*J. Physiol.* (1975), **249**, *pp.* 445–468
*With* 11 *text-figures*
*Printed in Great Britain*



# THE VELOCITY TUNING OF SINGLE UNITS IN CAT STRIATE CORTEX

BY J. ANTHONY MOVSHON*

*From the Psychological and Physiological Laboratories, University of Cambridge, Downing Street, Cambridge CB2 3EB*

(*Received 30 October 1974*)

SUMMARY

1. The activity of single units was recorded from the striate cortex (area 17) of anaesthetized, paralysed cats. Reponses to stimuli moving at different velocities were examined.

2. Peak evoked firing frequency, rather than total evoked spikes, is used throughout as a measure of response. The former measure gives curves of response *vs.* velocity that correlate well with curves of contrast sensitivity *vs.* velocity, whereas the latter does not.

3. Cortical receptive fields were classified according to the criteria of Hubel & Wiesel. Simple cells were found to prefer lower velocities (mean 2·2 deg $sec^{-1}$) than complex cells (mean 18·8 deg $sec^{-1}$). The response of simple cells to stimuli moving faster than 20 deg $sec^{-1}$ is generally poor; complex cells usually discharge briskly to these speeds.

4. Cells classified as hypercomplex by the end-inhibition criterion were further characterized as type I or type II, according to the suggestion of Dreher (1972). Type I units are indistinguishable from simple cells in their velocity tuning, and type II units equally clearly resemble complex cells. These results are therefore consistent with Dreher's subdivision.

5. The selectivity of cells for velocity is variable but can be quite marked. The average selectivities of simple and complex cells are not significantly different. There is an inverse correlation between preferred velocity and the sharpness of velocity selectivity for simple cells; no trend is apparent for other cell types.

6. No clear correlation is observed between the velocity preferences of units and their degree of direction selectivity, or receptive field arrangement. Simple cells with 'sustained' temporal responses to flashed stimuli tend to prefer slower rates of movement than 'transient' ones, and to be less selective for velocity.

* Address from 1 October 1975: Department of Psychology, New York University, 4 Washington Place, New York, N.Y. 10003, U.S.A.

7. The results for different cortical cell-types are compared with the velocity tuning of X- and Y-cells in the lateral geniculate nucleus.

## INTRODUCTION

Single neurones in the primary visual cortex of the cat can be divided into three classes, simple, complex and hypercomplex, on the basis of their responses to visual stimuli. The groups, and the criteria by which they may be discriminated, were first described by Hubel & Wiesel (1962, 1965). Two response properties distinguish these three cortical cell-types from afferent fibres from the lateral geniculate nucleus: most can be activated by stimuli presented to either eye, and are sensitive to the orientation of a linear stimulus flashed on the receptive field or moved across it. In addition, many are sensitive to the direction of movement (Hubel & Wiesel, 1962).

Simple cells have receptive fields that can be subdivided into parallel 'on' and 'off' regions on the basis of their responses to flashed bars or spots of light. It is possible to demonstrate spatial summation of 'on' or 'off' responses within these subregions of the field, and antagonism between them. Furthermore the spatial configuration of the excitatory and inhibitory regions revealed in this way is an accurate indication of the optimal stimulus pattern, though it does not usually predict asymmetries in response to different directions of movement of an optimally oriented stimulus (Bishop, Goodwin & Henry, 1974). Complex cells normally have receptive fields that cannot be divided into subregions in this manner; if they respond at all to flashed stimuli an 'on-off' discharge is usually obtained anywhere in the field. Furthermore, the width of the optimal stimulus is not simply related to the size of the region from which responses to flashed stimuli may be evoked. Cells of the third type, which are less commonly encountered in area 17, resemble the lower-order hypercomplex cells described in prestriate cortex by Hubel & Wiesel (1965) in that they are selectively responsive to stimuli limited in length at one or both ends. Apart from this single feature they resemble simple or complex cells, and Dreher (1972) has suggested that they should be classified as type I (simple-type) or type II (complex-type).

Hubel & Wiesel (1962) found that cells of all types but of similar preferred orientation tended to be clustered together in 'columns' extending radially in the cortex from surface to white matter, and that, in any particular region of the visual field, simple cells tend to have smaller receptive fields than complex cells. They also found that the various cell types were not uniformly distributed in the depth of the cortex: simple

cells occur most commonly in or near layer IV, the site of termination of almost all geniculocortical fibres (Garey & Powell, 1971), while complex and hypercomplex ecIls are more often found in the deeper or more superficial layers (see also Kelly & Van Essen, 1974). Hubel & Wiesel therefore proposed that the cell-types represented different levels in a *hierarchical*, or *serial* analysis of visual information. In this scheme simple cells receive the bulk of their synaptic input directly from the optic radiation, while complex cells gain most of theirs from the simple cells within the same column, which bestow on them the same orientation preference.

An alternative theory derives from the discovery by Enroth-Cugell & Robson (1966) that there are two classes of ganglion cells in the cat retina, which can be distinguished according to the linearity of spatial summation within their receptive fields: X-cells are linear while Y-cells are non-linear in their summation behaviour. It has been shown (Cleland, Dubin & Levick, 1971; Hoffman, Stone & Sherman, 1972) that these two systems remain functionally distinct at least to the level of the relay cells of the lateral geniculate nucleus, and that they are also morphologically distinct: X-cells in both the retina and lateral geniculate have smaller axons with slower conduction velocity, while Y-cells, are larger, and faster. Hoffmann & Stone (1971) were able to show that complex cells that could be monosynaptically activated by electrical stimuli applied to the optic tract or radiation had, on average, a shorter latency to such stimulation than simple cells that could be similarly activated. They took this as evidence that simple and complex units were the cortical representatives of the X- and Y-pathways respectively, two separate and *parallel* systems for processing visual information (see Stone, 1972).

If we could find some property of complex cells which could not be derived from simple cell input, or show that there is some stimulus dimension to which the two cell-types are differentially sensitive, we would have powerful evidence in favour of the parallel processing model. The specificity and selectivity of the cell-types for such stimulus features as orientation (Rose & Blakemore, 1974), spatial frequency (Maffei & Fiorentini, 1973) and length (Rose, 1974) have been compared, and found to be rather similar. But some of the data of Pettigrew, Nikara & Bishop (1968*a*), and the comments of other workers (Hoffmann & Stone, 1971; Stone & Dreher, 1973; Maffei & Fiorentini, 1973; Palmer & Rosenquist, 1974) suggest that there might be a substantial difference between the velocity tuning characteristics of simple and complex cells, though other authors have reported no apparent difference between them (Kelly & Van Essen, 1974).

The experiments described here are addressed to the problem of the

velocity tuning characteristics of cortical neurones. Some of these results have been briefly reported elsewhere (Movshon, 1974).

## METHODS

Adult cats were initially anaesthetized with halothane (Fluothane), and surgery was carried out under a short acting barbiturate (methohexitone sodium: Brietal). Light anaesthesia was maintained during recording with a mixture of 80% $N_2O$/19% $O_2$/1% $CO_2$, and eye movement was minimized by a continuous I.V. infusion of gallamine triethiodide (Flaxedil: 10 mg $kg^{-1}$ $hr^{-1}$) in 6% glucose-Ringer solution (4 ml. $hr^{-1}$), together with bilateral cervical sympathectomy. Body temperature was maintained at 37° C with a thermostatically controlled heating pad. E.e.g. and e.c.g. were monitored continuously. Peak expired $P_{CO_2}$ was checked at intervals with a Beckman infrared gas analyser (LB-1 or LB-2) and maintained at 4·0–5·0% by adjusting the tidal volume of the respiration pump.

Pupils were dilated with homatropine sulphate, and eyelids and nictitating membranes retracted with phenylephrine HCl. The corneae were protected with clear contact lenses, 3 mm artificial pupils were placed immediately in front of the eyes, and supplementary lenses used to focus the eyes on a screen 57 cm away.

Single units were isolated in area 17 using tungsten-in-glass micro-electrodes (Levick, 1972) with an exposed tip length of 8–15 $\mu$m, which were driven hydraulically into the cortex through a sealed chamber over a small craniotomy and durotomy. Action potentials were conventionally amplified and displayed.

