

DEVELOPMENT OF γ -AMINOBUTYRIC ACID MEDIATED INHIBITION OF X CELLS OF THE CAT LATERAL GENICULATE NUCLEUS

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SUMMARY

1. We studied the development of γ -aminobutyric (GABA) mediated inhibitory processes of the lateral geniculate nucleus cells in kittens of various age groups, by measuring the effect of ionophoretic application of GABA and bicuculline on cell response to sinusoidal gratings.

2. In young kittens (less than 30 days) we found very few Y cells only X cells and weakly responsive cells which fitted neither X nor Y classifications ('immature' cells).

3. As with adult cells, GABA inhibits the visual response of young kitten cells. Simultaneous application of bicuculline restored responsiveness. The mean GABA current to silence cell response in young kittens was significantly higher than that obtained in adult cats.

4. Application of bicuculline alone had little effect on young kitten X-cell responsiveness, either on the average discharge or on the amplitude of modulation to stimulation by sinusoidal gratings.

5. For older kittens (40–45 days), bicuculline increased X-cell responsiveness, and the increase in responsiveness was dependent on stimulus contrast and spatial frequency. However, the increased responsiveness was less than that for adults.

6. At 100 days the changes of slope of X-cell contrast–response curves during bicuculline application were similar to those observed for adult X cells.

7. We conclude that, although GABA receptors may be present at 30 days, the GABA mediated inhibitory system does not begin to function until about 45 days and does not mature fully until about 100 days.

INTRODUCTION

Both X- and Y-type neurones of the lateral geniculate nucleus (l.g.n.) of adult cats receive a powerful inhibitory input which exerts a strong influence on the organization of their receptive fields (Hubel & Wiesel, 1961; Singer & Creutzfeldt, 1970; Singer, Poppel & Creutzfeldt, 1972; Singer & Bedworth, 1973; Morgan, Sillito & Wolstencroft, 1974; Dubin & Clelland, 1977; Sillito & Kemp, 1983). The inhibitory input is also evident on recording their response to gratings (Berardi & Morrone, 1984). The transmitter mediating this inhibitory input appears to be γ -aminobutyric acid

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(GABA) (Curtis & Tebecis, 1972; Morgan *et al.* 1974; Sterling & Davis, 1980; Hunt, Liebermann, Ohara & Wu, 1982; Sillito & Kemp, 1983).

Anatomical and electrophysiological studies (see Sherman & Spear, 1982 for review), have shown that many properties of the cat visual system, not mature at birth, develop over the first months of life. For example, most kitten l.g.n. cells show low spontaneous discharge, poor spatial acuity, poor temporal resolution, high contrast thresholds, long response latency and poorly defined centre-surround organization with weak antagonism (Adrien & Roffwarg, 1974; Norman, Pettigrew & Daniels, 1977; Daniels, Pettigrew & Norman, 1978; Ikeda & Tremain, 1978). In addition, many l.g.n. cells in kittens younger than 35 days are difficult to classify as X or Y cells. These cells fail to respond reliably to visual stimuli, fatigue easily and exhibit a very low discharge rate (0–4 spikes/s under stimulation) (Norman *et al.* 1977; Daniels *et al.* 1978). We term these cells 'immature'.

Anatomical studies show that l.g.n. cell morphology develops slowly. For example the neurones of kitten l.g.n. are small with poorly developed dendritic arborization (Garey, Fisker & Powell, 1973; Gragg, 1975; Kalil, 1978; Friedlander, 1983). Furthermore, the development of symmetric synapses, which are thought to be inhibitory, lags behind the development of the asymmetric synapses, which are thought to be excitatory (Winfield, Headon & Powell, 1976; Winfield & Powell, 1980; Winfield, Hiorns & Powell, 1980).

Retinal ganglion cells mature early, development being nearly complete by about 28 days (Hamasaki & Flynn, 1977; Rusoff & Dubin, 1977; Hamasaki & Sutija, 1979). Ganglion cell centre-surround organization is almost mature at 28 days, whereas that for l.g.n. cells is much weaker at 28 days than for adults.

A possible explanation for the late development of the surround antagonism of l.g.n. cells is that inhibitory mechanisms develop late, an idea which receives some support from the anatomical results outlined above. The aim of the present study was to investigate this possibility, using ionophoretic techniques. We examined the change induced by bicuculline application in the contrast-response curves of X cells at different stages during l.g.n. development. We concentrated on X rather than Y cells because X l.g.n. cells have been shown to mature earlier than Y cells (Daniels *et al.* 1978). X cells also seem to receive a more powerful inhibitory input than Y cells (Fukuda & Stone, 1976; Berardi & Morrone, 1984). Preliminary results of this study have been reported by Morrone & Berardi (1983).

