Periodic excitability changes across the receptive fields of complex cells in the striate and parastriate cortex of the cat.

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PERIODIC EXCITABILITY
CHANGES ACROSS THE RECEPTIVE FIELDS OF COMPLEX
CELLS IN THE STRIATE AND PARASTRIATE CORTEX
OF THE CAT

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SUMMARY

1. Complex cells in cortical areas 17 and 18 of the cat have been studied in response to narrow slits and edges moving across the receptive field in the preferred direction and also to stationary slits of different widths.

2. Average response histograms, recorded as a narrow slit was moved across the receptive field, displayed a periodic series of peaks above a baseline level. The response histogram for most area 17 and 18 cells contained five principal peaks; sometimes one or two weaker peaks were present at receptive field borders. The histogram for one cell located at the area 17–18 border showed thirteen distinct peaks. Periodic response patterns were also generated as an extended edge was moved across the receptive field. Plots of cell response versus slit width for stationary slits of different widths also indicated a periodic response pattern.

3. The accuracy of determining the preferred slit orientation was the single most important requirement for demonstrating the periodic response pattern. Significant changes in the appearance of the periodic pattern occurred even upon 5° rotations away from the preferred orientation.

4. Average response histograms were also studied over a wide range of moving slit velocities. The number of peaks across corresponding spacings within the receptive field remained constant over a range of velocities. Response amplitudes, however, were velocity dependent. Thus the response peaks remain associated with fixed positions within visual space independent of stimulus velocity, even though temporal as well as spatial factors may be involved in response selectivity and the periodic modulation. The most striking periodic response histograms were generated at the velocities which produced the greatest cell firing rates. Area 17 complex cells

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responded well to velocities of less than $0.5^\circ$ to $6.0^\circ$/sec, but cells in area 18 generally required higher velocities, sometimes as high as $20^\circ$–$30^\circ$/sec, for a good response.

5. Spatial frequencies for the periodic component of the receptive field for area 17 cells in the central visual area covered a range of three octaves up to 5 cycles/degree, and area 18 cells included another octave on the low frequency side. The spatial frequency of a cell was found to be roughly inversely proportional to the receptive field width. Only a small sample of area 18 cells was studied, but these cells tended to represent low spatial frequencies and to respond selectively to high velocity stimuli.

6. Simple cells were also studied with stationary and moving slits. Both width-selective and edge-selective cells were found. The width-response function of a width-selective simple cell shows a single maximum; beyond the optimal width the response decreases monotonically.

7. Individual cell responses to single sweeps were also studied. Variability in the response onset from corresponding discharge zones was noted. This response variability resulted in a partial overlap of adjacent peaks in the histogram response and contributed to building up the base line or ‘bias’ level in the response histograms.

8. The receptive field excitability profiles of complex cells were Fourier analysed. The transform amplitudes indicated that the periodic component of the receptive field could be well described by a single ‘preferred’ frequency. There were no significant peaks at higher harmonics, which indicates that to a first approximation the periodic component may be considered sinusoidal.

For typical complex cells in area 17 and 18, the half band width of the preferred frequency on the high frequency side was about one-fifth of an octave. The half-amplitude band width on the low frequency side was either similar or slightly broader. For one cell at the area 17–18 border, the half band width was about one-tenth of an octave.

9. Complex cells in areas 17 and 18 have a periodic component in their receptive field shape which could allow them to contribute to a spatial frequency analysis of discrete regions of visual space. Additional experiments will be required to determine coupling characteristics between different discharge zones when diverse parts of the receptive field are stimulated.

**INTRODUCTION**

Ever since Hubel & Wiesel (1959, 1962) discovered the orientation selective properties of most neurones in the cat visual cortex, there has been considerable interest in how visual information is encoded along the spatial axis perpendicular to a cell’s preferred orientation. Receptive fields
with elongated excitatory receptive field centres, flanked on each side by parallel inhibitory regions, were believed to impart an optimal width selectivity for light bars with a converse arrangement for dark bars. In another type of simple cell, excitatory and inhibitory regions met along a boundary defining a border region that suggested an edge selective function (Hubel & Wiesel 1959, 1962). The optimal response required a precise positioning of the bar or edge. Hubel & Wiesel (1962) termed other striate neurones 'complex'; these neurones seemed to respond selectively to either edges or bars of an optimal width and orientation over a larger receptive field than was the case for simple cells. These width and edge selective properties of striate neurones have served as the basis for many models of how the visual system carries out pattern recognition.

Schade (1956) initiated a linear systems-analysis approach to the human visual system. He measured the separate thresholds for detecting a given sine wave grating (i.e. a pattern whose luminance varies sinusoidally in one direction) over a wide range of spatial frequencies (i.e. the number of cycles of the grating included within, say, one degree of visual angle). Lenses and optical filters are commonly evaluated in terms of their response to a particular frequency range of sine wave gratings. The test situation can also be applied to any spatial filter such as the receptive field shape of a visual neurone. Enroth-Cugell & Robson (1966) measured the contrast sensitivity (the reciprocal of the threshold) of cat retinal ganglion cells as a function of the spatial frequency of sine wave gratings and found a relatively broad type of spatial frequency selectivity. Campbell, Cooper & Enroth-Cugell (1969) used sine wave gratings to determine the spatial frequency selectivity of unidentified neurones in the cat visual cortex and found that some of their cells had band pass characteristics quite similar to those found in the psychophysical grating adaptation experiments of Blakemore & Campbell (1969) where the bandwidth of the adapted channels was estimated as just over an octave at half amplitude. Maffei & Fiorentini (1973) identified striate cell types and reported that the simple cells have the bandwidth characteristics of the channels inferred from the psychophysical studies.

Pollen, Lee & Taylor (1971) took a pattern-recognition approach and realized that, since the firing rate of a single simple cell has a dual dependence on relative brightness and area, it cannot signal uniquely either size or brightness information. It was further realized that many of the stimulus-equivalence propositions of Lashley (1942) could be satisfied in the Fourier transform domain where, for example, the amplitudes of Fourier coefficients are invariant to translational displacement of an image. Such a transform could be derived from the sets of width-selective simple cells which were realized to be mathematically sufficient for such a
derivation. Pollen et al. (1971) proposed as an hypothesis that complex cell responses might be encoding a Fourier or spatial frequency transform over restricted regions of visual space.

Glezer, Ivanoff & Tscherbach (1972, 1973) independently proposed essentially the same hypothesis. They tested complex cells with a limited set of periodic bar patterns of several different wave shapes and reported that, in certain cases, multiple bar patterns produced either greater or lesser cell firing than did single bars. Glezer et al. (1973) reported that the

Text-fig. 1. I, schematic representation of a narrow slit moving across the receptive field of a complex cell.

