The effect of moving textures on the responses of cells in the cat's dorsal lateral geniculate nucleus

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Abstract

Neurons in the dorsal lateral geniculate nucleus (dLGN) of the anaesthetized cat were activated with test stimuli (flashing spots, counterphased gratings and moving bars) in the presence of a moving background texture. Moving texture alone produced mild excitation, as a result of stimulation of the receptive field centre. Fast moving coarse textures were more effective than fine slow moving textures. The predominant effect of texture motion, however, was to reduce the response to all test stimuli displayed in the receptive field centre. The effects were similar for X- and Y-like cells. In the case of flashed spots, the sustained response was more strongly suppressed than the transient response. The direction of motion of the texture and differences in the relative motion of bar and texture had no influence on the degree of suppression. These observations are similar to effects seen on cat retinal ganglion cells, and are probably a form of gain control. Such suppressive effects are transmitted to the cortex and are likely to be evoked by large gratings, textures and by natural stimuli, all of which activate extensive regions of the receptive field surround.

Introduction

There is considerable evidence that neurons in the primary visual cortex of the cat are influenced by stimuli presented outside their 'classical' receptive field (e.g. Hammond & McKay, 1977, 1981; Allman *et al*., 1985; Gulyás *et al*., 1987; Sengpiel *et al*., 1997; Walker *et al*., 2000). These surround stimuli suppress the responses to optimal stimuli presented in the classical receptive field. The tuning of the responses to these suppressive stimuli is characteristically much broader than that elicited by classical stimuli, such as bars and edges. The suppressive effects are thought to arise from lateral inhibitory circuits within the cortex (Blakemore & Tobin, 1972; Sillito *et al*., 1980; Lauritzen *et al*., 2001).

The question arises as to whether earlier stages of processing also contribute to the suppression seen at cortical level. In the cat retina the effects reported are mainly excitatory. In the 'periphery effect', continuous movement of a remote stimulus facilitates responses of the classical receptive field (Levick *et al*., 1964; McIlwain, 1964; Ikeda & Wright, 1972; Fischer & Krüger, 1980; Passaglia *et al*., 2001), whereas in the 'shift effect', sudden displacements of remote stimuli evoke strong excitatory responses in ganglion cells (Krüger & Fischer, 1973; Noda & Adey, 1974; Barlow *et al*., 1977; Fischer & Krüger, 1980; Li *et al*., 1991; Felisberti & Derrington, 1999). Nevertheless, remote stimuli can also evoke suppressive effects at the level of the ganglion cells (Enroth-Cugell & Jakiela, 1980; Passaglia *et al*., 2001). These effects may underlie the phenomenon of saccadic suppression, which is also visible at cortical levels.

In contrast to the predominantly excitatory effects of remote stimulation on the responses of retinal ganglion cells, mainly suppressive effects have been reported in cat lateral geniculate neurons. When remote stimuli are suddenly shifted (Derrington & Felisberti, 1998; Felisberti & Derrington, 1999) the response to flashed spots presented to the classical receptive field is reduced. Eysel and colleagues (Eysel & Ringler, 1985; Eysel *et al*., 1986, 1987) were able to isolate an intrageniculate inhibitory mechanism evoked by stimulation of the peripheral field. However, both excitatory and inhibitory effects of remote stimuli were reported by Fischer & Krüger (1974). Continuous motion of a large static texture stimulus suppressed the response of cat dorsal lateral geniculate neurons (dLGN) to a bar moving across the classical receptive field (Gulyás *et al*., 1987). It is noteworthy that presented alone, a large moving texture stimulus excites both cortical (Hammond & McKay, 1975, 1977; Edelstyn & Hammond, 1988) and retinal neurons (Ahmed & Hammond, 1984), an effect resulting from activation of the classical receptive field centre.

Gulyás *et al*. (1987) concluded that the suppressive effects they observed in the cortex were largely a reflection of the prior effects transmitted by the dLGN. As this conclusion is of some consequence for views of long range suppressive interactions in the cortex, we have followed up their brief report using similar 'static' texture stimuli. We find that moving background textures have a predominantly suppressive effect on visually evoked responses in both X- and Y-like dLGN cells, probably resulting from retinal gain control mechanisms.

Materials and methods

Animal preparation

Six adult cats (2.5–6.6 kg) were used for this study. All experiments were carried out under authorization of the Cantonal Veterinary Authority of Zurich. After an initial subcutaneous injection of a mixture of 0.5 mg/kg xylazine (Rompun; Bayer, Leverkusen,

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Germany) and 10 mg/kg ketamine (Narketan; Chassot, Bern, Switzerland) the animals were surgically anaesthetized with a 30 : 70 mixture of O_2 : N_2O and halothane (1–2%) and additional intravenous (i.v.) Saffan (alphaxolone + alphadolone; Schering-Plough Animal Health, Welwyn Garden City, UK) if required. The femoral vein and artery and the trachea were cannulated. During recording Saffan was infused continuously intravenously (i.v.) at ~0.1–0.2 mL/kg/h) and the cats were ventilated on 30 : 70 O_2 : N_2O and ~0.5% halothane. After a loading dose of 40 mg/kg gallamine triethiodide (May & Baker, UK), a mixture of gallamine triethiodide (5 mg/kg/h) and d-tubocurarine chloride (0.5 mg/kg/h; Sigma-Aldrich Co., St. Louis, MO, USA) were infused continuously i.v. to maintain muscle relaxation. After muscle relaxants were given the cats were artificially ventilated with 30 : 70 O_2 : N_2O and supplementary halothane (~0.5%) and Saffan was administered in boluses i.v. The mixed anaesthetic dosages were calibrated to maintained the electroencephalogram (EEG) in a spindling pattern. Additional Saffan was injected i.v. if required, e.g. during durotomy. A second cannula in the femoral artery was used to measure the blood pressure. Electrocardiogram, EEG, heart rate, blood pressure, rectal temperature and expired CO_2 were recorded continuously. Atropine was applied to the eyes and neutral power gas permeable contact lenses were inserted. The eyes were refracted and test lenses applied to focus on the screen placed 57 cm from the eyes.