Small electrolytic lesions were made at points along each penetration (total length 1–4 mm) by passing current through the electrode tip (5–10 $\mu$A for 5 sec, tip negative). At the end of the experiment the animal was sacrificed and perfused with 10% formalin in Ringer solution. The brain was sectioned at 40 $\mu$m, stained with cresyl violet and sometimes counterstained with luxol fast blue. Most penetrations were histologically verified to lie within area 17. In the few cases where such confirmation was not obtained, the point of entry of the electrode, the drift of receptive field positions into the contralateral visual field and the occurrence of simple receptive fields (Hubel & Wiesel, 1962, 1965) were taken to indicate that the penetration lay within area 17.

Stimulus control was obtained with a television technique, modified from Campbell & Green (1965). Bright or dark bars, or edges were generated on the face of a display oscilloscope (Hewlett-Packard 1300A; P31 phosphor). The frame frequency of the display was normally 500 Hz, increased to as much as 2000 Hz for very high velocity stimuli. The stimulus was swept at a controlled rate by injecting a gated low-frequency triangle or sawtooth wave pulse into the time base; stimuli could be moved at velocities from 0·05 to over 100 deg $sec^{-1}$. The mean luminance of the display was 5–10 cd $m^{-2}$, and the luminance difference between the brightest and darkest parts was 0·2–0·5 log units, except in the experiments on sensitivity described below, when the contrast was varied with a decade attenuator to determine the unit's contrast threshold. Stimuli were appropriately positioned and oriented by physically moving and rotating the display; where stimuli of limited length were required, the appropriate portions of the screen were masked.

The responses of cortical units were analysed on-line with a multichannel averaging computer (Biomac 1000) gated by the stimulus sweep to produce smoothed pulse-density histograms (Enroth-Cugell & Robson, 1966). In addition, an external counter-printer was sometimes used to print out the total spike count in a sweep-gated interval. The response to twenty stimulus presentations was normally averaged.

Receptive fields were initially plotted by hand on a tangent screen with flashed and moving slits, bars, edges and spots. They were classified as simple, complex or hypercomplex (type I or type II) by the criteria of Hubel & Wiesel (1962) and Dreher (1972) as discussed above. Units with the brisk response, monocular drive, concentric receptive field organization and brief spike wave form of fibres from the lateral geniculate nucleus were characterized as on- or off-centre and *X*- or *Y*-type using some of the criteria of Cleland *et al.* (1971) and Hoffmann *et al.* (1972). If a unit was judged to be sufficiently stable after this qualitative investigation, quantitative analysis was undertaken over a period of 1½–8 hr.

The configuration, dimensions and orientation of the optimal bar or edge stimulus for this analysis were established during the initial qualitative investigation of the receptive field. In the case of simple cells, the optimum stimulus reflected the spatial arrangement of 'on' and 'off' regions in the receptive field (Hubel & Wiesel, 1962). Stimuli were normally delivered to the dominant eye, and the other eye was covered. In two cases, however, units showed marked facilitation of an otherwise poor response to an appropriately positioned binocular stimulus (Barlow, Blakemore & Pettigrew, 1967; Pettigrew, Nikara & Bishop, 1968*b*). For these units, the disparity was optimized with a variable bi-prism, and stimuli delivered binocularly.

To determine a unit's 'tuning curve' for velocity, different rates of movement were presented in pseudo-random order. The first velocity tested was often retested at the end of the run to ensure that responsiveness had not grossly changed. These repeat determinations almost invariably agreed with the first to within 10–20%, and the difference was often smaller when the experiment was more than 12 hr old and the animal's condition had completely stabilized. Stimulus sweeps were externally gated to provide an interval between presentations of at least 7 sec.

Each unit was tested with five to fifteen velocities, covering a range of two to ten octaves. It was not usually possible to follow the extreme ends of the tuning curves down to zero or negligible response, but the low-velocity end of many complex cells' tuning curves, and the high-velocity end of most simple cells' tuning curves was determined. Otherwise a 50% drop in response from the optimum was accepted as a reasonable limit for quantitative investigation; each unit was qualitatively tested well beyond these limits to ensure that the response declined monotonically beyond the ends of the assessed tuning curve.

Ninety-six units were recorded from twelve penetrations in seven cats, and the behaviour of sixty-six was fully analysed. Of these, sixty were cortical cells: twenty-five simple, twenty-eight complex and seven hypercomplex (four of type I and three of type II). In addition, the responses of six fibres from the lateral geniculate nucleus were examined; four were X-type and two Y-type. All units had receptive fields within 10 deg of the *area centralis*, and most were within 5 deg.

## RESULTS

### *The measurement of response*

In order to determine the velocity tuning curve for a cell it is necessary to choose between the two fundamentally different ways of measuring the response: as a function of time, and as a function of space.

*Measurement as a function of space: a time-independent measure.* This method involves counting the number of spikes per sweep of the stimulus, and subtracting any maintained activity to determine the evoked response during the sweep (Barlow, Hill & Levick, 1964; Rose & Blakemore, 1974).

Since this measure takes no account of the fact that the stimulus spends less and less time in the receptive field as the velocity increases, it favours low rates of movement. It produces a measure of the number of spikes evoked by the stimulus per unit of space. In these terms a unit that shows a maintained elevation of discharge to an appropriately positioned stimulus has a preferred velocity of zero (an infinite response in an infinite sweep time).

*Measurement as a function of time: a space-independent measure.* Either the mean frequency during the response (Finkelstein & Grüsser, 1965) or the peak firing frequency (Pettigrew *et al.* 1968*a*) can be determined, and these two measures are highly correlated, since the shape of the pulse-density histogram plotted as a function of space rarely undergoes gross changes as the velocity is varied (Figs. 3 and 4). This reflects the fact that the apparent spatial dimensions of the receptive field do not change dramatically as a function of stimulus velocity. Since the amount of time the stimulus spends in the receptive field varies widely it seems more appropriate to use a

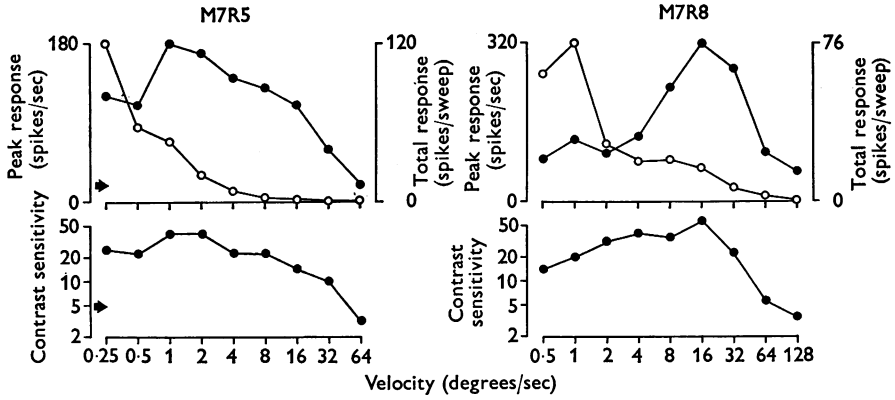


Fig. 1. Comparison between contrast sensitivity as a function of velocity and response as a function of velocity using the two response measures discussed in the text. The upper graphs show velocity tuning curves for a simple cell (left) and a complex cell (right), with response expressed as peak firing frequency (filled symbols, left-hand ordinates) and total spikes per sweep (open symbols, right-hand ordinates). The lower graphs show the cells' contrast sensitivities at the same velocities, for the stimuli used to produce the velocity tuning curves (a bright bar, 5 deg by $\frac{1}{4}$ deg in each case). The arrows in the left-hand graphs represent the simple cell's maintained firing frequency (upper graph) and contrast sensitivity (lower graph) to a stationary optimally positioned stimulus turned on in the receptive field. The cell's response in total spikes to this stimulus is practically infinite, since the sweep time at zero velocity is infinitely long.

Contrast sensitivity is the inverse of the threshold contrast. Contrast is defined as $L_{max} - L_{min}/L_{max} + L_{min}$.

measure that takes account of the time element but not the space element, rather than vice versa.

