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# Cortical Off Response Tuning for Stimulus Duration

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To answer the question whether OFF response amplitude (firing rate) of visual cortical cells varies as a function of stimulus duration, a series of such cells from areas 17 and 18 of the cat were investigated with a stationary light bar, presented for different durations (10–3200 msec) over the receptive field. Out of a sample of 174 cells tested, 58 cells were found for which the OFF responses varied as a function of ON stimulus duration. Of these cells, 29 showed a continuous increase up to the longest duration tested, six showed a sharp tuning for medium range durations (between 50 and 400 msec) and the remaining 23 cells had an intermediate profile (increase to optimum followed by slight decrease). For some of these cells this tuning could be used to predict adequately the velocity tuning. Similar recordings in 13 lateral geniculate nucleus cells failed to show duration tuning. Copyright © 1996 Elsevier Science Ltd.

OFF responses    Duration tuning    Cat areas 17 and 18    Visual cortex    Velocity tuning

## INTRODUCTION

Temporal characteristics of cortical and geniculate responses differ considerably. While cells in the LGN (lateral geniculate nucleus) respond with short latency to stimuli of very short duration, the cells in cat areas 17 or 18 often require longer-lasting stimuli to which they respond with a long latency (Duysens *et al.*, 1985b, Duysens *et al.*, 1987; Cremieux *et al.*, 1983). Recent work has shed light on the reasons for these differences. Geniculate cells may contribute as few as 5% of the excitatory input in layer 4 (Ahmed *et al.*, 1994) but this input may be especially amplified through activation of regenerative Ca<sup>2+</sup> potentials (Hirsch *et al.*, 1995) and/or through strong excitatory intracortical connections (Douglas & Martin, 1990). Furthermore, the responses in cortical simple cells have been proposed to result both from excitatory input from LGN and from disinhibition of other simple cells with overlapping receptive fields (Hubel & Wiesel, 1962; Palmer & Davis, 1981; Duysens *et al.*, 1987; Ferster, 1988). Given these differences between LGN and visual cortex, it is surprising that little attention has been given to changes in the time course and the temporal characteristics of the responses at these two

levels (see, however, Ferster, 1988). In previous work we have concentrated mainly on ON responses (Duysens *et al.*, 1985a,b; 1991). At present, special attention will be given to OFF responses and the question will be asked whether these responses show characteristics which are not present in LGN. To test these characteristics the duration of stimulation was the variable manipulated.

This type of testing allows one to answer a second type of question. In the visual system, the coding of stimulus duration relies on a coding in terms of response duration, while a coding in terms of frequency of discharge has not yet been demonstrated. In cat visual cortex, many cells show ON responses which depend on the duration of presentation of a stationary bar (Duysens *et al.*, 1985a,b; 1991) but a duration tuning for ON responses (resulting in largest ON response amplitude for a clear optimum stimulus duration and smaller responses for either shorter or longer durations) was not observed. In the present study the question was asked whether OFF responses are able to code the duration of ON stimuli.

A third reason for studying the duration dependency of OFF responses is that the classification of cortical cells relies on the detection of regions from which one obtains ON and OFF responses. If OFF responses depend on ON stimulus duration, then the classification of cell types may be influenced by the use of different ON durations in the quantitative tests performed in different laboratories.

Fourthly, in previous studies it was shown that the velocity characteristics of many cortical cells, stimulated with a moving light bar, can be predicted from a knowledge of the ON responses to stationary presenta-