1A, hypothetical average response histogram to moving slit showing more or less uniform response across the receptive field.

1B, hypothetical response to slit movement showing a periodic response pattern.

II, schematic representation of an extended edge, i.e. a rectangular stimulus so long that the trailing edge never enters the receptive field, moving across the receptive field.

IIA, hypothetical more or less uniform average response histogram as the edge moves across the main body of the receptive field.

IIB, two hypothetical curves showing a narrow optimal width curve (continuous line) and broader optimal width curve (interrupted line) in response to an edge moving across the receptive field.

IIC, hypothetical periodic response as an edge is moved across the receptive field.
average response histogram obtained with '... a single slit moving across the receptive field was continuous', but some histograms '... had peaks corresponding to excitatory zones' and they illustrated an example showing three peaks. Their evidence that 'stripedness' may be a factor in complex cell response would be consistent with a spatial frequency model.

In an attempt to determine whether complex cells are encoding edge selectivity, width selectivity, spatial frequency selectivity, or some other spatial attribute, we have performed a number of experiments using stationary and moving slits and edges. The average response histogram produced as a narrow properly oriented slit is moved across the complex cell receptive field may be considered as defining field shape under these conditions (Text-fig. 1, I). Hypothetically, the receptive field profile might be more or less uniform (Text-fig. 1, IA), periodic (Text-fig. 1, IB), or of any other shape. A uniform profile would be consistent with both edge selective and width selective hypotheses, which could then be distinguished by moving an extended edge across the field (Text-fig. 1, II). A uniform response to the edge (Text-fig. 1, II A) as well as to the slit would support an edge selectivity hypothesis. However, a single peaked response to the edge as its effective width within the receptive field increased (Text-fig. 1-IB) would support an optimal width selectivity hypothesis.

A Fourier transform representation could be expressed in either of two ways. Cell firing rate could represent a particular spatial frequency amplitude with phase represented in some other way. In such a case the response to a moving slit might be essentially uniform (Text-fig. 1, IA). Alternatively, a sine and cosine representation would be sufficient for the subsequent recovery of both amplitude and phase information. In such a case the cosine filter would have the same periodicity as the sine wave filter but be placed 90° out of phase with respect to it. The responses of these filters to a narrow moving slit and an extended edge would exhibit similar periodicity (Text-fig. 1, IB and 1, II C).

These hypothetical cases cover a very limited number of models, and obviously are not sufficient to prove the validity of any one of them. Nevertheless, the simplified models are useful, as they provide a convenient framework for understanding some of the methods used and interpreting the experimental results which follow.

METHODS

Sixty-one experiments were carried out in cats initially anaesthetized with 4% halothane in oxygen. All operative procedures including tracheotomy, insertion of a venous cannula, craniotomy and opening of the dura, and in ten experiments a
femoral arterial cannulation for blood pressure recording were carried out under surgical anaesthetic levels of at least 1-5% halothane. Halothane can produce cardiac arrhythmias and hypotension. After halothane was discontinued, the arrhythmias ceased and the blood pressure returned to normal levels. After surgery the animal was maintained on a mixture of 70% nitrous oxide and 30% oxygen for light anaesthesia and analgesia (Venes, Collins & Taub, 1971). Local anaesthetics were used at pressure points.

Pancuronium bromide (Pavulon, Organon, Inc.) was used to paralyse the extraocular muscles, and the animals were then mechanically respired with a Harvard pump. A direct i.v. injection of 0-1 mg/kg was made, followed by application of a continuous intravenous drip via a paediatric IV set of 0-15 mg/kg.hour in 5% dextrose and normal saline. This dose level was satisfactory for preventing significant eye movement in most experiments; occasionally a receptive field drift was noted and the dose increased. Blood pressure remained stable over a 24 hr test period even when the dose was increased severalfold. Stroke volume of the Harvard pump was adjusted to maintain end expired $P_{CO_2}$ between 3-5 and 4% as measured with a Beckman LB2 CO$_2$ analyser. The e.e.g. and e.e.g. were monitored on a Grass polygraph. A thermal heating underpad was used to maintain body temperature.

Atropine sulphate was used for cycloplegia and mydriasis and phenylephrine HCl for retraction of the nictitating membrane. A streak retinoscope was used to select the corneal contact lens which would best focus the eye on a screen 1-5 m away. It was convenient to refract with the aid of a 5 mm artificial pupil temporarily placed directly in front of the cat's eye. After the correct corneal lens was selected the optic disk and area centralis for each eye were back projected and marked on the tangent screen. The estimation of the area centralis by back projection was subject to an error of 1-2 degrees. A 3 mm artificial pupil was then placed in the optical axis directly over the contact lens.

For a recording chamber a 2-3 mm high ring of $\frac{1}{4}$ in. outer diameter polyethylene tubing was cemented with dental acrylic to the bone around the 6 mm trephine hole. A gel of 4% agar in artificial cerebrospinal fluid was placed over the brain at 41°C and allowed to cool and harden. After a tungsten micro-electrode (Hubel, 1957) was lowered into the gel, the chamber was sealed with melted bone wax, the agar beneath serving as a heat shield (Bishop, Coombs & Henry, 1971). A hydraulically driven micromanipulator was used for micro-electrode advance.

Conventional amplification and filtering were used. The signal was led to an oscilloscope for monitoring spike wave form and isolation, and to a Synax 100 computer for generating average response histograms. These were displayed on a second oscilloscope for visual inspection or Polaroid photography. Electrical activity and shutter synchronization signals were stored on magnetic tape. A pulse counter was used for counting the events in any specified time interval.

In studies of area 17, micro-electrodes were inserted between Horsley–Clarke A–P planes −2-0 to −5-0 mm and laterally from 0-5 to 2-0 mm. In nine experiments, usually after some studies in area 17 had been made, a single penetration was carried out in area 18 at the same frontal planes but from 3-0 to 5-0 mm laterally. During the experiment probes of area 18 were readily distinguished from penetrations in area 17 by the larger field sizes in area 18 for the retinal region studied, the absence of simple cells in area 18, and by the need for a very rapidly moving target to make many of the cells respond. In especially important cases electrolytic lesions were made by passing 40–60 μA electrode tip negative for 20–30 sec. The brains were fixed in 10% formalin, embedded in celloidin, and alternate 20 μm sections were stained with cresyl violet (Nissl) and Loyez (myelin) respectively. In one case frozen sections were cut and similarly stained.
The criteria of Hubel & Wiesel (1965) were used for distinguishing electrode placements in area 17 from those in area 18. The more lateral cortex of area 18 was identified principally by the larger pyramidal cells of layer III and the coarser myelination of radial fibres.

