Visual Neuroscience (1998), **15**, 875–880. Printed in the USA.

Peripheral shift reduces visual sensitivity in cat geniculate neurones

ANDREW M. DERRINGTON AND FATIMA FELISBERTI
Department of Psychology, University Park, Nottingham, NG7 2RD, UK

(RECEIVED December 1, 1997; ACCEPTED March 9, 1998)

Abstract

The sudden displacement of the retinal image during a saccade raises the visual threshold of human observers to foveal stimuli. The fall in visual sensitivity observed during this phenomenon, known as saccadic suppression, seems to occur very early in the visual processing chain. The lateral geniculate nucleus (LGN) is a likely locus for the multiple retinal and extraretinal interactions occurring during saccadic eye movements, therefore we used the responses of relay cells of adult cats to simulate a pychophysical experiment. We first measured the responses of X and Y relay cells (27 X and 13 Y) to central spots of optimal size and different contrasts. The spots were presented either alone or time locked with the rapid movement of a large, high-contrast peripheral pattern, referred to as *shift*. We measured the percentage of trials on which the relay cell fired more spikes when the spot (contrast: 0.03–1.0) was present than when it was absent. In experiments with human observers the task was to indicate, by a keypress, which of two otherwise identical temporal intervals contained the spot. The shift reduces the sensitivity (raises the contrast threshold) of neurones in the cat relay cells to brief, stationary targets presented to the receptive-field center. The suppression of visual sensitivity is significantly greater in Y cells than in X cells (average sensitivity ratios 5.6 ± 5.4 in Y cells, 1.59 ± 0.9 in X cells: $P < 0.001$, *U* test). The shift also reduces the sensitivity of human observers to the same target. This suggests that the LGN is a potential locus for the modulation of visual responses that leads to saccadic suppression.

Keywords: Shift effect, Cat LGN, Geniculate relay cells, Saccadic suppression, Visual sensitivity

Introduction

The fall in human visual sensitivity observed during saccades affects the magnocellular visual pathway. Luminance patterns and low spatial-frequency patterns are suppressed during saccades (Burr et al., 1982), whereas color and high spatial frequency patterns are not affected (Burr et al., 1994). In addition, the detectability of a briefly presented foveal target can be reduced by a saccadic-like movement or oscillation of a border or grating pattern, which may be several degrees away from the target (MacKay, 1970; Derrington, 1984; Volkmann, 1986).

The rise in visual thresholds during saccades seems to occur very early in the human visual processing chain. Retinal ganglion cells and relay cells of the lateral geniculate nucleus (LGN) of cats are known to be excited by saccades and by the movement of a large pattern presented far beyond the conventionally defined receptive field, a phenomenon generally referred to as the "periphery effect" or "shift effect" (McIlwain, 1966; Noda, 1975*b*; Fischer et al., 1996). It is something of a puzzle that the response of some relay cells to visual or electrical stimulation could also be suppressed by saccades (Noda & Adey, 1974; Noda, 1975*a*). Similarly, passive eye movements suppress visual responses of relay cells of cats in the early phase of a saccade (Lal & Friedlander, 1989, 1990).

The LGN with its large number of nonretinal synapses (Guillery, 1969; Montero, 1991; Wilson, 1993) is a likely locus for visual modulation of visual signals. Although the LGN is the main relay in the pathway from retina to striate cortex, neurones in the LGN are influenced by projections from other visual and visuomotor centers (Molotchnikoff et al., 1983; Wahle et al., 1994; Schmidt, 1996), which makes it an ideal locus for modulation of sensitivity by eye movements. It may be that the apparent disagreement between earlier experiments arises because saccades and pattern movements in conscious cats produce variable effects on the receptive-field center of LGN neurones due to uncontrolled stimulation generating additional direct excitatory or inhibitory effects.

To control this possibility and to examine how the remote visual stimulation that occurs during saccades affects the responses to real stimuli on the receptive field, we recorded the activity of LGN relay cells of anesthetised, paralyzed cats. We report how responses of relay cells to their optimal stimuli are modulated by saccade-like movements of a high-contrast peripheral pattern, referred to as *shift*.

