses on texture sample. Responses to three texture-bars formed from different samples of visual noise are illustrated in the right-hand curves. The texture-bars were moved against a field of stationary visual noise of similar texture and equal mean luminance. For comparison, tuning for a field of visual noise and a moving contrast bar are illustrated on the left-hand side.

Unit number: 177/12 Standard complex cell of the supragranular layers.
Receptive field size: 4.6 deg. sq.

Contrast bar dimensions: 9.5 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 9.5 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for texture-field and texture-bars 2.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
X AXIS OF TUNING CURVES: DIRECTION OF MOTION [DEG.]
FIG 4.22

Comparison of Tuning for a Texture-bar Moving Across a Field of Similar Texture and of Equal Mean Luminance with Tuning for a Moving Contrast Bar and a Moving Field of Texture

Compared to response to a moving field of visual noise or contrast bar, the response to a moving texture-bar is reduced. The tuning for texture-bar motion is typical for a cell unimodal in its texture-field response with peaks in texture-field and contrast bar in register. Response to texture-bar is strong compared with units with well separated peaks in tuning for moving bar and texture-field. The breadth of tuning for texture-bar is wider than for the contrast bar of equal dimensions but matches the width of the texture-field tuning curve. Width of the contrast and texture-bar were set at dimensions which produced an optimal response to the contrast bar.

Unit number: 169/49 Unclassified complex cell of the infragranular layers.
Receptive field size: 3.2 deg. sq.

Bar dimensions: 8.5 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 8.5 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving contrast bar, texture-bar and texture-field 1.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
MOVING TEXTURE FIELD

X AXIS OF TUNING CURVES: DIRECTION OF MOTION (DEG.)
FIG 4.23

Comparison of Tuning for a Moving Texture-bar with Tuning for a Moving Contrast Bar and Texture-field for a Cell Unimodal in Texture-field Tuning with Well-Separated Peaks in Bar and Texture-field Tuning

The response of this cell to texture-bar motion is typical for a cell with a large receptive-field and well-separated bar and texture-field tuning curves. Response to a texture-bar of dimensions producing optimal response to a contrast bar is negligible.

Unit number: 178/6 Standard complex cell of the infragranular layers.
Receptive field size: 11.8 deg. sq.
Bar dimensions: 8.5 x 0.5 deg. Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 8.5 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving contrast bar, texture-field and texture-bar 3.5 deg./sec.
Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]
Comparison of Tuning for a Moving Texture-bar with Tuning for Moving Contrast Bar and Texture-field with a Small Separation of Tuning Peaks for Bar and Texture-field Motion

The response of this cell to a moving texture-bar is intermediate between that of the two preceding units illustrated. The tuning curve for bar motion is contained within the envelope of the tuning curve for moving texture-field. The peak positions of bar and texture-field tuning curves are separated by a small distance compared with many units of the infragranular layers. The response to texture-bar motion is intermediate compared with the cells illustrated in Figs. 4.22 and 4.23. The tuning curve for moving texture-bar is broader than that for the moving contrast bar and broader than that for the texture-field. As with a number of units, response to the texture-bar is dependent on clustering of elements in the texture sample.

Unit number: 177/10 Standard complex cell of the infragranular layers.
Receptive field size: 7.3 deg. sq.
Bar dimensions: 9 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 9 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving contrast bar, texture-bar and texture-field 2.5 deg./sec.
Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG]
Comparison of Tuning for a Moving Texture-bar with Tuning for a Moving Contrast Bar and Texture-field for a Complex Cell Bimodal in Its Texture-field Tuning

The response of this cell to a moving texture-bar is typical for one with a large receptive field. In response to a moving contrast bar, the cell produces a strong discharge and is sharply tuned. To a texture-bar of the same dimensions as the contrast bar, response is limited to a weak modulation of the resting discharge.

Unit number: 175/35. Standard complex cell of the infragranular layers.
Receptive field size: 12.5 deg. sq.
Bar dimensions: 9.0 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 9.0 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving contrast bar, texture-bar and texture-field 3.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]
FIG 4.26

Comparison of Tuning for a Moving Texture-bar in Comparison with Tuning for a Moving Contrast Bar and Texture-field for a Complex Cell Bimodal In Its Texture-field Tuning

The tuning curve for moving texture-bar is typical for a complex cell showing a weakly bimodal tuning curve for texture-field motion. Response to the moving texture-bar is more broadly tuned than for the corresponding contrast bar of the same dimensions. In breadth of tuning, the response to the texture-bar is broader than that for a moving texture-field. The response to the texture-bar lacks the depression in sensitivity for directions optimal for the moving contrast bar seen for some cells with bimodal texture-field tuning.

Unit number: 175/15. A special complex cell of the infragranular layers.
Receptive field size: 8.5 deg. sq.

Bar dimensions: 9 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 9 x 0.4 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving contrast bar, texture-bar and texture-field 3.5 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]
The response to a moving texture-field, at a velocity optimal for bar motion, was bimodal for this cell. The tuning curve for a moving texture-bar is clearly more broadly tuned than the corresponding contrast bar of the same dimensions. The tuning curve for moving texture-bar matches the tuning curve for moving texture-field in breadth of tuning. The response to the texture-bar shows some depression of response in directions optimal for contrast bar motion.

Unit number: 175/14 Special complex cell of the infragranular layers.
Receptive field size: 3.2 deg. sq.
Bar dimensions: 9 x 0.5 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 9 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for contrast bar, texture-bar and texture-field 2 deg./sec.
Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]
The response to a dynamic texture contour is illustrated. Response to the contour is weak and restricted to a small modulation of response around the resting discharge level. A greater response is produced by a moving texture-bar. Tuning for the texture-bar matches the corresponding texture-field response in breadth, though no depression in texture sensitivity is seen in the texture-bar response. The dimensions of the texture-bar were identical to those for a contrast bar. Separation of the two contours of the moving texture-bar contour equalled the width of the contrast bar.

Unit number: 169/17. Special complex cell of the infragranular layers.
Receptive field size: 7.4 deg. sq.

Bar dimensions: 9.2 x 0.4 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 9.2 x 0.4 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for contrast bar, texture-bar, texture-contour and texture-field 3 deg./sec.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
MOVING CONTRAST BAR

MOVING TEXTURE BAR

MOVING TEXTURE BAR CONTOUR

X AXIS OF TUNING CURVES: DIRECTION OF MOTION (DEG.)
Temporal Summation with a Moving Texture-bar

At a velocity optimal for a moving contrast bar, the cell was only weakly responsive to a texture-bar of equal dimensions. The effect of temporal summation is illustrated in the tuning curves obtained at a range of velocities. At the lowest velocity illustrated, there is a weak excitatory response to the texture-bar. As velocity was increased, there was a small excitatory response to the texture-bar at 2 deg./sec. with suppression of response below the level of the resting discharge apparent for non-preferred directions. When the velocity was increased to 3.5 deg./sec., there was little evidence of an excitatory response, but very clear suppression of response below the resting discharge level for a range of directions over which there was a suppression of response for a moving texture-field.

Unit number: 178/71 An unclassified complex cell of the infragranular layers.
Receptive field size: 5.3 deg. sq.