METHODS

We recorded from ten kittens between 25 and 100 days of age, and from six adult cats. The initial anaesthesia was induced with halothane, whereafter the general techniques of life support maintenance and monitoring, optical refraction and cornea maintenance were identical to those described by Berardi & Morrone (1984).

Glass three-barrelled pipettes were used for extracellular recording of neuronal activity and the ionophoretic application of drugs. The recording barrel, also used to mark the recording sites, contained 1% Pontamine Sky Blue (PSB) in 0.5 M-sodium acetate, and the other two contained *N*-methylbicyculline as chloride (5 mM, pH 3) and GABA (0.5 M, pH 3). At the end of each penetration, PSB was continuously ejected (20 μ A, negative polarity) during electrode withdrawal for subsequent histological reconstruction of the electrode track. In this paper we report only the results obtained from cells clearly located in the A laminae of the l.g.n. within 20 deg from the area centralis.

We studied the effect of bicuculline on cell response to gratings; the use of gratings allowed us a more direct comparison with our data in the adult cat and also permitted us to acquire more complete information about bicuculline effects than receptive field analysis would have done.

Vertical sinusoidal gratings were used to elicit cell responses. A Digital PDP11/03 laboratory

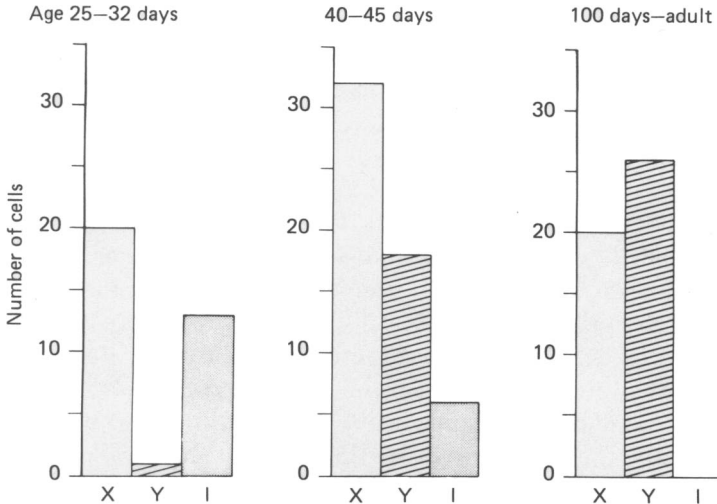


Fig. 1. Total number of X, Y and immature (I) cells recorded in animals of three age groups. The total number of cells is thirty-four in the 25-32 day old kittens group, fifty-six in the intermediate age group and forty-six in the 100 day old kittens group. This last group includes also results obtained from one adult cat.

computer generated the gratings, which were then displayed on the face of an oscilloscope (HP1300A), using the standard television technique of Schade (1956). The computer was programmed both to display a sequence of stimuli which varied either in contrast or in spatial frequency (depending on which parameter was under investigation) according to a pre-programmed sequence, and also to make a simultaneous recording of the cell response. This procedure, which is an improvement of that used for the previous study (Berardi & Morrone, 1984) allowed us to collect a contrast-response curve or a spatial frequency tuning curve for a cell in less than 4 min, thus reducing the possibility of changes in cell excitability. We repeated the observations at least twice both under normal conditions and under bicuculline application, and again after a suitable period of recovery as a control.

The experimental points of the contrast-response curves were fitted with polynomials up to the 3rd order by the method of least squares. When the slope of the curve was to be evaluated, however, the data were fitted linearly. We considered a curve well fitted by a straight line when the correlation coefficient was greater than 0.9.

The pharmacological effectiveness of bicuculline was always assessed following the procedure described in Sillito & Kemp (1983; see also Berardi & Morrone, 1984).

RESULTS

For each age group, we classified cells as X, Y or immature. The X-Y classification was made using the null point technique (Enroth-Cugell & Robson, 1966; Hochstein & Shapley, 1976). Cells were classified as 'immature' when they failed to respond reliably to visual stimuli, fatigued easily and exhibited very low discharge rates (0-4 spikes/s under stimulation). In addition, immature cells generally had very high

contrast thresholds (sometimes as high as 30%), responded to only a very narrow range of spatial frequencies and displayed on-off responses to small spots of light. This last observation confirms previous findings on kitten l.g.n. cells (Daniels *et al.* 1978).