I performed a control experiment to determine which method of assessment more nearly reflected the cell's sensitivity to stimuli of low contrast as a function of velocity. The results for two cells, one simple and one complex, are shown in Fig. 1; three other cells (two simple and one complex) showed similar behaviour. The cells were tested for their response to a range of stimulus velocities with both frequency and space measures, and to standing contrast in the case of the simple cell, which showed a maintained discharge to an appropriately positioned bright bar. A cell's contrast threshold at each velocity was determined by adjusting the contrast of the stimulus in 0·05 log unit steps until a contrast level was found to which the cell responded on eight of ten stimulus sweeps. Neither of the cells illustrated had any maintained activity, which made it easy to recognize a response (usually one spike at threshold); when spontaneous activity was present the results were similar.

Notice that the contrast threshold of both cells was lowest at that velocity which gave the best response measured in *frequency* terms, 1 deg $sec^{-1}$ and 16 deg $sec^{-1}$ respectively. In *space* terms the simple cell had a preferred velocity of zero, since it showed a maintained discharge of 19 spikes $sec^{-1}$ over several minutes to standing contrast, and the complex cell had a preferred velocity of 1 deg $sec^{-1}$; these clearly do not correlate with the observed sensitivities. As a result, and for the other reasons discussed above, the peak firing frequency measured from the smoothed pulse-density histogram is used as a measure of response.

### *The analysis of response*

Fig. 2 shows pulse-density histograms of the responses of two simple cells to stimuli moving at a number of velocities. Cell M4R12 had a very brisk discharge to very slow stimulus movement. The cell's response to 0·5 deg $sec^{-1}$ was slightly better than to the other velocities, and its activity declined gradually from there. There was little discharge to movement at 8 deg $sec^{-1}$, and no response to 16 deg $sec^{-1}$. The cell had a preference for movement to the right, which is expressed more or less equally at all velocities below 4 deg $sec^{-1}$; above this velocity the response, such as it was, was roughly equal in the two directions of the sweep. This was a typical 'slow' simple unit.

Cell M4R17 showed a rather sharper selectivity for one velocity of movement (4 deg $sec^{-1}$). The response declined abruptly above this value (there was no response to 16 deg $sec^{-1}$) and rather more gradually below it. This was a typical 'fast' simple cell, though not all such cells showed such

an abrupt decline in activity at velocities higher than the optimum. This cell was almost completely direction selective, and responses in the null direction are not shown.

Fig. 3 shows similar histograms for three complex cells. All of these cells had a direction preference or were completely direction selective, and responses are only shown for movement in the optimum direction. Cell M4R4 showed a moderately strong preference for stimuli moving between 2·5 and 5 deg sec$^{-1}$; the response declined fairly sharply either side of

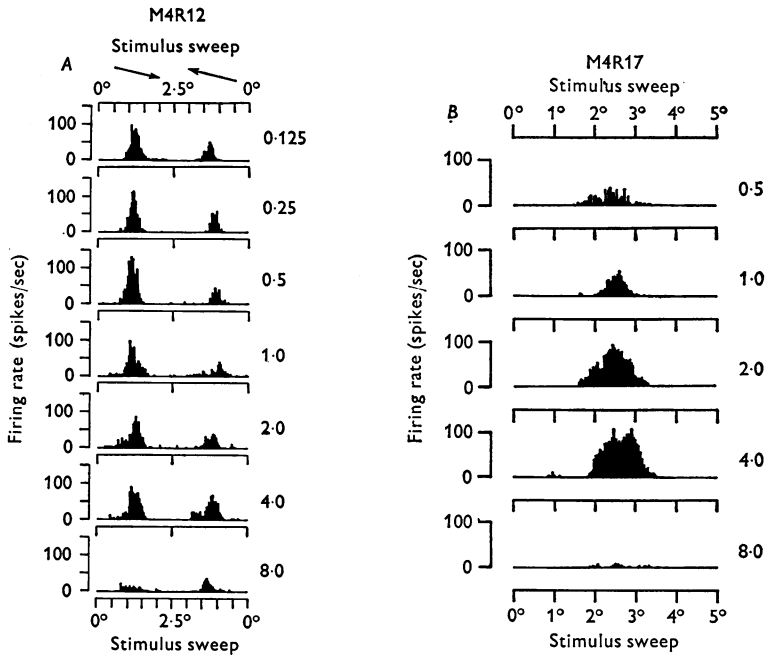


Fig. 2. Pulse density histograms of the responses of two simple cells to various stimulus velocities. *A*, cell M4R12. Stimulus was a 10 deg by $\frac{1}{4}$ deg bright bar, moving back and forth across the receptive field. *B*, cell M4R17. Stimulus was a 10 deg by $\frac{1}{2}$ deg bright bar, moving across the receptive field. For each histogram space is shown on the abscissa and firing rate on the ordinate. The velocity of each stimulus in deg sec$^{-1}$ is indicated beside each record. Each histogram shows the average of twenty stimulus sweeps.

these values. This preference for moderately slow velocities made it one of the 'slowest' complex cells seen, and it was also unusual in that its response dropped to almost nothing at 40 deg sec$^{-1}$. The relatively sharp fall in activity below the preferred velocity was, however, typical. Cell M4R18 showed a relatively poor response to a velocity of 3 deg sec$^{-1}$. The discharge increased up to a velocity of 18 deg sec$^{-1}$, and declined above it. The response to 36 deg sec$^{-1}$ was relatively poor, but the cell

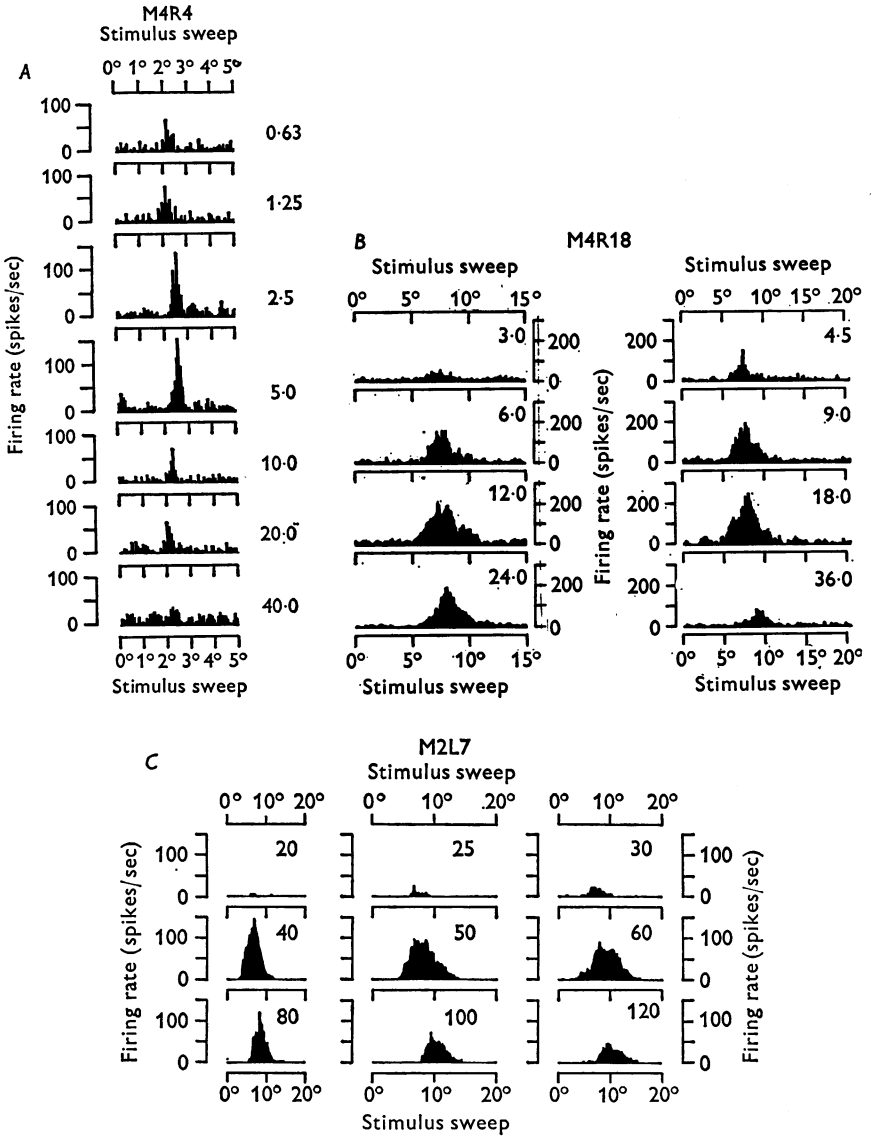


Fig. 3. Pulse density histograms of the responses of three complex cells to various stimulus velocities. *A*, cell M4R4. Stimulus was a 4 deg by $\frac{1}{4}$ deg dark bar. *B*, cell M4R18. Stimulus was a 10 deg by $\frac{3}{4}$ deg bright bar. *C*, cell M2L7. Stimulus was a 20 deg long *light* edge, producing a step *increase* in luminance as it moved across the receptive field. Responses are shown only in the preferred direction. Conventions otherwise as in Fig. 2.

