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# THE CONTRIBUTION OF EXCITATORY AND INHIBITORY INPUTS TO THE LENGTH PREFERENCE OF HYPERCOMPLEX CELLS IN LAYERS II AND III OF THE CAT'S STRIATE CORTEX

BY A. M. SILLITO AND VERA VERSIANI

*From the Department of Physiology, the Medical School, Birmingham University, Birmingham B15 2TJ*

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SUMMARY

1. The GABA antagonist bicuculline has been applied to hypercomplex cells in layers II and III of the cat's striate cortex in an attempt to test the hypothesis that their length preference derives from the action of a GABA mediated post-synaptic inhibitory input.

2. Iontophoretic application of bicuculline to these cells resulted in a reduction but not an elimination of the length preference. The reduction in length preference was only observed in the case of slits extended to one side of the receptive field or to slits only partially covering what appeared to be inhibitory flanking regions either side of the field centre. In cells normally showing a clear and stable length preference it was never possible to produce by the application of bicuculline a significant response to a slit fully extended to cover both flanking regions.

3. The orientation tuning was basically eliminated by the application of bicuculline. In contrast the directional specificity was relatively unaffected.

4. The action of bicuculline on hypercomplex cell orientation tuning supports the view that GABA mediated inhibitory inputs were effectively blocked and suggests that the partial effect on length preference and lack of effect on directional specificity reflect the varying degree of involvement of a GABA mediated inhibitory input to these receptive field properties.

5. These observations introduce the possibility that the excitatory input to the superficial layer hypercomplex cells exhibits directional specificity, length preference with respect to a slit extended to both sides of the field and a low degree of orientation selectivity. Evidence is presented indicating that certain layer V cells with hypercomplex type

receptive field properties exhibit some of the characteristics required of this input.

## INTRODUCTION

Neurones in the visual cortex exhibiting a selectivity to the length as well as the orientation of an elongated visual stimulus were first described by Hubel & Wiesel (1965, 1968) who referred to them as 'hypercomplex cells'. Basically these cells show an optimal excitatory response to an appropriately oriented slit of light of a certain length moving over their receptive field; extension of the slit length beyond this value results in a marked decrease in or even loss of the original response. The term 'end stopping' is sometimes used to describe this particular receptive field characteristic. The end-stopping effect is often more powerfully elicited by slit extension to one side of the receptive field than to the other. Hubel & Wiesel (1965) postulated a very simple model to explain the receptive field characteristics of hypercomplex cells. This involved hypercomplex cells receiving an input from several complex cells with similar preferred orientations but spatially displaced receptive fields. They suggested that a cell with a centrally placed field provided an excitatory input whilst cells with receptive fields displaced to either end of this along the plane of the preferred orientation provided an inhibitory input. They also noted as likely variations of this model that the receptive fields of the inhibitory input cells may overlap the excitatory field or be spatially displaced to one side only.

The possibility of testing the model for hypercomplex cell length preference was introduced by evidence that GABA may be an inhibitory transmitter in the visual cortex (Iversen, Mitchell & Srinivasan, 1971) and that its action in the visual cortex be blocked locally by the iontophoretic application of bicuculline (Sillito, 1975*a*, *b*). If the iontophoretic application of bicuculline to hypercomplex cells blocks the inhibitory inputs acting on them the length preference should be abolished but other properties such as the orientation tuning already determined by the characteristics of the excitatory input from complex cells should be unaffected. In the experiments described here this prediction has been examined. A preliminary report of some aspects of this work has already been made (Sillito & Versiani, 1976). The observations here refer to hypercomplex cells in layers II and III of area 17.

## METHODS

The experiments have been carried out on cats in the weight range 2·2–3·0 kg. Details of anaesthesia, techniques and general procedures have been given in previous papers (Sillito, 1975*a*, *b*, 1977).

Five barrel micropipettes were used for the extracellular recording of neuronal activity and the iontophoretic application of drugs. The centre recording barrel contained a solution of 0·5 M-Na acetate with 1% pontamine blue which enabled the recording site to be marked by the technique described by Hellon (1971). The other four barrels contained a selection of the following drugs made up in aqueous solution: D,L-homocysteate (Fluka Chemicals Ltd.) 0·2 or 0·5 M adjusted to pH 7·5 with NaOH; L-glutamate (Sigma Chemical Company), 0·2 M adjusted to pH 8 with NaOH; $\gamma$-aminobutyric acid, GABA (Sigma Chemical Company), 0·5 M adjusted to pH 3 with HCl; bicuculline (Fluka Chemicals Ltd.) 5 mM in 165 mM-NaCl, solution adjusted to pH 3 with HCl; strychnine (Sigma Chemical Company) 2 or 10 mM in 165 mM-NaCl; ammonium acetate or chloride (B.D.H.), 1·5 M solution. The retaining and ejecting currents used for controlling the release of the drugs were respectively: D,L-homocysteate + 12 nA (retaining) and −2–15 nA (ejecting); glutamate + 12 nA (retaining) and −10–50 nA (ejecting); GABA −18 nA (retaining) and +1–50 nA (ejecting); bicuculline −10 nA (retaining) and +20–160 nA (ejecting); strychnine −10 nA (retaining) and +20–60 nA (ejecting); ammonium ions −30 nA (retaining) and +100–300 nA (ejecting).