Fig. 1 shows the total number of X, Y and immature cells recorded in animals of three age groups. The probability of recording from immature cells decreased as the age of kittens increased, from 35% in kittens younger than 35 days to none in 100 day old kittens. A constant proportion of clearly defined X cells was found in all age groups. Very few clearly defined Y cells, however, were observed when recording from the youngest kittens.

Effect of bicuculline on response to drifting gratings

The X cells of new-born kittens responded to drifting gratings with a modulation of their discharge, as do those of adult cats. However, the responses of kitten X cells are more rectified than those of adult X cells, even at low contrast (compare left and right columns in Fig. 2). This response rectification probably results from the low resting discharge of young kitten cells (around 2 spikes/s; $n = 24$; s.d. = 1). The cells of older kittens have higher spontaneous activity (mean = 8 spikes/s; $n = 24$; s.d. = 7 spikes/s) and their response to drifting gratings show less rectification (Fig. 2, middle column).

Bicuculline application increased both the spontaneous and the visually elicited discharge of the majority of kitten cells of all age groups, but the effect was much less for the younger than the older kittens. The average spontaneous discharge increase for the 25–32 day old groups was only 2 spikes/s ($n = 20$; s.d. = 1) compared with 6 spikes/s ($n = 24$; s.d. = 5) for the 40–45 day group, 12 spikes/s ($n = 34$; s.d. = 8) for the 100 day group and 13 spikes/s for adult X cells. Ten out of the twenty-four young kitten cells showed no measurable increase of spontaneous activity during bicuculline application. Similarly, bicuculline caused little increase in the amplitude of modulation of young kittens' (25–32 days old) cell response to grating stimulation. The maximum increase obtained was by a factor of 1.2; this value is negligible compared with that of a typical X cell from an adult (see Fig. 2, right column).

Despite the fact that bicuculline produces only a slight increase in X-cell activity of young kittens GABA was always effective in blocking the cell response to a visual stimulus. For instance, application of GABA (10 nA) abolished all response from the cell of Fig. 2 (left column). Application of bicuculline (60 nA) was sufficient to antagonize the action of GABA (40 nA). The distributions of the minimum GABA current necessary, to block a cell response to a grating of 10 times the threshold contrast for the youngest animals and the adult group are shown in Fig. 3. The amount of GABA required varied between the two groups, the current being 59 nA on average for the 25–41 day old kittens and 9 nA for the adult cats. These differences are significant ($P < 0.05$).

Effect of bicuculline on contrast-response curves

Our data for the adult cat (Berardi & Morrone, 1984) show that X cells receive a visually driven inhibitory input which can be blocked by bicuculline to produce

a change in slope of the cell contrast-response curves. The effect of bicuculline application on kitten X-cell contrast-response curves, when measured both by average cell discharge and by amplitude of modulation, is reported in Fig. 4 for the three age groups of animals.