continued to respond quite briskly to velocities in excess of 80 deg sec$^{-1}$ (not shown). Cell M2L7 was one of the 'fastest' cells seen. It gave little response to rates of movement less than 30 deg sec$^{-1}$. There was a clear preference for 40 deg sec$^{-1}$, but the drop in activity as velocity increased was very gradual, and a brisk response was obtained to 120 deg sec$^{-1}$, the highest velocity tested. This unresponsiveness to velocities below 20 deg sec$^{-1}$

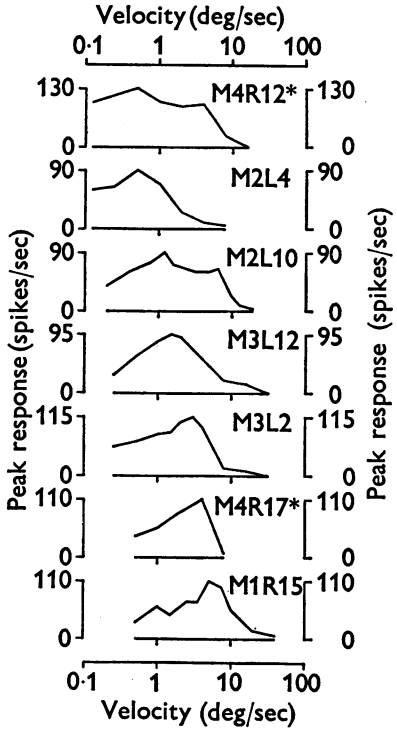


Fig. 4. The velocity tuning curves of seven simple cells. Pulse density histograms for cells marked with an asterisk (*) are shown in Fig. 2.

was not common: only three of twenty-eight complex cells (11%) showed similar behaviour.

Figs. 4 and 5 show velocity tuning curves for a number of simple and complex cells respectively. They give some idea of the range of preferred velocity and velocity selectivity encountered; both plainly vary considerably. However, it is clear that simple cells show a markedly lower range of preferred velocities than complex cells. On the logarithmic abscissae used, their response tends to decline more sharply above the preferred velocity than below it, and they rarely respond well to velocities over 20 deg sec$^{-1}$. Twenty of twenty-five simple cells (80%) gave less than

20% of their maximum response to stimuli moving at any velocity faster than 20 deg sec$^{-1}$. Conversely, twenty-six of twenty-eight complex cells (93%) gave more than 20% of their best response to these stimuli. Complex cells, in addition to showing a rather higher range of preferred velocities, often had tuning curves whose slope was more gradual above the

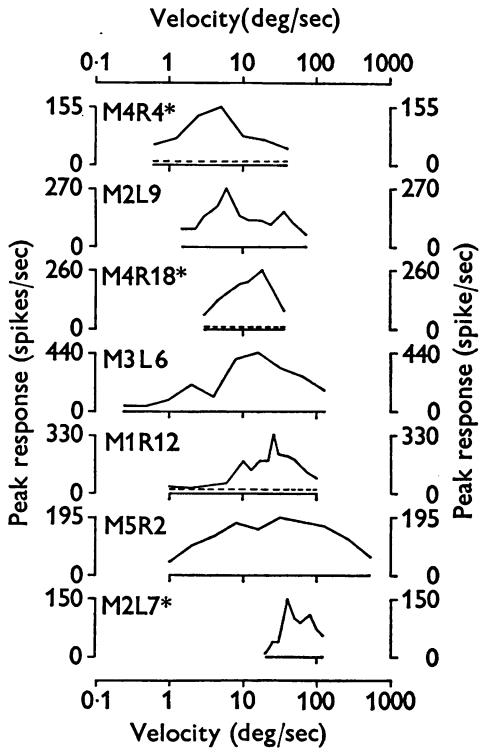


Fig. 5. The velocity tuning curves of seven complex cells. Pulse density histograms for cells marked with an asterisk (*) are shown in Fig. 3. Interrupted lines indicate spontaneous activity.

preferred velocity than below it. Seventeen of twenty-eight complex cells (61%) gave less than 40% of their maximum response to stimuli moving at any velocity below 5 deg sec$^{-1}$. In marked contrast, twenty-four of twenty-five simple cells (96%) gave their maximum response below this value. Thus, a large proportion of complex cells respond briskly to stimulus velocities to which simple cells respond poorly, if at all.

Tuning curves for two hypercomplex cells are shown in Fig. 6. The upper curve, for M1R19, a type I cell, is similar to that of a simple cell in all respects. The preferred velocity (1·5 deg sec$^{-1}$) and the relatively sharp drop in activity at higher velocities are typical of simple cells. The lower

graph shows that cell M5R5, a type II cell, resembled a complex cell in its velocity tuning. It showed a relatively high preferred velocity (16 deg $sec^{-1}$) and a brisk response to stimuli moving at over 30 deg $sec^{-1}$.

Histograms of the preferred velocities of all sixty cells in the four classes are shown in Fig. 7. The difference between simple and complex distributions is absolutely clear. In fact, with hindsight, thirty-seven of

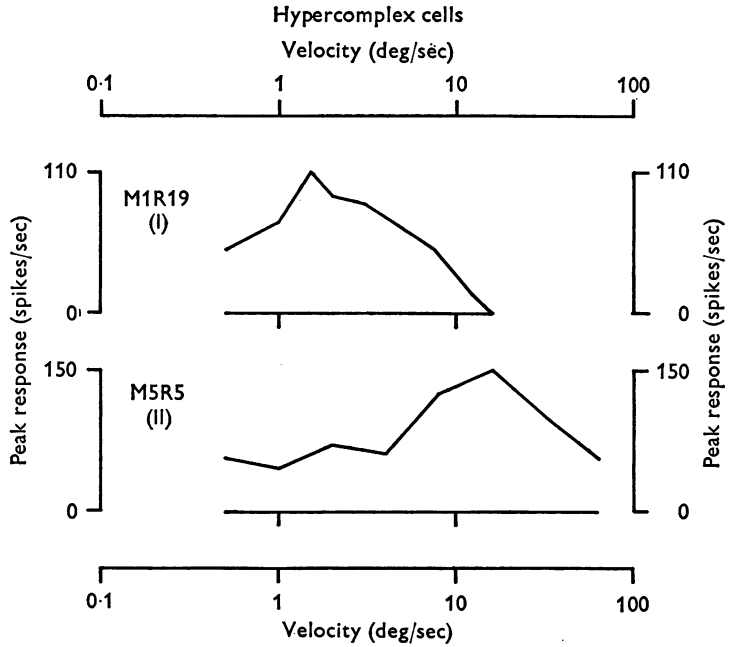


Fig. 6. The velocity tuning curves of two hypercomplex cells. The upper curve is for a type I cell; note its resemblance to the curves for simple cells in Fig. 4. The lower curve is for a type II cell; note its resemblance to those for complex cells in Fig. 5.

the fifty-three cells in these two groups could be appropriately classified as simple or complex simply by their velocity preferences; only sixteen have ambiguous preferred velocities between 2 and 8 deg $sec^{-1}$. The mean preferred velocity for simple cells is 2·2 deg $sec^{-1}$ (S.D. = 1·7); for complex cells it is 18·8 deg $sec^{-1}$ (S.D. = 12·8). The results for hypercomplex cells are consistent with Dreher's (1972) subdivision: type I cells (mean preferred velocity 2·4 deg $sec^{-1}$) fit clearly with the simple distribution and type II (mean 15·5 deg $sec^{-1}$) with the complex.