Address correspondence and reprint requests to: Andrew M. Derrington, Department of Psychology, University Park, Nottingham, NG7 2RD, UK.

Material and methods

Physiological preparation

Experiments were carried out on five adult female cats anesthetised with intramuscular alphadalone/alphaxalone acetate (saffan; 1.5 ml/kg). After cannulation of a forelimb vein, Saffan was given intravenously as required. The trachea was cannulated and a craniotomy was performed to allow access to the right LGN. During recording the animal was paralyzed with pancuronium bromide (60 $\mu g \cdot kg^{-1} \cdot h$; i.v.) and artificially respired with N_2O (70%), O_2 (30%) and halothane (0.2–1%). Light anesthesia, assessed by continuous monitoring of the ECG, and EEG waveform, was maintained by adjusting the level of halothane. Respiration at 25 strokes/min was adjusted to keep end expiratory CO_2 levels between 4.5–5%, Body temperature was maintained close to 38°C by an electric blanket controlled by a subscapular thermistor. The pupils were dilated with atropine sulphate and phenylephrine hydrochloride was applied to retract the nictitating membranes. The eyes were protected by rigid gas-permeable contact lenses of zero added power. Refractive errors were assessed initially by ophthalmoscopic inspection and later by optimizing the response to high spatial-frequency gratings. They were corrected by miniature spectacle lenses placed in front of 3-mm artificial pupils. The *area centralis* and optic disk of each eye were plotted on a tangent screen using a reversing ophthalmoscope.

Visual stimulation and recording

Recordings of single-unit activity in the right LGN were obtained with glass-insulated tungsten electrodes. Recorded cells were established to be in laminae A and A1 either using standard histological techniques or from the sequence of ocular dominance changes during a penetration.

The visual stimuli (400 pixels square) were generated by a Macintosh computer using a NuVista graphics adapter and presented on a color CRT display monitor (Mitsubishi, model no. HL7955SKTKL) at 125-Hz frame rate. The display subtended 30 deg × 30 deg at the viewing distance of 0.57 m and had a luminance of 50 $cd \cdot m^{-2}$. A front-surfaced mirror was used to position the receptive field on the center of the display. The red, green, and blue inputs to the display were driven in parallel using a signal generated by combining three outputs from the graphics adapter to give high resolution of intensity (Pelli & Zhang, 1991). Stimulus luminances were set using a lookup table to compensate for the nonlinear relation between luminance and applied voltage of the display and to divide the available display luminance into 4096 equal steps. A digital signal processor housed in the computer sampled the amplified signal from the microelectrode, sorted action potential spikes according to their shape, and time-stamped them with a resolution of 100 μs.

Measuring detection thresholds

Human subjects

Two trained subjects (the authors) viewed the stimuli with their appropriate spectacle correction from 0.57 cm and fixating on a mark 10 deg above the point where the central target, or spot, was presented. The spot diameter was 1 deg. On each trial, two intervals 1 s long were marked by tone bursts and the spot was presented in the middle of one of them, chosen at random. The subject's task was to indicate, by a keypress, which interval had contained the spot.

Relay cells

Data were obtained using the same visual stimuli, except that the spot was adjusted in size to give the maximum response and so presumably had approximately the size of the cell receptive-field center. On half of the trials, chosen at random, the peripheral grating was turned on gradually during the first half of each observation interval, shifted rapidly through 0.5 cycles at the midpoint of the interval, and then turned off gradually during the second half of the interval. Data were analyzed as follows. For each condition, we plotted the percentage of trials on which the cell fired more spikes during the 80 ms of maximal activity when the spot was present than during a comparable period when it was absent, against the contrast of the spot. The contrasts of the spots were selected to cover the range of performance from near chance to near perfect.