Recording

Tungsten-in-glass 12–15 μm exposed tip electrodes (manufactured by A. Ainsworth) were used to record neurons in the A-layers of the dLGN, within 5 ° of the estimated position of the area centralis. The receptive field of the cells was plotted by hand on the tangent screen using spots of light. A battery of tests was used to classify the cells as X- or Y-like cells (Friedlander *et al.*, 1981). The tests included responses to surround stimulation with large fast stimuli of opposite sign to the centre (light or dark disks, subtending about 30° of visual angle, moved by hand at ~100 °/s), search for a 'null' position of a counterphased grating (Hochstein & Shapley, 1976), and in three animals, measures of the response latency after electrical stimulation of the optic chiasm.

Visual stimulation

Three different stimuli were used: flashed spots; counterphased gratings; and moving bars. They were displayed on a screen (Tektronix 608 monitor, phosphor P31; USA) placed at a distance of 57 cm from the eyes. In all cases a stationary textured background was present and the stimuli were superimposed on it. The texture covered 10° × 10° of the visual field and consisted of random clusters of dark and light squares. It was generated by a dual channel velocity field and stereogram generator and controlled through the Picasso cathode ray tube Image Synthesizer and a computer (Innisfree, Cambridge, UK). The texture was either stationary or moving fast at 4.43 °/s or slowly at 0.54 °/s and in one of two orthogonal directions: upward or rightward with the bar and the grating, and rightward or downward with the spot. Two different texture grain sizes were used: coarse, which had pixels (small squares) about 0.2° in size; and fine texture, which had pixels of about 0.1° in size. Thus, to each cell, we showed eight different moving textures (two grain sizes + two velocities + two directions) plus two different stationary textures (two grain sizes), for a total of 10 different texture conditions. The luminance of the texture dark and white pixels was 3.6 and 16 cd m^{-2}, respectively, which give a contrast of 63% and a mean luminance of 9.8 cd m^{-2}. The contrast is defined as $c = 100 \times (L_{max} - L_{min})/(L_{max} + L_{min})$, where L_{max} and
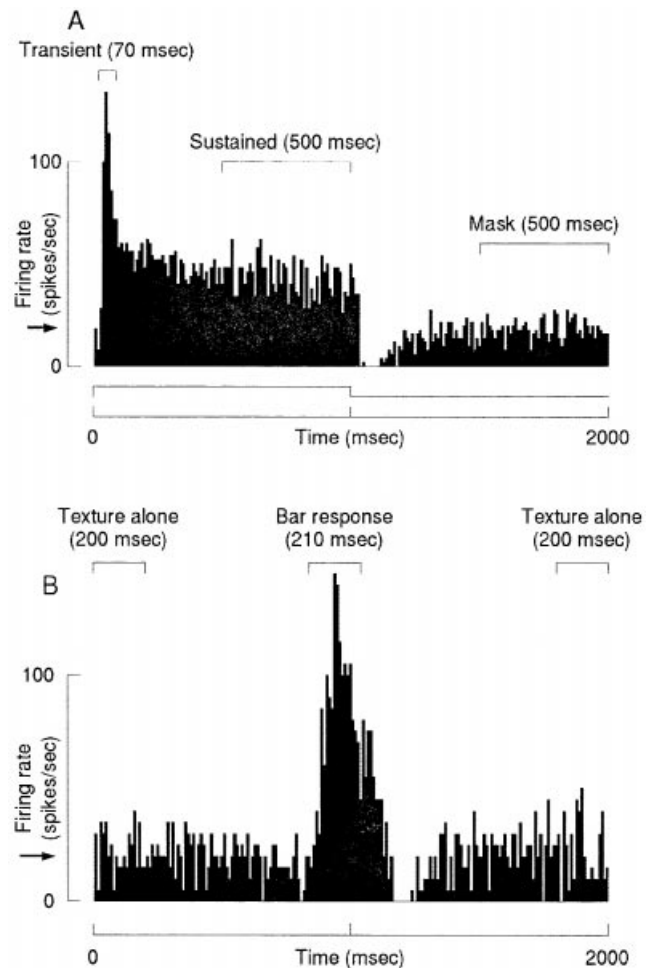

FIG. 1. Response to the spot and bar stimuli. (A) The peristimulus time histogram shows an example of a cell's response to a flashed spot. The transient and the sustained parts are shown with the time windows used to quantify them. The spot onset at time 0 is indicated by the upward deflection of the stimulus line (above the time axis) and its offset at time 1000 ms by a downward deflection. The last 500 ms of the response indicate the time window used to quantify the response when the receptive field centre was not stimulated by the texture (masked). (B) The peristimulus time histogram shows an example of a response to a bar sweeping across the receptive field. The response to the texture moving alone was measured at the beginning and at the end of each trial, when the bar was clearly outside the receptive field. The bar response itself was measured in a 210-ms window centred on the peak. The arrow on the left in A and B shows the mean spontaneous firing rate of the cell with stationary texture.

L_{min} are the maximal and the minimal luminance found in the texture, respectively.

Flashed spot

The spot was flashed on the centre of the receptive field. The spot size was chosen to optimize the response of the cell. A light spot with a luminance of 38.8 cd m^{-2} was used with ON centre cells and a dark spot with a luminance of 0.4 cd m^{-2} was flashed on OFF centre cells. When the test spot was off, the centre was illuminated with a spot of 12 cd m^{-2} luminance. Five series of 10 trials were presented, with 1.8 s between the series and 1 s between the trials. Thus the responses shown in Fig. 4 are the averages of 50 presentations. The segments used are shown in Fig. 1. The response to the spot going off decayed in less than 500 ms. The last 500 ms of the responses were used to

quantify the response when the receptive field centre was masked, but the texture moved over the receptive field surround and periphery (out to 10° from the receptive field centre).