It is clear from the tuning curves in Figs. 4, 5 and 6 that the selectivity of cells for velocity varies widely. Some cells show relatively sharp tuning for the preferred rate of movement, while others respond briskly to a wide

range of stimulus velocities. An index of this selectivity is provided by the full-width at half-amplitude of a cell's tuning curve, determined by noting the velocities at which the line of half-maximum response intersects the tuning curve, and expressing the difference between them as a ratio of the higher over the lower; this is equivalent to a linear measure on the logarithmic velocity abscissae of Figs. 4, 5, 6, 10 and 11.

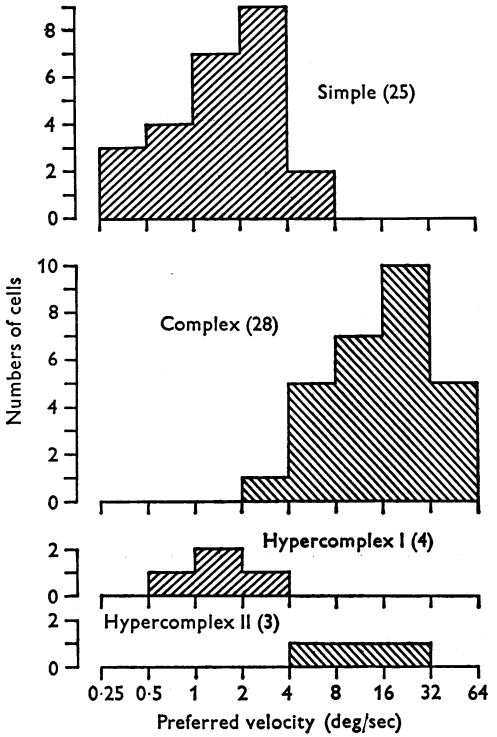


Fig. 7. Histograms showing the distributions of preferred velocities for all sixty cells of the four major types.

It was possible to calculate the full-widths for nineteen of the twenty-five simple cells, twenty-seven of the twenty-eight complex cells and all seven hypercomplex cells. The remaining seven cells were not tested at velocities low enough (in the case of the simple cells) or high enough (in the case of the complex cell) to cause a 50% drop in response from that obtained at the preferred velocity. The full-widths of these cells must of course be greater than some value which can be determined from that extreme end of the tuning curve which does not drop by 50%. Histograms of the full-widths for the fifty-three cells for which this parameter was calculated are shown in Fig. 9. Both major cell-types show a wide range of velocity

selectivity, and complex cells (mean full-width: 18·5) show a slight but non-significant tendency to be more narrowly tuned than simple cells (mean 21·0).

A scatter plot of preferred velocity against full-width is shown in Fig. 9 for all cells. There is a weak tendency for cells preferring lower velocities to be more broadly tuned than those preferring higher ones; there is a significant inverse correlation ($r = -0{\cdot}26$, $n = 60$, $P < 0{\cdot}05$) between the

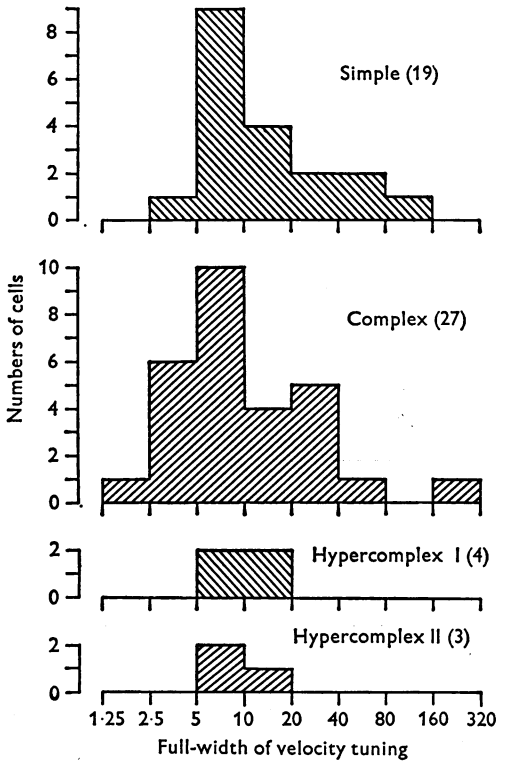


Fig. 8. Histograms showing the distributions of velocity full-widths for fifty-three units of the four major types. The method for deriving this measure of velocity selectivity is described in the text.

variables. Separate analysis of the cell-types showed no significant trend in the complex or hypercomplex categories, but the correlation is apparent among the simple cells (filled circles; $r = -0{\cdot}43$, $n = 25$, $P < 0{\cdot}02$).

It might be that the velocity tuning of a cell depends on some temporal property of the stimulus' traverse of its receptive field, such as the time between the arrival of the two edges of a bar. The velocity tuning might therefore depend on the width of the particular bar stimulus

employed. This possibility was investigated in five cells (three simple and two complex) by determining the velocity tuning a number of times with bars of several different widths. In no case, despite considerable variation in response magnitude, was there a systematic change in the preferred velocity or velocity selectivity, despite a range of bar widths varying by a factor of 16 to 32. Therefore, when spatially aperiodic stimuli are used to determine velocity tuning, the characteristics of that tuning do not depend on the width of the stimulus.

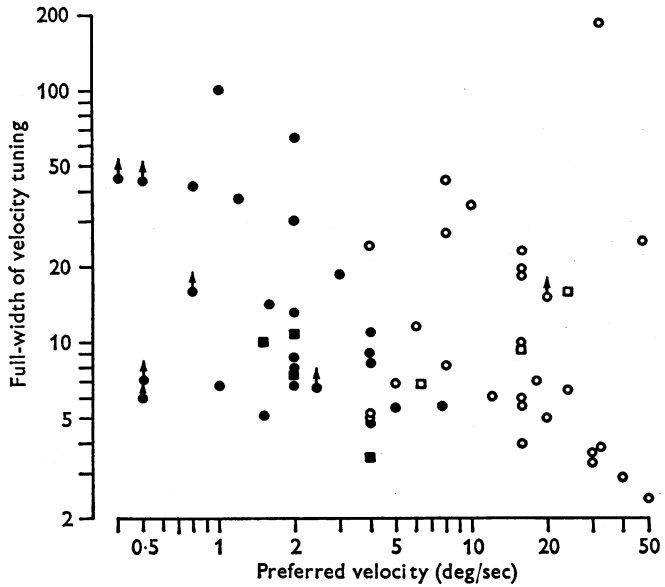


Fig. 9. A scatter-plot of full-width of velocity tuning *vs.* preferred velocity for all units. Simple cells are shown as filled circles, complex cells as open circles, type I hypercomplex cells as filled squares and type II hypercomplex cells as open squares. For seven units, only the minimum full-width is indicated (see text); these are shown under upward-pointing arrows.

Cells in both major classes can be subgrouped according to various properties of their receptive fields, such as the temporal character of their response to flashed stimuli, the presence or absence of direction selectivity and the spatial arrangement of receptive field subregions.

I was able to divide simple cells into a 'sustained' (nine of twenty-five, 36%) and 'transient' (sixteen of twenty-five; 64%) group, according to whether a stimulus could be found which, when turned on in the receptive field, caused a change in discharge rate lasting more than 5 sec (Ikeda & Wright, 1974). All the complex cells in the present study which responded to flashed stimuli (twenty-two of twenty-eight; 78%) appeared transient

in their responses to flashed stimuli. 'Transient' simple cells (mean 2·5 deg $sec^{-1}$) have a slight tendency to prefer higher velocities than 'sustained' ones (mean 1·7 deg $sec^{-1}$). 'Transient' cells (mean full-width 17·7) also tend to be more selective for velocity than 'sustained' ones (mean 26·9) – this is largely due to the fact that tuning curves for 'transient' cells generally show a rather sharper drop in response below the preferred velocity than 'sustained' ones. This coupled tendency probably accounts for the inverse correlation between preferred velocity and velocity full-width shown for simple cells in Fig. 9. One simple cell of each type is shown in Fig. 2: M4R12 is 'sustained' and M4R17 is 'transient'.