Light stimuli were presented using a Leitz Prado projector. A Compur electronic shutter was used when stimuli of set duration were required. The diaphragm setting of the shutter was used to adjust stimulus intensity which was measured using a SEI exposure meter. Background lighting was provided by overhead diffuse nonglare incandescent lamps. Background luminance was 0.54 log cd/m² except when background luminance was itself the factor studied. Slit and edge stimuli were tested at luminances of 0.3–0.6 log units above background except when changes in stimulus luminance were studied.

Slits of various lengths and widths were projected using a rotatable detented slit device which, with the aid of a set screw, allowed change of the aperture in fixed steps. In stationary slit-width studies, different slits were tested in a random manner with 10–20 stimuli presented at each width. In ‘symmetric’ slit width studies, a line was lightly drawn through the centre of the receptive field map and the slit width was increased equally on each side. In ‘asymmetric’ slit width studies a fine line was drawn at one receptive field flank and the slit widths were increased only on one side of the line. Moving slits (Text-fig. 1, I) and ‘extended edges’ (Text-fig. 1, II) were presented with the aid of a galvanometer-driven mirror arrangement. Slits could be moved across the receptive field at any angle in either direction over a variable set excursion and velocity range.

Over 200 complex cells in area 17, and twelve complex cells in area 18 were studied. Our main interest was in complex cells, so most simple cells and all hypercomplex, though frequently found, were passed up once they had been identified as such. However, twenty-five simple cells were extensively studied in order to compare their spatial properties with those found for complex cells. The experimental programme for each cell studied took from 3 to 4 hr. An average of three cells, and sometimes four or five, were studied in each experiment. Experiments were rarely carried beyond the morning of the second day; orientation selectivity remained intact beyond this time, but cell firing was frequently very bursty, making it more difficult to obtain statistically significant data about spatial characteristics.

Cells were classified according to the criteria of Hubel & Wiesel (1962). Simple cell receptive fields could be broken up into separate ‘on’ and ‘off’ regions in response to stationary stimuli. Complex cells usually gave mixed ‘on–off’ responses to stationary stimuli over the entire receptive field; less often there was an ‘off’ region to one side of the larger ‘on–off’ region. By trial and error the approximate best orientation for a receptive field was found, using both stationary and moving stimuli. The borders parallel to the preferred orientation were determined by moving and flashing slits at the field edges until response ceased. The borders perpendicular to the preferred orientation were similarly determined. Orientation selectivity was then tested by moving a slit or flashing a stationary slit and counting the total number of responses at the tentative preferred angle and in 10° steps on each side until peak sensitivity was established. The orientation ‘tuning curves’ with moving and stationary slits were similar, although a moving slit produced a stronger response than did the stationary one at any given angle (Text-fig. 2A, B).

When necessary, receptive borders field were remapped. Responses to moving slits in both directions were then tested. Cells were called ‘bidirectional’ if the two directions gave similar responses within a 2:1 ratio, ‘asymmetric bidirectional’ if the ratio ranged between 2:1 and 4:1, and ‘unidirectional’ for cells with complete directional preference or ratios greater than 4:1. The response to each eye was
tested and the eye giving the stronger response was used, the other eye being covered.

After each receptive field had been mapped the narrowest slit of light which produced a clearly recognizable increase in cell firing rate was selected to move across the receptive field. Increase in slit length produced an increase in response until the field borders were reached. Slits of optimal length were generally used, but length was not found to be a significant factor in determining spatial characteristics along the preferred direction.

At least 25 sweeps and often 50–200 sweeps were carried out to generate each histogram. Sweep excursions were selected so that each slit spent about half of its excursion within the receptive field. Responses per sweep might fall off 15–30%.

Text-fig. 2. Complex cells. A, orientation selectivity tuning curve as a narrow slit is moved across the receptive field of a complex cell. A horizontal orientation is indicated by 0°, with clockwise inclinations from the horizontal indicated by positive numbers. Each data point in this and subsequent graphs indicates mean with its standard error. Cell 50–3. Velocity = 1°/sec.

B, orientation study for the same cell but carried out using stationary flashed stimuli of 500 msec.

C, average responses for each of twenty successive groups of ten responses to a moving slit are shown. Note the response fall off during the first fifty responses. Cell 47–1.

D, same experimental plan as in C, but in this cell the responses remain relatively stable. Cell 58–4.

The cell in C was in area 17, that in D in area 18; however, both stable and mildly adapting complex cells have been found in both area 17 and area 18.
COMPLEX CELL RECEPTIVE FIELDS during the first 50 responses and then become relatively stable (Text-fig. 2C) or in other cases remain relatively constant for 200 sweeps (Text-fig. 2D). Whenever quantitative comparisons were made between responses at different widths, orientations, velocities or luminances, we measured responses for corresponding numbers of consecutive sweeps after the cell had 1–2 min of rest under stimulus-free conditions.

The receptive field shape functions, as determined in the moving-slit studies, were also subjected to Fourier analysis. For this purpose it was necessary to obtain the number of events in each of the 100 bins in each histogram. The analogue voltages from the Synax computer for each bin were measured using a digital panel meter, and the Fourier coefficients were evaluated from the usual formulae for discrete Fourier transforms (see, for example, Bracewell, 1965).

RESULTS

Moving slit studies in complex cells. After the receptive field borders had been established and the optimal orientation selectivity and preferred direction of movement had been determined, a narrow slit was moved across the field at a velocity selected so as to produce a strong response. The effect of different velocities on response will be considered in a later section. For most complex cells in area 17 and 18 the average response histograms which were generated presented a periodic receptive field profile consisting of a series of successive maxima and minima riding above some base line level (Text-fig. 3A–F).

For convenience, we will consider the periodic part of the response as the modulated or high frequency component and the base line response as the ‘bias level’ or low frequency component. The peak to peak amplitude of the modulated component in the central region of the receptive field usually ranged from about one half to two thirds of the total response amplitude (Text-fig. 3). In the histograms shown, 100 bins were used for resolution of the receptive field shape. An increase in resolution by using 200 bins did not significantly modify receptive field shape or change the relative amplitude of the periodic component.

For most area 17 and 18 cells, five principal peaks were found in the average response histograms (Text-fig. 3A, D–F). One or two much weaker peaks might also be seen at receptive field borders (Text-fig. 3A, D). In two area 17 cells, histograms with only four principal peaks were found (Text-fig. 3B). Periodic histograms were found for both unidirectional and bidirectional complex cells in both areas 17 and 18. During one penetration two successively encountered cells were found to have identical periodicities but opposite directional selectivities (Table 2, cells 51–3, 51–4).