Counterphased grating

The counterphased grating stimulus was a stationary sinewave grating whose contrast reversed sinusoidally. The grating was presented in a circular window covering only the centre of the receptive field. The spatial frequency and phase of the grating were adjusted to give the maximal response. Two temporal frequencies were used; either 1 Hz or 1.33 Hz. Twelve repetitions of 8 (temporal frequency = 1 Hz) or 6 (temporal frequency = 1.33 Hz) seconds stimulus were presented.

Moving bar

The third stimulus was a vertical bar moving back and forth across the receptive field. The width and the length of the bar were chosen to optimize the cell's response. Typically the bar width was about the same as the diameter of the hand plotted receptive field centre and its length about 2–3-times the diameter. The bar moved with a velocity of 2 °/s. We used dark bars for OFF centre cells, and light bars for ON centre cells. Five repetitions of four complete bar movements (forward + backward) were carried out for each texture condition. This means that the post stimulus histograms of Fig. 7 correspond to the mean value for 20 passages of the bar across the receptive field. A complete movement of the bar lasted for 4 s (2 s in each direction). The segments used for the analysis of the bar responses are described in Fig. 1.

Data analysis

Peristimulus time histograms

We plotted peristimulus time histograms (psth) for each stimulus condition, with a bin size of 10 ms. Different segments of the psth were analysed depending on the stimulus condition, as illustrated in Fig. 1. For flashed spots, the responses consisted of a transient and a sustained part. The peak of the transient was approximately 70 ms long, with a sharp onset and a slower decay. The transient response was thus quantified by taking the mean firing rate over a 70 ms period, beginning 20 ms before the peak. The sustained rate was measured during the 500 ms preceding the spot offset. For bars, responses were calculated from a time window of 210 ms, centred on the peak of the response.

Statistical tests

We used the t-test for two samples to analyse our data. For all stimuli, we compare the cells' mean response in the presence of a stationary texture to the mean response in the presence of a moving texture. The different samples of cells (for example comparison between X- and Y-like cells) and the different texture conditions (for example, comparison between fine and coarse textures) were also compared with the t-test.

Results

We recorded from a total of 50 cells, all located in the A laminae of the dLGN, as judged by eye dominance changes.

Response to texture alone

We were interested to discover the contributions of velocity and grain size to the response. We found that the full-field texture stimulus had only a small effect on the response of neurons ($n = 29$), regardless of velocity, grain size, direction of movement, or whether the neuron
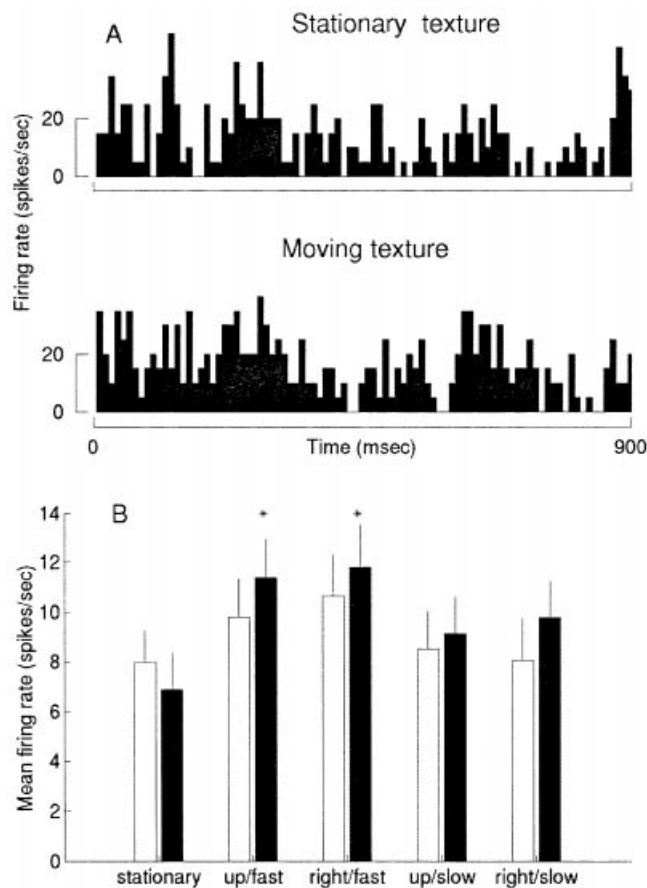

FIG. 2. (A) Response to the static texture alone moving over the whole receptive field. This cell's response increased slightly when the texture moved. The mean firing rate while the texture was stationary (top) was 14 spikes/s and 16 spikes/s when the texture moved (bottom). The cell was an OFF centre, Y-like cell. In this example, the texture was fine and moving up and fast. (B) Mean response of 29 cells tested with the texture moving alone. The error bars indicate the standard errors. The white and black bars correspond to the fine and the coarse texture, respectively. The asterisks indicate responses that were significantly different from the response to coarse, stationary textures (t-test for two samples, $P < 0.05$). The texture motion condition is given on the x-axis.

was X- or Y-like. The effect was almost always excitatory. An example of response to the texture alone is given in Fig. 2A. The top psth shows a Y-like cell's spontaneous activity to a stationary texture; the bottom psth shows the response to a moving texture. Figure 2B shows the average firing rate of the entire sample to the same stimulus. The fast-moving coarse textures were slightly more effective in driving the cells and gave significant increases of firing above the rate measured with stationary texture (t-test for two samples, $P < 0.05$). Figure 3A summarizes the results for the whole sample. The left column shows scatterplots of the responses to moving texture compared with the response to the stationary texture.