Simple cells can also be divided into groups on the basis of the organization of 'on' and 'off' regions in their receptive fields. Three configurations are common: an 'on' region flanked by two 'off' regions of roughly equal strength (hereafter called on-centre); the obverse of this, an 'off' region flanked by two 'on' regions (off-centre); and a side-by-side pair of opposing regions (edge-detector). Pettigrew *et al.* (1968*a*), who used only bright slits as stimuli, reported that simple cells with a 'bimodal' discharge pattern (presumably corresponding to the off-centre category) show a preference for rather higher-velocity stimuli than 'unimodal' simple cells (presumably the on-centre and edge-detector groups); the three groups of simple cells in the present study all showed similar velocity preferences. Pettigrew *et al.* judged the preferred velocities of most of their cells simply by listening to the response on a loudspeaker, and it may be that the bimodal response of an off-centre cell to a drifting bright bar sounds greater at high velocities when the two bursts run together.

Cortical cells can also be grouped on the basis of asymmetries in their responses to the two directions of movement of an optimally oriented stimulus. Direction selective cells often show the 'true direction selectivity' examined by Barlow & Levick (1965) in the rabbit retina. The response asymmetry survives reversal of the contrast of the stimulus, and small movements of the stimulus within the receptive field evoke direction selective discharges (Bishop *et al.* 1974; J. A. Movshon, unpublished observations). Barlow & Levick were able to show that an inhibitory mechanism within the receptive field was responsible for the effects they observed; such a mechanism must have certain timing properties and might therefore itself be expected to show some velocity selectivity, and perhaps to influence the cell's velocity tuning in the preferred direction. It could be that the presence or absence of direction selectivity is largely responsible for the scatter of preferred velocities and velocity half-widths shown in Figs. 7–9.

Such an effect on optimal velocity, if it exists, is slight. Complex cells with some direction selectivity show a very slight tendency to prefer

higher velocities than non-directional ones; no trend is discernible among the simple cells. And there is no apparent difference in velocity selectivity among the groups.

Most units of both types which showed direction selectivity and which were tested in both directions of movement showed the response asymmetry roughly uniformly across the velocity spectrum examined. Some, however, showed more complicated behaviour, and tuning curves for both directions of movement of three such cells (all complex) are shown in Fig. 10.

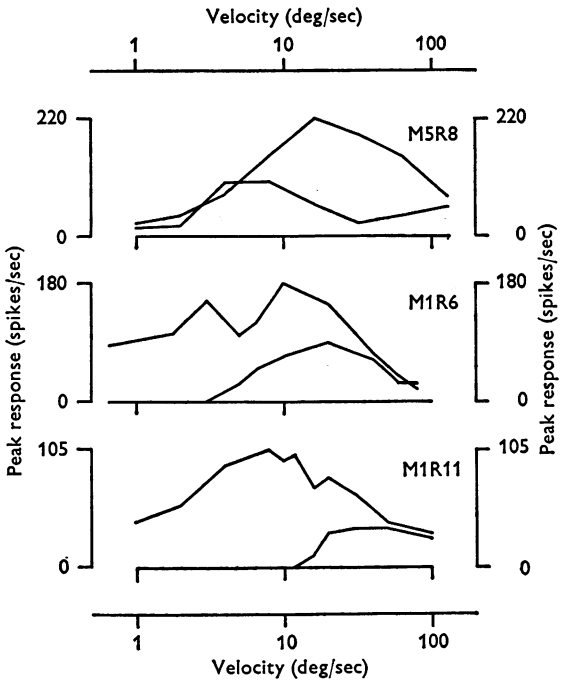


Fig. 10. The velocity tuning curves of three complex cells which showed some degree of direction selectivity. Curves are shown for both directions of movement of an optimally oriented stimulus.

Cell M5R8 showed no direction preference for stimuli moving more slowly than 8 deg $sec^{-1}$. Above that velocity a strong direction bias developed, and then waned at a velocity of over 100 deg $sec^{-1}$. The direction selectivity of this unit was therefore itself tuned for velocity. Note that the bias is most marked near the unit's preferred velocity. Units M1R6 and M1R11 show a rather more common pattern, which has also been reported in on-type direction selective units in the rabbit retina (Oyster, 1968). These units are completely direction selective for slow rates of movement. As stimulus velocity is increased, a response in the opposite direction appears (at

5 deg sec$^{-1}$ for M1R6 and at 16 deg sec$^{-1}$ for M1R11) and comes nearly to equal the response in the preferred direction (at 40–50 deg sec$^{-1}$ in both cases). It is possible to understand both these behaviours in terms of restrictions in the timing properties of an inhibitory mechanism in a system similar to that proposed by Barlow & Levick (1965): in the first case the inhibition would be postulated to decay too quickly to affect slow-moving stimuli, and in all three cases it would also seem to have too long a rise-time or too short a space constant to affect stimuli moving very rapidly.

Cell M1R6 (Fig. 10) is one of five complex cells (18%) that show an interesting pattern in their response to stimuli moving more slowly than the preferred velocity: there is a secondary peak in the tuning curve for

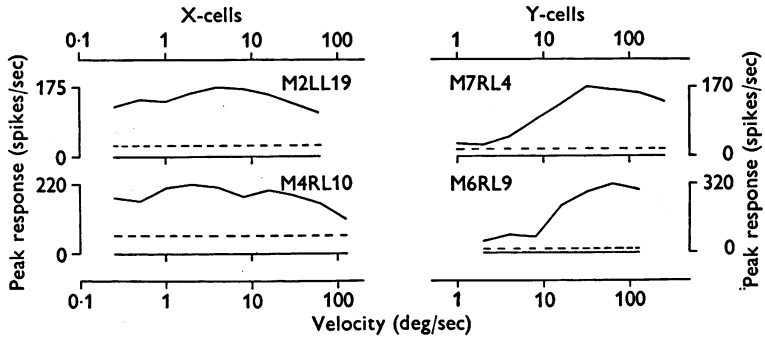


Fig. 11. The velocity tuning curves of four LGN fibres recorded in the visual cortex. The left-hand pair are X-cells; the right-hand pair, Y-cells. Unit M6RL9 is off-centre; all others are on-centre. The stimuli in all cases were long bars whose width approximately matched the diameter of the centre of the receptive field. The bars were bright for the three on-centre units, and dark for the off-centre one. Dotted lines indicate spontaneous activity.

the preferred direction at about 3 deg sec$^{-1}$, near the preferred velocity of many simple cells (Figs. 4 and 7), which could reflect an input from such cells. Cell M3L6, whose tuning curve for the preferred direction is shown in Fig. 5, showed similar behaviour. It is difficult to attribute the effect to short-term changes in responsiveness, since the tuning curves in the non-preferred direction, which were accumulated at the same time, show no apparent peaks or dips (e.g. cell M1R6 in Fig. 10). When the effect occurred in complex cells which responded to both directions of movement, the tuning curves in the opposite direction showed no effect. It also seems unlikely that the secondary peaks are due to timing properties of inhibitory direction selecting mechanisms, since they always occur in the preferred direction of movement. Since they usually occur at velocities

between 1 and 4 deg $sec^{-1}$, it is tempting to suppose that they do represent input from simple cells.

Fig. 11 shows the velocity tuning curves for 4 LGN fibres recorded in the deep layers of area 17 or the underlying optic radiation. The X-fibres are very responsive to a wide range of velocities, including very slow rates of movement, while the Y-fibres respond relatively poorly to slow-moving stimuli, and well to faster ones. These results are in good agreement with those shown in Fig. 5 of Dreher & Sanderson (1973), who also report that some LGN X-cells with receptive fields in the *area centralis* are strongly selective for very slow rates of movement; some responses of one cell that is presumably of this type are shown in Fig. 9*H* of Stone & Dreher (1973).