The electrode tract for the complex cell study of Text-fig. 3A and also the simple cell study of Text-fig. 13 is shown (Pl. 1A, B). In one study a histogram with thirteen peaks, about twice the usual number found, was
Complex Cells
Moving slit studies

Text-fig. 3. Average response histograms representing receptive field shape for complex cells as a narrow slit is moved across the receptive field. In this and subsequent illustrations \( n \) equals the number of stimulus presentations. Periodic changes in excitability across the receptive field may be noted for cells in area 17 (A and B), area 18 (D–F) and for one cell near the 17–18 border (C). Additional data about these cells may be found in Table 2. Stimulus luminance in these and all other cases is 0.3–0.6 log cd/m\(^2\) above background of 0.54 log cd/m\(^2\) unless otherwise indicated. In A, D–F, the zero level is indicated by the lowermost horizontal line. In B and C the zero level is indicated by the lowest filled bin. In C, the spontaneous level had fallen to zero during the period in which the histogram was taken.
en countered (Text-fig. 3 C). The electrode was in the right side of the brain and the contralateral eye was open. The receptive field extended bilaterally across the estimated back projection of the area centralis and the three largest peaks on the left side of the estimated mid line were much larger than the three largest peaks on the right of the marked border. The electrolytic lesion at the electrode tip (Pl. 1C, D) seemed close to the 17–18 border. Our data are not sufficient to prove whether or not this cell was in the area representing the vertical meridian, which is best located by physiological methods (Hubel & Wiesel, 1967).

The velocities at which studies of area 17 cells were carried out ranged from less than 0.5°/sec to 6.0°/sec. Much higher velocities were often necessary to make area 18 cells respond at all. In one case a velocity of over 20°/sec was required to make the cell respond to a moving slit; in another case a velocity of close to 30°/sec was needed. Test velocities as well as a number of other parameter values which will be considered in subsequent sections are enumerated in Table 2 for 24 complex cells in areas 17 and 18.

The effect of changes in slit orientation on receptive field excitability profiles. The single most important factor for demonstrating the response periodicity was the accuracy in determining the preferred orientation. Histogram responses to a moving slit rotated 20° to either side of the preferred orientation may fail to show any significant periodicity. Significant changes in the periodic pattern occur for successive rotations of even 5° around the preferred orientation (Text-fig. 4).

The periodic response pattern in Text-fig. 4 A was clear when the slit was moved in the preferred direction but was not at all evident when the slit was moved in the non-preferred direction. Response patterns in the preferred direction were very stable; the histogram generated by the first 100 sweeps looked very similar to that generated by the second 100 sweeps (Text-fig. 4 B). The preferred orientation had been determined by counting the responses/sweep for the first 50 sweeps at 5° slit rotations after a tentative estimate of the preferred orientation had been made. The response plot (Text-fig. 4 C) showed that the preferred slit orientation was 5° clockwise to the horizontal, and a periodic histogram with five principal peaks was generated when the slit was moved downward perpendicularly to this angle (Text-fig. 4 F, upper trace). The fifth peak on the right is no longer clear when the slit was rotated either to the right or left by only 5° (Text-fig. 4 F, lower trace, and 4 E, lower trace). At a 20° counterclockwise rotation (Text-fig. 4 D, upper trace) the two central peaks are relatively much more prominent than the other peaks and the separation between the peaks seems slightly greater than in the case of the peaks at the preferred orientation. At −10° the histogram appears jagged (Text-fig. 4 D, lower trace); a resemblance to a periodic pattern is not obvious. The sense
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Text-fig. 4. Complex cell, area 18. Cell 58-4 A, histogram responses to a narrow slit in the preferred direction (upper trace) and non-preferred direction trace.

B, the first and second 100 responses to a moving slit are shown in the upper and lower traces respectively.

C, orientation response plot in 5° steps around preferred orientation. A horizontal orientation is indicated by 0°.

D–F, histograms in response to successive 5° rotations from −15° to 10°. Note the clearest periodicity at 5° in F (upper trace), which angle had been determined in C as the preferred angle. Other details in the text.
of a smooth periodic pattern begins to occur at $-5^\circ$ (Text-fig. 4E, upper trace) and becomes clearer at $0^\circ$ (Text-fig. 4E, lower trace).

When we have had the time to adjust orientation and other parameters quite carefully we have found periodic average response histograms for about 70% of the last sixty area 17 cells so studied and in all twelve area 18 cells so studied. The preferred direction of movement for a number of these cells is indicated in column 3 of Table 2. When clear periodicity could not be demonstrated, there were still several irregularly spaced peaks in the response histograms, much as in Text-fig. 4D, lower trace.

**Moving extended edge studies in complex cells.** Slits of light so wide that the trailing edge could never enter the receptive field were moved across the receptive field under the same conditions as in the narrow moving slit studies. The extended edge may be considered as both a moving edge test and a slit of continuously increasing width within the receptive field. Response patterns showing the same periodicities found with single narrow slits were found (Text-fig. 5A, B). In some cases the extended edge brought out peaks on the falling phase of the histogram more clearly (Text-fig. 5A, lower trace) than did the moving slit (Text-fig. 5A, upper trace). In one area 18 cell, the initial peaks generated in response to the extended edge (Text-fig. 5B, lower trace) were of relatively lower amplitude compared to later peaks than was the case when the cell was tested with the narrow slit (Text-fig. 5B, upper trace). The lower initial responses with the edge might indicate the presence of an inhibitory region peripheral to the excitatory borders of this cell.

Stationary single slit responses were also tested to see whether complex cells yielding periodic histograms to the moving slits or edges fell into either the phasic (very rapidly adapting) or tonic (prolonged response) category. In many complex cells essentially phasic responses to stationary flashed stimuli were seen (Text-fig. 5C). In other complex cells there was an initial large response followed by a much weaker prolonged response component that might be considered ‘tonic’ (Text-fig. 5D). Tonic components of complex cell responses were always much weaker than that found for those simple cells with strong tonic components.