The right columns show histograms of the number of cells whose firing rate was increased (white bars), decreased (black bars), or unaffected (grey bars) by the moving texture. Coarse textures moving fast were most effective, and they significantly increased the firing rate of more than half of the sample.

Because of the strong effects of surround stimulation in the retina, we were interested to know how much the surround contributed to the small excitatory response evoked by the texture. We analysed the responses of the cells ($n = 50$) at the end of the flashed spot trials,

when the receptive field centre was masked by a spot of approximately the same mean luminance as the texture (see Fig. 1), so that the texture stimulated only the classical and remote surrounds. As shown in Figs 1 and 4, the cell responses returned to steady state level 500 ms after the spot offset. Figure 3B shows the results of this analysis. Masking the centre gave different results from the whole field stimulation. The majority of cells were unaffected by the texture moving in the surround (grey histograms in Fig. 3B; right column). A minority of cells were either suppressed or facilitated by the texture (black and white histograms in Fig. 3B; right column). Thus, the predominantly excitatory effect of the whole field stimulation (Fig. 3A) was mainly due to direct excitation of the centre itself. However, it should be emphasized that the significant changes in rate, above or below the spontaneous rate, amounted to a change of only a few spikes per second on average.

To examine the interactions between a stimulus presented to the classical receptive field and the moving texture background, we used a number of different stationary and moving stimuli. The simplest of these was a flashed spot placed on the receptive field centre.

Flashed spot

Fifty cells (15 Y-like, 35 X-like) were tested with flashed spots. With a stationary texture background, a flashed spot placed on the receptive centre gave the well-documented transient response in both X- and Y-like cells followed by a sustained tail in all but three 'lagged' cells (see Fig. 4).

Comparison between the transient and the sustained responses

The major effect of the moving textures was to suppress the response to the flashed spot. However, the transient and sustained components of the response were affected quite differently, as shown in Fig. 5. The transient part (Fig. 5A) was suppressed less by the moving texture than the sustained part (Fig. 5B). Although significant facilitation or suppression was seen for the transient component in some cells, the data tended to cluster along the diagonal (Fig. 5A). In contrast, for the sustained response, much more of the data lay beneath the diagonal (Fig. 5B). In all but one of the stimulation conditions (fine texture moving down and fast), the sustained response of most cells was suppressed by the moving texture. For some cells the suppression was up to 95% of the control value. In the transient part, the suppression rarely exceeded 50%. It was noticeable that when facilitation was seen it was for cells with low firing rates; cells with high firing rates were all suppressed. The distributions for X-like ($n = 35$) and Y-like ($n = 15$) cells were not significantly different (*t*-test for two samples, significance level < 0.01). The three X-like, 'lagged' cells had no transient response at stimulus onset, as

reported previously (Mastronarde, 1987a, b; Humphrey & Weller, 1988). However, their sustained responses were also significantly suppressed by moving texture (Fig. 4).

Counterphased grating

Because the major effect of the moving texture on the responses to the flashed spot seemed to be on the sustained component, we tested the effects of slowly varying stimuli presented to the receptive field
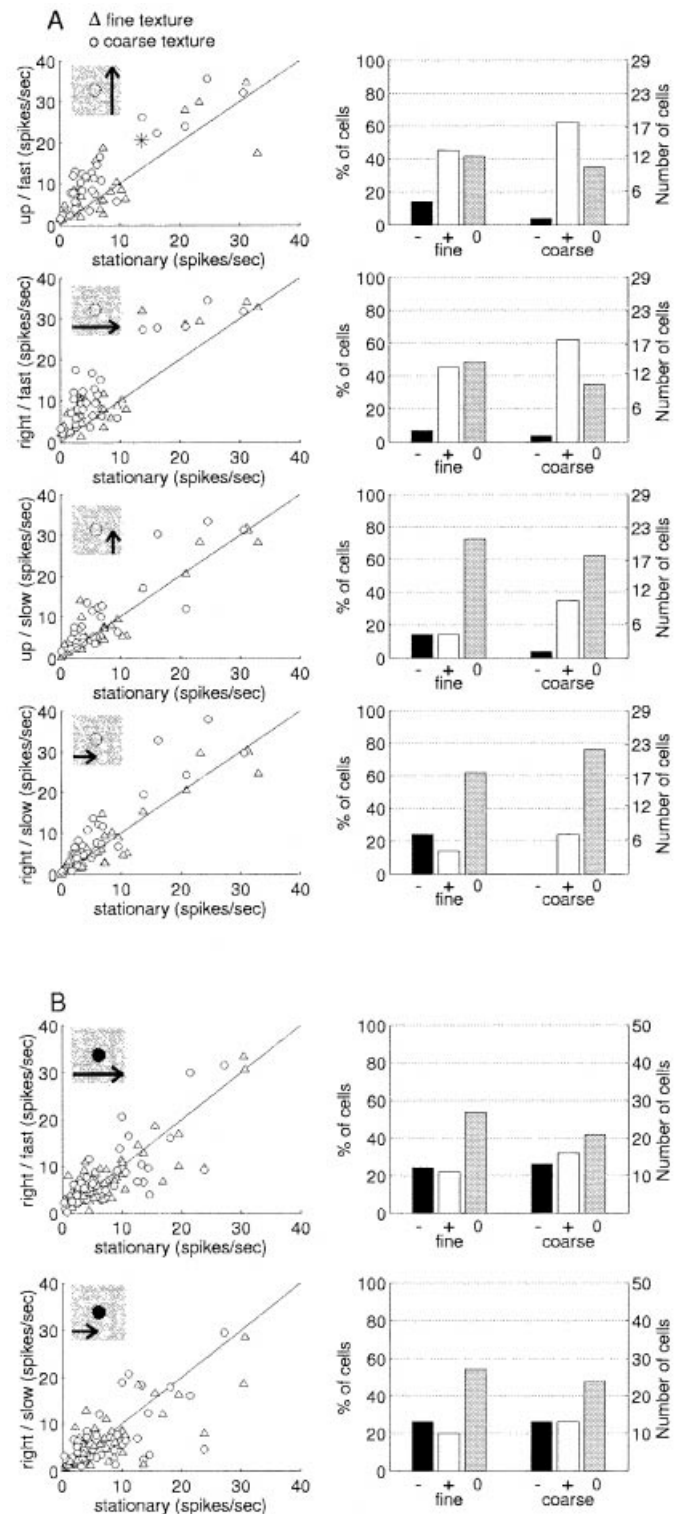