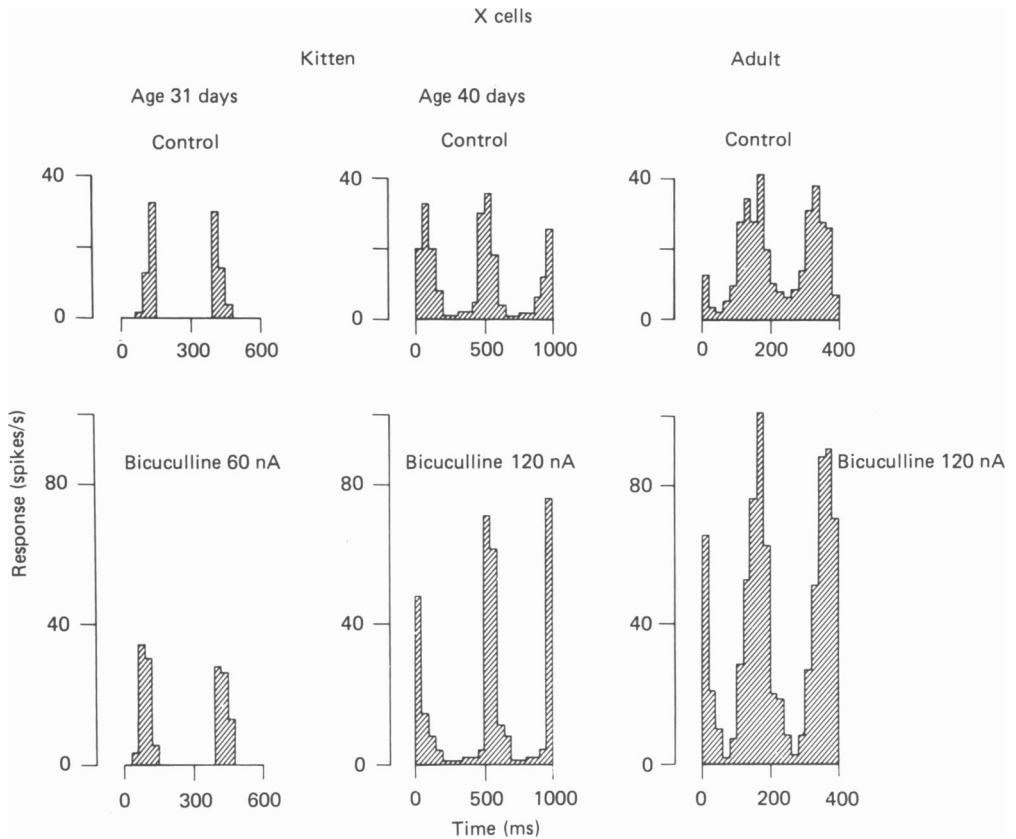


Fig. 2. Peri-stimulus time histograms of the response to sinusoidal drifting gratings of three X cells recorded from 31 and 40 day old kittens and from an adult cat. The top row shows the response in normal conditions, the bottom one during application of bicuculline. The current values used are reported in the Figure. The histograms have been calculated for two periods of the stimulus averaging on forty repetitions. The stimulus parameters for the three cells were the following. For the 31 day old kitten: spatial frequency 0.2 cycle/deg, contrast 15%. For the 41 day old kitten: spatial frequency 0.4 cycle/deg, contrast 20%. For the adult cat: spatial frequency 2 cycles/deg, contrast 20%.

Consider first the contrast-response curves of the X cell recorded from a new-born kitten (25 days old, Fig. 4, top row). In normal conditions, both the average discharge and amplitude of modulation curves differ from those of adult-like cells. For modulation amplitude, the contrast threshold is higher and the contrast gain (slope) lower. However, the slope of the average discharge curve is steeper than that for adult cats, particularly at low contrasts. The increase of average discharge with contrast could result from the rectification of the cell response shown in Fig. 2.

Bicuculline application does not change substantially the slope of either the average discharge or the amplitude of modulation curve (as it does for adult cats). For the cell of Fig. 4 (top row), bicuculline induced a slight increase in over-all responsiveness at all contrasts (shown by the upward shift of the curves) but in many

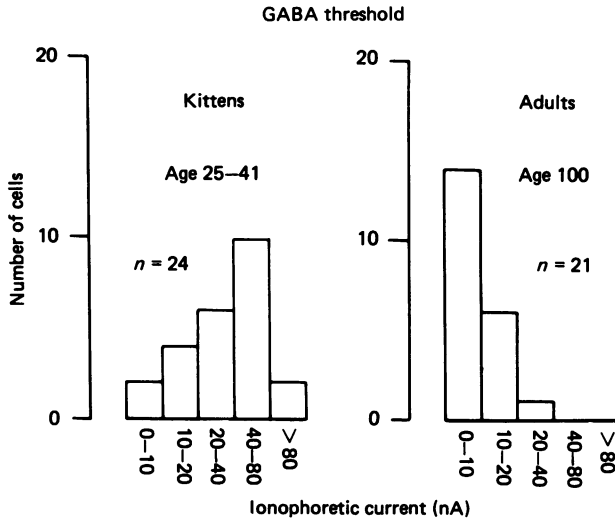


Fig. 3. Distributions of the minimum GABA currents necessary to block a cell response to a grating of about 10 times threshold contrast. The two distributions are for X cells recorded in animals between 25 and 41 days of age and from adult cats. The mean GABA current threshold was 59 nA (s.d. = 35 nA) for the kittens and 9 nA (s.d. = 7 nA) for the adults.

other cells (nine out of twenty), bicuculline had no effect at all. The cells where bicuculline had no effect at all had receptive fields within 5 deg from the area centralis, whereas those for which bicuculline produced a parallel shift in the response curves (like the cell in Fig. 4) had more peripheral receptive fields. In the X cells of this age group we also studied the receptive field organization and, in agreement with previous results (Daniels *et al.* 1978; Ikeda & Tremain, 1978), we failed to find any strong antagonistic centre-surround organization.

X cells from kittens of intermediate age had intermediate behaviour. Some of them behaved like the X cells from young kittens, showing no increase in contrast gain during bicuculline application, others more like cells of adult cats, showing bicuculline-induced increase of the slope of the contrast-response curves (although this increase was less than that of the adult cells). Fig. 4 (middle row) shows the results obtained from a cell recorded from a 43 day old kitten for which bicuculline did affect the dependence of its response on contrast. However, unlike adult cat l.g.n. cells, the average discharge in normal conditions increased with contrast, as it did in very young kittens, and bicuculline application made this increase more pronounced.