Bar dimensions: 9 x 0.6 deg.
Contrast: 0.6 log units below noise background.
Texture-bar dimensions: 9 x 0.6 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocities for moving texture-field and texture-bar are indicated in the diagram.

Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
TEXTURE FIELD

TEXTURE BAR

3.5 deg/sec

2 deg/sec

1 deg/sec

X AXIS OF TUNING CURVES : DIRECTION OF MOTION [DEG.]
FIG 4.30

Spatial Summation for a Moving Texture-bar.

The effect of spatial summation on response to a moving texture-bar is illustrated. Stimulus velocity was set at that optimal for a moving contrast bar. The width of the texture-bar was increased and the tuning curves for each width are illustrated. Increased stimulus width is associated with increased response but no change in the range of directions from which response is elicited.

Unit number: 182/64 An unclassified complex cell of the infragranular layers.
Receptive field size: 4.6 deg. sq.
Texture-bar dimensions: 8.5 x 0.5 deg.; 8.5 x 0.5 deg.; 8.5 x 0.5 deg.
Contrast bar dimensions: 8.5 x 0.5 deg.
Texture-field dimensions: 10 x 10 deg.
Stimulus velocity for moving texture-field and texture-bar 2 deg./sec.
Calibration signal: 50 spikes/sec.
Binwidth: 10 deg.
Resting discharge indicated by the dotted line.
CHAPTER FIVE: Implications of the Tuning of Complex Cells for Contrast and Textured Stimuli for Models and the Role of the Complex Cell in Visual Analysis

5.1 An Overview

The main findings of the experimental investigation can be summarized. Tuning of complex cells for a stationary, flashed bar has poor predictive value for response to moving stimuli; typically, tuning for a stationary bar is sharper and more symmetrical than the same bar in motion and preferred direction for a moving spot is not orthogonal to preferred orientation for a stationary bar. Preferred direction for a moving texture-field can be predicted from the preferred direction for a moving spot. Features of texture-field tuning due its spatial extent are breadth of tuning and bimodality. Comparison of tuning for a moving texture-bar with tuning for a moving contrast bar and texture-field indicates that, in the absence of luminance cues, complex cells are sensitive only to texture motion. Implications of these findings for models for the role of intracortical inhibition in the generation of tuning properties and for the role of the complex cell in visual analysis are discussed.

The findings that tuning for a stationary bar is sharper and more symmetrical than the same bar in motion and that preferred direction for a spot is not orthogonal to preferred orientation for a stationary bar are reviewed in the context of Goodwin and Henry's (1975) model for direction selectivity. A functional interpretation is given to the asymmetry in tuning
for a moving bar. The present study has established that the degree of asymmetry in bar tuning is unrelated to the complex cell's preferred orientation but arises from bar motion. The greater asymmetry in tuning for a moving contrast bar of complex cells compared to simple cells, it is argued, reflects a functional difference which may be related to the distinct role of the complex cell in visual analysis.

Features of the complex cell's tuning curve for texture-field motion attributable to spatial and temporal factors are considered. Comparison of tuning for spot and texture-field is interpreted to be consistent with the view that bimodality of texture-field tuning arises from an interaction between orientation and direction selective mechanisms. The functional implication of the absence of a contour response by complex cells to a moving texture-bar is evaluated in the context of Hubel and Wiesel's model for form representation by contour analysis.

The role of the complex cell in visual analysis is discussed and the proposition that the complex cell has a distinct role is considered. The tuning properties of complex cells for contrast and textured stimuli reported in the present study are related to the role of the complex cell in visual analysis. A starting point for the discussion is a review of models for the role of the striate cortex in the representation of form. "Feature extraction" and "population coding" models are reviewed. The feature-extraction model of Hubel and Wiesel (1962, 1963) is rejected on the basis that (1) the tuning properties and receptive field structure of the single cell do
not correspond to the requirements of a feature-extraction model and (2) intracortical connectivity is incompatible with a serial, feature-extraction role. A population coding model of representation is adopted and the roles that simple and complex cells might play in population coding considered. A role for complex cells in the analysis of moving objects is established. Two important conclusions are reached from the discussion; (1) that the asymmetrical coupling conferring on complex cells their direction selectivity also provides a compensation for the distortion of an object associated with its movement and (2) the perception of form of a moving texture-bar under conditions in which complex cells respond only to texture motion prescribes a role for direction-selective units in the representation of form.

5.2 The Tuning of Complex Cells for Contrast Stimuli

For most striate cortical neurones, the tuning curve for a moving bar is asymmetrical (Hammond and Andrews, 1978b). The degree of asymmetry of bar tuning does not increase with recording depth in penetrations normal to the cortical surface (Lee, Heggelund, Hulme and Creutzfeldt, 1977; Hammond, 1978). Areal differences between A.17 and A.18 in asymmetry of tuning have been reported (Hammond and Andrews, 1978b) which are consistent with known areal differences in the extent of horizontal anisotropies of horizontal fibres (Creutzfeldt, Garey, Kuroda and Wolff, 1977). Asymmetries are not therefore a byproduct of damage to the fine intracortical wiring with electrode advance. In the present study, tuning for a stationary contrast bar was seen to be sharper and more
symmetrical than for the same bar in motion; asymmetries in bar tuning arise from stimulus motion.

Conditions of stimulus presentation cannot have contributed to the result. For the simple cell, there is evidence for figure/ground interactions between a contrast bar and a textured background (Hammond and Mackay, 1978; Hammond and Mackay, 1981). The importance of a homogeneous background for obtaining a flash response from simple cells has been reported (Emerson and Gerstein, 1977). Hammond and Mackay (1981) found that moving a field of visual noise in synchrony with a contrast bar depressed bar response in 70% of simple cells. By contrast, Hammond (1978) found that the presence of a stationary background of visual noise did not influence tuning for a moving contrast bar for his sample of complex cells. In the present study, interactions between moving bar and stationary texture were not found.

Complex cells are not only more broadly tuned than simple cells (Henry, Dreher and Bishop, 1974; Watkins and Berkley, 1974; Albus, 1975; Hammond and Andrews, 1978b; Leventhal and Hirsch, 1978; DeValois, Yund and Hepler, 1982) but also more asymmetrical (Henry, Dreher and Bishop, 1974; Hammond and Andrews, 1978b) in tuning for a moving bar. The possibility is raised that this represents a functional difference in tuning between simple and complex cells. This interpretation is made in discussion of the role of the complex cell in visual analysis. It is therefore important, at this stage, to rule out the possibility that the greater asymmetry of tuning of complex cells is artefactual. Deviations from linearity of the
tuning curve for moving bar are associated with broadly tuned units (DeValois, Yund and Hepler, 1980). It should be emphasised, as is illustrated in the tuning curves for comparisons of tuning for stationary and moving contrast bars (chapt. 4) that asymmetries of bar tuning are found for complex cells of a broad range of tuning widths.