Results

A bright spot presented for about 80 ms in the receptive-field center of an ON-center LGN relay cell elicits a brief burst of spikes above the baseline firing level (Fig. 1A). If a high-contrast grating pattern outside the classical receptive field is gradually turned on and then jumps rapidly rightward or leftward just as the spot is presented, the response to the spot is substantially reduced (Figs. 1E–1F). The shift stimulus can also suppress the firing rate of the cell even when no stimulus is being presented to the receptive-field center (Fig. 1B).

To minimize the possibility that the shift suppressed the response of the cell simply by scattering light onto an inhibitory region of the receptive field, we compared the effects of shift elicited by surround gratings that were negatives of each other; i.e. 180 deg out of phase and moved in opposite directions. Because these complementary stimuli were exact opposites of each other, they deliver equal and opposite luminance increments to the receptive field. Consequently, they would have equal and opposite effects on linear receptive field mechanisms. Fig. 1E shows the response of the neurone to the spot when the peripheral stimulus shifted to the right, while Fig. 1F shows the cell response to the spot combined with the complementary grating shifting in the opposite direction. Both shifts are similarly suppressive. For all the cells in our analysis, the effects produced by the two complementary gratings on the responses were similar indicating that linear receptive-field surround mechanisms were unlikely to be responsible for the suppressive effect of the grating.

In a number of cells, we also tested the effect of covering the shifting peripheral pattern in order to demonstrate that the suppressive effect arises within the visual system rather than by some interaction in the display monitor. Covering the peripheral pattern destroys its suppressive effect (Fig. 1C). The firing rate of the cell in response to the steady background luminance is plotted in Fig. 1D.

In our experiments the moving peripheral pattern was almost always inhibitory or neutral in its direct effect on the cell. Only one relay neurone, an X cell, out of 40 (27 X and 13 Y cells), was excited by the shift.

Our main aim was to see how the shift would affect the visual sensitivity of LGN neurones. To do this, we used the responses of each cell to simulate a pychophysical experiment as follows. On each trial, we counted the number of spikes fired by the cells