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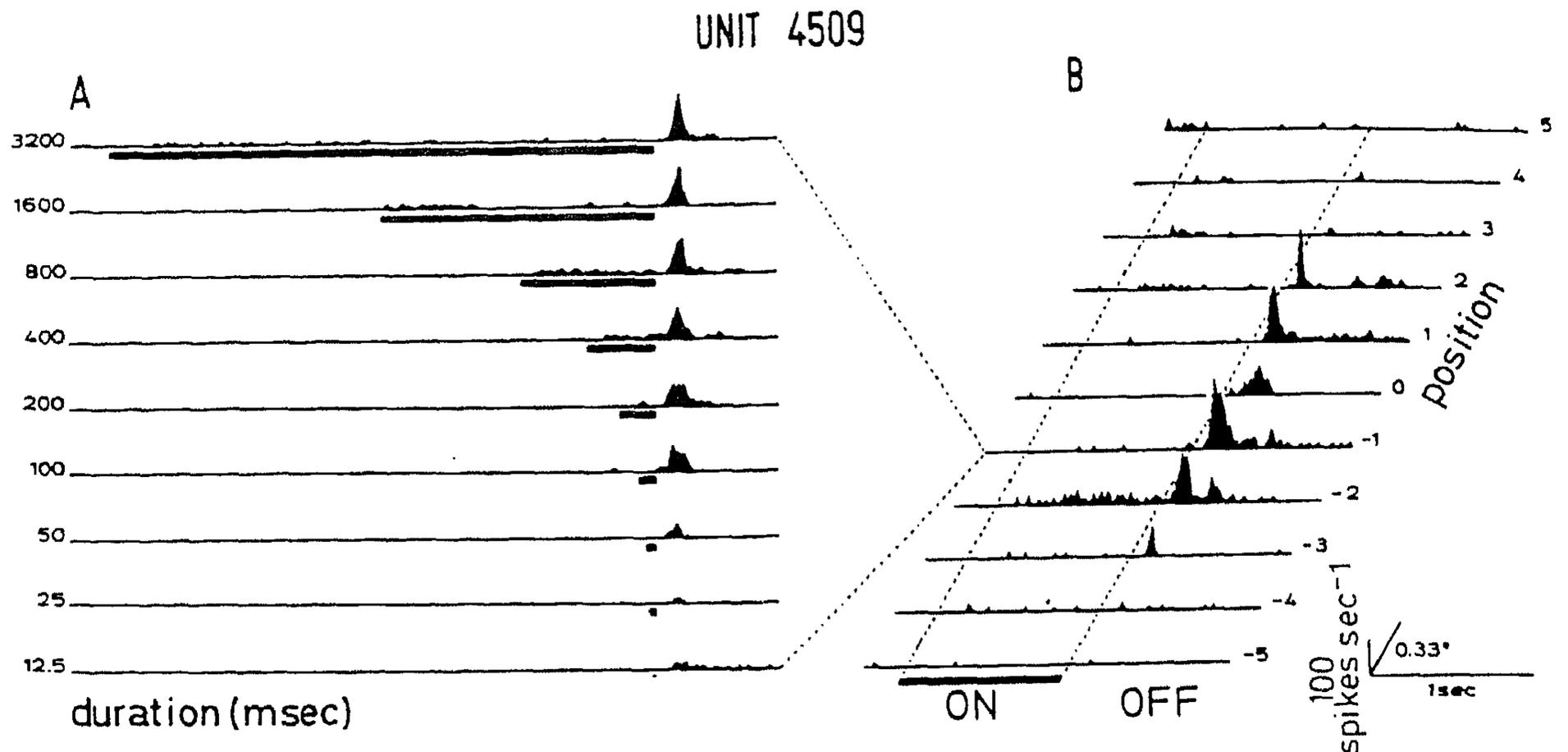


FIGURE 1. Responses of a single cell from area 17 to a flashed bar presented with different durations, at a single location of the receptive field (A) or with constant duration (1 sec) at various positions (B). Horizontal bar: ON stimulus. Histograms in (B) are presented in oblique order to avoid overlap of the response peaks. Area 17, layer 5-6 S cell with 2.5 deg eccentricity.

tions of the same light bar for different durations (Duysens *et al.*, 1985b). Some cortical cells, however, give mostly OFF responses and for such cells it is more appropriate to try to predict the responses to a moving light bar on the basis of the OFF responses following ON stimulation of various durations. In the present study we determined the OFF responses of cells in the visual cortex (areas 17 and 18) as a function of the duration of the light bar presentations, preceding the responses. These OFF responses were then compared with those obtained with the same bar moving at different velocities.

### METHODS

A detailed description of the methods used can be found in previous publications (Duysens *et al.*, 1985a,b; 1987; for summary see Orban, 1984). Cats were anaesthetized with Alfatesin (Glaxo) for initial surgical procedures. Thereafter they were curarized with a continuous perfusion of Flaxedil at 5 mg/kg/hr with D-tubocurarine added at 0.14 mg/kg/hr. The cats were given pentobarbitone intravenously (0.2-1 mg/kg/hr) and the effectiveness of the anaesthesia was checked by recording the E.C.G. and, on occasion, the E.E.G. as well. The animal was respirated with a Bird 8 respirator supplying a N<sub>2</sub>O:O<sub>2</sub> (70:30) mixture. The end-tidal CO<sub>2</sub> level was maintained at 4%. The temperature was maintained at 38°C. Pupils were dilated with atropine. Except for some of the early experiments, artificial pupils with a diameter of 2 mm were placed in front of the eyes. Afocal contact lenses prevented the cornea from drying and corrective lenses were used to focus the eyes. The daily care of the optics included the local use of antibiotics.

### Quantitative testing

Varnished tungsten electrodes were used to record single units which could be separated from other units with one or two level discriminators. On the plotting table the optimal stimulus dimensions (length, width, orientation) were determined with hand-held stimuli. The same optimal stimulus (usually a light bar of 0.3 deg width with a luminance of 3.43 cd/m<sup>2</sup> against a background luminance of 0.05 or 0.65 cd/m<sup>2</sup>) was rear projected on a translucent screen by means of a computer-controlled slide projector. The computer operated on a program which allowed interleaving of different stimulus conditions and construction of multiple interleaved peristimulus time histograms (PSTH). Each PSTH corresponds to a stimulus condition and the set of PSTHs constitutes a multihistogram. Impulses corresponding to neuron activity were stored on disks together with the stimulus parameter settings.