### *Histological procedures*

The electrode recording sites were marked by passing a current of 2–8 $\mu$A for 3–10 min through the recording barrel with the electrode as the cathode, this deposited a small amount of pontamine blue in the tissue around the electrode tip. At the end of the experiment the surface of the cortex underlying the small aperture in the skull (4 mm diam.) through which the penetrations had been made, was lightly marked with a black dye. The brain was then fixed in a solution of 10% formol saline. A photographic record was made of the location of the mark on the surface of the cortex. Serial sections 50 $\mu$m thick were taken on a freezing microtome through the marked region of the cortex. The sections were stained with 1% neutral red, mounted and the location of the blue spots marking the recording sites determined. Where statements are made about the distribution of cells in terms of cortical layer these refer only to those cases where the recording position was marked clearly by pontamine blue dye. Layers were distinguished by criteria following the comments of Otsuka & Hassler (1962) and Garey (1971).

### *Experimental procedure*

Oblique rather than vertical electrode penetrations were made into the cortex. The objective of this was to increase as far as possible the length of penetration through layers II and III and also with respect to the likely damage to these superficial layers at the point of electrode entry, to enable sampling of cells in columns remote to this potentially damaged region. Penetrations were routinely continued through to layer V and VI. It was always found that cell responsiveness in the superficial layers was markedly depressed immediately following initial penetration into the cortex. The number of responsive cells encountered was considerably improved by allowing a period of 1–2 hr after initial penetration into the cortex before starting the recording session.

Many hypercomplex cells in the superficial layers exhibited no spontaneous activity. These were initially isolated by moving the electrode in very small steps

and iontophoretically applying the excitant amino acid D,L-homocysteate at each point. This induced firing in cells which would have otherwise been missed.

For stimuli at non-optimal orientations simple cells and some complex cells show a larger response to a shorter as opposed to a longer slit, i.e. the orientation selectivity is lower for a short slit than it is for a long slit (Henry, Bishop & Dreher, 1974; Henry, Dreher & Bishop, 1974). Consequently it is theoretically possible to see apparently hypercomplex properties in these cells if the optimal orientation is incorrectly defined. For this reason in the present experiments great care was taken to check the optimal orientation of cells believed to show length preference. Once the optimal orientation had been assessed qualitatively, it was checked quantitatively by constructing peristimulus histograms for orientations varying in a series of 5° steps on either side of the optimum. If this suggested a slightly different optimum the whole process was repeated. All evaluations of length preference were made with stimuli at the optimal orientation. In practice it was found that the length preference of most hypercomplex cells was so marked as to be clearly distinguishable from the variations in response with stimulus length seen at non-optimal orientations in simple and complex cells. The approximate spatial extent of the central excitatory region and the inhibitory flanking regions were assessed in the following way. First the length of the stimulus and the location of the path of motion through the receptive field that gave the largest excitatory response (as judged by the area under the peristimulus time histogram) were determined. This was considered to define an excitatory zone. Then the reduction in response produced by a successively increasing slit extension to one side of this excitatory zone was observed and an estimate of the length of extension required to produce a maximal reduction or elimination of the original response made. This procedure appeared to define an inhibitory zone. It was repeated for both sides of the receptive field. Further detailed analysis of the receptive field subdivisions carried out on the cells showed that the situation was rather more complicated than the results of the above tests alone implied and this is discussed in the following paper (Sillito, 1977). All observations refer to monocular stimulus presentation with a 34 cd $m^{-2}$ stimulus on a 17 cd $m^{-2}$ background.

The effect of bicuculline on hypercomplex cell properties was routinely assessed using a standard set of stimulus conditions. These were: a slit of optimal length at the optimal orientation, a slit of optimal orientation extended to one side of the field and then the other, a slit of optimal orientation extended to both sides of the receptive field, a slit of optimal length but at 45° clockwise, 45° anticlockwise and 90° to the optimal. In some cases the observation with the slit at the 45° anticlockwise orientation was omitted. Responses to these stimuli were assessed before, during and after the application of bicuculline. The pharmacological effectiveness of bicuculline was checked by determining the degree of block produced in the inhibitory action of iontophoretically applied GABA. The time for which a stable state could be achieved during the application of bicuculline was generally limited (30–45 min) by the capability of the electrode to sustain a constant ejecting current and this in turn restricted the number of tests that could be carried out. For this reason with respect to the time taken to document and check the effects on length preference it was impossible to produce a full orientation tuning curve to document completely the effects on orientation selectivity. Consequently the comparative observations on orientation selectivity were restricted to the three or four testing orientations referred to above. Whilst these tests could clearly not reveal small changes in orientation selectivity they were adequate for demonstrating the large reductions in selectivity that were actually observed during the application of bicuculline.