## DISCUSSION

### *Parallel or serial processing in the visual cortex?*

Simple and complex cells show marked differences in the ranges of velocity to which they respond, and in their preferred velocities; it is difficult to see how a straightforward hierarchical model of visual cortical information processing can account for these facts. One could perhaps suggest that the input on to each complex cell from simple cells with spatially distributed receptive fields shows strict sequential temporal summation properties organized to select a higher velocity preference. Indeed, Pollen & Taylor (1973) have reported that the latency of response to a flashed stimulus can vary systematically across the receptive field of a complex cell, perhaps reflecting the action of such a mechanism. But in order for the mechanism to have much effect on velocity preference, it would have to have such fine temporal discrimination as to enforce a narrow velocity selectivity on the complex cells. And complex cells are only slightly more selective than simple cells (Fig. 8). More importantly, no simple hierarchical model can explain the generally excellent response of complex cells to stimuli moving faster than 20–30 deg $sec^{-1}$ (Fig. 5), since simple cells rarely respond at all well to these speeds (Fig. 4).

A parallel process of the kind proposed by Hoffmann & Stone (1971, see also Stone, 1972) seems better equipped to account for these data. X- and Y-cells in the lateral geniculate nucleus show characteristic differences in velocity preference, with Y-cells responding better to high velocity stimuli and X-cells responding better to slower movement (Fig. 11, and Cleland *et al.* 1971; Dreher & Sanderson, 1973; Singer & Bedworth, 1973). The results therefore lend some support to the parallel processing hypothesis: X-cells, like simple cells, respond very well to slow rates of movement, while Y-cells, like complex cells, prefer higher velocities.

It is however clear that many lateral geniculate X-cells respond very

much better to fast-moving stimuli than simple cells do. The fall in simple cells' discharge to high velocities could be due to inhibition from some mechanism with Y-cell properties. Since the available anatomical (Garey & Powell, 1971) and physiological (Watanabe, Konishi & Creutzfeldt, 1966) evidence suggests that all geniculocortical terminals are excitatory in their action, such inhibition would presumably have to come from interneurones driven directly by Y-axons, or indirectly by basic complex cells. There is other evidence to indicate that inhibitory interneurones in the visual cortex have complex properties. Innocenti & Fiore (1974) have recently shown that marked i.p.s.p. activity can be seen in cortical cells' responses to stimuli moving at between 2 and over 70 deg $sec^{-1}$. This is obviously consistent with inhibition from complex cells. And Creutzfeldt & Ito (1968) reported that the low rate of maintained discharge in the (mostly simple) cortical cells from which they obtained intracellular or 'quasi-intracellular' records appeared to be due to a tonic inhibitory input, revealed by a continuous i.p.s.p. frequency of 150–300 Hz. Very few simple cells have maintained activity greater than a few spikes $sec^{-1}$, while complex cells with higher resting rates are not uncommon (Pettigrew *et al.* 1968*a*; Rose & Blakemore, 1974; Kelly & Van Essen, 1974). Furthermore, the latency of i.p.s.p. responses to electrical stimulation reported to Watanabe *et al.* (1966) are consistent with a disynaptic fast-fibre mechanism.

Many complex cells respond more briskly to slow rates of movement than do Y-cells of the lateral geniculate nucleus (compare Figs. 5 and 11, and see Dreher & Sanderson, 1973). This response to low velocities could be due either to the direct action of X-cells, or to excitation from simple cells. Stone & Dreher (1973) report that a number of cells with complex receptive fields can be activated electrically from the optic radiation at latencies which could represent the monosynaptic action of slow (X) fibres. It could be that these cells are 'slow' complex cells, like M4R4 in Fig. 5, whose tuning curve shows little resemblance to those of Y-cells in the lateral geniculate nucleus. On the other hand, the low-velocity response peak in the tuning curve of complex cells such as M1R6 (Fig. 10) and M3L6 (Fig. 5) can show direction selectivity, which is more easily accounted for by postulating an input from simple cells to a complex cell whose primary input come directly or indirectly from Y-cells; the electrical stimulation latencies of Stone & Dreher's 'slow afferent' complex cells are also consistent with disynaptic activation by fast fibres.

It is therefore possible to account for the observed data by suggesting that simple and complex cells receive their prime excitation from lateral geniculate nucleus X- and Y-cells respectively, but that simple cells are inhibited by complex cells, and that some complex cells can receive

excitatory input from either lateral geniculate X-cells or cortical simple cells (or perhaps both).

Ikeda & Wright (1974) have attempted to extend the sustained/transient distinction found in cells in the retina and lateral geniculate nucleus to visual cortical neurones. They report that, in contrast to the situation at more peripheral levels of the visual system, the sustained/transient classification is orthogonal to the accepted classification of cells; both sustained and transient simple and complex cells are described. Following the equation by Cleland *et al.* (1971) of the X/Y and sustained/transient grouping systems, they propose that both simple and complex cells can receive X- or Y-type afferents. However, it seems likely that the inhibitory interactions described in the lateral geniculate nucleus (Singer & Creutzfeldt, 1970; Singer Pöppel & Creutzfeldt, 1972; Singer & Bedworth, 1973) and visual cortex (Blakemore & Tobin, 1972; Creutzfeldt, Kuhnt & Benevento, 1974) would have a marked effect on the temporal response properties of cells in these areas, and that these properties may not adequately discriminate between X- and Y-type units beyond the retina; simple cells in the cortex, whether sustained or transient in their responses to flashed stimuli, have properties strongly reminiscent of X-cells, while complex cells resemble Y-cells (Movshon & Tolhurst, 1975, and in preparation).

On the basis of my data, and the work of Rose (1974), who showed that end-inhibition is graded in cortical cells, and may not afford a sufficient criterion for distinguishing simple and complex cells from hypercomplex ones, it might also be suggested that 'hypercomplex' cells in area 17 are merely unusual examples of simple and complex fields, differing from other cells of these types only in that they have a more marked length selectivity. They seem clearly different from the types of hypercomplex cells described in areas 18 and 19 by Hubel & Wiesel (1965).

### *The processing of velocity information in the visual cortex*

The rate of stimulus movement might be determined by the visual system in two fundamentally different ways. Each neurone could signal stimulus velocity over a wide range by simply changing its response as some monotonic function of stimulus velocity, or it could be selective for a relatively narrow range of velocities, and signal its preferred velocity as a 'trigger feature' of the stimulus (Barlow, 1961).

The velocity tuning curves of movement-detecting neurones in the visual systems of lower vertebrates are commonly seen to show a monotonic increase in response with an increase in stimulus velocity over a very wide range, and similar behaviour has occasionally been reported in the mammalian visual system (see Grüsser & Grüsser-Cornehls, 1973). These

neurones are obviously well suited to a 'single-channel' analysis, the first of the two possibilities mentioned above.

In a 'multiple-channel' model, velocity information would be abstracted by determining the most active neural group in a population of such channels, each selective to a relatively narrow range of velocity. There is psychophysical evidence to suggest that such a system operates in the human visual system (Tolhurst, Sharpe & Hart, 1973), and the results of this study tend to indicate that a similar process is at work in the cat's visual cortex. Many neurones show relatively fine tuning for rate of stimulus movement, and between them their preferred velocities cover a two-hundredfold range. Simple and type I hypercomplex cells form an apparent 'slow' group of these cells, responding optimally to stimuli moving at velocities from 0·25 to 7·5 deg $sec^{-1}$, while complex and type II hypercomplex cells form a 'fast' group, preferring velocities from 4 to 50 deg $sec^{-1}$ (Fig. 7).

The visual cortex of the cat has been held to increase selectivity for the orientation (Hubel & Wiesel, 1962; Rose & Blakemore, 1974) and spatial frequency (Maffei & Fiorentini, 1973) of the stimulus. These authors and others (Campbell, Cleland, Cooper & Enroth-Cugell, 1968; Campbell, Cooper & Enroth-Cugell, 1969) have provided measurements of the selectivity of cortical cells for these stimulus variables, and in both cases the width of each cell's tuning curve represents a relatively small fraction of the total range of the variable to which cells are selectively sensitive. It appears from my results that cortical cells are similarly selective for stimulus velocity; their mean velocity full-width (19·6) represents a similarly small proportion of the range of preferred velocities seen. This characteristic of visual cortical receptive fields is markedly different from the behaviour of visual neurones in lower animals (Grüsser & Grüsser-Cornehls, 1973) and the more peripheral levels of the cat visual system (Fig. 11, and Dreher & Sanderson, 1973). It therefore seems reasonable to ascribe to it some functional significance, and to suggest that the visual cortex, as well as increasing specificity for other aspects of a visual stimulus, sets up a multiple-channel system for analysing its rate of movement.