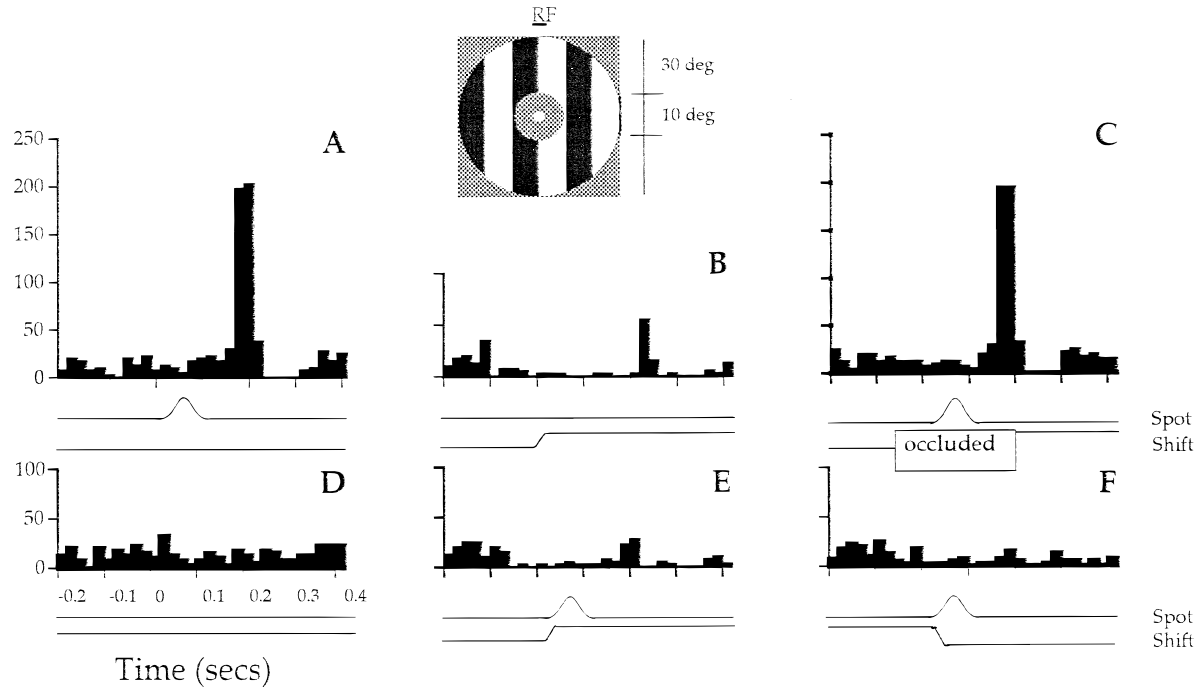

Fig. 1. Peri-stimulus time histograms (PSTHs, binwidth 20 ms, 50 repeats) showing the responses of an ON-center Y cell (9-deg eccentricity). The two traces underneath each histogram show the temporal luminance profile of the spot and the spatial phase of the peripheral grating. A: A bright spot (50 cd·m^{-2}, 2-deg diameter, 0.98 contrast) was presented for about 80 ms, 0.2 s after the start of the trace. The spot was turned on and off gradually as indicated by the marker trace. B: A peripheral grating (0.1 cycle/deg, 0.98 contrast) with a 30-deg surround diameter and at a distance of 5 deg from the center of the receptive field was turned on gradually over 0.5 s then jumped sideways by 5 deg and was turned off gradually. Apart from the spot, the central hole in the grating remained uniformly illuminated with the same mean luminance as the peripheral grating. A diagram of the stimulus configuration is given in the top of the figure. C: Control experiment in which the shifting grating is covered with an opaque occluder. D: Cell response to the background luminance alone. E: Cell response to the central spot from (**A)** combined with surround grating from (B). F: Same as (E) but the peripheral grating came on in the opposite phase and moved in the opposite direction.

during the 80-ms period in which its average response was greatest. These measurements were made for spots of different contrasts presented in the presence and in the absence of a shift.

For each condition, we plotted the percentage of trials on which the cell fired more spikes when the spot was present than when it was absent, against the contrast of the spot. Pairs of plots for an X cell and a Y cell are shown in Figs. 2A and 2C. The contrast at which performance on such a plot reaches 75% correct indicates the psychophysical threshold that would be recorded if performance depended only on the responses of that single neurone. The reciprocal of the threshold contrast is a measure of sensitivity. In some cells when the spot was presented alone, even the lowest contrast was above threshold. In those cells the lowest spot contrast was taken as an estimate of threshold. Data points from these cells are plotted differently in Fig. 3.

The shift raises the threshold of the Y relay cell whose data are plotted in Fig. 2A by about 0.7 log units and the X relay cell threshold by about 0.1 log unit (Fig. 2C). Figs. 2B and 2D show psychophysical measurements made on human subjects using the same stimuli presented at a location 10 deg below the fixation point. The shift raises the threshold by about 0.4 log units.

Fig. 3 shows how the shift affected the contrast threshold in each of the cells for which we were able to collect data. The threshold for the optimal central spot when its presentation coincided with a shift is plotted against the threshold for the same spot presented alone. All the data points fall either along the diagonal of the graph, indicating that the threshold for the central spot was not affected by shift, or above the diagonal, indicating that the threshold was raised by the shift. The threshold ratio (spot + shift)/(spot) of our sample of X cells was 1.6 ± 0.9 (arithmetic mean of individual cell threshold ratios ± S.D.) and of our sample of Y cells was 5.6 ± 5.4. A value of 1.0 would indicate no change in threshold. Thresholds of Y cells are increased by the shift substantially more than are X-cell thresholds (U test; $P < 0.001$).

Discussion

The results presented here are the first to show a fall in visual sensitivity of LGN relay cells during the shift of a high-contrast peripheral pattern presented outside the classical receptive field. This points to the LGN as a strong candidate for the locus of at least some of the visually mediated components of saccadic suppression.

Taken together, our findings suggest that the rise of contrast thresholds caused by the peripheral shift is likely to be mediated by purely visual mechanisms in Y-cell and (to a lesser extent) X-cell pathways no later than the LGN. The same pattern movements that elevate thresholds of cat relay cells also elevate human visual thresholds. The result is in line with the available evidence that both the shift effect (Derrington, 1984; Felisberti & Derrington, 1997) and saccades (Burr et al., 1994) reduce sensitivity to low spatial-frequency luminance targets.