To determine the receptive field (RF) structure, the response plane of the RF was constructed by flashing a light bar over the RF in several closely spaced positions. The presentations at different locations were interleaved and randomized. Each 1 sec ON period was followed by a 1 sec OFF period and preceded by a period of 250 msec during which spontaneous activity was sampled. When a long series of different procedures were used the quantitative determination of the receptive field was repeated to ensure that no shift of the field had occurred due to eye movements. In other cases the back projection of the receptive field was used to check for drifts in eye position. In the rare cases when such drifts were found to

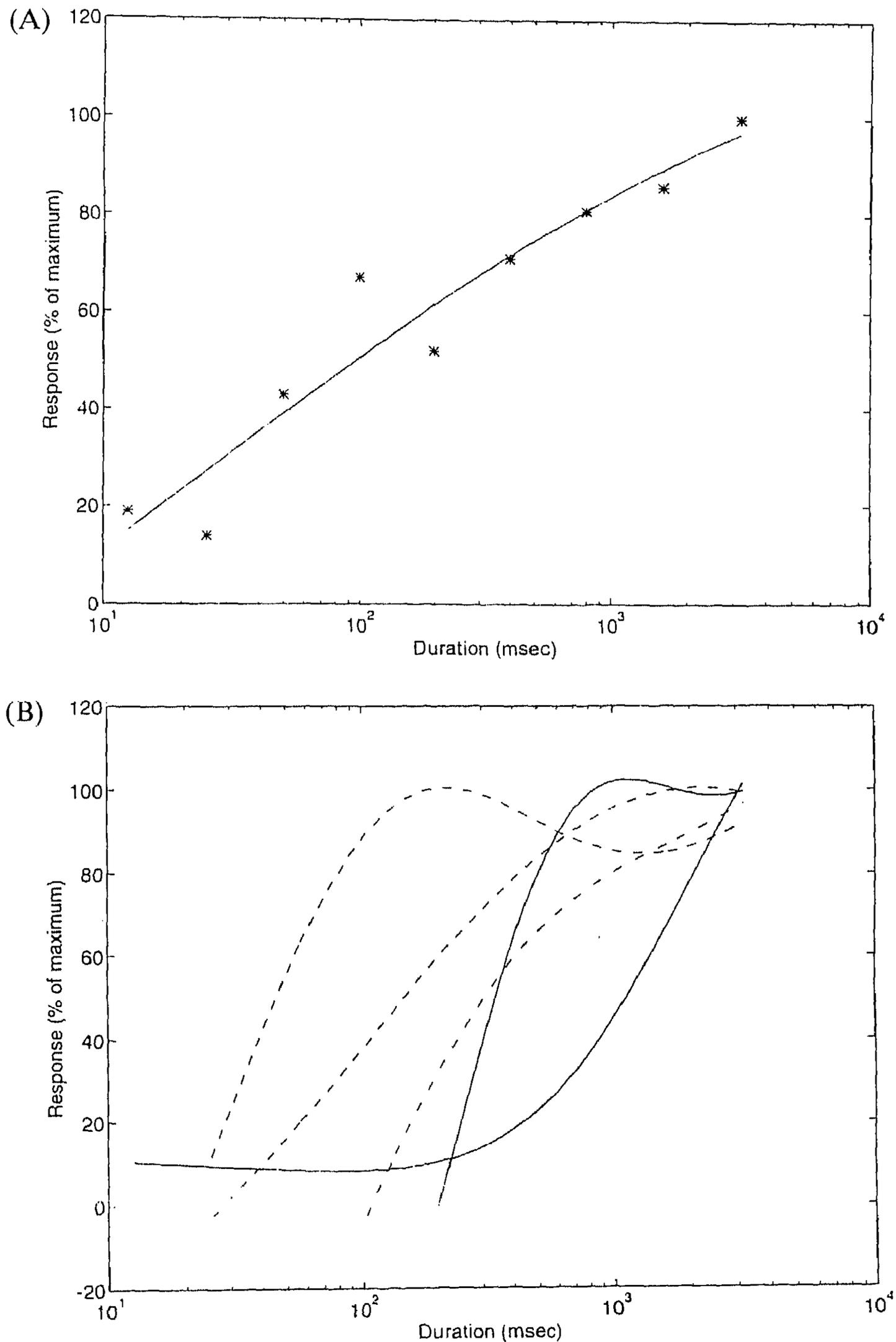


FIGURE 2. Duration response curves for same cell as shown in Fig. 1(A) and for a set of cells with a duration threshold for OFF responses (B). All data were fitted with a spline function. (A) Area 17 cell with 16.5 deg eccentricity; (B) two cells from area 17 and three from area 18. Eccentricities ranging from 1.6 to 19.9 deg. Cell types: HC, B, C, HC and S (for definitions see Orban, 1984). Layers: 2-3 (two cells), 5 (two cells) and 6.

occur, the data, sampled during such an unstable period, were discarded.

For the variable duration test the stimulus was the same as in the previously described test except that the ON period ranged from 10 to 3200 msec and that only one

position (the one yielding the largest OFF responses) was tested. As for the response plane test, the stimulation was repeated 10-50 times and all conditions were interleaved and randomized.

In the "velocity test" the influence of angular velocity

was tested over a range from 0.5 to 900 deg/sec (19 velocities in total). The responses were sampled using a multiple interleaved peristimulus time histogram. Each of the interleaved PSTHs corresponds to a 250-msec rest period followed by a forward and backward sweep at a given velocity. For at least 5 sec between the movements, the stimulus was stationary outside the field over which either facilitatory or suppressive responses could be evoked (see Orban, 1984). For all tests described, the different PSTHs could be visualized as well as the resulting summary curves.