## RESULTS

### *Hypercomplex cells in layers II and III*

A total of thirty-four hypercomplex cells in layers II and III were examined in detail. They all exhibited a very low resting discharge (0–3 impulses/sec), all but two exhibited directional specificity and all

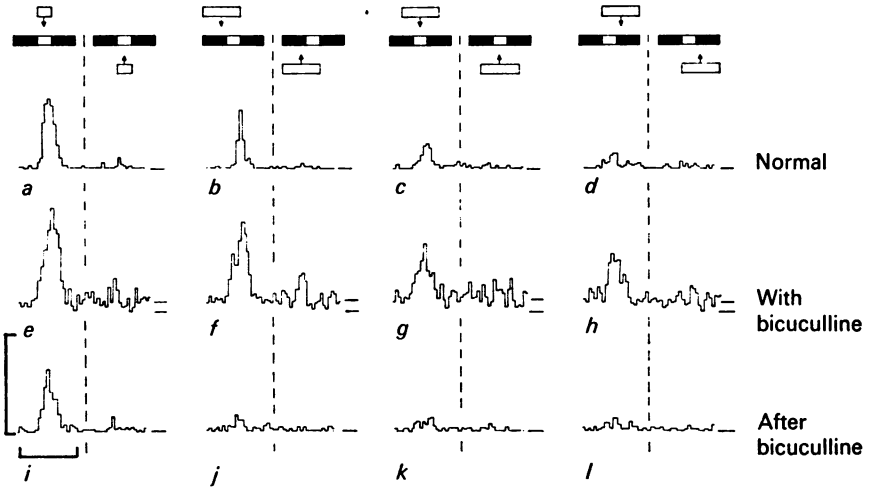


Fig. 1. Peristimulus histograms illustrating the action of bicuculline on the length selectivity of a superficial layer hypercomplex cell. Diagrams above each set of records summarize the stimulus situation. Receptive field is diagrammatically represented as an unshaded central excitatory zone flanked by shaded inhibitory regions. Stimulus is shown as an unshaded bar with an arrow indicating direction of motion. The portions of the histograms to the left and right of the dashed lines show the response of the cell to respectively the forwards and backwards motion of the slit over the receptive field. Upper records show the normal response of the cell, the middle records the response during the iontophoretic application of bicuculline (140 nA ejecting current) and the lower records the response after recovery from the application of bicuculline. Stimuli were respectively 2 and 10° long. Peristimulus histograms constructed from 25 cycles of stimulus motion. Bin size 50 msec. Vertical calibration indicates range corresponding to 0–100 counts per bin (0–80 impulses/sec). Horizontal calibration 1 sec.

exhibited a high degree of length preference and orientation specificity. The over-all stimulus specificity was consequently very high with a cell responding to only direction of motion of a short slit at a particular orientation through a very restricted region of visual space. These characteristics were consistent with those described by Dreher (1972) for type I 'simple hypercomplex cells'. However, in agreement with the recent

observations of Camarda & Rizzolatti (1975) on hypercomplex cells in the superficial layers of the cat's visual cortex, it was not possible to demonstrate a convincing subdivision of the receptive field into the spatially discrete 'on' and 'off' regions seen in the simple cell receptive field (Hubel & Wiesel, 1962). The cells either gave no response to a stationary flashing stimulus or a weak 'on–off' response.