**The effect of slit velocity upon receptive field excitability profiles.** The previous findings demonstrate that a moving narrow slit or extended edge may generate a series of periodic responses as it moves across the receptive field of a complex cell. It remains to be determined whether the periodicities are spatial or temporal functions, or a combination of the two. In order to try to resolve this issue, we studied ten cells in area 17 at three or more velocities covering a range of several octaves. For example, a periodic response histogram with five peaks was demonstrated for cell 55–2 at a slit velocity of $2\cdot36^\circ$/sec (Text-fig. 6B). For this cell, unlike the case in Text-
fig. 4A, there was a suggestion of a weak periodic response when the slit was moved in the non-preferred direction (Text-fig. 6D). When the slit velocity was decreased to 0.8°/sec the first three peaks (Text-fig. 6A) may be discerned in relation to the corresponding peaks in Text-fig. 6B, but the fourth and fifth peaks are not evident. When the slit velocity was increased to 5.08°/sec, the first three peaks may also be seen (Text-fig. 6C), but not as clearly as in Text-fig. 6B, and two smaller response elevations possibly representing fourth and fifth peaks may be seen (Fig. 6C).

The receptive field widths as judged from the histogram records did not change when slit velocity was altered (Table 1). Periodic responses were much more striking at the velocity of 2.36°/sec than at 0.8°/sec and 5.08°/sec. However, the number of peaks across corresponding spacings within the receptive field remained essentially constant (Text-fig. 6A–C, Table 1).

Text-fig. 5. Complex cells. A, response of an area 17 cell to a moving narrow slit (upper trace) and extended edge (lower trace). Cell 48-2.
B, response of an area 18 cell to a moving narrow slit (upper trace) and extended edge (lower trace). Cell 56-5.
C, D, histogram responses to flashed stationary slit in two different positions in the receptive field for two different complex cells. In C, the ‘on’ response for cell 48-2 shown above is largely phasic; in D, for cell 32-1, a weak tonic response follows the primary response peak. Both cells showed prominent ‘off’ responses throughout the receptive field.

A–C, histograms generated in response to a moving slit at three different velocities. A periodic response histogram is most striking at the intermediate velocity in B.

D, response to non-preferred direction of movement. This cell had considerable spontaneous activity and the zero level is indicated on all histogram traces, by the bottom line.

E, plot shows the number of responses per stimulus for the first 250 msec of the response versus the slit width as slits of various widths were randomly presented asymmetrically to one side of a reference line just outside the receptive field border on one side. The spontaneous firing level is indicated by the dashed line. Receptive field width is about 4.3°.

F, cell responses have been plotted against velocity in three different representations. Please see text for other details. R equals total response.
Table 1. Table shows measurements for receptive field width, spatial frequencies and response density considered on either a response per sweep or response per second basis for three complex cells in area 17 studied at three different slit velocities. Cell 55–2 was also studied at 'zero velocity' with stationary slits of different width.

<table>
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<th>Expt. no.</th>
<th>Cell no.</th>
<th>Velocity (deg/sec)</th>
<th>Counting interval</th>
<th>Calculated receptive field width (deg)</th>
<th>Average spatial frequency (deg/sec)</th>
<th>Response per sweep</th>
<th>Spontaneous per sec</th>
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<td></td>
<td></td>
<td>0</td>
<td>0·25 sec</td>
<td>4·3*</td>
<td>1·7*</td>
<td>—</td>
<td>14·8</td>
<td>3·7</td>
<td>—</td>
</tr>
<tr>
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<td>2</td>
<td>0·54</td>
<td>2·8 sec</td>
<td>1·3</td>
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<td>0</td>
<td>0</td>
<td>12·5 ± 4·2</td>
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<tr>
<td></td>
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<td>1 sec</td>
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<td>0</td>
<td>87·7 ± 7·9</td>
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<tr>
<td></td>
<td></td>
<td>3·13</td>
<td>0·5 sec</td>
<td>1·6</td>
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<td>0</td>
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<td>54 ± 3·1</td>
<td>44</td>
<td>35·2</td>
<td>24·7 ± 3·1</td>
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<td>16 ± 1·5</td>
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<td>0·45 sec</td>
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<td>36 ± 1·3</td>
<td>44</td>
<td>19·8</td>
<td>36 ± 1·3</td>
</tr>
</tbody>
</table>

* As determined during a stationary slit width study.
† 1st and 2nd peaks merged, 4th peak weak. Difficult to obtain accurate value for spatial frequency.
This was also the case for nine other cells so studied and the calculated values for several cells are given in Table 1. The periodicity for each cell measured in spatial terms remained constant over a particular range of velocities, although peak response amplitudes were velocity dependent.

For cell 55–2 we also carried out an asymmetric slit width study in which stationary slits of various widths were flashed in random order with one border of the slit always placed in fixed relation to a reference line lightly drawn just to one side of the receptive field boundary. The responses to stationary stimuli were highly variable, producing large standard errors of the mean; even so the results of the random slit width presentation yield a response slit width plot (Text-fig. 6E) which also has a periodic component similar to that found in the moving slit studies (Table 1).

Individual records of cell responses to sweeps at different velocities were studied and we observed that the separate discharge zones of increased excitability occurred at fixed spatial intervals (Text-fig. 7). It was also possible to open a shutter and start the sweep at different portions within the receptive field and show that the spatial position of the subsequent peaks remained independent of the portion of the receptive field in which the sweep was first projected on to the screen.

We plotted velocity–response curves to try to determine whether the histograms showing the strongest periodic responses to moving slits could predictably be related to velocity selectivity factors. Because it is uncertain whether an ‘optimal velocity’ should be estimated in terms of ‘response per sweep’ or ‘response per second’, we followed the example of Pettigrew, Nikara & Bishop (1968) and plotted the data both ways (Text-fig. 6F). In the case illustrated the net response per second was maximal at the intermediate velocity of 2.36°/sec at which velocity the response histogram showed the strongest periodic responses (Text-fig. 6F).

In general the most striking periodic histograms were generated at velocities producing the greatest number of responses per second. The maximum response per second represents the strongest average signal at any instant; the signal-to-noise ratio is thus greatest at this velocity. It is uncertain whether the reduced amplitude of the periodic component in Text-fig. 6A is due to a lower signal to noise ratio at the velocity tested or to some other velocity-dependent function.

Even if the cell in Text-fig 6F is considered ‘velocity tuned’ in terms of response per second, that tuning is quite broad, and the cell also responded well to stationary stimuli (Text-fig. 6E). Complex cells in area 17 consistently generated periodic histograms at slit velocities less than 6.0°/sec (Table 2). Many complex cells in area 18 did not respond at all to stationary stimuli, and even those that did respond weakly gave little or no response to moving slits until velocities greater than 20°/sec were tested (Table 2).
Effect of slit luminance upon receptive field excitability profiles. When the background was kept constant and the luminance of the slit was increased in steps, both the periodic and non-periodic part of the response increased (Text-fig. 8A, B). Sometimes slight differences in the relative modulation were seen when the stimulus luminance was changed, but the effects were small and the direction was not predictable. The usual background level was 0.54 log cd/m², but in three experiments the background level was raised by 0.3–0.6 log units. Histogram shapes were not greatly different as long as the stimulus luminance was raised by about the same amount (Text-fig. 8C). In one experiment the background room lights were turned off, and a moving slit was tested at a background level of -1.5 log cd/m². The periodic shape of the histogram was not significantly modified.