The significance of the responses was tested with respect to the spontaneous activity preceding the stimulus trials. A response was considered to be above threshold if the response criterion (the maximum firing rate measured over 8 msec binwidth) was larger than the mean spontaneous activity plus 2 standard deviations. Unless stated otherwise, the data were fitted both with a spline function (see Orban, 1984) or, in order to obtain a better fit for the relative low number of data points, with Levenberg–Marquardt nonlinear regression (Gaussian with a linear function added for increasing duration). An example is shown in Fig. 2(A).

At the end of the experiment the animal was sacrificed. The location of cortical units was verified in a histological reconstruction, using 40  $\mu\text{m}$  sections of the brain which was previously perfused with 1.0% formaldehyde. At least two electrolytic lesions were made in each penetration.

## RESULTS

A group of 174 cells from areas 17 and 18 was examined quantitatively to test the sensitivity of OFF responses to changes in duration of the preceding ON periods. In a first step the structure of the receptive field was determined quantitatively by flashing a 0.3 deg wide light bar over the receptive field [Fig. 1(B)]. In the present sample, the majority of the cells ( $n = 116$ ) showed no ON duration sensitivity for the OFF responses, if such responses were present at all. However, the remaining third (58/174 cells) had OFF responses with an amplitude which depended on the ON duration. The criterion used was that the maximum OFF response at a given ON duration had to be at least twice as large as the smallest OFF response. The 58 cells meeting this criterion had receptive field sizes with a mean width of 2 deg, which was not significantly different from the mean RF width of the duration-insensitive population (2 deg, see also Duysens *et al.*, 1985b). All these 58 cells showed an increment in amplitude of OFF responses for increasing ON durations over at least part of the range of durations tested. They will therefore be termed ‘increment’ cells. The receptive fields of these cells had eccentricities ranging from 0.3 to 25 deg.

In all cells, the position yielding the largest OFF responses was used to evaluate the effect of changes in the duration of the ON stimulus preceding the OFF responses. In the example of Fig. 1, the receptive field consisted mainly of a large OFF subregion [Fig. 1(B)].

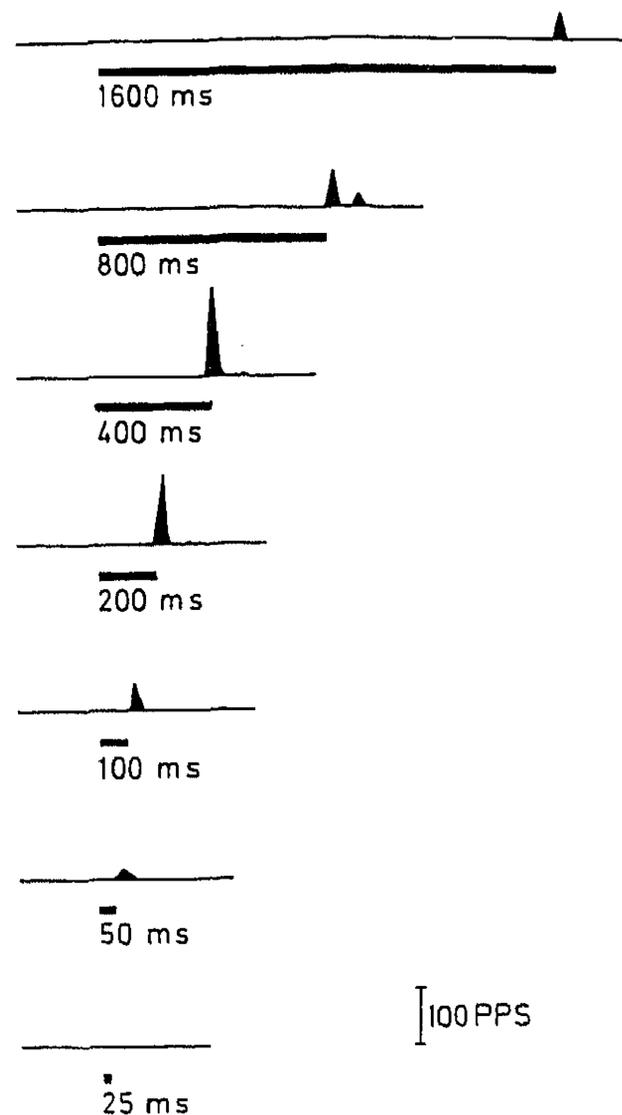


FIGURE 3. Example of an area 17 S cell (#3215; layer 4) with a duration tuning for OFF responses. Conventions as in Fig. 1.

Repetition of the ON stimuli for various durations over the position yielding the largest OFF responses revealed that the amplitude of the OFF responses increased as a function of ON duration [Fig. 1(A) and Fig. 2(A)].

In the example shown in Fig. 1(A) and Fig. 2(A) an OFF response was present even following the shortest ON duration tested (12.5 msec). This was also the case for 25 of the 58 cells with OFF responses. The other cells in the group had thresholds with a median of 42 msec (first quartile Q1:28 and third quartile Q3:140 msec; median instead of mean was used since the duration scale was logarithmic and as a result there was no normal distribution).