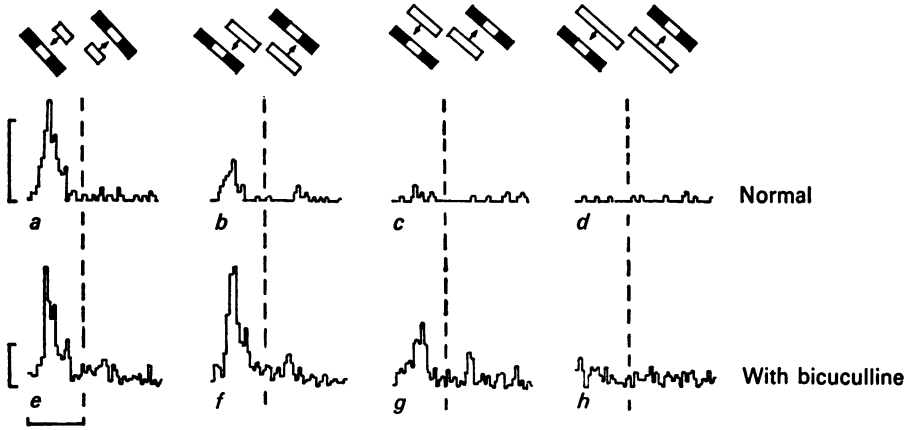


Fig. 2. Further example of the action of bicuculline on hypercomplex cell length preference. Upper records show normal response of the cell, lower records show the response during the application of bicuculline (50 nA ejecting current). All details as for Fig. 1 except that vertical calibration indicates range corresponding to 0–25 counts per 50 msec bin (0–20 impulses/sec). Stimulus lengths respectively 2° (*a*, *e*), 8° (*b*, *c*, *f*, *g*) and 14°(*d*, *h*).

Iontophoretic application of bicuculline caused a variable but clear reduction in the length preference of all the hypercomplex cells examined but in no case did it eliminate it. The action of bicuculline on hypercomplex cell length preference is illustrated in Fig. 1. The upper records show the normal response of the cell (Fig. 1*a–d*). It was clearly end stopped on both sides but the effect of stimulus extension over the right side (Fig. 1*d*) produced the largest reduction of the response. A stimulus partially covering both inhibitory zones (Fig. 1*c*) produced a larger excitatory response than the stimulus covering the right inhibitory zone only. It is also notable that the cell only gave a significant response to one direction of stimulus motion. The middle records in Fig. 1*e–h* show the response during the iontophoretic application of bicuculline. There was an increase in the magnitude of the evoked response and a small but clear reduction in the relative amplitude of the response to the optimal stimulus (Fig. 1*e*) with respect to the other stimuli (Fig. 1*c–d*) but, for example, the response to the stimulus extended to cover the right flank (Fig. 1*h*) was still

considerably less than that to the optimal stimulus (Fig. 1*e*). As the lower records indicate (Fig. 1*i–l*), after termination of the bicuculline application there was an increase in the length selectivity of the cell. This type of increase in selectivity after termination of bicuculline application has been observed in the context of other receptive field characteristics in simple and complex cells (Sillito, 1975*b*).

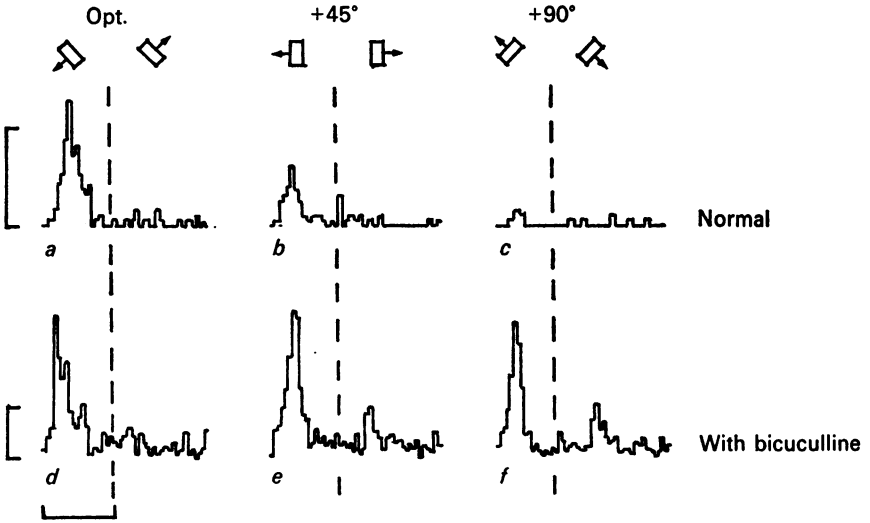


Fig. 3. Action of bicuculline on the orientation selectivity of the cell in Fig. 2 to an optimal length stimulus. Upper records show the normal response of the cell to a stimulus at the optimal orientation and 45 and 90° to the optimal orientation. Lower records show response during the iontophoretic application of bicuculline. Calibration details as for Fig. 2.

The records in Fig. 2 show the response of another hypercomplex cell to the same range of tests. The stimulus for the records in column *d*, however, extended to cover both inhibitory zones completely instead of partially covering them as in Fig. 1*c*. In this example stimulus extension to the left (Fig. 2*c*) as opposed to the right (Fig. 2*b*) of the excitatory zone produced the largest reduction in the response and the stimulus extended to cover both inhibitory zones (Fig. 2*d*) produced no response. During the application of bicuculline the 'end-stopping effect' deriving from the right inhibitory zone was clearly eliminated by the application of bicuculline (Fig. 2*f*) whilst that from the left inhibitory zone was reduced (Fig. 2*g*). Despite the apparent elimination of the effectiveness of the right inhibitory zone and the reduction in the effectiveness of the left zone, the extension of the stimulus to cover both zones (Fig. 2*g*) resulted in a complete loss of the response. In no case was it possible to produce during the

application of bicuculline a significant response to a slit extended to cover both inhibitory flanks.