Relationship between receptive field width and spatial frequency. The spatial periodicities of area 17 and 18 cells may be expressed in cycles/degree, and some individual values are listed in Table 2. For most area 17 cells, at least one border of the receptive field was within 2–3° of, and

![Text-fig. 7. Complex cell responses. Three individual records of single cell response to a slit moving at 10.3°/sec (A–C) and a 5.15°/sec (D–F). The time bases are the same in the two cases. Note the greater temporal separation between discharge zones at the lower velocity. The spikes in D–F have been retouched.](image)
slightly inferior to, the area centralis, which cannot be fixed in these experiments with an accuracy better than 1–2°. The cells studied are probably representative of central visual field neurones in the cat. The spatial frequencies of the periodic component of the receptive field shape for cells in area 17 cover an almost three octave range approaching a maximum value of 5 cycles/degree. The low frequency range might have been greater had cortex subserving peripheral regions of the visual field been explored.

The area 18 neurones represented roughly similar areas of central visual space and had, as noted by Hubel & Wiesel (1965), receptive fields 2–3 times larger than the fields of area 17 cells for similar regions of visual


A, average response histogram to a moving slit at background and luminance levels indicated.

B, stimulus luminance was increased at constant background level.

C, similar histogram shape after background level has been increased.
Table 2. Columns 1 and 2 represent cell number and cortical area studied respectively. The preferred direction, the receptive field width, and the principal velocity at which the cell was tested with moving slits and edges are indicated in columns 3, 4 and 5. In column 3 double equal arrows indicate ‘bidirectional’ selectivity within a 2:1 ratio; single arrows indicate that the response was essentially ‘unidirectional’ with a response ratio in the preferred direction of at least 4:1. Response ratios between 2:1 and 4:1 are roughly indicated by relative sizes of the two arrows shown. The test slit width is indicated in column 6. The spatial frequencies calculated from histogram responses as is Text-fig. 3 are indicated in column 7 and the half period, or the reciprocal of twice the spatial frequency is indicated in column 8. The ratio of the test slit width to the half period is shown in the last column. In most cases this ratio was between 0·5 and 1·0.

<table>
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<tr>
<th>Complex cell</th>
<th>Cortical area</th>
<th>Directional preference</th>
<th>Receptive field width (deg)</th>
<th>Test velocity (deg/sec)</th>
<th>Test slit width x length (26·19 mm = 1°)</th>
<th>Spatial frequency (cycles/deg)</th>
<th>Half-period (deg)</th>
<th>Test slit width/( \text{Half period} )</th>
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</thead>
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<td>41–2</td>
<td>17</td>
<td>↑</td>
<td>2·2</td>
<td>0·73</td>
<td>ee*</td>
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<td>0·22</td>
<td>—</td>
</tr>
<tr>
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<td>17</td>
<td>←</td>
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<td>0·18</td>
<td>0·9</td>
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<td>↓</td>
<td>2·1</td>
<td>0·56</td>
<td>ee</td>
<td>3·85</td>
<td>0·13</td>
<td>—</td>
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<td>0·33</td>
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<td>0·8</td>
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<td>0·4</td>
<td>0·3</td>
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<td>0·66</td>
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<td>←</td>
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<td>11·1</td>
<td>ee</td>
<td>0·4</td>
<td>1·25</td>
<td>—</td>
</tr>
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<td>6 × 95</td>
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<td>8 × 94</td>
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<td>8 × 164</td>
<td>0·98</td>
<td>0·51</td>
<td>0·6</td>
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<td>5·15–10·3</td>
<td>5 × 112</td>
<td>2·82</td>
<td>0·18</td>
<td>1·1</td>
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</table>

* ee indicates that cell was tested with ‘extended edge’ only.
space. The spatial frequencies for area 18 cells were generally lower than for area 17 cells (Table 2), even for cells representing roughly corresponding regions in the visual field.

In Table 2 receptive field widths, spatial frequency, and the calculated optimal single slit width (which is the reciprocal of twice the spatial frequency) are listed. When these data are plotted (Text-fig. 9), there is an inverse type of relationship between receptive field width and spatial frequency. The same plot seems to fit both area 17 and area 18 cells.

The area 18 cells have larger receptive field widths but represent lower spatial frequencies; their receptive fields display about the same number of peaks as do area 17 complex cells. Thus, for these cells, the larger field sizes do not indicate any increase in the number of cycles within a receptive field. Additionally, area 18 cells are often responsive only to rapidly moving stimuli (Table 2).

However, in one cell, 61–2, the relationship between receptive field width and spatial frequency would not fit with the plot in Text-fig. 9. The moving-slit histogram (Text-fig. 3 C) had about twice as many peaks as we encountered in area 17 and 18 cells and, as described earlier, this cell may have been situated in the area representing the vertical meridian. If this is the case, this cell’s receptive field may have resulted from an assembly of periodic subunits from the two hemispheres.

The relationship between test slit width and the calculated half period
may also be considered here. In the methods section we had noted that in the moving slit studies we had selected the narrowest slit width that gave a strong response. As it turned out, the widths used were usually less than or about equal to the half-period values later calculated (Table 2).

Text-fig. 10. Complex cell responses. Three individual sweep records from two different complex cells in area 17 are shown in I and II and records from two area-18 complex cells are shown in III and IV. Sometimes the peak spacings are clear, as best seen in IV A–C. Note the variability in corresponding peak onsets from one trace to another for the same cell in II, III and IV. The spikes in IA–C have been retouched.

Analysis of individual records of complex cell responses to moving slits. Individual records were examined to assess the manner in which the periodic and non-periodic portions of the histogram responses were built up. Individual records are shown for complex cells in area 17 (Text-fig. 10, I, II) and area 18 (Text-fig. 10, III, IV). The records for cell 55–2 (Text-fig. 10, IA–C) show sporadic firing as the slit moves across the receptive field,
and periodically spaced discharged zones are not readily apparent. However, after looking at the average response histogram for this cell under the same conditions (Text-fig. 6B) and noting the relative positions of the five peaks, one can scan the three individual records and observe that there is some increase in cell firing rate at positions corresponding to the histogram peaks. There are also brief pauses in firing rate at certain intervals corresponding to minima.