### Types of increment cells

The group of 58 increment cells could be subdivided into three groups which were termed pure, tuned and mixed increment cells. In the pure increment group ( $n = 29$ ), the response increased up to the longest stimulus duration tested [3200 msec, see Fig. 2(B)]. For the remaining cells, increasing the stimulus duration beyond the level where maximum responses were obtained, led to a reduction in response level. When this reduction was severe, the cells were classified as tuned ( $n = 6$ ). In such cases, the duration response curve, fitted with a spline function, had to cross the 50% of maximum level both with its ascending and its descending limb. The remaining cells ( $n = 23$ ) which did not meet this criterion formed the third group. They were termed ‘mixed’ [for examples see Fig. 2(B)]. In this group the response

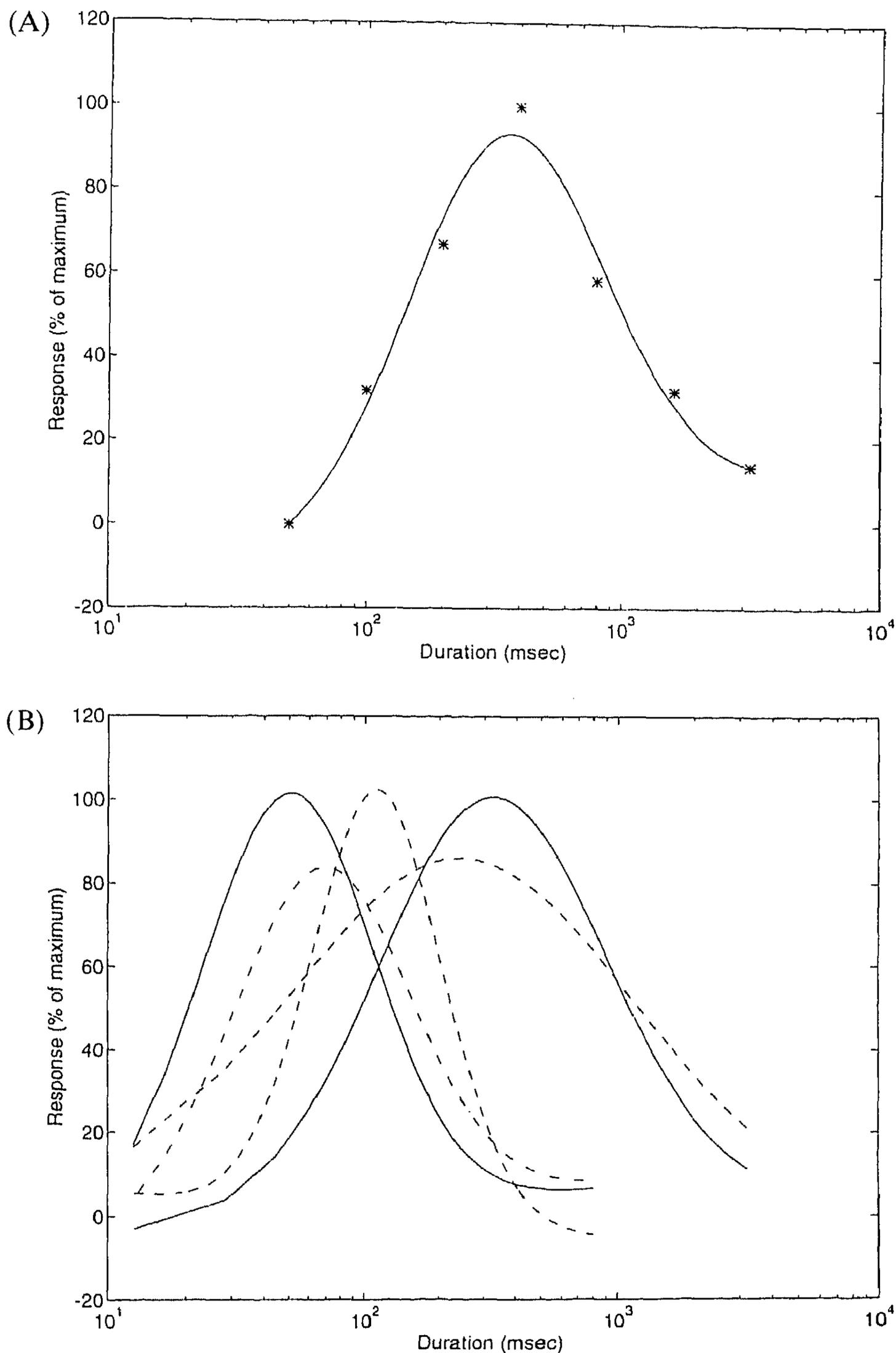


FIGURE 4. OFF response tuning for ON stimulus durations for the same cell as shown in Fig. 3 (A) and for five other cells (B). The maximum response was at 400 msec for (A) and for two cells in (B). The largest response for the remaining cells was 50 ( $n = 2$ ) and 100 msec ( $n = 1$ ). Cells in (B): two from area 18, three from area 17; cell types: B, HS, HA, HS, one unclassified; layer: 2-3, 4 (two cells), 5-6 and 6.

amplitude first increased but then stabilized or decreased again slightly when tested with the longest stimulus durations (with the descending limb not crossing the 50% of maximum level). Hence the three groups differ mainly with respect to the duration at which optimum responses

were obtained. For the pure group this was the longest duration tested (3200 msec), while it was increasingly shorter for the mixed and the tuned group, respectively. For the whole group of pure and mixed increment cells ( $n = 52$ ), the ON duration required to yield maximum