The suggestion of Rose and Blakemore (1974) that tuning width is inversely related to angular distance from the vertical and horizontal meridians raises the possibility that asymmetrical tuning is related to preferred orientation. The proposal was made by these authors for simple but not complex cells. In the present study, degree of asymmetry was not found to be related to preferred orientation, confirming Rose and Blakemore’s reports for the complex cell. It was argued earlier (chapt. 3) both that tuning width is unrelated to preferred orientation (Wilson and Sherman, 1976; Gilbert, 1977) and that cells with preferred orientations around the vertical and horizontal meridians are not over-represented (Rose and Blakemore, 1974; Finlay, Schiller and Volman, 1976; Wilson and Sherman, 1976; Poggio, Doty and Talbot, 1977). An over-representation of cells tuned to the vertical/horizontal or oblique was not found in the present study nor was a dependence of tuning width on preferred orientation.

Henry, Bishop and Dreher (1974) made no evaluation of tuning of complex cells for stationary and moving contrast bars. For simple cells, identical tuning for the two stimuli was reported. The finding in the present study, that complex cells symmetrically tuned for moving bar show similar tuning
for a stationary bar suggests that Henry, Bishop and Dreher's (1974) results for simple cells might be a consequence of sampling from symmetrically tuned units. The recent study by Heggelund and Moors (1983), with a much larger sample of simple cells, demonstrated that simple cells asymmetrically tuned for bar motion are more sharply and symmetrically tuned for a stationary bar. The discrepancy between Henry, Bishop and Dreher's (1974) study and investigations of receptive field structure with stationary and moving contrast bars by Benevento, Creutzfeldt and Kuhnt (1972), Creutzfeldt, Kuhnt and Benevento (1974), Innocenti and Fiore (1974) and Fries and Albus (1976) may therefore be resolved. The possibility exists that differences in the tuning properties of simple cells between Henry, Bishop and Dreher's (1974) and Heggelund and Moors (1983) studies may reflect sampling from different populations of simple cells differing in morphology and connectivity.

On the basis of the present study of complex cells and of the strong support given by Heggelund and Moors (1983) study for Rose's (1977) and Hammond and Andrews' (1978b) findings of sharper and more symmetrical tuning for stationary than moving bars for simple cells, it can be concluded that the direction selectivity of both simple and complex cells cannot be accounted for by the spatial organization of the receptive field mapped with a stationary, flashed bar rotated symmetrically about the cell's receptive field centre. However, the degree of asymmetry of complex cells' tuning for moving bars is greater than for simple cells, suggesting a functional difference.
Henry, Bishop and Dreher's (1974) study of simple cells indicated that preferred direction for a moving spot is orthogonal to preferred orientation for a stationary bar. Also, these authors reported that, for a population of five complex cells, preferred direction of a moving spot was identical to that for a moving bar. The present study does not contradict these findings but suggests they have limited validity in describing complex cells' tuning characteristics. Only those cells symmetrically tuned for bar motion showed identical preferred direction for spot and moving bar with preferred direction for spot orthogonal to preferred orientation for a stationary bar. Directional bias could not be predicted from tuning for a stationary bar. Given the complex non-linearities of the length-response curve (Bodis-Wollner, Pollen and Ronner, 1976; Rose, 1977; Hammond and Andrews, 1978c) one question for future investigation is the contribution of interactions within and between the component parts of the receptive field in the shift in preferred direction with bar length.

In one aspect, the present study is at variance with Henry, Bishop and Dreher's (1974) study. The existence of those authors' second group of complex cells, for which reduced stimulus length brought reduced response but no change in breadth of tuning was not confirmed. Their result was probably a consequence of deriving tuning curves over a limited range of orientations in their study.
5.3 Implications for Models

In the earlier discussion of models for the role of intracortical inhibition, it was suggested that insufficient data were available for evaluation of Goodwin, Henry and Bishop (1975) model for direction selectivity; Goodwin, Henry and Bishop (1975) made no evaluation of stationary flash and movement components in response to a moving contrast bar and Henry, Bishop and Dreher’s (1974) data were based on symmetrically tuned units.

The validity of Goodwin, Henry and Bishop’s (1975) model can be assessed on two levels: the descriptive level and at the level of mechanism. Earlier evaluation of the model focused on mechanism. At that stage, it was argued that assumptions derived from Hubel and Wiesel’s (1962, 1963) and Bishop’s (Bishop, Coombs and Henry, 1971b; Bishop, Coombs and Henry, 1973) models, of convergence of afferent input and a fixed spatial relationship between intracortical inhibition and afferent excitation, are untenable. Also, it was established that the simple cell is not invariably the recipient of input from LGN cells showing linear summation. Goodwin, Henry and Bishop (1975) attempted an explanation of simple cell’s direction selectivity from assuming the properties of intracortical inhibition derive from the spatial organization and summatory properties of the geniculate input to the cell.

Goodwin, Henry and Bishop’s (1975) model had its antecedent in Rodieck and Stone’s (1965) analysis of response by retinal ganglion cells to moving stimuli. Rodieck and Stone
(1965) reported that the response to a moving spot was "directly correlated with the gradient of the receptive field defined by flashing lights" (i.e. spots). By making the assumptions of (1) a constant time course for a cell's responses to a stationary flashing spot stimulus, whatever its position in the receptive field and (2) a linear summation of influences reaching it from different parts of the receptive field, its responses to various moving stimuli (spots and bars of various dimensions) would be predictable from its sensitivity profile. This analysis provided the basis for Goodwin, Henry and Bishop's (1975) suggestion that the direction selectivity of simple cells might be predictable from the sensitivity profile mapped with a stationary flashed bar. Linearity of summation and a constant time course for inhibition were assumed; intracortical inhibition would reflect the properties of the afferent input and afferent input would be provided by cells showing linear summation.

Goodwin, Henry and Bishop's (1975) model fails not only at the level of mechanism but also at the descriptive level. Since, in the present study, preferred direction for a moving spot was seen to change as a function of velocity, the complex cell receptive field must reflect temporal as well as spatial factors (c.f. also Hammond and Reck, 1980 in the context of the dependence of texture-field tuning on velocity). As revealed in both physiological and anatomical studies (chapter two), most, if not all, complex cells receive intracortical excitatory inputs with many complex cells additionally receiving a direct excitatory input from the LGN. The complex cell receptive field comprises components from intracortical
inhibition which are not in a fixed spatial relationship to the excitatory input.

Contained within the model of Goodwin and Henry (1975) was the assumption that direction-selective inhibition is initiated by a stationary edge, whilst the study of Henry, Bishop and Dreher (1974) provided evidence that the receptive field profile mapped with a stationary bar rotated around the geometric centre of the receptive field is identical to the receptive field structure determining the tuning curve for a moving bar. The present study indicates that the component of the receptive field mediating the direction selective response to a moving bar is not reflected in the receptive field element mapped with a stationary bar rotated around the cell's receptive field geometric centre. Though the asymmetry in tuning for a moving bar arises from bar motion, the result does not demonstrate a dependence on temporal factors independent of the spatial organization of the receptive field.