We also investigated qualitatively the centre-surround organization of l.g.n. cells in this age group. Some antagonism was present in the majority of these cells, demonstrated by the reduced response to stimulation by a large spot compared with

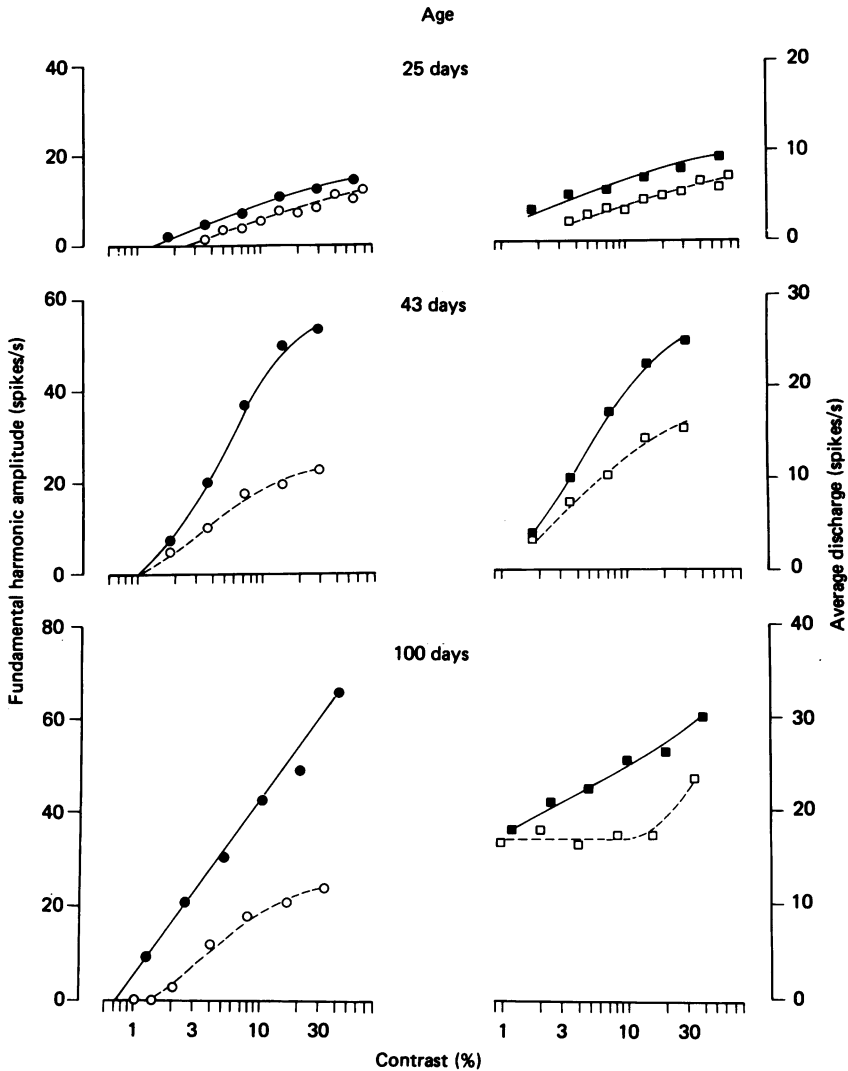


Fig. 4. Contrast-response curves of three cells recorded in kittens of three different ages. In the left column the response of the cells is reported as the fundamental harmonic amplitude, in the right column as the average discharge. Open symbols, normal conditions; filled symbols, bicuculline application. Top row: spatial frequency of the stimulus, 0.14 cycle/deg, temporal frequency 1.5 Hz, bicuculline current 60 nA. Middle row: spatial frequency 0.1 cycle/deg, temporal frequency 2 Hz, bicuculline current 60 nA. Bottom row: spatial frequency 0.15 cycle/deg, temporal frequency 5 Hz, bicuculline current 90 nA.

that by a small spot. As with adult cats, the difference in response to small and large spots was attenuated during bicuculline application.

Fig. 4 (bottom row) shows the curve of a 100 day old kitten. The behaviour of this cell in normal conditions was very similar to that of an adult X cell. The amplitude of modulation of the X-cell response increased monotonically with contrast, while the average discharge was constant over most of the contrast range. Under bicuculline

application, both parameters of the cell response increased with increasing contrast, and the amplitude of modulation curve increased in slope. This cell, and the majority of those in this age group, can therefore be considered to be adult-like.