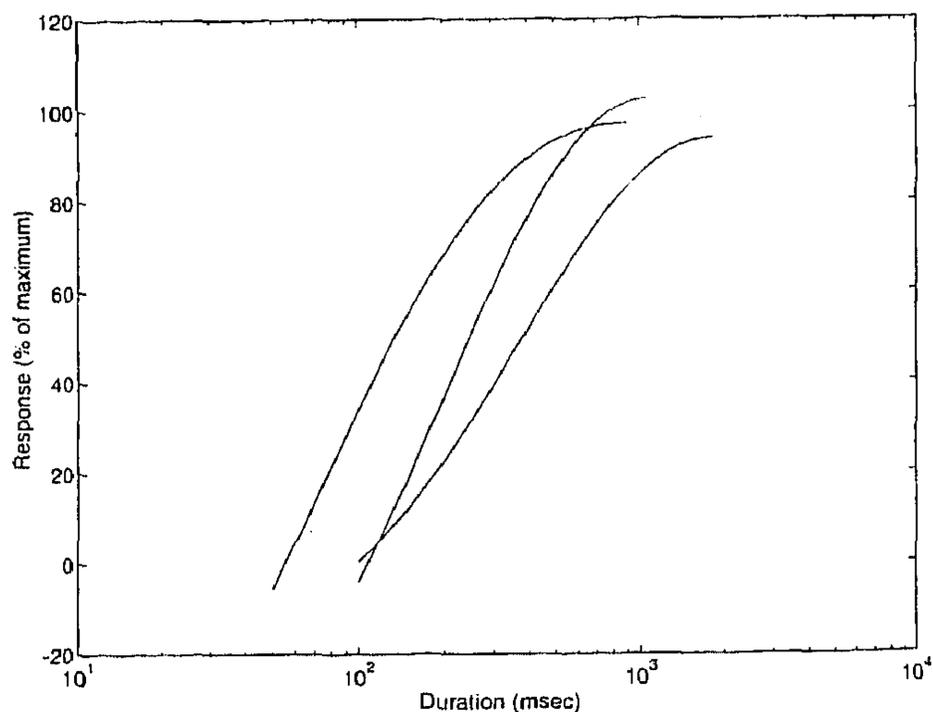


FIGURE 5. Increments in OFF response amplitude as a function of ON stimulus duration in 3 Y-OFF cells.

OFF responses was 1300 msec (median with Q1:450 and Q3:1700 msec). In contrast, for the tuned group the median was 250 msec (range 50–400 msec).

In all three groups a large proportion of cells (13/29 pure; 10/23 mixed and 5/6 tuned) had receptive fields with predominant OFF responses, such as shown in the example of Fig. 1. The maximum OFF responses in these OFF-dominant cells were at least 1.5 times larger than the maximum ON response obtained anywhere in the receptive field. The remaining cells had more equal ON and OFF responses.

The duration response curves were constructed as illustrated in Fig. 2(A). To show the variation both in slope and position of the ascending slope, a set of five other curves is shown [Fig. 2(B)]. Four of these cells lacked an OFF response for the shortest ON duration tested (i.e., they had a duration threshold).

#### Tuned cells

Tuned increment cells had an optimum at short ON stimulus durations and such cells showed sharp tuning curves. These cells deserve some special attention because they potentially can code ON stimulus duration. An example of such a cell is given in Fig. 3. This area 17 cell was classified as simple and had a dominant OFF subregion (16 deg eccentricity; 1.2 deg receptive field width). The amplitude of the OFF responses in this cell increased up to a maximum for an ON stimulus duration of 400 msec and then declined when longer ON durations were used. The resulting duration tuning curve is shown in Fig. 4(A). In a separate test (not illustrated) the robustness of the tuning was tested. Lowering the luminance of the light bar to a level near the threshold for OFF responses (maximum OFF response reduced to 31% of the maximum shown in Fig. 3) broadened the tuning but there was no shift in optimum duration. Five other examples of such curves were found and they are shown in Fig. 4(B). Such tuning curves were restricted to simple cells [as those five shown in Fig. 4(B)], while