Both Goodwin, Henry and Bishop (1975) and Schiller, Finlay and Volman, (1976) assumed each cell to have a single preferred direction for stimulus motion. Functionally, such tuning characteristics would support a feature extraction model of representation; the single cell would signal movement in a particular direction. Not only preferred direction for bar and texture differ (Hammond 1978 and subsequently), but also reduction of stimulus length produces a change in preferred direction. Such tuning behaviour is incompatible with a feature-extraction model but consistent with a population coding model of representation; the tuning properties of
complex cells depend on the configurational properties of the stimulus.

5.4 The Tuning of Complex Cells for Textured Stimuli

Though moving fields of visual noise provide a stimulus free from orientation, a complicating factor in interpreting the tuning curve for moving texture-field arises from the spatial extent of the stimulus. A comparison of tuning for spot and texture-field is interesting in this context. Tuning for spot has a high predictive value for preferred direction for texture-field motion; for cells unimodal in texture-field tuning at all velocities and for bimodal cells at low velocities. For cells bimodal in texture-field tuning at higher velocities, spot tuning remains unimodal and shifts to the prominent peak in texture-tuning with increased velocity.

In the discussion of the bimodality of texture-field tuning, two possibilities raised by Hammond (Hammond, 1978; Hammond and Reck, 1980; Hammond and Smith, 1983) were considered plausible interpretations for the origin of the bimodality. These were that the bimodal tuning is a product of the direction mechanism alone or that it arises from an interaction between orientation and direction selective mechanisms. In the framework of Goodwin, Henry and Bishop's (1975) model for direction selectivity one would predict bimodal spot tuning as a product of a bipartite spatial division of the receptive field.

Bishop, Kato and Orban (1980) reported bimodal spot tuning
for a cell bimodal in texture-field tuning. In one respect only is the present study in agreement with Bishop, Kato and Orban's; reduction in bar length produces a shift in preferred direction. Bimodal spot tuning curves were seen in no case. Bishop, Kato and Orban's (1980) result was based on a complex cell with marked end-inhibition. A possible explanation for the discrepancy may be that complex cells with marked end-inhibition differ in their tuning properties.

Early reports suggested differences in direction selectivity of complex cells with and without end-inhibition (Kato, Bishop and Orban, 1978; Orban, Kato and Bishop, 1979ab). Also, Sillito (1977) has reported contrasting differences in the effect of bicuculline on Type I complex cells of lamina III and hypercomplex cells of the same lamina. Direction selectivity of Type I cells was eliminated following the iontophoretic application of bicuculline but the direction selectivity of hypercomplex cells from layer III was unaffected. Sillito (1977) interpreted this to suggest the possibility of differing synaptic organization underlying the directional specificity of the two types of cell. However, as Bishop, Kato and Orban (1980) themselves found, direction-selective and end-inhibition are derived from separate mechanisms.

Bimodal tuning for spot would imply a bipartite spatial division of the receptive field, a result which would be surprising given the unimodal tuning for texture of bimodal cells at low velocities (Hammond and Reck, 1980a, b). In the present study, in addition to the population of complex cells
recorded, three complex cells with significant end-inhibition were recorded. Two of these cells were bimodal in texture-field tuning. Both showed unimodal spot tuning curves. In summary, Bishop, Kato and Orban's (1980) report of bimodal spot tuning is without support.

On the basis of comparison of tuning for spot and texture-field motion it is reasonable to suggest that cells have a single preferred direction for texture motion and depression of texture sensitivity in the tuning curve for cells showing bimodal tuning arises from an interaction between orientation and direction selective mechanisms. It remains problematical for such a view (c.f. Hammond and Smith, 1983a, b) that bimodal texture-tuning persists at velocities beyond the cut-off velocity for bar response. A second problem is that some cells show identical preferred direction for spot and bar motion but that these cells are distributed among cells unimodal and bimodal for texture tuning. A functional diversity is suggested, as is implied by the studies of Hammond and Smith (1983a,b) that some complex cells respond to the relative motion of bar and texture whilst others respond to the bar regardless of the context in which motion occurs. Connectivity differences remain obscure.

Comparisons of tuning for moving texture-bar with moving contrast bar and texture-field were undertaken in the context of Hubel and Wiesel's hypothesis of form representation by contour-selective neurones. The study reported here has shown that whilst complex cells differ in sensitivity to moving texture-bars, they are uniform in tuning properties; complex
cells do not respond to the dynamic contour of a moving texture-bar.

Hammond and MacKay (1977) reported that the majority of complex cells are less sensitive to texture-bar motion than to a contrast bar of optimal dimensions for the cell and a moving texture-field. Differences in preferred direction for texture and contrast bars were reported in the same study. These findings were confirmed. The present study extends the work of Hammond and MacKay in providing a systematic quantitative evaluation of tuning for a moving texture-bar with contrast bar and texture-field.

For cells unimodal in their texture-field tuning, tuning for moving texture-bar can be simply described. In both peak position and breadth of tuning, texture-bar tuning matched the cell's tuning for moving texture-field. In the limited case of cells with identical peaks for texture-field and contrast bar tuning curves was preferred direction for texture-bar identical to that for contrast bar. Breadth of texture-bar tuning, however, matched the texture-field curve.

Complications arise in the case of cells bimodally tuned for texture motion because of depressed sensitivity to texture motion for directions optimal for contrast bar motion. Interactions between orientational and directional mechanisms were evident in the bimodal response to a texture-bar seen for some neurones. The velocity dependent response to a moving texture-bar was not investigated for bimodal cells. Several observations rule out the possibility that cells bimodal in
texture-field tuning respond to the texture-bar contour. Given the number of units from which data were collected, some evidence of response to the texture-bar contour, even if reduced in amplitude, would have been seen. More directly, many units produced a tuning curve, matching in breadth the tuning curve for moving texture-field, with no suppression of response in directions optimal for bar motion.

The conclusion from comparisons of tuning for moving texture-bar with moving contrast bar and texture-field is that, given certain limitations of spatial summation, complex cells are uniform in tuning; in the absence of luminance cues, complex cells are responsive only to texture motion. Support for the conclusion is given by the absence of an orientation-selective response to a dynamic contour. The result indicates that the representation of form cannot be achieved solely by contour detectors.

Effects of spatial and temporal summation with a texture-bar produced several interesting results. It is important to emphasise that reducing or broadening the texture-bar width brought no transition from an edge response, as seen with the contrast bar, to a purely directional response as seen with a texture-field. Another feature seen with broadening of the texture-bar was that the range of directions to which the cell responded did not change with stimulus width; in the conceptual framework of Barlow and Levick (1965), there was no evidence of recruitment of "sub-units".

Two aspects of experiments concerned with temporal
summation with texture-bars of dimensions optimal for a contrast bar warrant discussion. Firstly, it was clear that one could not "trade-off" temporal for spatial summation. A cell might be unresponsive to a bar of dimensions optimal for a moving contrast bar and broadening of the texture-bar's width would produce an excitatory response. Maintaining the same dimensions for the texture-bar at those optimal for a contrast bar, but increasing stimulus speed, did not produce an excitatory response from the units tested. By contrast, increased stimulus velocity was accompanied by suppression of response in directions in which suppression of response was seen in the texture-field tuning curve. These observations cast doubt on Bishop, Kato and Orban's (1980) observation for complex cells that inhibition in the non-preferred direction is augmented by the same stimulus parameters that increase the excitatory response in the preferred direction.