The regions of increased cell firing and the regions of pauses are more clearly seen in records from another cell (Text-fig. 10, III) which may be compared to the histogram of Text-fig. 3F. The responses from each discharge zone and the interpeak pauses are especially clear in Text-fig. 10, IV corresponding to the histogram of Text-fig. 3E. The bursts of cell firing corresponding to any given histogram peak fall a bit earlier or later in different individual records. This results in a partial overlap of discharge zones, which in turn generates the 'bias level' observed in the histograms of Text-fig. 3E. The response variability of maxima and minima may also be noted in Text-fig. 10, II, III. Firing levels for the increased neural activity as the slit crossed discharge zones ranged from 250 to 500/sec (Text-fig. 10, III) or higher (Text-fig. 10, IV). In individual records one or another entire set of responses from individual discharge zones may drop out from time to time (Text-fig. 10, IV).

**Fourier transforms of the receptive field excitability profiles of complex cells.** The receptive field profiles shown in Text-fig. 3 were Fourier analysed, and the resulting spectra are shown in Text-fig. 11. The plots have been normalized so that the peak amplitude of the periodic component is assigned the value 1·0. The transforms indicate that the periodic response can be described reasonably well by a single preferred frequency. At frequencies above the principal peak there is no clear evidence of higher harmonic content. Consequently, the phase information in the transforms is not of particular interest and is not shown.

The very low frequency terms in the spectra are a measure of the reciprocal of the receptive field width. The values for the DC and low frequency terms are greater than those of the periodic terms. Much of the magnitude of the very low frequency terms may be a consequence of the temporal variability of responses from each discharge zone with neighbouring peaks partially overlapping and building up a bias level and need not indicate a prediction of a biological response.

In typical Fourier transforms for area 17 and 18 cells, the half band width of the centre frequency on the high frequency side is about one fifth of an octave (Text-fig. 11A, D). The half-amplitude band width on the low frequency side is either of similar width (Text-fig. 11A, B, F) or slightly broader (Text-fig. 11D, E). For cell 61-2 at the 17-18 border
region, the half band width of the centre frequency is about one tenth of an octave (Text-fig. 11C).

Simple cell studies. A number of simple cells were studied in the same experiments in which the periodicities in complex cell responses were found, so as to determine whether or not simple cells studied under the same conditions would also give spatially periodic average response histograms. In all simple cells, 'on' and 'off' regions were first mapped out with stationary stimuli before moving stimuli were used. Whenever a purely unidirectional simple cell was found, the cell was found to be 'edge selective' with a single excitatory region bordering an inhibitory zone. In some cells the preferred direction was from the excitatory to the inhibitory region, in which case a moving slit generated a strong response as it traversed the 'on' region and in some such cells there was another response as the slit left the 'off' region (Text-fig. 12E, upper trace).
When an extended edge crossed this cell's field in the preferred direction, it produced a ramp-like summation as it crossed through the 'on' area with a very abrupt fall in response as the slit entered the inhibitory region (Text-fig. 12 E, lower trace). Moving slit responses for a typical cell with preferred direction from the inhibitory to the excitatory region are shown for a slit moved in the preferred (Text-fig. 12 F, upper trace) and

Text-fig. 12. Simple cell response histograms to moving slits and edges are shown. The direction of movement across excitatory and inhibitory regions is indicated above each histogram. Records from on-centre cells are shown in A, B and D. Results from an off-centre cell are shown in C, and responses from edge selective cells with different directional preferences are shown in E and F. Cell 57–4 in A and B, slit width 11 mm. Cell 56–4 in C, slit width 14 mm. Cell 56–1 in D, slit width 4 mm. Cell 42–5 in E. Slit width for upper trace is 3 mm. Cell 42–1 in F, slit width 2 mm (26.19 mm = 1°).
non-preferred (Text-fig. 12 F, lower trace) directions. There might be some minor irregularities or inflexions on the rising phase of the average response histograms (Text-fig. 12 E, F), but no clearly periodic responses were seen for edge selective simple cells.

Text-fig. 13. Simple cell. A, average response per stimulus for the first 500 msec of the on-response is plotted against slit width for a number of slits presented symmetrically around the receptive field centre in a random sequence for an on-centre simple cell. Most of the response occurred within the first 250 msec but some response persisted for a longer period, so the 500 msec counting interval was selected. The spontaneous level is indicated by the dashed line. Cell 57-4. Stimulus duration is 500 msec.

B, the response amplitudes are normalized for a peak response of 1 and are plotted on a log scale against the reciprocal of twice the width to give an 'equivalent spatial frequency' for one cycle of a square wave grating.

Both on-centre and off-centre width selective simple cells were also studied. These cells responded well to slit movements in either direction, although the response might be greater for one direction of movement. In an off-centre cell, the two excitatory flanks respond in turn as the slit moves across the field (Text-fig. 12 C). Simple cells with on-centres might
also give two responses to a moving slit, one response when the slit traversed the ‘on’ region and in some cells another response occurred as the slit left the ‘off’ region with either direction of movement (Text-fig. 12A, B). For other on-centre simple cells, only the central ‘on’ response might be generated (Text-fig. 12D).

Symmetric slit width responses were also carried out on several on-centre simple cells, including the one whose responses to moving slits are shown in Text-fig. 12A, B. Slits of different widths were presented at random and the results are plotted (Text-fig. 13A). As the slit width increased, an optimal width was found, beyond which the response progressively decreased. No subsequent relative maxima were found, unlike the case in complex cells where a series of relative maxima and minima resulted.

In order to facilitate comparison of the slit width selectivity of this cell with the spatial frequency selectivity of identified simple cells studied by Maffei & Fiorentini (1973) with sine wave gratings, the normalized responses are plotted versus the reciprocal of twice the width, which would represent the spatial frequency for a one cycle section of an equivalent square wave grating. The curve in Text-fig. 13B is similar to some of the spatial frequency selectivity curves of Maffei & Fiorentini (1973) and has a full band width at half-amplitude of over an octave. By comparison they indicated an even broader tuning for complex cells than for simple cells. This result may reflect their measurement of an average receptive field shape rather than of the periodic component we have observed. Their result is not unexpected insofar as they measured the average discharge rate as gratings moved across the receptive field over a one minute period rather than the amplitude of the modulation of the firing rate. Moreover, some of their stronger responses to low frequency gratings when the grating period was greater than the receptive field may be comparable to the average density of responses obtained with single moving edges.