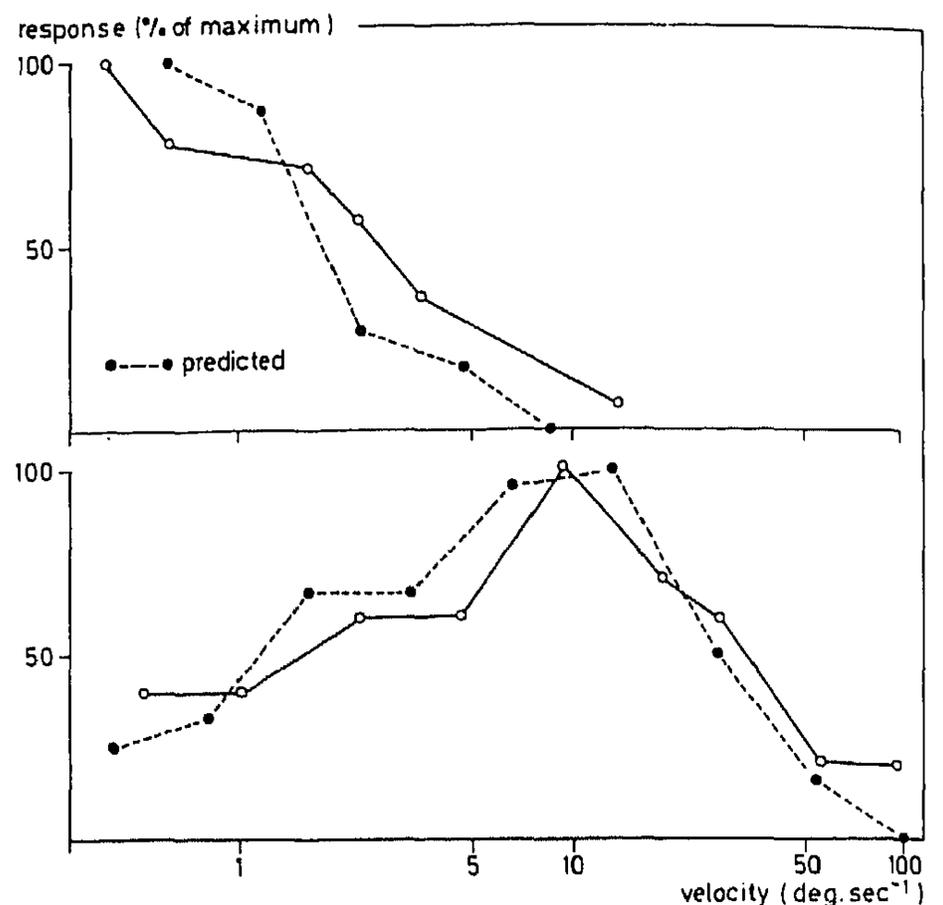


FIGURE 6. Comparison of velocity response curves, as measured with a moving light bar, with predictions made on the basis of the responses to a stationary light bar, presented with different durations. To accentuate the similarities, the data points were simply connected, either with full lines (measured values) or with dashed lines (predictions). Top: area 17 (layer 2–3) B cell with eccentricity of 2.5 deg. Bottom: area 18 C cell with 15.9 deg eccentricity.

complex cells did not show tuning. Four of the five cells had predominant OFF responses (according to the definition given earlier). Among the five cells of Fig. 4(B), two were from area 18 and the others were from area 17. Their receptive fields were all within 15 deg from the area centralis and their field width was between 0.9 and 2.7 deg.

#### Lateral geniculate units

An obvious question arising from these data is whether the increments and the tuning of OFF responses as a function of ON stimulus duration are cortical or subcortical phenomena. To answer this question a sample of 13 geniculate units was studied with exactly the same ON stimuli of different durations as used for the cortical cells. The sample consisted of 6 X-ON, 1 X-OFF, 3 Y-ON and 3 Y-OFF cells. None of these cells had a tuned response curve but three cells showed a clear increment in response amplitude as a function of stimulus duration (Fig. 5). These cells were all of the Y-OFF type and they all had a duration threshold for OFF responses.

#### Implications for velocity sensitivity

If an OFF subregion is sensitive to the duration of flashed ON stimuli, then one might expect it to be sensitive to the velocity of a moving light bar as well. At low speeds, the light bar would remain over the receptive field for a long period of time and this might be equivalent to flashing a light bar for a long duration. For cells with a predominant ON subregion, a similar type of

reasoning was previously shown to be successful in predicting velocity characteristics of visual cortical cells (Duysens *et al.*, 1985b).

For the cells in the present sample equally successful predictions were limited to two cells which had a single dominant OFF subregion. The results are shown in Fig. 6, one for a cell with an OFF increment curve (top) and one for a tuned OFF response curve (bottom). To make the predicted curves, the velocity equivalent to each ON duration was calculated as the ratio of the receptive field width over the ON duration. Hence the ON stimulation by the moving bar was assumed to be equivalent to the time spent by the leading edge of the light bar in the receptive field. For a cell which has the largest OFF responses at long ON durations one predicts that the lowest velocities elicit the largest responses, as was indeed found for cells such as illustrated in Fig. 6 (top). From the six cells showing OFF response tuning, only one cell was also tuned for velocity ("velocity tuned" cell according to the definitions used by Orban, 1984). For this one velocity tuned cell, responding optimally to medium ON durations, the best velocities were also intermediate and well predicted by the OFF responses (Fig. 6, bottom).

## DISCUSSION

The main finding of the present paper is that the temporal characteristics of OFF responses of cortical cells show both similarities and differences with those seen in LGN cells. First, there is the finding that one-third of the cortical cells tested showed increased amplitudes of OFF responses as a function of the duration of the (ON) stimulation. At the geniculate level such "increment" behaviour was only seen in Y-OFF cells. Other authors, however, have seen duration-dependent increments in other LGN cells as well. Brooks & Huber (1972) reported that OFF responses of ON centre cells increased following the prolongation of the preceding ON stimulation up to 700 msec. In analogy with this, Singer & Phillips (1974) found that the ON responses of geniculate ON centre cells were inhibited when preceded by OFF stimulation periods ranging from 30 to 500 msec. The duration-dependent increase in OFF responses of geniculate cells may itself arise from retinal input. The OFF responses of retinal ganglion cells have been found to increase in amplitude as a function of the preceding ON stimulation (Enroth-Cugell & Pinto, 1972). Similar observations were made by Steinberg (1969).