Differences in Tuning Properties Between Different Classes of Complex Cells

MacKay (1976), commenting on the concept of the columnar organization of orientation in the striate cortex, suggested that, given a wider range of stimuli, a wider diversity of functional properties/trigger features between cells showing the same orientation preference may be seen. Potentially, a combination of contrast and textured stimuli provides an opportunity for investigating the functional diversity of complex cell sub-groups.

The classification of complex cells has primarily been
based on properties of summation along the "orientation axis". It is an unresolved question whether this property indicates separate roles for "standard" (including B cells) and "special" complex cells. Laminar differences in distribution of these cell types does suggest differences in afferent and intracortical connectivity and potentially distinct roles.

There is some evidence to suggest that "standard", "special" and B cells differ in geniculate input. Tanaka (1983) reported that "special" cells receive only Y cell input but "standard" complex cells receive both Y and X fibre input. Henry, Mustari and Bullier (1983) reported that B cells receive only W input. The association, suggested by Tanaka (1983), of a differential input to standard and special complex cells with the summatory properties of those two cell groups would suggest a link between, if not a dependence on, summatory behaviour and afferent input which is, at best, unproven and difficult to reconcile with the particular connectivity scheme suggested. Patterns of intracortical connectivity suggest separation of intracortical pathways between standard and special complex cells; lamina VI "standard" complex cells receptive field structure is principally determined by input from lamina V "standard" complex cells (Gilbert and Wiesel, 1979, 1981). Anatomical and physiological evidence has revealed a prominent pathway from lamina III to lamina V potentially linking "standard" and "special" complex cells of lamina III with their counterparts in lamina V (Creutzfeldt, Garey, Kuroda and Wolff, 1977; Lund, Henry and Harvey, 1979; Mitzdorf and Singer, 1978; Gilbert and Wiesel, 1979, 1981). However, there is no evidence for a segregation of pathways such that lamina III
"standard" complex cells contact lamina V "standard" complex cells and "special" complex cells in lamina III provide the exclusive supragranular input to lamina V "special" complex cells.

Segregation of outputs of "standard", "special" and B cells is suggested by the selective input from B cells to the Clare-Bishop area (Henry, Lund and Harvey, 1978), that lamina VI complex cells are exclusively "standard" complex (Gilbert and Wiesel, 1981) and from the early report that "special" complex cells provide the striate cortical input to the superior colliculus (Palmer and Rosenquist, 1974). However, Sillito reported differences within the standard complex group in the derivation of their orientation selectivity (Sillito, 1979). Also, Harvey (1980) has reported "standard" as well as "special" complex cells project to the superior colliculus.

The results of the present investigation emphasise the independence of many tuning properties of the "standard"/"special" dichotomy. It is clear that "standard" and "special" complex cells are not distinguished by many aspects of response. Both "standard" and "special" complex cells are distributed among cells unimodal and bimodal in texture-field tuning, as Hammond (1978) has also reported. The tuning of both categories of cell for texture-bar motion showed an identity to the cell's texture field response. Not only are some "special" complex cells unresponsive to bar flash but also some "standard" complex cells show this behaviour (see also Gilbert, 1977). It was, however, apparent that cells of both the "special" and "standard" populations unresponsive to bar
flash are more broadly tuned than cells responsive to bar flash suggesting a functional difference.

Some distinctions between "standard" and "special" complex tuning characteristics were, however, noticeable. While both groups showed a shift in the peak of spot tuning compared to bar tuning, the shift was more pronounced for "special" complex cells. Also, as a group, "standard" complex cells were more sharply tuned for a moving bar than "special" complex cells. Harvey (1980) has commented on the inverse relationship between orientation and direction selectivity. There was also some indication of class-specific differences in directional bias between "standard" and "special" complex cells; "standard" complex cells direction biased for bar were directionally selective for spot but "special" complex cells direction biased for bar could also be biased for spot. Data are too limited to draw firm conclusions. Differences in breadth of tuning for spot and texture-field tuning were clearly class-specific. It remains an unanswered question the extent to which differences amongst the complex cell population are obscured by a lack of information about laminar distribution of recorded units.

The finding of a cell with bimodal tuning for a moving contrast bar is interesting in suggesting a greater diversity of complex cells' tuning characteristics and receptive field organization than has previously been described for striate cortex. Cells with more than one preferred orientation have been reported in extrastriate cortex by Hubel and Wiesel (1965). Hubel and Wiesel (1965) described "higher order" hypercomplex cells in area 19, the distinguishing
characteristic of which was the property of responding to a moving contrast bar at two different, orthogonal orientations. Such neurones were exclusive to area 19, typically in "columns" which contained complex and "lower order" hypercomplex cells, some of which responded to one of the two orientations to which the "higher order" hypercomplex cell would respond, other members of the column responding to the other orientation (Hubel and Wiesel, 1965). Hubel and Wiesel (1965) suggested the construction of the "higher order" hypercomplex cell receptive field by input from complex and "lower order" hypercomplex cells of the same column with each of the two preferred orientations deriving from the preferred orientations of the two populations of complex and "lower order" hypercomplex cells. "Higher order" hypercomplex cells had receptive fields close to the representation of the area centralis.

The unit described in the present study had peaks in the moving bar tuning curve separated by 40 deg. Stability of the bimodal tuning for a moving contrast bar over a period of two hours would argue against an artefactual basis for the tuning curve. While caution should be exercised in putting too much weight on the observations from one unit, recently other such units have been recorded (P. Hammond; J. Crook; personal communications) giving support to the existence of a group of complex cells with bimodal tuning for a moving bar.

A characterization of the tuning properties of these neurones would be a precondition for an understanding of the receptive field structure underlying their stimulus selectivity.
and functional role. A primary question is whether the bimodality is related to the bimodality in tuning for a moving texture-field seen for some complex cells. The unit recorded in the present study would argue against this; it was unimodal in texture field tuning. Hubel and Wiesel's (1965) suggestion of formation of "higher order" hypercomplex cells' receptive field structure from excitatory input from two populations of cells of the same "column" with orthogonal preferred orientations is clearly an inappropriate basis for explaining bimodality of bar tuning in area 17. How such neurones in area 17 might have their receptive fields constructed is unclear. Whether such neurones "cluster" in distribution as was the case for Hubel and Wiesel's (1965) population of higher order hypercomplex cells in area 19 would be interesting to investigate. The point emphasised at this stage is that of a greater diversity of tuning properties of complex cells than previously suggested and that such neurones exist in striate cortex and are not exclusive to extrastriate cortex.

5.5 The Role of the Complex Cell in Visual Analysis

1. The Representation of Form

Approaches to the representation of form are broadly divided between those models which posit single cell modes of representation and those which suggest representation in the responses of a population of neurones; these quite different approaches are labelled "feature extraction" and "population coding" models respectively. The latter includes Fourier models. Hubel and Wiesel's (1962, 1963) model falls into the
category of a feature extraction model. The feature-extraction models have their origin in studies of the stimulus specificity shown by retinal ganglion cells of frog and rabbit (Barlow 1953; Lettvin, Maturana, McCulloch and Pitts, 1959, Lettvin, 1961; Maturana, Lettvin, McCulloch and Pitts, 1960; Barlow, 1964). These early studies revealed cells with highly specific stimulus requirements suggesting a feature extraction role for the single cell. The coding operations which a cell performs would be delineated by reference to the feature of the visual scene to which the single cell seems optimally sensitive. The role of the single cell is to extract that feature from the visual environment.