To investigate further the effect of bicuculline on the intermediate age group

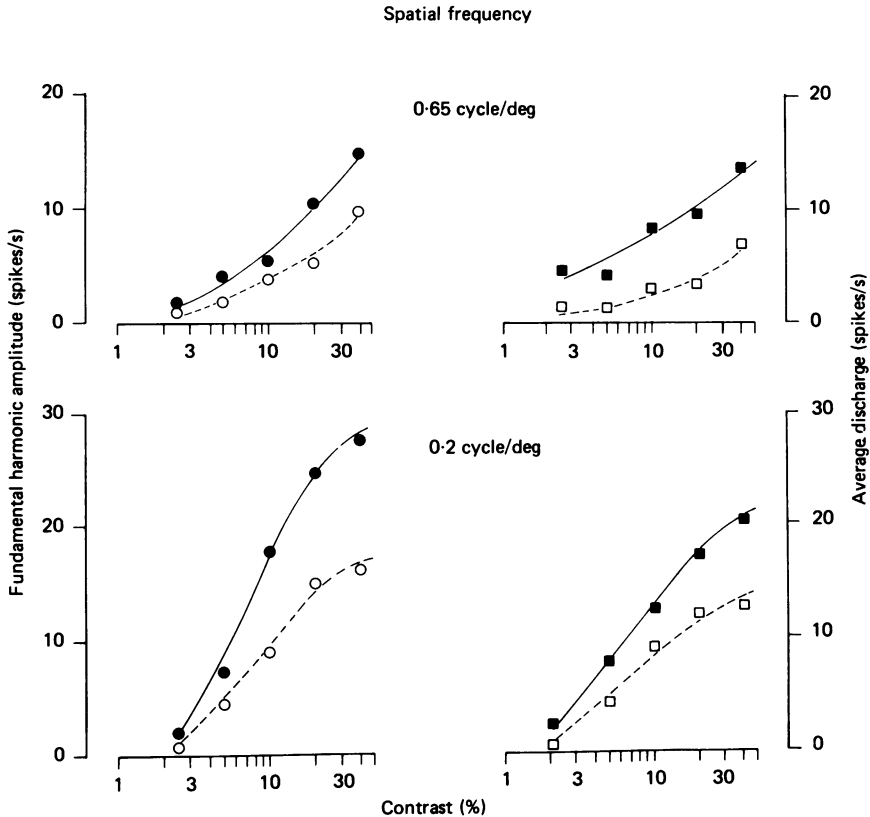


Fig. 5. Contrast-response curves of an X cell recorded in a 45 day old kitten for two different spatial frequencies (0.65 and 0.2 cycle/deg) of the sinusoidal gratings (temporal frequency 4.5 Hz). Symbols as in Fig. 3 (bicuculline current 60 nA). The linear fit of the amplitude of modulation-contrast curves is as follows: top row: filled circles, $y = 4.4 + 10.7x$, correlation coefficient (c.c.) 0.97; open circles, $y = -3.2 + 7x$, c.c. 0.95. Bottom row: filled circles, $y = -10 + 24x$, c.c. 0.98; open circles, $y = -6.4 + 14x$, c.c. 0.99. Where y is the cell response and x the logarithm of the stimulus contrast.

(kittens between 40 and 45 days old), we measured the contrast-response curves for two different spatial frequencies. Fig. 5 reports an example of the contrast-response curves obtained on stimulating an X cell with gratings of low spatial frequency (two octaves lower than cell acuity), and of high spatial frequency (half an octave lower than cell acuity). Bicuculline induced a change in the contrast-response curve for both conditions, but the change was less pronounced for the higher spatial frequency (upper curves). Thus, as for adult X cells, the effect of bicuculline was greater in the

low spatial frequency range. This suggests that the changes of slope result from the removal of a visually driven inhibition (see Berardi & Morrone, 1984, for discussion).

Properties of the Y cells recorded in the intermediate age group

From the 40–45 day old kittens we were able to record from some Y cells. These cells showed many signs of incomplete development, such as low spontaneous discharge, low contrast gain and usually had on-off centres.