FIG. 3. Static texture moving alone. (A) The four plots correspond to different textures conditions, indicated on the *y*-axis. The responses to fine and coarse textures are represented with triangles and circles, respectively. The diagonal has a slope of one. The histograms on the right show the number (right axis) and the percentage (left axis) of cells that appear in the corresponding scatter plot. The black histograms represent significantly suppressed (–) cells, the white histograms significantly facilitated (+) cells and the grey histograms the cells that were not significantly affected (0), *t*-test for two samples with $P < 0.01$. The asterisk in the first scatter plot corresponds to the cell of Fig. 2A. (B) Responses to texture alone when the receptive field centre was masked. Only two texture conditions are shown here as the other conditions had similar effects. The icons on the top left corner of each scatterplot summarize the texture motion (long and short arrows for fast and slow moving textures, respectively). Similar icons will be used in Figs 5, 6B and 7B. The circle represents the receptive field centre (A) and the filled circle the mask (B), which was shown at the same mean luminance as the texture.
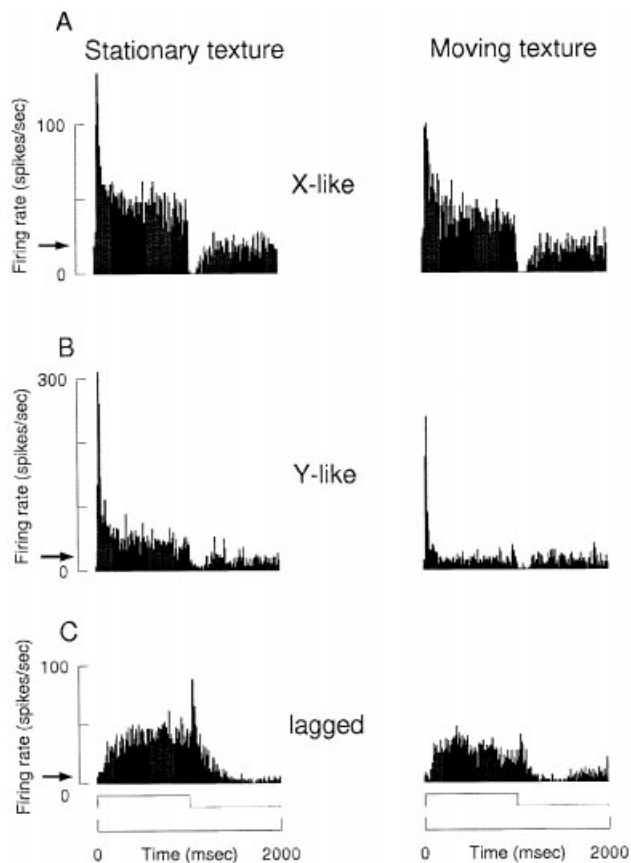
FIG. 4. (A) Responses of an OFF centre, X-like cell to a flashed spot and coarse, stationary texture (left) and coarse texture, moving fast downward (right). The mean firing rate fell from 86 to 83 spikes/s in the transient response and from 43 to 35 spikes/s in the sustained response when the texture moved. (B) Response of an OFF centre, Y-like cell (same cell as in Fig. 2A) to a flashed spot with a fine stationary texture (left) and a fine texture, moving fast downward. The mean firing rate fell from 150 to 89 spikes/s in the transient response and from 42 to 16 spikes/s in the sustained response when the texture moved. (C) Response of an OFF centre, lagged cell to a flashed spot with a fine stationary texture (left) and a fine texture, moving fast and downward. The mean firing rate fell from 42 to 24 spikes/s in the sustained response while the texture moved. The stimulus line shows onset (upward deflection) and offset (downward) of the spot. The arrow on the left shows the mean spontaneous firing rate of the cell with stationary texture.

centre. The stimulus was a circular patch of stationary sine wave grating, the contrast of which was sinusoidally counterphased. Figure 6A shows a particularly strong suppressive effect on the responses of an ON X-like neuron. The suppression lasted as long as the background texture moved. For analysis, the first 500 ms of each set of trials was discarded because of the transient response resulting from the grating onset. The mean firing rate was calculated from the 6 (temporal frequency = 1.33 Hz) or 8 s (temporal frequency = 1 Hz) duration of the presentation, minus the first 500 ms. Figure 6B shows the results for the eight cells we tested with these stimuli. The fast, coarse background texture was again the most effective in changing the response elicited by the centre stimulation. Where significant changes were seen, they were all suppressive (5 of 8), as anticipated from the effect on the sustained responses to flashed spots.

Moving bar

The third type of stimulation we used was a bar moving back and forth over the receptive field. The responses were not directional, so the responses to both directions of motion were pooled. An example of a cell's response to this stimulus is shown in Fig. 7A.