Between trigger feature and receptive field structure a relationship of key to lock is implied. Feature-extraction models require that the firing of the single cell signifies to the brain the occurrence of a particular stimulus in a certain part of the visual field. The formation of a "Gestalt" from elementary features requires a hierarchical organization of neurones with convergence at each level with higher order neurones whose firing represents a stimulus symbolized by a word (Creutzfeldt and Nothdurft, 1978). Feature extraction implies that perceptions are caused by the activity of a small number of neurones selected from a very large population of predominantly silent cells (Barlow, 1972).

Feature-extraction models have been held to be logically and empirically untenable (see Uttal, 1971; Szentagothai and Arbib, 1974; Creutzfeldt, 1977, 1978 for reviews). A central argument against the feature extraction approach is that the
single cell cannot signify the presence of a stimulus since few, if any, neurones increase their firing rate as a function of only one stimulus parameter (Erikson, 1968; Uttal, 1971; Poggio, 1972; Hoepfner, 1974; Bartlett and Doty, 1974; Hammond and MacKay, 1977). Even for one stimulus parameter cortical neurones are often broadly tuned so that widely separated values of the presumed trigger feature produce equivalent discharge rates (Erikson, 1968; 1974).

Hubel and Wiesel (1962, 1963) proposed a role for the single cell in contour analysis. In their variant of the feature extraction model the striate cortex was divided into functional units or "columns" within which serial analysis was undertaken by the simple, complex, hypercomplex chain. Serial analysis by such a hierarchical chain, with convergence at each stage, is theoretically unsound and contradicted by known patterns of intracortical connections. Creutzfeldt and Nothdurft (1978) commented that convergence from simple to complex to hypercomplex cells would lead to a loss of information from one level to the next without gaining unequivocal and sufficiently exact information on the feature that is supposed to be represented at the next level. Patterns of connectivity between simple and complex cells are not constrained by a serial chain (Hoffmann and Stone, 1971; Stone, 1972; Stone and Dreher, 1973; Toyama, Mackawa and Takeda, 1973; Toyama, Kimura, Shida and Takeda, 1977; Movshon, 1975; Hammond and MacKay, 1977). In striate cortex, there is no hypercomplex cell stage (Dreher, 1972; Camarda and Rizzolatti, 1976; Wilson and Sherman, 1976; Hammond and Andrews, 1978a, b; Leventhal and Hirsch, 1978), though cells
with complex tuning properties have been described in area 18 and 19 of the cat (Hubel and Wiesel, 1965; Hammond and Andrews, 1978b) and in the inferotemporal cortex of monkey (Gross, Rocho-Miranda and Bender, 1972). Evidence for papal neurones (Barlow, 1972) remains, however, scant.

A question of importance for the "orientation detector" model is in the synthesis of elements of contour to represent shapes. Creutzfeldt and Nothdurft (1978) have raised objections to Hubel and Wiesel's (1962, 1963) model if it is assumed that the synthesis occurs in striate cortex and that the cortical representation is an affine transformation of the visual scene. Creutzfeldt and Nothdurft (1978) suggested that the necessary, but also sufficient condition for synthesis is that the responses elicited by the successive points of a line should be represented in an orderly sequence in the cortical map of the visual field i.e. the representation of the visual field, at the cortical level, should be an equivalent transformation of the real world. Splitting up of the continuous representation of contours in the cortex because of clustering of cells with similar orientations into columns impedes formation of a Gestalt. A counter argument to this criticism would be either to assume that continuity of line elements to form shapes is produced by specific patterns of connectivity within the striate cortex or that the synthesis of elements occurs at a stage beyond the striate cortex. However, when the shape of an object is defined by a texture contour the problem of continuity of contour elements is particularly acute (see Caelli, Preston and Howell, 1978).
The alternative to the representation of form by a hierarchical process of feature extraction is some form of population coding. Population coding does not necessarily preclude form representation by contour analysis.Positing a model of population coding, however, raises the question of the roles performed by simple and complex cells in the population response.

(i1) The Role of the Complex Cell in Visual Analysis

It has been suggested that simple and complex cells perform parallel roles in visual analysis by virtue of differential input from the lateral geniculate nucleus (Hoffmann and Stone, 1971; Stone, 1972). The retino-geniculate pathway has been conceived as comprising distinct channels beginning with the major groupings of ganglion cells which subserve distinct functions (Rowe and Stone, 1980). Separate channels mediating information about form or motion have been suggested (Tolhurst, 1973; Kulikowski and Tolhurst, 1973). Segregation of parallel pathways at the geniculo-cortical synapse could determine that simple and complex cells receive and process different aspects of the visual image. If X and Y pathways were to be equated with "form" and "motion" channels (Tolhurst, 1973; Kulikowski and Tolhurst, 1973), and if the X and Y streams were to segregate at the geniculo-cortical synapse with X input to simple cells and Y input to complex cells (Hoffmann and Stone, 1971; Stone, 1972), this might suggest that simple and complex cells constitute form and motion analysing systems respectively. Psychophysical evidence for form and motion channels, the
equation of these with X and Y pathways and the association of simple and complex cells with form and motion analysing systems is therefore evaluated.

Psychophysical evidence for separate "form" and "motion" channels is substantial. For example, Tulunay-Keesey (1969) reported that flashing or flickering a bar-shaped stimulus pattern prolonged its visibility but that, at flicker frequencies 5-30 Hz perception of the flicker of the stimulus persists after the perception of its shape is lost. Tolhurst (1973) confirmed Robson's (1966) observation that flicker increases the visibility of coarse but not fine grating stimuli and Blakemore and Campbell's (1969) observation of a lowest adaptable spatial frequency channel. But, additionally, Tolhurst (1973) reported that when the adapting grating was moving instead of stationary, channels selective for frequencies much coarser than the coarsest channels detected with stationary gratings were evident. Kulikowski (1971) reported that the psychophysical threshold for the perception of flickering gratings depends on whether they are switched on or off or counterphased and that the threshold for counterphase was half that for on-off flicker at low spatial frequency but fine gratings' threshold for counterphase and on-off modulation did not differ. Interpretation of some of these experiments has been questioned (see Macleod, 1970 for review).

Behavioural studies with the cat have produced evidence consistent with human data in suggesting separate form and motion channels (Blake and Camisa, 1977). Identification of form and motion channels with cat X and Y fibre systems was
suggested by Tolhurst's studies (1973). Tolhurst (1973) noted that 'movement' channels were very sensitive to low spatial frequencies (≤3 cycles/deg.) and 'pattern' channels to high spatial frequencies (>3 cycles/deg.), properties similar to Y and X fibres respectively.