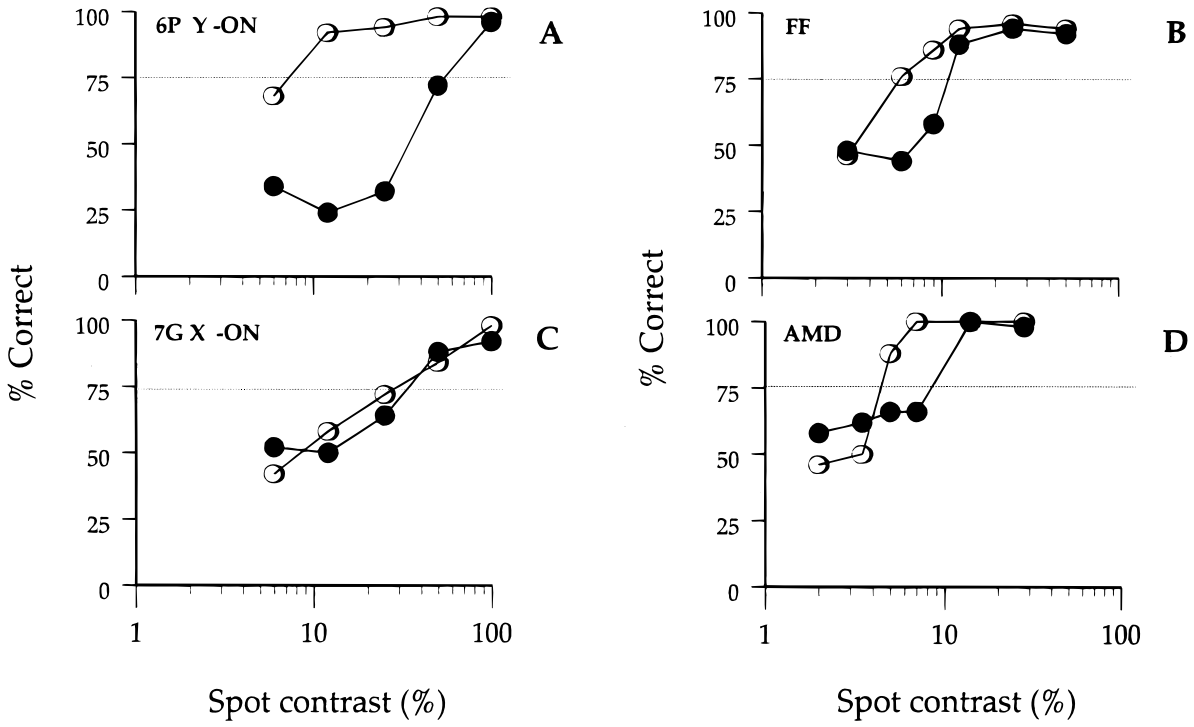

Fig. 2. Examples of effects of the sudden motion of a high-contrast peripheral grating on the performance of LGN relay neurones (A,C) and human observers (B,D) signalling the presence of a brief central spot. Each data point is based on 50 trials. A: The percentage of trials on which an ON-center Y geniculate cell (13-deg eccentricity) fired more spikes during the 80 ms of maximal activity, when the central spot was presented than during a 80-ms control period, is plotted against the contrast of the central spot. Open circles (○) show results when only the spot was displayed, filled circles (●) show results when a peripheral grating was gradually presented and suddenly moved through 5 deg just as the spot was presented. C: An ON-center X cell (8-deg eccentricity). B, D: Psychophysical measurements made on human subjects using the same shifting grating as in (A,C) and a target spot presented at a location 10 deg below the fixation point.