Altogether 27 cells were tested, and their responses are shown in Fig. 7B. Again, the moving textures suppressed the responses of a large proportion of the cells. When the texture was coarse and moving fast, the responses of most cells were suppressed relative to the stationary texture condition. Most cells were not affected by fine textures. Finally, very few cells showed a response increase for any of the moving texture conditions relative to the stationary texture. These results are similar qualitatively to those obtained with the flashed spot.

Discussion

The results show that moving backgrounds of static texture can strongly affect the responses to flashed, counterphased and moving stimuli presented to the classical receptive field. In combination with these stimuli, the predominant effect of the texture was to reduce the response. The moving texture presented alone, however, produced only a slight elevation in firing rate, which masking experiments showed to result largely from activation of the centre. This is consistent with the observations of Ahmed & Hammond (1984) who found that cat retinal ganglion cells were driven by moving whole field static textures, but did not respond when the centre was masked, or when the stimulus was presented outside the classical receptive field. Texture presented to the centre of the receptive field alone evoked excitation. The excitatory responses seen by Ahmed & Hammond (1984) were because of local changes in contrast produced by the individual grains (maximum size 0.12° diameter) of the texture, rather than to the whole texture motion itself. Thus, they found an inverse correlation between the strength of the response and the receptive field diameter. It is not surprising then that in our case, fast moving or coarse textures were more effective in driving the cells than slow moving or fine textures.

The only comparable study of the response of dLGN cells to texture is that of Gulyás et al. (1987), who used Hammond's static texture stimulus. They found that the response to moving bars was suppressed by background moving texture. They did not use different texture grain sizes and only moved the background in the same axis as the moving bar stimulus. However, their results, based on 19 cells, are qualitatively similar to ours, in that the effects were independent of the relative motion of the bar and background texture, and dependent on the velocity of the texture. Faster velocities produced more suppression. The lack of a directional effect and the lack of an effect of relative motion argue against the involvement of cortical feedback in the suppression. Indeed, the texture sensitive cortical neurons lie mainly in layer 5 (Wagner et al., 1981; Edelstyn & Hammond, 1988), and not in layer 6 where the cortical projection to the thalamus arises. Hence, the suppression is most likely generated in the retina and/or thalamus. As Gulyás et al. (1987) suggested, this offers the simplest explanation for the widespread suppressive effects they found in neurons of cortical area 17 that were exposed to moving background textures.

We explored the spatial source and the dynamics of the suppression. Masking the receptive field centre in the presence of moving texture revealed that the mild excitation seen for full field moving textures was generated from the centre. Textures presented to the classical surround and periphery did not suppress the ongoing spontaneous activity. Transient responses evoked by the onset of a light or dark spot on the receptive field centre were somewhat suppressed, but much more marked was the suppression of the
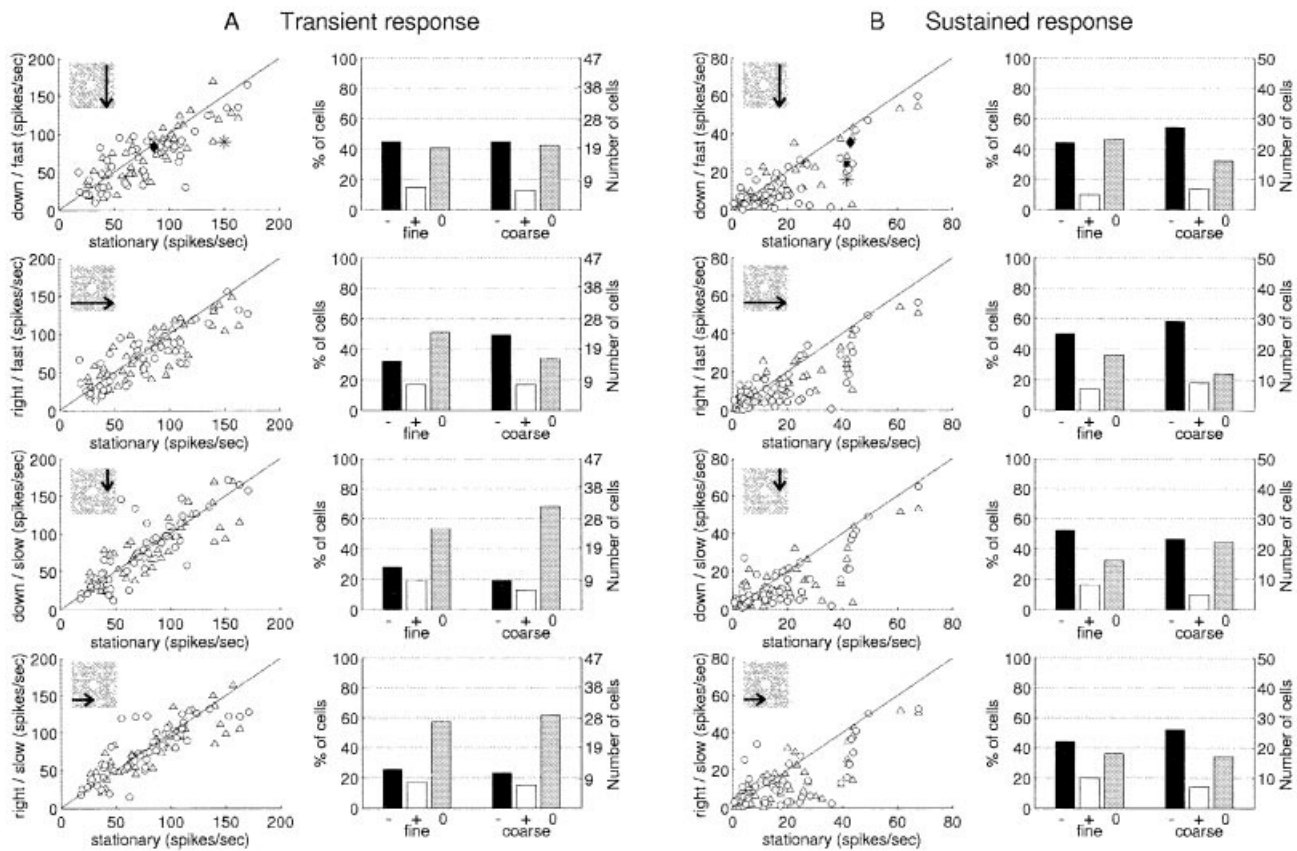
FIG. 5. Scatter plots and histograms for the transient (A) and the sustained (B) responses to a flashed spot. The asterisks in A and B show the Y-like cell, the black diamonds show the X-like cell, and the black squares the lagged cell of Fig. 4. The white dot in the icon (B) represents the flashed spot. Other symbols as in Fig. 3.