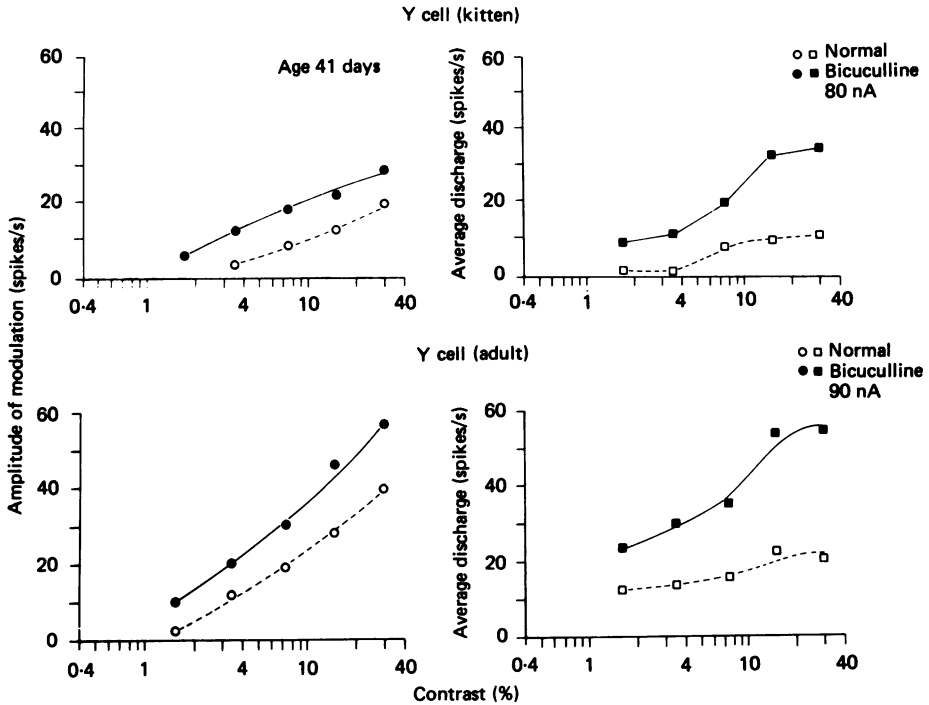


Fig. 6. Contrast-response curve of two Y cells recorded from a 41 day old kitten and from an adult cat. Symbols as in Fig. 4. The grating spatial frequency was 0.15 cycle/deg for the kitten cell and 0.8 cycle/deg for the adult. The temporal frequency was 5 Hz in both cases.

As for X cells, the response of Y cells could be blocked by application of GABA. The GABA threshold current for these cells had a mean value of 55 nA ($n = 11$; s.d. = 42); this value is not significantly different from that for X cells of the same animals (mean = 36 nA; $n = 13$; s.d. = 25).

In many of the Y cells we tested the effect of bicuculline in antagonizing ejected GABA and in raising the cell spontaneous discharge. The results show that young kitten Y cells are sensitive to bicuculline application, the mean increase in spontaneous activity being 6 spikes/s ($n = 11$; s.d. = 3.2).

Unfortunately, only for two Y cells do we have complete information for the effects of bicuculline on contrast-response curves, as in this age group we rarely encountered

Y cells that responded reliably. These preliminary results, however, indicate that, as for the adult Y cells, bicuculline induces an upward shift of the amplitude of modulation contrast curve, without inducing any change in the slope of the curve. The average discharge curves, like those of adult cats, do change slope under bicuculline application (compare top and bottom row of Fig. 6).

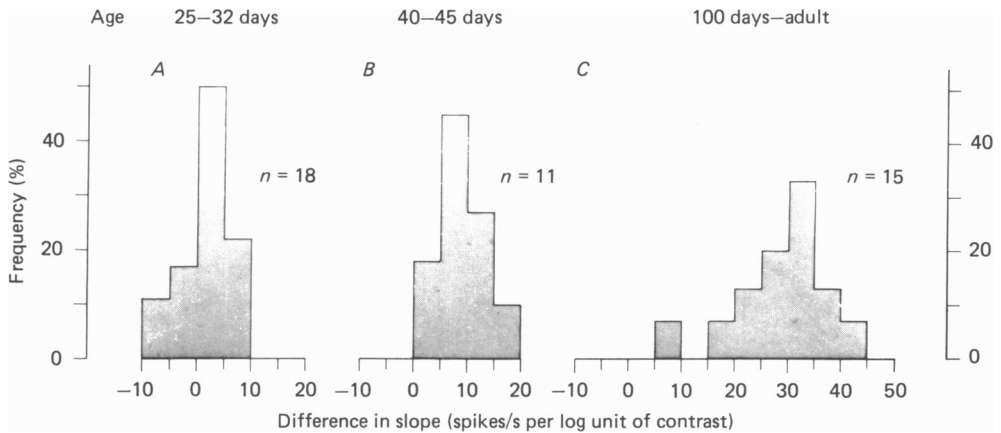


Fig. 7. Frequency distribution of the slopes of the difference curves (the difference between the amplitude of modulation-contrast curves with and without bicuculline) for the three age groups. Slope is expressed in spikes/s per logarithmic unit of contrast. Only those cells whose responses could be well fitted linearly (with a correlation coefficient greater than 0.9) have been included in the distributions. Note that 18% of the cells in the intermediate age group have slopes of the difference curves near zero; this fact follows from the heterogeneity of this cell population.