The picture is more complex. Kulikowski and Tolhurst (1973) have shown that pattern detection is mediated by the X-like system at high spatial frequencies and by the Y-like system at low frequencies. At intermediate frequencies, both systems are likely to contribute to this function. Lennie (1980) reported that when the temporal contrast sensitivities of X and Y ganglion cells, in cat, are measured under conditions in which shape and motion channels are demonstrated psychophysically, Y cells are no less sensitive than X cells to stimuli at low temporal frequency. X/Y pathways do not segregate into parallel and independent simple/complex streams at the geniculo-cortical synapse (Ikeda and Wright, 1975; Singer, Tretter and Cynader, 1975; Movshon, Thompson and Tolhurst, 1978a, b, c; Lee, Meggelund, Hulme and Creutzfeldt, 1977; Bullier and Henry, 1979a, b, c; Tanaka, 1983). Simple and complex cells cannot be equated with 'form' and 'motion' processing systems. The existence of a third retino-striate pathway, for W cells, provides a further complication in understanding information transfer via parallel pathways to the striate cortex.

Though distinct roles for simple and complex cells cannot be established as a product of differential input from the lateral geniculate nucleus, a number of properties do, however,
suggest distinct roles for simple and complex cells in visual analysis: the sharper tuning of simple compared with complex cells (Henry, Dreher and Bishop, 1974; Watkins and Berkley, 1974; Albus, 1975; Hammond and Andrews, 1978b; Leventhal and Hirsch, 1978; DeValois, Yund and Hepler, 1982); the greater symmetry of tuning of simple compared with complex cells (Henry, Dreher and Bishop, 1974; Hammond and Andrews, 1978b); constancy of tuning for simple cells, but increased breadth of tuning for complex cells with eccentricity (Gilbert, 1977; Leventhal and Hirsch, 1978; Watkins and Sherman, 1976); an increase in the proportion of complex cells with eccentricity (Wilson and Sherman, 1976). Moreover, preferred velocity and velocity cut-off are typically higher for complex than simple cells (Movshon, 1975; Wilson and Sherman, 1976). Simple and complex cells are differentially sensitive to texture-field motion (Hammond and Mackay, 1977 and subsequently). Complex cells produce excitatory responses during saccadic eye movements, but simple cells are inhibited (Kimura, Komatsu and Toyama, 1980). In sum, simple and complex cells are distinguished by tuning properties and function under different circumstances.

In the following analysis it is suggested that both simple and complex cells have a role in the representation of form but that the role of the complex cell is distinct from that of the simple cell. Form representation is viewed as a non-unitary mechanism and complex cells are ascribed a role in the representation of the form of moving objects. A functional interpretation is given to asymmetries of tuning for a moving bar. The central contention is that asymmetries provide not
only a pre-condition for direction-selectivity but also a compensation for distortion of form associated with stimulus movement. Consideration is also given to the fact that the form of a moving texture-bar can be seen under conditions in which cells respond only to texture motion. It is concluded that this result requires a role for direction-selective units in the representation of form.

Creutzfeldt and Nothdurft's (1978) investigation of the transfer properties of simple and complex cells emphasised a role for simple cells in foveal vision. These authors suggested that the (orientation-selective) simple cells could play an important role for static hold and guide functions of gaze during foveal exploration, fixation and binocular fusion as simple cells are ideally suited to localise and monitor contours. Creutzfeldt and Nothdurft (1978) noted the sensitivity of complex cells to movement of texture and contrast and to higher speeds of movement; complex cells become active if a contour or texture of the fixated visual environment moves relative to it. Creutzfeldt and Nothdurft (1978) therefore suggested a role for the complex cell system in representing movement relative to a still structure as it is represented by simple cells and to guide visual behaviour towards the moving object.

The role of the complex cell in monitoring the movement of a textured surface receives firm support from the work of Hammond and associates (Hammond and MacKay, 1977; Hammond, 1978; Hammond and Reck, 1980, for example). Hammond and Smith (1983a, b) have demonstrated that complex, but not simple
cells, can resolve relative motion.

There is a specific problem relating to pattern recognition of moving objects which may provide a functional interpretation for the asymmetry shown in tuning for a moving bar. The interpretation derives from Fromel's (Fromel, 1977, 1980a, b) and Dinse and von Seelen's (1981a, b) analyses of problems of feature extraction in the context of studies of the superior colliculus and area 18 respectively.

Dinse and Von Seelen (1981a, b) have argued that since the (cat's) visual environment is not recognizably asymmetrical, there is no reason for implementing the recognition of stationary patterns with asymmetrical coupling of neurones. It is known that the projection of the retino-geniculate pathway onto the striate cortex is retinotopically organized (Whitteridge, 1973; Tusa, Palmer and Rosenquist, 1978). Both Fromel and Von Seelen and Dinse have argued that the conditions of pattern recognition change under conditions of stimulus movement. Fromel (1980a) has commented that symmetrical spatial coupling (as for example seen in the retina) shows distortion in the temporal domain so that pattern recognition is rendered difficult. As a product of the temporal properties of the symmetrical coupling, determination of where a moving object is located is subject to a systematic spatial error which is dependent on velocity. As velocity increases, the maximum of the output value lags behind that of the input value so that an error occurs when determining the position of a moving object.
In the same vein, Dinse and Von Seelen (1981b) stressed that in conditions of stimulus movement, "a time dependent variable must be involved in the space transformations necessary for pattern recognition due to the time lag at synapses. Due to causality, the time domain is in principle asymmetrical. So, when the pattern moves, there is always dispersion in 2-dimensional networks i.e. the patterns are distorted in a way dependent on their velocity and appear to the analysing system to be positioned wrongly with reference to the external co-ordinate system."

Potentially, distortion of pattern associated with its movement might be overcome by a central computation from simultaneously measuring the spatial error in localisation of a moving object or by compensating for the error. Both Fromel (1980a, b) and Dinse and Von Seelen (1981b) argue for compensation; distortion is compensated by asymmetrical coupling of neurones. One may therefore argue that the asymmetry of bar tuning of complex cells for a moving bar reflects not only the coupling determining direction selectivity but also provides compensation for distortion associated with stimulus movement. The present study provides evidence for Dinse and Von Seelen's (1981) contention that asymmetrical coupling is probably a general principle of neuronal connectivity that eliminates distortions of moving patterns and allows the direction of movement of stimuli to be coded by a neuronal network. Most important, asymmetrical coupling of neurones means that form analysis does not require a stationary image.
The results from comparison of tuning for a texture-bar with moving contrast bar and texture-field are problematical both for a hierarchical feature-extraction model and for a model invoking population coding by contour analysers; simple cells are unresponsive to moving texture-bars (Hammond and Mackay, 1977) and complex cells respond only to texture-bar motion. Perception of form, under conditions in which cells are unresponsive to contour, prescribes a role for direction-selective units in the mediation of form. That role is provided by complex cells.