sustained response following the onset transient. The suppression in the transient and sustained responses was from activation of the surround, because the stimulus spot itself masked the texture from the centre. With the counterphased grating, we were able to avoid an onset transient and show that responses evoked in the centre were suppressed by the moving texture in the surround. Suppression was also seen in the lagged cells, which lacked the onset transient. The difference in effectiveness of the texture in suppressing sustained vs. transient responses could simply be in the strength of the excitatory synaptic conductances evoked by the onset of the stimulus, which overwhelm the opposing inhibitory conductances set up by the moving texture. Inhibition evoked by peripheral stimuli was discovered by Eysel and colleagues (Eysel & Ringler, 1985; Eysel *et al.*, 1986, 1987) who studied the shift effect in cat dLGN cells. They found that if the direct retinal input to dLGN cells was removed by focal retinal coagulation, the normally excitatory shift effect was replaced by a GABAergic mediated inhibitory response of very short latency. They conjectured that the source of this synaptic inhibition was the perigeniculate nucleus. They showed (Eysel *et al.*, 1987) that acetylcholine enhanced the late part of the shift response through disinhibition, but that in X-cells a late tonic component was only revealed under acetylcholine plus barbiturate anaesthesia (which we did not use). Although the stimuli we used most likely activated the intrathalamic inhibitory circuits, the fact that moving texture alone did not suppress the spontaneous activity when the centre was masked seems to indicate that the mechanism of suppression we studied, and which had its strongest effects on the sustained response, is somewhat

other than an intrathalamic synaptic inhibition evoked by the moving texture.

The dual effect of the moving texture – excitation and suppression – was seen best in the experiments with moving bars. As the texture moved, it stimulated the receptive field centre and evoked a mild increase in firing. As the bar moved from the periphery through the classical receptive field, the normal excitation evoked by the bar did not summate with the texture-evoked excitation, but instead the texture motion depressed the bar response. It is also notable that the texture motion did not obviously potentiate the inhibitory response produced either by the bar moving through the surround, or by the offset of the spot. Thus the suppression appears to be effected not through a traditional postsynaptic inhibition, but through changing the gain of the excitatory response.