In contradistinction to expectations the orientation tuning of hypercomplex cells was essentially eliminated during the application of bicuculline. The peristimulus histograms in Fig. 3 show the response of the hypercomplex cell of Fig. 2 to an optimal length stimulus moving over the receptive field at respectively the optimal orientation and 45 and 90° to the optimal orientation. During the application of bicuculline the response to all three orientations was nearly equal (Fig. 3*e–g*). Conversely, for all but one of the cells discussed in this section the directional specificity was not significantly changed during the application of bicuculline. The lack of effect on directional specificity is clear in Figs. 1–3. The term directional selectivity used here refers to a preference for one of the two directions of motion over the receptive field of an optimally oriented slit travelling in a plane at 90° to its long axis. However, directional selectivity was also present in the responses to non-optimal orientations revealed during the application of bicuculline as shown in Fig. 3. Under these conditions the cells' responses were reminiscent of pure directional cells (Blakemore & Van Sluyters, 1974). In summary the results obtained show almost paradoxically that the application of bicuculline to these cells will produce a large change in orientation preference, a small reduction of length preference and no significant effect on directional specificity.

*Hypercomplex cells in layers II and III showing a variable length preference*

A number of cells (five) were encountered that on the basis of an initial qualitative examination justified inclusion in the general category of hypercomplex cells, but they were excluded from the group of cells discussed above because during the long testing period involved in the present experiments it became apparent that the length preference was a highly variable receptive field property. They further differed from the cells analysed above, in so far as when present, the response reduction produced by slit extension to one side or the other was not marked, it only became significant when the slit was extended to both sides of the field centre and moreover even then the response was not completely suppressed. The presence of these cells did not correlate with any abnormality of the preparation or any general deterioration in the properties of other stable hypercomplex, complex or simple cells recorded earlier or later in the same penetration.

Because there was a spontaneous variation in the degree of length preference it was difficult to assess with confidence the effect of bicuculline on this receptive field parameter. Data taken from one of these cells is

shown in Figs. 4 and 5. In Fig. 4*a* and *b* the normal responses to a long and short slit are illustrated. They indicate a clear preference to the short slit which over a series of eight tests (each of twenty-five trials) was found to vary above and below this level. During the application of bicuculline this length preference was completely abolished (Fig. 4*c*, *d*) but it did not reappear after termination of the bicuculline application (Fig. 4*e*, *f*). The action of bicuculline on the orientation selectivity of the

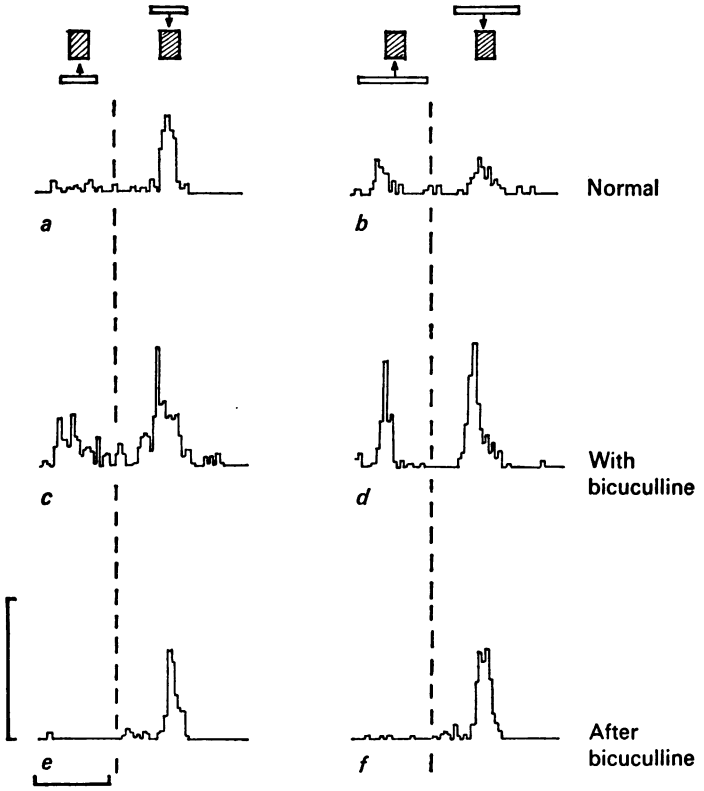


Fig. 4. Hypercomplex type cell showing variable length preference. Records show response to short (2°) and long (10°) slit before application of bicuculline (*a*, *b*), during application of bicuculline (*c*, *d*, 80 nA ejecting current) and 40 min after cessation of application (*e*, *f*). See text for further details. Calibration as for Fig. 1.