Psychophysical evidence has suggested both that form representation is not mediated by a unitary mechanism and that some aspects of form analysis may be achieved by direction-selective units; separation of moving objects from one another and from a background or the reconstruction of a three dimensional object (Wallach and O'Connell, 1953; Gibson, Gibson, Smith and Flock, 1959; Julesz, 1971; Ullman, 1979). Harr and Ullman (1981) have suggested that a population of direction-selective units may be used to separate figure from ground by instantaneous measurements of the motions of elements in the visual field. Phenomenologically, the shape of an object would arise from discontinuities in the motion field as defined by the population of direction-selective units. The theoretical perspective is neatly summarized in the following quotation from Marr and Ullman, 1981.

"If the complex velocity field is given (i.e. speed and duration at each location) boundaries will be indicated by discontinuities in this field. This is because the motion of a
rigid object is locally continuous in space and time. The
continuity is preserved by the imagery process, and gives rise
to what might be called the principle of continuous flow,
according to which the velocity field of motion within the
range of rigid objects varies continuously everywhere except at
self-occluding boundaries. Since the motions of unconnected
objects are unrelated, the velocity field will often be
discontinuous at object boundaries. Conversely, lines of
discontinuity are reliable evidence of an object boundary.”

In conclusion, there is an interesting paradox presented
by the work reported in this thesis; evaluation of orientation
tuning of complex cells has revealed much about the mechanism
determining direction selectivity but consideration of the
complex cell’s direction selectivity has revealed even more
about the role of the complex cell in the representation of
form.
REFERENCES


AHMED B., HAMMOND P. and NOTHDURFT H-CHR. (1977) A reappraisal of the feline mesopic range. J. Physiol. (Lond.) 266: 94P.


ALBUS K. (1979) 14C-Deoxyglucose mapping of orientation sub-units in the cat's visual cortical areas. Exp. Brain Res. 37: 609-613.


ANDREWS D.P., HAMMOND P. and JAMES C.R. (1975) Absence of spontaneous variability of orientational and directional tuning in cat visual cortical cells. J. Physiol. (Lond.) 251P.


between layers IV and V in central parts of the cat striate cortex. Exp. Brain Res. 48: 245-255.


J. Physiol. (Lond) 25-26P.

CAJAL R. (1921) Textura de la corteza visual del gato. Trabajos del Laboratorio de Investigaciones Biológicas de la Universidad de Madrid. 19: 113-144.


127-139.


DREHER B. (1972) Hypercomplex cells in the cat's striate
FAIREN A. and VALVERDE F. (1979) Specific thalamo-cortical


11: 227-240.


Neurol. 163: 81-106.


HAMMOND P. (1979a) A semi-chronic preparation for cortical recording. J. Physiol. (Lond.) 298: 3-4P.


HAMMOND P. (1979d) Simultaneous determination of directional tuning of complex cells in cat striate cortex for bar and
HAMMOND P. and ANDREWS D.M. (1975a) Differential responses of
HAMMOND P. and MACKAY D.M. (1975b) Responses of cat visual cortical cells to kinetic contours and static noise. J. Physiol. (Lond.) 252: 43P.


HAMMOND P. and RECK J. (1979) A method for the simultaneous determination of directional tuning of visual cortical cells for two dissimilar stimuli. J. Physiol. (Lond.) 298, 4-5P.


HAMMOND P. and RECK J. (1980b) Influence of velocity on directional tuning of complex cells in cat striate cortex for


HEGGELUND P. and MOORS J. (1978) Direction selectivity and


HENRY G.H., BISHOP P.O. and DREHER B. (1974) Orientation,


HUBEL D.H and WIESEL T.N. (1963) Shape and arrangements of columns in cat's striate cortex. J. Physiol. (Lond.) 165:

559-560.


LEVICK W.R. (1967) Receptive fields and trigger features of
ganglion cells in the visual streak of the rabbit's retina.


NODA M., FREEMAN R.B., GIESAND B.Jr. and CREUTZFELDT O.D.


ORBAN G.A. and VANDENBUSCHE (1979) Behavioural evidence for
the oblique effect in the cat. J. Physiol. (Lond.) 295: 15P.


PETERS A. and KAISERMAN-ABRAMOF J.R. (1980) Synaptic relationships between a multipolar stellate cell and a pyramidal neuron in the rat visual cortex. A combined


RIBAK C.E., HARRIS A.B., VAUGHN J.E. and ROBERTS (1979) Inhibitory GABA-ergic nerve terminals decrease at sites of


SCHILLER P.H., FINLAY B.L. and VOLMAN S.F. (1976) Quantitative studies of single cell properties in monkey striate cortex. J. Neurophysiol. 39:
(a) Spatiotemporal Organization of Receptive fields. 1288-1319.
(b) Orientation Specificity and Ocular Dominance. 1320-1333.
(c) Spatial Frequency. 1334-1351.
(d) Cortico-tectal Cells. 1352-1361.
(e) Multi-variate Statistical Analyses and Models. 1362-1374.


SILLITO A.M. (1974a) Modification of the receptive field properties of neurones in the visual cortex by bicuculline, a GABA antagonist. J. Physiol. (Lond.) 239: 36-37P.


cortex as revealed by Golgi staining of the labelled neurones. 
Brain Res. 223: 431-436.
STONE J. and HOFFMANN K.P. (1972) Very slow conducting


TIEMAN S.B and HIRSCH H.V.B. (1982) Exposure to lines of only one orientation modifies dendritic morphology of cells in the

TIGNES J., SPATZ W.B. and TIGNES M. (1973) Reciprocal point
to point connections between parastriate and striate cortex in

TOLHURST D.J. (1973) Separate channels for the analysis of
the shape and movement of a moving visual stimulus. J.
Physiol. (Lond) 231: 385-402.

direction of movement as an element in the organization of cat


TOMBOL T. (1978) Comparative data on the Golgi architecture
of interneurones of different cortical areas in cat and
rabbit. In Architectonics of the Cerebral Cortex. (eds.)
Brazier M.A.B. and Petsche H. Raven Press, 59-76.

TOYAMA K., MACKAWA K. and TAKEDA T. (1973) An analysis of
neuronal circuitry for two types of visual cortical neurones
classified on the basis of their responses to photic stimuli.
Brain Res. 61: 385-399.

intracellular study of neuronal organization in the visual

TOYAMA K., MAEKAWA K. and TAKEDA T. (1977) Convergence of
retinal inputs onto visual cortical cells I: a study of cells
monosynaptically excited from the lateral geniculate body.
Brain Res. 137 207-220.

TOYAMA K., KIMURA M., SHIDA T. and TAKEDA T. (1977)
Convergence of retinal inputs onto visual cortical cells II:
a study of the cells disynaptically excited from the lateral
geniculate body. Brain Res. 137: 221-231.


WILSON P.D., ROWE M.H. and STONE J. (1976) Properties of

TITLE

DIRECTIONAL AND ORIENTATIONAL TUNING IN THE STRIATE CORTEX OF THE CAT FOR CONTRAST AND TEXTURED STIMULI.

AUTHOR

Tigwell, D.A.

INSTITUTION and DATE

University of Keele.
1985

Attention is drawn to the fact that the copyright of this thesis rests with its author.

This copy of the thesis has been supplied on condition that anyone who consults it is understood to recognise that its copyright rests with its author and that no information derived from it may be published without the author's prior written consent.