This gain mechanism therefore extends through the surround and can be altered by the velocity and by the grain size of the texture. These spatial and temporal features are reminiscent of the contrast gain control mechanisms explored in cat retinal ganglion cells by Shapley & Victor (1979) and Enroth-Cugell & Jakiela (1980) who found that responses to a central test stimulus were suppressed by moving background stimuli. The stimuli used by Enroth-Cugell & Jakiela (1980) were either fine gratings or a rotating 'windmill' stimulus that produced no modulation of the activity when presented alone, but produced strong suppression when the centre was activated by flashed spots or bars. This is very similar to our findings. As with our data, they found that the sustained responses were more affected by background motion than the transient. Also, the suppression had a
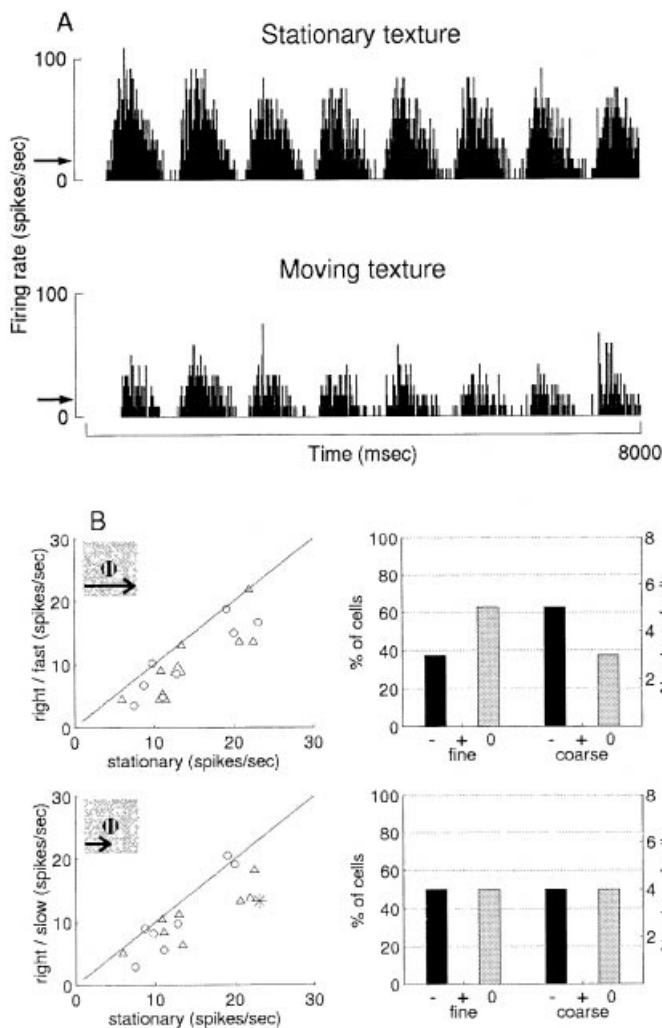
FIG. 6. (A) Response of an ON centre, X-like cell to the counterphased grating with a coarse, stationary texture (top) and the same texture, moving slowly to the right (bottom). The mean firing rate was 23 spikes/s when the texture was stationary and 13 spikes/s when it moved. The arrows on the left show the mean spontaneous firing rate of the cell with stationary texture. (B) Responses of cells to the counterphased grating. The asterisk shows the cell of A. Other symbols as in Fig. 3.
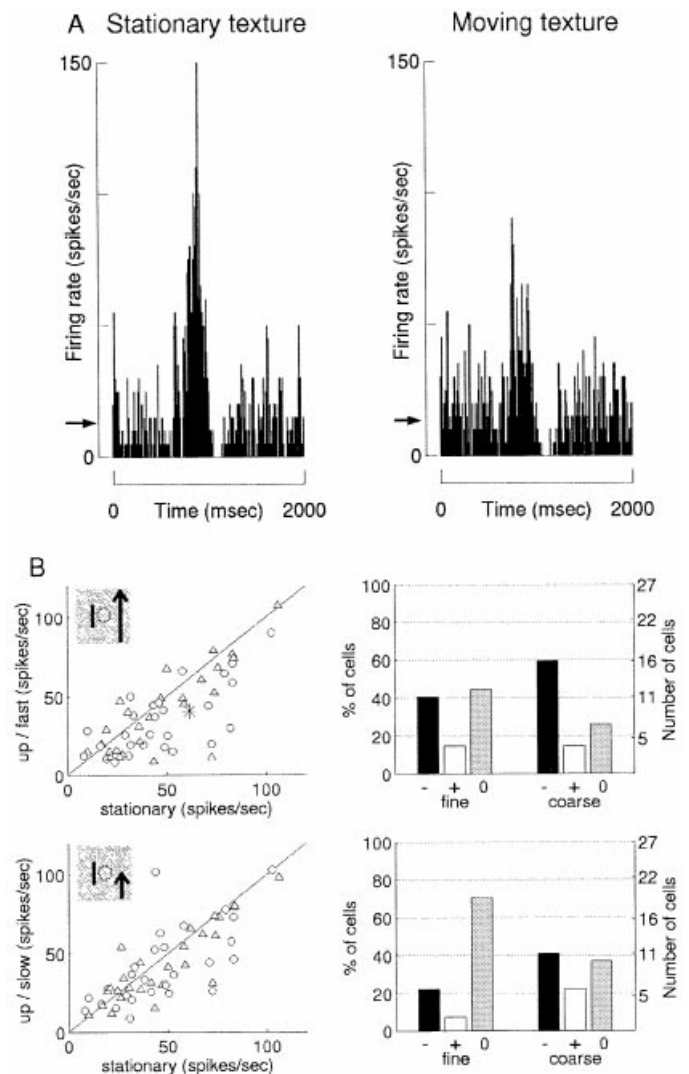

FIG. 7. (A) Response of an OFF centre, Y-like cell (same cell as in Fig. 2) to the moving bar superimposed on a stationary fine texture (left), and a fine texture moving fast and upward (right). The mean firing rate was 61 spikes/s with stationary texture and 41 spikes/s when the texture moved. The arrows on the left show the mean spontaneous firing rate of the cell with stationary texture. (B) Responses to moving bars. The asterisk shows the cell of A. Other symbols as in Fig. 3.

fast onset and remained as long as the background motion continued, as we found also in the dLGN. One difference is that they found that the suppression was stronger in Y than X cells, as was later confirmed by Freeman (1991), whereas in our sample of dLGN cells the effects on X and Y cells were not significantly different. Nevertheless, the striking similarities in most of the effects make it likely that the suppression in the dLGN neurons reflects that of a contrast gain control mechanism of the retinal ganglion cells. The mechanism is thought to act at the level of the inner plexiform layer and result from a steady depolarization of the amacrine cells (Werblin, 1972; Werblin & Copenhagen, 1974; Thibos & Werblin, 1978; Enroth-Cugell & Jakiela, 1980). One role of the contrast gain control is to reduce possible distortions that would be produced at high contrasts, thereby maintaining the ganglion cell output in a reasonable operating range.

The suppressive effects of moving background stimuli on the response to stimulation of the classical receptive field have important implications for studies of the nonclassical receptive field of cortical neurons. The interaction between classical and nonclassical receptive

fields is thought to be important for some perceptual properties, such as segregation of figure and ground (Lamme, 1995; Zipser et al., 1996; Akasaki et al. 2002). However, nonlinear mechanisms evoked by peripheral stimuli operating in the retina and additional inhibitory mechanisms in the dLGN (Eysel & Ringler, 1985; Eysel et al., 1986, 1987) make it clear that interpretations of the generally suppressive effects of stimuli present beyond the classical cortical receptive field cannot simply be accounted for by lateral inhibitory mechanisms at the cortical level (e.g. Blakemore & Tobin, 1972; Sillito, 1975; Morrone et al., 1987; see Fitzpatrick, 2000 for a review). Because current circuits in the cortex amplify the dLGN input, even relatively small changes in gain at the retinal and dLGN level might significantly alter the responses of cortex. In this respect, it will be important to look for signatures of cortical input in the suppressive mechanisms at the cortical level. As the stimuli used in visual cortical research shift from simple orientated bars to the more complex stimuli of natural scenes, it is evident that the influence of the contrast

gain control mechanisms we have observed here will be brought more and more into play and have increased influence on cortical responses.

Acknowledgements

Abbreviations

dLGN, dorsal lateral geniculate nucleus; ECG, electrocardiogram; EEG, electroencephalogram; psth, peristimulus time histogram; i.v., intravenous

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