The shift stimulus which elicits the inhibitory effects described here is a smaller, intermittent version of the shift stimulus which causes transient excitation in retinal ganglion cells (Krüger & Fischer, 1973; Krüger et al., 1975). This makes it surprising that the shift effect is inhibitory rather than excitatory. We have checked that, on its own, the shift also increases the firing rate of the majority of retinal ganglion cells. We are testing a number of possible explanations for the difference in effect between the shift

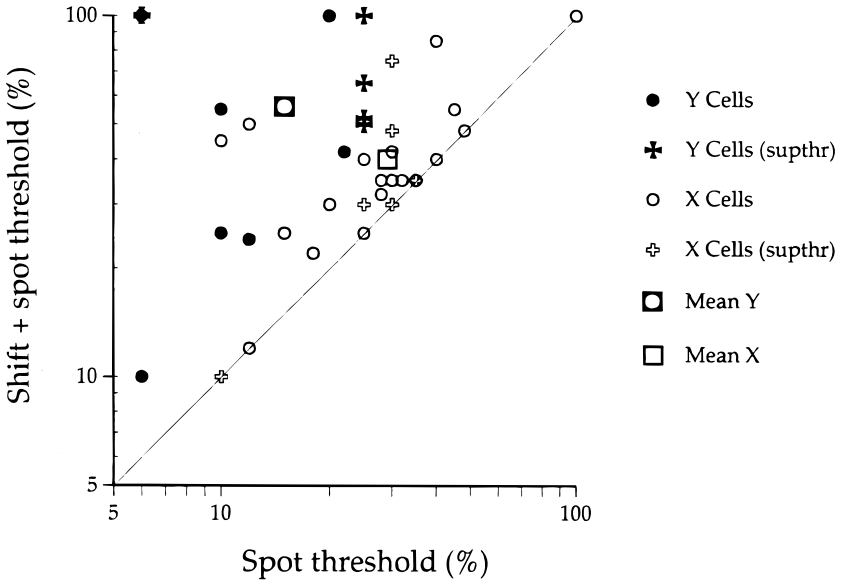

Fig. 3. Contrast thresholds of X and Y LGN neurones measured during the shift are plotted against the thresholds measured with no shift. Filled symbols (●) represent direct threshold values obtained in Y cells whereas (✚) represent the lowest suprathreshold contrast values in those Y cells for which the lowest contrast presented was still above threshold. Similarly, open symbols (○) represent threshold of X cells whereas (✚) represent the lowest suprathreshold contrast values in X cells. Note that the suprathreshold data give a conservative estimate of threshold elevations, because they only relate to the spot-alone presentation condition.

stimuli used in our experiments and the shift stimuli used in previous papers (Fischer et al., 1978; Derrington et al., 1979).

The geniculate suppression of visual signals by the shift could originate in retinal ganglion cells, where different effects of remote retinal stimulation have been observed. Enroth Cugell and Jakiela (1980) found that continuous motion of a pattern that surrounded the classical receptive field suppressed the responses to spots of light on the receptive-field center although a sudden movement of the same pattern was excitatory. Others have also found that single sudden movements of a peripheral shifting pattern produced excitatory responses in retinal ganglion cells (McIlwain, 1966; Krüger & Fischer, 1973). It seems likely that the balance between excitatory and inhibitory effects depends on spatial and temporal patterns of activity in retinal and geniculate processing networks (Troy, 1983; Essock et al., 1985). The inhibition we observe could be a manifestation of the retinal contrast gain control (Shapley & Victor, 1981) which has also been suggested as a mediator of the changes in human visual processing during saccades (Burr & Morrone, 1996). The net effect was that the motion of the peripheral pattern makes it more difficult to detect the response to stimuli on the receptive-field center.

Two general mechanisms have been proposed to account for the rise of visual thresholds caused by rapid motion of peripheral patterns (Valberg & Breitmeyer, 1980; Breitmeyer et al., 1980). The first mechanism involves an increase in the background noise. The second mechanism encompasses inhibitory effects exerted at low level in the visual pathway, presumably at the LGN. The inhibitory mechanism is supported by our present results.