same cell is shown in Fig. 5. The records illustrate the development of the full effect of bicuculline on the response of the cell to an optimum length slit at the preferred orientation and 45 and 90° to the preferred orientation. There is an almost complete elimination of the orientation tuning and directional selectivity. The elimination of the directional selectivity

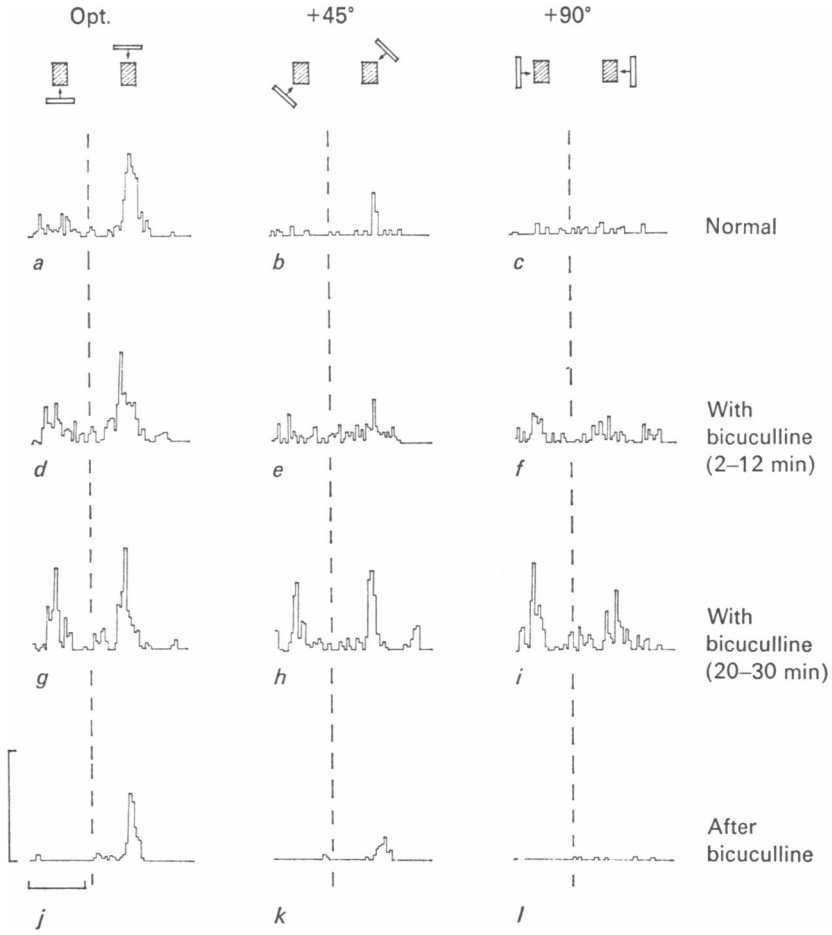


Fig. 5. Action of bicuculline on orientation selectivity of cell illustrated in Fig. 4. Records show response to a 2° slit at the optimal orientation and 45 and 90° to the optimal. Records *a–c*: normal response. Records *d–f*: response during application of bicuculline with 80 nA ejecting current, records taken in period 2–12 min after onset of application. Records *g–i*: records taken in period 20–30 min after onset of bicuculline application (steady 80 nA ejecting current). Records *j–l*: records taken 40 min after cessation of bicuculline application. Calibration details as for Fig. 1.

contrasts with the lack of effect on this receptive field characteristic in the cells referred to in the previous section. In contrast to the length preference which failed to recover from the action of bicuculline (last tested 2 hr after termination of the application) the orientation and direction selectivity of this cell had recovered within 40 min of terminating the bicuculline application. It seems doubtful that the bicuculline appli-

cation could have been responsible for the total and apparently irreversible loss of the length preference of this cell, rather this loss is likely to relate to some other coincidental change reflecting those processes that were already contributing to the response variability with respect to this receptive field parameter. It must be emphasized that the length preference of these cells showed variability in the absence of bicuculline application. In three of the five studied there was actually no large change in length preference during the bicuculline application and in one case the length preference disappeared and then reappeared during the application period. Thus even in the case of these cells the data does not seem to support the view that bicuculline application itself directly eliminated length preference, although it does support the conclusion that it directly modified orientation tuning and directional preference.