DISCUSSION

When a narrow slit is moved in the preferred direction across the receptive field of complex cells in area 17 and 18, average response histograms were generated which displayed a periodic receptive field profile consisting of a series of maxima and minima riding above some baseline level. The periodicity for each cell measured in cycles/degree remained constant over a particular range of velocity, although peak response amplitudes were velocity dependent. Thus, the peaks remain referable to fixed positions within visual space independent of the test velocity, even though temporal as well as spatial factors may be involved.
in response selectivity and the periodic modulation. Such an arrangement would allow a visual system to identify an object as the same object independent of its velocity across the retina within certain velocity ranges. The average response histograms of complex cells to extended edges were also periodic. The periodic component of the receptive field could also be demonstrated for some area 17 complex cells when stationary slits of different widths were tested.

Resolution of the periodic component was critically dependent upon first determining the precise preferred orientation selectivity. Once this was established, periodic histograms in area 17 and 18 generally showed five principal peaks with one or two weaker peaks sometimes noted at the receptive field edges. The receptive fields for complex cells of area 18 cells are wider than for area 17 cells subserving roughly similar regions of the visual field. There tends to be an inverse relationship between spatial frequency and receptive field width, the greater receptive field widths of area 18 cells being associated with a lower range of spatial frequencies. In one case we recorded from a cell close to the 17–18 border and the histogram for the receptive field, which covered both sides of our back projection of the area centralis, showed thirteen distinct peaks.

Histogram response amplitudes were velocity related functions. The periodic response pattern was usually best brought out at velocities producing the maximal level of cell firing per second. For area 17 cells the optimal velocities used were relatively low, ranging from less than 0.5°/sec to 6.0°/sec, and the velocity selectivity on a response per second basis was relatively broadly tuned. The central visual region in area 17 had complex cells with spatial frequencies covering a three octave range up to 5 cycles/degree. These findings suggest that complex cells in area 17 may be involved in pattern recognition tasks demanding relatively fine resolution of detail during the viewing of stationary or slowly moving objects.

By contrast, even though our sample of area 18 cells was very small, many of the cells studied required very high velocities to make them respond well, and the spatial frequencies measured were generally lower than in area 17 cells representing roughly corresponding regions in the visual field. The correspondence is only partly similar in the two cases, because the outer borders of the wider field area 18 cells may extend out more peripherally than the fields of area 17 cells. This class of area 18 complex cells might be involved in abstracting relatively coarse details of form from objects moving rapidly across a fixed retina.

Simple cell receptive field shapes. Our results with simple cells were consistent with those of Hubel & Wiesel (1962). Using stationary stimuli, we found simple cells whose responses suggested optimal selectivity to a given width or to a single edge. Moreover, when width selective simple
cells were tested as a function of slit width, the resultant curve indicated a single optimal width. Hubel & Wiesel (1962) suggested that simple cells might project on to complex cells. The presence of five to seven peaks in the average response histogram for complex cells might be indicative of multiple simple cell inputs.

Hubel & Wiesel (1962) also suggested that edge selective simple cells might project on to complex cells with edge selective properties. Given the velocity response selectivity of complex cells, especially in area 18, and mindful of the findings of Bishop et al. (1971) stressing the spatio-temporal aspects of both slit width and velocity upon simple cell responses, the possibility remains open that a series of edge selective simple cells may be connected to complex cells in such a way as to produce a spatially periodic receptive field shape. The foregoing discussion assumes after Hubel & Wiesel (1962) that simple cells may project on to complex cells. However, it should be realized that Hoffman & Stone (1971) have reported results which may indicate the existence of monosynaptic geniculate inputs to complex cells; even so, that finding alone is neither sufficient for excluding a simple cell input as well nor for determining whether such a direct geniculate input is responsible for any of the spatially periodic or orientation selective properties of complex cell responses.

Spatially periodic responses and the 'bias level' of complex cells. The average response histograms to moving slits and edges displayed a series of periodic peaks riding above a background or 'bias level'. When single cell responses to single sweeps were examined, intervals of increased cell firing upon a background of seemingly sporadic cell firing were often observed. At other times each set of responses from successive discharge zones was distinct, but there was some variability in response onset from one record to another. We cannot determine whether the magnitude of the bias level due to response overlap is due to response variability or to some independent synaptic drive which provides a steady background level of excitation.

The Fourier transforms of the receptive field excitability profiles of complex cells. The Fourier transforms indicated that the periodic component of the response could be well described by a single preferred frequency. Beyond the principal peak, there was within the noise level no clear harmonic content, so relative phase plots were not deemed to be relevant here. The general absence of significant higher harmonics also indicates that to a first approximation the periodic component may be considered sinusoidal.

The DC and low frequency terms in the transform provide a measure of the bias level, which to a certain but usually unknown extent is built up by partial overlap of neighbouring peaks as discussed above. Even if all minima had reached zero, the Fourier transform of the receptive field
shape would still have shown a considerable DC term equal to the average level of the histogram response.

In typical Fourier transforms for area 17 and 18 cells, the half-band width on the high frequency side of the centre frequency was about one fifth of an octave with either a similar or slightly broader half-band width on the low frequency side. For the cell at the 17–18 border, the half-band width was about one-tenth of an octave. These same Fourier transforms would, apart from the DC and low frequency terms, predict the modulation transfer function for the responses of a family of gratings assuming that the spatial filter had linear response characteristics. The bias level terms, even if not largely exaggerated due to response overlap, need not constitute a serious analytical problem for subsequent stages of neural processing which could operate either on a high threshold detection basis or by filtering out lower interspike interval firing. On the other hand, if the bias level represents a broadly tuned filter in itself, then there may be serious difficulty in considering the periodic component of the receptive field as a dominant narrow band filter.

Two important steps remain ahead to determine whether these periodic receptive field shapes contribute to a narrow band spatial frequency analysis of discrete regions of visual space. First, ‘slit-length’ studies must be carried out to determine the function relating slit length to cell response. Secondly, it would be of interest to know whether there are conditions under which the coupling between discharge zones follows reasonably linear rules of summation as periodic multiple bar stimuli are tested. Work relating to these problems is in progress.

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REFERENCES


COMPLEX CELL RECEPTIVE FIELDS


EXPLANATION OF PLATE

A,B, Nissl and Loyez stained celloidin sections showing electrode tract in area 17 in which penetration complex cell 57–2 (Text-fig. 3A) and the simple cell of Text-figs. 12A,B and 13 were studied. The black material over the cortical surface and in the tract in B is India ink which was used to mark where the electrode penetrated the surface so as to aid in cutting blocks of tissue down to the relevant regions. Only one electrode penetration was made in this brain, but the electrolytic lesion in this case was not recovered.

C,D, Nissl and Loyez stained frozen sections for cell 61–2 showing a large electrolytic lesion near the area 17–18 border. Note the prominent large pyramidal cells of layer 3 beginning just lateral to the lesion.
Periodic excitability changes across the receptive fields of complex cells in the striate and parastriate cortex of the cat.

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