Interestingly, the average rise in contrast threshold that occurs in human observers during a shift is comparable to that observed in the population of LGN neurones. Although comparisons between cats and primates have to be considered cautiously, the psychophysical results suggest that at least some components of saccadic suppression are concentrated on the magnocellular pathway of primates, which contains Y cells and spare the parvocellular pathway which does not (Kaplan & Shapley, 1982; Derrington & Lennie, 1984). This also suggests that at least some components of the saccadic suppression of visual sensitivity are produced by geniculate processing involving long-range visual interactions.

Whether or not extraretinal projections to the LGN from pretectal areas (Schweigart & Hoffmann, 1992; Funke & Eysel, 1995; Schmidt, 1996) and the visual cortex (Sillito et al., 1993) interact within the visual suppressive effects that we describe here, their projections to the LGN provide a route by which visuomotor commands could modulate visual signals even in the absence of visually generated saccadic input, as has been observed by Riggs and Manning (1982).

Acknowledgments

We are grateful to the Biotechnology and Biological Sciences Research Council and Wellcome Trust for financial support and to Peter Lennie for allowing us to use his computer program.

References

Breitmeyer, B., Valberg, A., Kurtenbach, W. & Neumeyer, C. (1980). The lateral effect of oscillation of peripheral luminance gratings on the foveal increment threshold. *Vision Research* **20**, 799–805.

Burr, D.C., Holt, J., Johnstone, J.R. & Ross, J. (1982). Selective depression of motion sensitivity during saccades. *Journal of Physiology* **333**, 1–16.

Burr, D.C. & Morrone, M.C. (1996). Temporal impulse response functions for luminance and color during saccades. *Vision Research* **36**, 2069–2078.

Burr, D.C., Morrone, M.C. & Ross, J. (1994). Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature* **371**, 511–513.

Derrington, A.M. & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. *Journal of Physiology* **357**, 219–240.

Derrington, A.M., Lennie, P. & Wright, M.J. (1979). The mechanism of peripherally evoked responses in retinal ganglion cells. *Journal of Physiology* **289**, 299–310.

Derrington, A.M. (1984). Spatial frequency selectivity of remote pattern masking. *Vision Research* **24**, 1965–1968.

Derrington, A.M. (1985). Interactions between receptive field and periphery in cat LGN cells. *Journal of Physiology* **358**, 14P.

Enroth-Cugell, C. & Jakiela, H.G. (1980). Suppression of cat retinal ganglion cell responses by moving patterns. *Journal of Physiology* **302**, 49–72.

Essock, E.A., Lehmkuhle, S., Frascella, J. & Enoch, J.M. (1985). Temporal modulation of the background affects the sensitization response of X- and Y-cells in the dLGN of cat. *Vision Research*, **25**, 1007–1019.

Felisberti, F. & Derrington, A.M. (1997). Virtual saccades suppresses visual signals in the cat LGN. *Investigative Ophthalmology and Visual Science* **38**, 1800.

Fischer, B., Barth, R. & Sternheim, C.E. (1978). Interaction of receptive field responses and shift-effect in cat retinal and geniculate neurons. *Experimental Brain Research* **31**, 235–248.

Fischer, B., Krüger, J. & Droll, W. (1975). Quantitative aspects of the shift-effect in cat retinal ganglion cells. *Brain Research* **83**, 391–403.

Fischer, W.H., Schmidt, M., Stuphorn, V. & Hoffmann, K.P. (1996). Response properties of relay cells in the A-laminae of the cats dorsal lateral geniculate nucleus after saccades. *Experimental Brain Research* **110**, 435–445.

Funke, K. & Eysel, U.T. (1995). Pharmacological inactivation of pretectal nuclei reveals different modulatory effects on retinogeniculate transmission by X-cells and Y-cells the cat. *Visual Neuroscience* **12**, 21–33.

Guillery, R.W. (1969). The organization of synaptic interconnections in the laminae of the dorsal lateral geniculate nucleus of the cat. *Zeitschrift für Zellforschung und Mikroskopische Anatomie* **96**, 1–38.