*Cells with hypercomplex type receptive field properties in layer V*

This refers to a population of cells in layer V which are highly directionally specific and this aspect of their receptive field properties has

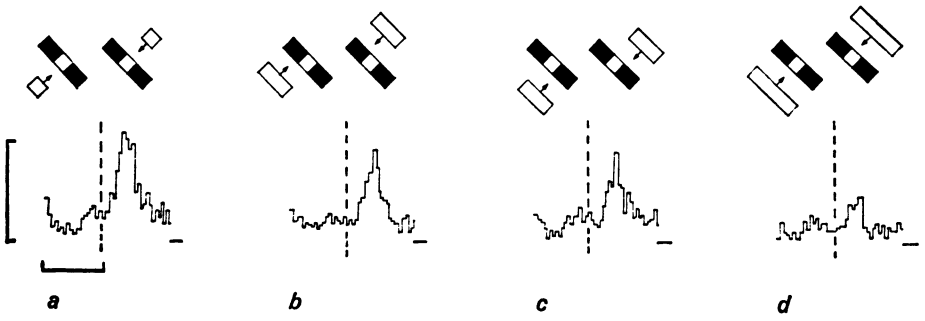


Fig. 6. Length preference tests on layer V hypercomplex cell. Representation of stimulus details and calibration as for Fig. 1. Test slit lengths 2° (*a*), 8° (*b*, *c*) and 14° (*d*).

been discussed in detail elsewhere (Sillito, 1977). They appear to correspond in many ways to those cells described by Palmer & Rosenquist (1974) as projecting to the superior colliculus. Some of them show a marked degree of length preference. Bicuculline does not appear to be particularly effective in blocking inhibitory inputs acting on these cells (Sillito, 1977). Although only a preliminary study of their length preference has been made, some aspects of their receptive field properties are documented here because it is proposed in the discussion that this type of cell could provide an excitatory drive to the superficial layer hypercomplex cells.

The peristimulus histograms in Fig. 6 show the response of one of these cells to the standard length preference tests used for the superficial layer hypercomplex cells. It gave a highly directionally specific response to an optimal length stimulus (Fig. 6*a*) and it is notable that there was a suppression of the high spontaneous activity of this cell when the stimulus moved in the non-preferred direction. Extension of the slit to either side of the field centre produced a small reduction in the response (Fig. 6*b*, *c*). However, extension of the slit to both sides of the field produced a marked reduction although not an elimination of the response (Fig. 6*d*). The data obtained so far indicates that the excitatory zone when tested

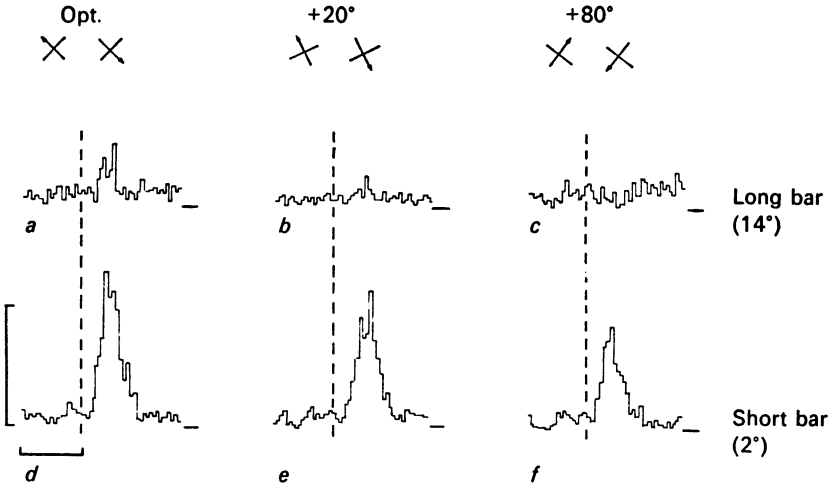


Fig. 7. Effect of slit length on orientation selectivity of cell shown in Fig. 9. Records show response to optimal orientation and 20 and 80° to the optimal. Upper records produced from the response to 14° bar and lower records from response to 2° bar. Calibration as for Fig. 1.

with a small slit extends into the apparent flanking regions, but there is no spatial summation, rather an occlusion of the response suggestive of overlapping inhibitory zones when longer slits are used. The orientation selectivity of these cells varied with stimulus length. They were generally quite sharply orientation tuned to a long slit, but to a short slit they exhibited a much lower level of orientation selectivity. This is illustrated in Fig. 7, which shows the response of one of these cells to a long and short slit at the optimal orientation and 20 and 80° to the optimal. For some of these cells it was very difficult to determine the optimal orientation using a short slit.