Statistical difference

The effect of bicuculline on the slope of the contrast-response curve is best expressed as the difference between the slopes of the contrast-response curves recorded with and without bicuculline. The difference in curve slopes for all the cells we recorded in all age groups are summarized in Fig. 7 (see legend for details of curve fitting). Slopes greater than zero indicate that under bicuculline application the contrast gain of the cell was higher. The greater the difference in slope, the greater was the bicuculline effect. For example, the change in slope shown in Fig. 4 (group aged 100 days) bottom left, yields a slope value of the difference curve equal to 30 spikes/s per log unit of contrast. The frequency distributions in Fig. 7 indicate that the slopes of the difference curves are clustered around zero in the 25-32 day old kittens, around 10 in the intermediate group and around 30 in the third group, for cats older than 100 days.

DISCUSSION

The kitten l.g.n. matures late (Kalil, 1978) and the sequence of the developmental events is different for the various cell types (Norman *et al.* 1977; Daniels *et al.* 1978; Ikeda & Tremain, 1978; Winfield *et al.* 1979; Winfield *et al.* 1980). Although cellular

size, spontaneous discharge and response latency are almost adult-like by the eighth week, other properties, such as contrast sensitivity, visual acuity and strength of antagonistic surround develop more slowly to become adult-like only in the twelfth week. The present study shows that GABA mediated inhibition acting on l.g.n. cells also matures late, in the seventh post-natal week.

The effect of bicuculline application on both the spontaneous discharge and on the cell response to gratings increased with the age of the kittens. In the very young kittens (aged 25–35 days) the increase in cell activity was negligible, especially for those cells with more central receptive fields. Only for kittens around 40–45 days old did we record some cells whose response as a function of contrast (gain) increased during bicuculline application. However, in the same kittens the response of other cells was virtually unaffected by the drug. In addition only those cells that showed a change of contrast gain during application of bicuculline had a powerful antagonistic receptive field surround. These two results agree in suggesting that GABA mediated inhibition starts to develop in this period.

Although bicuculline had little effect in changing the contrast–response curve of young kittens, application of GABA did block cell response (although a greater quantity was required than for adult cells). This suggests that the GABA mediated receptors are present on the cell membrane in kittens as young as 25 days old (although there may be fewer or they may be less effective than in the adult cat). Thus the ineffectiveness of bicuculline for raising cell activity in the X cells on young kittens probably reflects an absence of an inhibitory input to the cell rather than an absence of GABA receptors. This suggestion agrees with the anatomical data on l.g.n. development. It is known that while the dendrites of relay cells assume their mature characteristics gradually over the first 20 days, the dendrites of interneurons undergo their most rapid development between 20 and 40 days and continue to mature into the latter half of the second post-natal month. Moreover, the number of symmetrical synapses increases dramatically around 40–45 days, about the same time that we start to find evidence of an inhibitory input on X cells (Winfield & Powell, 1980; Winfield *et al.* 1976, 1980).

Our results support those of Daniels *et al.* (1978) in showing that Y cells develop later than X cells. We found many X-like cells in the very youngest kittens, but virtually no Y cells in this age group. The earliest age at which we recorded Y cells was 40 days, which restricted our sample. However, preliminary results suggest that as soon as Y cells appear (at about 40–45 days) bicuculline application increases cell discharge gain as it does for adult Y cells. If confirmed, this would suggest that when the functional properties of Y cells begin to appear, some Y cells are already receiving an inhibitory input. Furthermore, it seems that the Y system develops at about the same time as the inhibition on both X and Y cells begins to become evident. Although this may be coincidental, it is possible, considering the anatomical data, that the development of both X- and Y-excitatory input is needed to 'trigger' the development of the inhibition.

In conclusion, our results suggest that GABA mediated inhibition develops relatively late, when many of the X-cell properties related to excitatory inputs are already mature. It is interesting to note that inhibitory input begin to appear after the kitten starts to interact with its environment. It is therefore conceivable that the

development of the inhibitory system may be influenced by, or even modulated by, the visual experience of the cat, and this could be the major component in some plasticity phenomena demonstrated in the cat visual system.

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