Kaplan, E., & Shapley, R.M. (1982). X and Y cells in the lateral geniculate nucleus of macaque monkeys. *Journal of Physiology* **330**, 125–144.

Krüger, J. & Fischer, B. (1973). Strong periphery effect in cat retinal ganglion cells. Excitatory responses in ON- and OFF-center neurones to single grid displacements. *Experimental Brain Research* **18**, 316–318.

Krüger, J., Fischer, B. & Barth, R. (1975). The shift-effect in retinal ganglion cells of the rhesus monkey. *Experimental Brain Research* **23**, 443–446.

Lal, R. & Friedlander, M.J. (1989). Gating of retinal transmission by afferent eye position and movement signals. *Science* **243**, 93–96.

Lal, R. & Friedlander, M.J. (1990). Effect of passive eye movement on retinogeniculate transmission in the cat. *Journal Neurophysiology* **63**, 523–538.

MacKay, D.M. (1970). Elevation of visual threshold by displacement of retinal image. *Nature* **225**, 90–92.

McIlwain, J.T. (1966). Some evidence concerning the physiological basis of the periphery effect in the cat's retina. *Experimental Brain Research* **1**, 265–271.

Molotchnikoff, S., Casanova, C., Laferriere, C. & Delaunais, D. (1983). The superior colliculus simultaneously modifies the responses of the lateral geniculate cells and of the oculomotor nuclei. *Brain Research Bulletin* **10**, 719–722.

Montero, V.M. (1991). A quantitative study of synaptic contacts on interneurons and relay cells of the cat lateral geniculate nucleus. *Experimental Brain Research* **86**, 257–270.

Noda, H. (1975*a*). Depression in the excitability of relay cells of lateral geniculate nucleus following saccadic eye movements in the cat. *Journal of Physiology* **249**, 87–102.

Noda, H. (1975*b*). Discharges of relay cells in lateral geniculate nucleus of the cat during spontaneous eye movements in light and darkness. *Journal of Physiology* **250**, 579–595.

Noda, H. & Adey, W.R. (1974). Retinal ganglion cells of the cat transfer information on saccadic eye movement and quick target motion. *Brain Research* **70**, 340–345.

Pelli, D.G. & Zhang, L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research* **31**, 1337–1350.

Riggs, L.A. & Manning, K.A. (1982). Saccadic suppression under conditions of whiteout. *Investigative Ophthalmology and Visual Science* **23**, 138–143.

Schmidt, M. (1996). Neurons in the cat pretectum that project to the dorsal lateral geniculate nucleus are activated during saccades. *Journal of Neurophysiology* **76**, 2907–2918.

Schweigart, G. & Hoffmann, K.-P. (1992). Pretectal jerk neuron activity during saccadic eye movements and visual stimulations in the cat. *Experimental Brain Research* **91**, 273–283.

Shapley, R.M. & Victor, J.D. (1981). How the contrast gain control modifies the frequency responses of cat retinal ganglion cells. *Journal of Physiology* **318**, 161–180.

Sillito, A.M., Cudeiro, J. & Murphy, P.C. (1993). Orientation sensitive elements in the corticofugal influence on center-surround interactions in the dorsal lateral geniculate nucleus. *Experimental Brain Research* **93**, 6–16.

Troy, J.B. (1983). Spatio-temporal interaction in neurones of the cat's dorsal lateral geniculate nucleus. *Journal of Physiology* **344**, 419–432.

Valberg, A. & Breitmeyer, B. (1980). The lateral effect of oscillation of peripheral luminance gratings: Test of various hypotheses. *Vision Research* **20**, 789–798.

Volkmann, F.C. (1986). Human visual suppression. *Vision Research* **26**, 1401–1416.

Wahle, P., Stuphorn, V., Schmidt, M. & Hoffmann, K.P. (1994). LGN-projecting neurons of the cats pretectum express glutamic-acid decarboxylase messensger-RNA. *European Journal of Neuroscience* **6**, 454–460.

Wilson, J.R. (1993). Circuitry of the dorsal lateral geniculate nucleus in the cat and monkey. *Acta Anatomica* **147**, 1.