I thank Dr Colin Blakemore for his help and advice throughout this work, Dr Peter Lennie and Professor Horace Barlow for helpful discussion, and Janet Dormer and Philip Taylor for technical help. The author holds a research training studentship from the Wellcome Trust, and the work was supported by a programme grant to Dr Blakemore from the Medical Research Council (no. G. 972/463/B).

REFERENCES

BARLOW, H. B. (1961). The coding of sensory messages. In *Current Problems in Animal Behaviour* ed. THORPE, W. H. & ZANGWILL, O. L., pp. 331–360. Cambridge: Cambridge University Press.

BARLOW, H. B., BLAKEMORE, C. & PETTIGREW, J. D. (1967). The neural mechanism of binocular depth discrimination. *J. Physiol.* **193**, 327–342.

BARLOW, H. B., HILL, R. M. & LEVICK, W. R. (1964). Retinal ganglion cells responding selectively to direction and speed of image motion in the rabbit. *J. Physiol.* **173**, 377–407.

BARLOW, H. B. & LEVICK, W. R. (1965). The mechanism of directionally selective units in the rabbit's retina. *J. Physiol.* **178**, 477–504.

BISHOP, P. O., GOODWIN, A. W. & HENRY, G. H. (1974). Direction selective subregions in striate simple cell receptive fields. *J. Physiol.* **238**, 25–27*P*.

BLAKEMORE, C. & TOBIN, E. A. (1972). Lateral inhibition between orientation detectors in the cat's visual cortex. *Expl Brain Res.* **15**, 439–440.

CAMPBELL, F. W., CLELAND, B. G., COOPER, G. F. & ENROTH-CUGELL, C. (1968). The angular selectivity of visual cortical cells to moving gratings. *J. Physiol.* **198**, 237–250.

CAMPBELL, F. W., COOPER, G. F. & ENROTH-CUGELL, C. (1969). The spatial selectivity of the visual cells of the cat. *J. Physiol.* **203**, 223–235.

CAMPBELL, F. W. & GREEN, D. G. (1965). Optical and retinal factors affecting visual resolution. *J. Physiol.* **181**, 576–593.

CLELAND, B. G., DUBIN, M. W. & LEVICK, W. R. (1971). Sustained and transient neurones in the cat's retina and lateral geniculate nucleus. *J. Physiol.* **217**, 473–496.

CREUTZFELDT, O. D. & ITO, M. (1968). Functional synaptic organization of primary visual cortex neurones in the cat. *Expl Brain Res.* **6**, 324–352.

CREUTZFELDT, O. D., KUHNT, U. & BENEVENTO, L. A. (1974). An intracellular analysis of visual cortical neurones to moving stimuli: responses in a cooperative neuronal network. *Expl Brain Res.* **21**, 251–274.

DREHER, B. (1972). Hypercomplex cells in the cat's striate cortex. *Investve Ophth.* **11**, 355–356.

DREHER, B. & SANDERSON, K. J. (1973). Receptive field analysis: responses to moving visual contours by single lateral geniculate neurones in the cat. *J. Physiol.* **234**, 95–118.

ENROTH-CUGELL, C. & ROBSON, J. G. (1966). The contrast sensitivity of retinal ganglion cells of the cat. *J. Physiol.* **187**, 517–552.

FINKELSTEIN, D. & GRÜSSER, O. J. (1965). Frog retina: detection of movement. *Science, N.Y.* **150**, 1050–1051.

GAREY, L. J. & POWELL, T. P. S. (1971). An experimental study of the termination of the lateral geniculo-cortical pathway in the cat and monkey. *Proc. R. Soc.* B **179**, 41–63.

GRÜSSER, O. J. & GRÜSSER-CORNEHLS, U. (1973). Neuronal mechanisms of visual movement perception and some psychophysical and behavioral correlations. In *Handbook of Sensory Physiology*, vol. VII/3A, ed. JUNG, R. pp. 333–429. Berlin: Springer-Verlag.

HOFFMANN, K-P. & STONE, J. (1971). Conduction velocity of afferents to cat visual cortex: a correlation with cortical receptive field properties. *Brain Res.* **32**, 460–466.

HOFFMANN, K-P., STONE, J. & SHERMAN, S. M. (1972). Relay of receptive field properties in dorsal lateral geniculate nucleus of the cat. *J. Neurophysiol.* **35**, 518–531.

HUBEL, D. H. & WIESEL, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* **160**, 106–154.

HUBEL, D. H. & WIESEL, T. N. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *J. Neurophysiol.* **28**, 229–289.

IKEDA, H. & WRIGHT, M. J. (1974). Evidence for 'sustained' and 'transient' neurones in the cat's visual cortex. *Vision Res.* **14**, 133–136.

INNOCENTI, G. M. & FIORE, L. (1974). Post-synaptic inhibitory components of the responses to moving stimuli in area 17. *Brain Res.* **80**, 122–126.

KELLY, J. P. & VAN ESSEN, D. C. (1974). Cell structure and function in the visual cortex of the cat. *J. Physiol.* **238**, 515–547.

LEVICK, W. R. (1972). Another tungsten microelectrode. *Med. & biol. Engng* **10**, 510–515.

MAFFEI, L. & FIORENTINI, A. (1973). The visual cortex as a spatial frequency analyzer. *Vision Res.* **13**, 1255–1267.

MOVSHON, J. A. (1974). Velocity preferences of simple and complex cells in the cat striate cortex. *J. Physiol.* **242**, 121–123*P*.

MOVSHON, J. A. & TOLHURST, D. J. (1975). On the response linearity of neurones in cat visual cortex. *J. Physiol.* **249**, 56–57*P*.

OYSTER, C. (1968). The analysis of image motion by the rabbit retina. *J. Physiol.* **199**, 613–635.

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

PETTIGREW, J. D., NIKARA, T. & BISHOP, P. O. (1968*a*). Responses to moving slits by single units in cat striate cortex. *Expl Brain Res.* **6**, 373–390.

PETTIGREW, J. D., NIKARA, T. & BISHOP, P. O. (1968*b*). Binocular interaction on single units in cat striate cortex: simultaneous stimulation by single moving slit with receptive fields in correspondence. *Expl Brain Res.* **6**, 391–410.

POLLEN, D. A. & TAYLOR, J. H. (1973). The striate cortex and the spatial analysis of visual space. In *The Neurosciences Third Study Program*, ed. SCHMITT, F. O. & WORDEN, F. G., pp. 239–247. Cambridge, Mass.: The M.I.T. Press.

ROSE, D. (1974). The hypercomplex cell classification in the cat's striate cortex. *J. Physiol.* **242**, 123–125*P*.

ROSE, D. & BLAKEMORE, C. (1974). An analysis of orientation selectivity in the cat's visual cortex. *Expl Brain Res.* **20**, 1–17.

SINGER, W. & BEDWORTH, N. (1973). Inhibitory interaction between *X* and *Y* units in the cat lateral geniculate nucleus. *Brain Res.* **49**, 291–307.

SINGER, W. & CREUTZFELDT, O. D. (1970). Reciprocal lateral inhibition of on- and off-center neurones in the lateral geniculate body of the cat. *Expl Brain Res.* **10**, 311–330.

SINGER, W., PÖPPEL, E. & CREUTZFELDT, O. D. (1972). Inhibitory interaction in the cat's lateral geniculate nucleus. *Expl Brain Res.* **14**, 210–226.

STONE, J. (1972). Morphology and physiology of the geniculocortical synapse in the cat: the question of parallel input to the striate cortex. *Investve Ophth.* **11**, 338–346.

STONE, J. & DREHER, B. (1973). Projection of *X*- and *Y*-cells of the cat's lateral geniculate nucleus to areas 17 and 18 of visual cortex. *J. Neurophysiol.* **36**, 551–567.

TOLHURST, D. J., SHARPE, C. R. & HART, G. (1973). The analysis of the drift rate of moving sinusoidal gratings. *Vision Res.* **13**, 2545–2555.

WATANABE, S., KONISHI, M. & CREUTZFELDT, O. D. (1966). Postsynaptic potentials in the cat's visual cortex following electrical stimulation of afferent pathways. *Expl Brain Res.* **1**, 272–283.