The present finding that geniculate Y-OFF cells all showed OFF responses which increased as a function of ON duration, while other cell types (within the small sample tested) did not show this behaviour (at least not under the present luminance conditions) has important implications. Input from Y-OFF cells should be especially prominent in cells from area 18 and in some area 17 cells with peripheral RF (Ferster, 1990). However, "OFF increment" cells were also found in the part of area 17 representing the central retina. Since these cells do not receive Y input they must rely on other, possibly cortical,

mechanisms to generate the variations in OFF responses observed.

A similar conclusion about intracortical processing is reached when considering the result that the amplitude of OFF responses of some cortical cells is sharply tuned over the range of durations tested. Indeed such tuning was not observed in the geniculate sample and therefore should be generated at a cortical level. In this respect it is important to point out that, unlike for geniculate cells, the OFF responses of cortical cells presumably rely on a "push-pull" mechanism (see Introduction). Hence the presence of duration-dependent increments in OFF amplitude in cortical cells lacking Y-OFF input may be related to disinhibition (release from inhibition of another cortical cell with ON input over the same region). Similarly, the tuning may be explained by a complex interaction between excitatory input (for example, from a geniculate "increment" cell) and the removal of inhibition from another cortical cell. For example, it is possible that the disinhibition is optimal for a given preceding ON duration, thereby causing a duration tuning of the OFF responses (since the latter result from a combination of direct excitation and disinhibition). Alternatively, the tuning may be the result of the complex amplification circuits which transform the incoming geniculate input (see Introduction). Future intracellular studies on the duration dependency of OFF responses could aid in determining the precise mechanisms involved.

### *Velocity sensitivity*

To investigate whether incremental OFF responses could explain velocity sensitivity, the cells were tested with a moving light bar and their responses were compared with those predicted on the basis of the duration tuning. In general, the velocity tuning was found to be broader than the duration tuning but at least one case was found in which the velocity tuning was sharp and well predicted by the results from the duration test. This indicates that in limited cases the responses to a light bar are pure OFF responses but in most cases a contribution of ON responses and additional spatiotemporal interactions were involved in shaping the velocity profile of the cells.

### *Cell classification*

The finding that the OFF response amplitude depends heavily on the preceding ON durations has obvious implications for quantitative studies using a flashed bar for the classification of cortical receptive field types. The duration of the shortest ON stimuli varies considerably in these studies, i.e., 32 msec (Movshon *et al.*, 1978), 128 msec (Emerson & Gerstein, 1977), 500 msec (Toyama *et al.*, 1977; Heggelund, 1981; Emerson & Coleman, 1981), 640 msec (Palmer & Davis, 1981), 1000 msec (Fries & Albus, 1976; Duysens *et al.*, 1982) and 2000 msec (Bullier *et al.*, 1982). When comparing the results of these studies one should take into account that the studies which used relatively brief ON stimuli may have underestimated the OFF responses and, related to

this, the size of OFF subregions of many cells. For ON responses a similar problem can arise. Shevelev *et al.* (1992) showed that by increasing the duration of ON stimuli from 10 to 400 msec the size of the RF decreased to less than 25% of the original size in cat area 17 cells.

A similar caution is needed when comparing studies with different contrast conditions since it was shown previously that conclusions about receptive field structure may be altered dramatically by changing the luminance of the stimulus (Duysens *et al.*, 1985a; Shevelev *et al.*, 1992). In view of these pitfalls it may be safe to base cell classification not only on the flashed bar technique but also on the method of moving sinewave gratings (for review of this point see Skottun *et al.*, 1991).

### Functional significance

From the tuning results it follows that there are two possible types of coding of visual stimulus duration. The first relies on the duration of the ON response and the second on the firing rate following the period of stimulation. The coding of stimulus duration by firing rate is not unique for the visual system. For sound stimuli, such frequency coding for stimulus duration has been reported in the frog's midbrain (Hall & Feng, 1986; Feng *et al.*, 1990) and in the inferior colliculus of the brown bat (*Eptesicus fuscus*, Casseday *et al.*, 1994). For the latter system, it was proposed that duration tuning arises in cells because of a combination of an early sustained inhibitory input and a delayed, transient excitatory input.

Despite the species difference, it has been possible in the past to link basic neurophysiological observations in animals with human psychophysics (e.g. Coenen & Eijkman, 1972; Duysens *et al.*, 1985a). For example, below the critical duration, which ranges between 50 and 100 msec, depending on background illumination (Barlow, 1985; Zacks, 1970), humans cannot distinguish between changes in duration or luminance (Bloch's law) and this is also well reflected in the behaviour of single cells in cat visual cortex (Duysens *et al.*, 1991). What are the psychophysical predictions which can be made on the basis of the present data? Since the optimum duration differs for the presently described tuned cells, it is not impossible that the amplitude of OFF responses contributes to the post-stimulus perceptual ability to discriminate stimulus durations above the critical duration. However, to our knowledge such perceptual ability has not yet been tested systematically.

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