## DISCUSSION

The main objective of the present work was to examine the synaptic mechanisms contributing to the length preference of hypercomplex cells in layers II and III of the striate cortex. The evidence obtained for the thirty-four stable length preference hypercomplex cells is not easily equated with previously held views on this matter because the application of bicuculline eliminated their orientation selectivity but did not eliminate their length selectivity. The original model of Hubel & Wiesel (1965) as discussed in the Introduction suggests that the excitatory input to hypercomplex cells is derived from complex cells in the same column and hence it is orientation tuned, whilst the length preference is produced by convergent inhibitory inputs from other complex cells with spatially displaced fields. If GABA is the inhibitory transmitter in question the application of bicuculline would be anticipated to eliminate length preference and not the orientation tuning. It could be argued that the modification of hypercomplex cell orientation selectivity reflects a diffusion of the bicuculline to the input complex cells. The application of bicuculline will eliminate the orientation tuning of some complex cells (Sillito, 1975*b*). The possibility of the diffusion of iontophoretically applied bicuculline to points remote from the cell under investigation such that it modifies the properties of the excitatory input neurones has already been discussed in the context of directional specificity (Sillito, 1977) and specifically for cells in the superficial layers of the cortex. Although this type of action cannot be totally excluded the available evidence suggests that it is not a major factor in the present experimental situation. Moreover, if the concentration of bicuculline was high enough to change the orientation selectivity of the input complex cells it is extremely unlikely that it would not block post synaptic GABA mediated inhibitory influences generating the length preference of the hypercomplex cell. The results thus suggest the possibility that the excitatory input to hypercomplex cells may not be orientation tuned.

If both length preference and orientation tuning are generated at the hypercomplex cell level by post-synaptic inhibitory inputs modifying the response to a non-specific excitatory input, then assuming that GABA is the inhibitory transmitter involved, it is necessary to postulate that the synapses concerned with length preference are in some way differentially located with respect to those mediating orientation tuning such that iontophoretically applied bicuculline would affect one group more than the other. This would require, for example, that inhibitory synapses mediating orientation tuning were located on the cell body whilst those generating length preference interact with excitatory synapses at locations on dendritic

processes remote from the cell body. This possibility is not without precedent in the literature. The apical dendrites of pyramidal cells in layers II and III receive what are thought to be inhibitory synapses from specific Golgi type II cells referred to as 'chandelier cells' (e.g. Szentagothai & Arbib, 1974) which contrast in location with other inhibitory synapses which are distributed in the region of the cell body and basal dendrites. Alternatively two transmitter systems could be involved, one GABA mediated for orientation tuning and one with some other transmitter for length preference.

The interpretation of the present data has to take note, however, of the fact that bicuculline although not eliminating length preference did reduce it. This would suggest that bicuculline was reaching and at least partially affecting the inhibitory synapses involved in length preference. This is particularly noticeable for the cell shown in Fig. 2. The application of bicuculline to this cell eliminated the end-stopping effect for one of the flanks and reduced it on the other. However, when a stimulus covering both flanks was used there was no response, which suggests that this stimulus was producing more than a simple spatial summation of the apparently reduced inhibitory components of the receptive field. Following from this a further possibility to be considered is that the excitatory input to layer II and layer III hypercomplex cells is derived from input cells which already exhibit a degree of length preference, and that GABA mediated inhibitory processes at the level of these superficial layer hypercomplex cells enhance rather than generate this specificity. Considering also the effect of bicuculline on hypercomplex cell orientation tuning and its general lack of effect on directional specificity, a similar line of reasoning leads to the suggestion that the input cells would also exhibit directional specificity and a low degree of orientation selectivity. The layer V cells briefly documented in the Results section exhibited many of these characteristics. They showed a marked decrease in responsiveness to a slit extended to both sides of the receptive field but a much smaller decrease to a slit extended to one side only, they were highly directionally specific but showed a low degree of orientation selectivity to a short slit of similar dimensions to that producing optimal activation of the superficial layer hypercomplex cells. On the other hand, the spontaneous activity was much greater than that of the superficial layer hypercomplex cells, but this could merely reflect a difference in the magnitude of tonic inhibitory influences acting on the superficial layer cells. The spontaneous activity of the superficial layer cells tended to increase to levels more compatible with that of the layer V cells during the application of bicuculline. There is anatomical justification for collateral inputs from layer V to the superficial layers (Szentagothai, 1972; Fisken, Garey & Powell, 1975).

Clearly even during the application of bicuculline the properties of the superficial layer hypercomplex cells do not completely match those of the layer V cells and the suggested relationship between the cell types can only be regarded as a working hypothesis. It is plausible that there is more than one type of excitatory input to the superficial layer hypercomplex cells. This appears to be the case for many complex cells in the visual cortex (Singer, Tretter & Cynader, 1975). The arguments presented here do not apply to the superficial layer cells exhibiting a variable length preference. If these are judged to be hypercomplex, it is likely that a different synaptic organization underlies their receptive field properties because, for example, the excitatory input does not appear to be directionally specific (in so far as it is eliminated by bicuculline). It is interesting however that even in the case of these cells local GABA mediated postsynaptic inhibitory inputs to the cell appear to be more directly concerned with orientation and direction selectivity than with length preference.

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