



Temporal Impulse Response Functions for Luminance and Colour During Saccades

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Previous work has shown that during saccadic eye movements, contrast sensitivity for low spatial frequency patterns modulated in luminance is selectively reduced by up to one logarithmic unit, while high spatial frequency patterns, and equiluminant patterns of all spatial frequencies are not suppressed at all [Burr *et al.* (1994). *Nature*, 371, 511–513]. Here we study the temporal characteristics for sensitivity to luminance and chromatic patterns during saccades, using the two-pulse summation technique. Sensitivity was measured for detecting two successive pulses as a function of stimulus-onset asynchrony, during normal viewing and during saccades. Impulse response functions were estimated from the summation data, for all conditions. For equiluminance, the functions were monophasic during normal viewing and saccades. For luminance modulation, the impulse response functions were di-phasic in both normal viewing and saccades. However, during saccades the impulse responses were faster in normal viewing. This result is consistent with the suggestion that saccadic suppression is mediated by contrast gain control mechanisms, known to occur in M-cells but not P-cells. Copyright © 1996, Published by Elsevier Science Ltd.

Saccadic suppression Temporal impulse response Magnocellular and parvocellular pathways
 Contrast gain Equiluminance

INTRODUCTION

As we view the world, we make frequent saccades in order to foveate different areas of interest. Saccades are fast (200–800 deg/sec), but saccadic velocities are certainly not beyond the resolution limit of human vision. Contrast sensitivity for direction discrimination is as good at 800 deg/sec for optimal (very low) spatial frequencies as it is for gratings of higher spatial frequency moving at slower speeds (Burr & Ross, 1982). As natural images tend to have most energy at low spatial frequencies (Field, 1987), retinal image motion during saccades should be a powerful stimulus for motion detectors. Yet we are unaware of this motion, and certainly not disturbed by it.

At least a part of the reason why we are undisturbed by the image motion is that vision is actively suppressed during saccades. This idea was first suggested by Holt (1903), with supporting evidence coming later from Volkman (1962), Latour (1962), Zuber & Stark (1966) and many others. However, Burr *et al.* (1982) showed the suppression to be highly selective for spatial frequency, occurring only at low spatial frequencies, the frequencies

that would otherwise be seen to move during saccades. The results suggested that motion sensitivity was selectively suppressed during saccades, an idea that has received further support from Shiori & Cavanagh (1989) and Ilg & Hoffmann (1993).

More recently, Burr *et al.* (1994) have shown that saccadic suppression occurs only for patterns modulated in luminance contrast. Sensitivity to equiluminant patterns is unaffected or even enhanced during saccades, leading to the suggestion that the magnocellular (M) pathway is selectively suppressed during saccades, while the parvocellular (P) pathway retains its normal function, or is even enhanced. This result has been reinforced by measures of spectral sensitivity functions, shown to acquire the characteristic “Sloan notch” during saccades, the signature for chromatically opponent mechanisms (Uchikawa & Sato, 1995), and during eyeblinks (Ridder & Tomlinson, 1995). Furthermore, thresholds for noticing image displacement are typically higher during saccades than in normal viewing, but not at equiluminance (Bridgeman & Macknik, 1995).

Although there remains considerable debate about the roles of the M- and P-pathways, and the degree to which they can be considered separate [for reviews see Shapley (1990); Merigan & Maunsell (1993)], it is generally agreed that the M-pathway carries no useful colour information (Merigan, 1989). At equiluminance, therefore, colours should be discriminated by the P-pathway alone. The selective suppression of low spatial frequen-

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cies is also consistent with a reduction in M-activity, as the M-system seems more sensitive than the P-system at low spatial frequencies (e.g., Merigan & Maunsell, 1990; Merigan, 1991). There is also good evidence that the M-pathway provides a major input to the putative motion centres MT (middle temporal cortex) and MST (middle superior temporal cortex) (Maunsell *et al.*, 1990), so its suppression during saccades would explain the selective suppression of motion perception.

The M- and P-pathways differ in their temporal responses, with M-cells responding to gratings at higher temporal frequencies than P-cells (Derrington & Lennie, 1984; but see also Discussion). We have, therefore, investigated the temporal properties of vision during saccades. Temporal characteristics are most conveniently measured by steady-state techniques, with counterphased or drifting stimuli (e.g., DeLange, 1952; Robson, 1966). However, these techniques require that the stimulus presentations be extended over time, and could, therefore, not be accommodated within the duration of the saccade. Curtailing a visual stimulus, even without temporal modulation, has the effect of spreading the temporal frequency spectrum, so stimuli exposed briefly will have wide range of frequencies around the nominal temporal frequency. For example, a brief stationary stimulus (say 20 msec) has a nominal temporal frequency of 0 Hz, but in fact contains considerable energy over a range of much higher frequencies (at least up to the inverse of its duration, 50 Hz), and therefore is not suitable to isolate the activity of detectors of low temporal frequency preference.

An alternative technique is to estimate the impulse response function from summation data for detection of two pulses, as a function of pulse separation. This technique has been applied to a variety of stimuli, including large and small fields, gratings, and most recently, equiluminant gratings and patches (e.g., Ikeda, 1965, 1986; Roufs, 1972; Watson & Nachmias, 1977; Burr & Morrone, 1993; Eskew *et al.*, 1994). The general finding is that the impulse response for luminance-modulated stimuli of low spatial frequency content is biphasic, or possibly triphasic (Tyler, 1992). At higher spatial frequencies, the response becomes monophasic, and somewhat slower (Watson & Nachmias, 1977). The impulse response to colour is also monophasic or only weakly biphasic, and slow (Uchikawa & Ikeda, 1986; Swanson *et al.*, 1987; Burr & Morrone, 1993; Eskew *et al.*, 1994).

Here we apply a version of the two-pulse summation technique to investigate impulse response during saccades, for patterns modulated in luminance and chromatic contrast. Somewhat surprisingly, we find that during saccades the impulse response for luminance contrast remains biphasic, and is actually faster than that for normal viewing. The impulse response for equiluminant stimuli remains monophasic during saccades, and very similar to that of normal vision.

METHODS

The stimuli were generated by framestore (Cambridge Research Systems) and displayed on the face of a Mitsubishi colour monitor, with suitable luminance linearization, at 120 frames/sec and 600 lines/frame. The waveforms were horizontal sinusoidal gratings of 0.075 c/deg, when viewed from 30 cm. The stimulus was vignettted within a Gaussian patch with vertical and horizontal space constants 13 and 17 deg (so the observer saw a couple of bars of sinusoid). The monitor was surrounded by a 1 × 1 m screen, floodlit to the same mean luminance (10 cd/m²), and of similar colour.

The stimuli were modulated either in luminance or in chromaticity, by combining red and green sinusoidal gratings of identical contrast and luminance. The luminance stimuli were made by summing the red and green gratings in the same phase, and the chromatic stimuli by summing them in counter-phase (subtracting them). The CIE co-ordinates (*x* and *y*, respectively) were: red — 0.59, 0.35; green — 0.29, 0.57. Equiluminance was established by flicker photometry, adjusting the ratio of the red-to-green luminance to produce minimal flicker of the stimulus when modulated at 16 Hz. This value, typically near the V_λ equiluminant point was also checked during saccades, (evaluated as the colour mix to yield least sensitivity of a brief flash), and found not to change.

To measure summation, the gratings were briefly presented (8 msec) twice, either in the same or opposite polarity, with variable stimulus-onset asynchronies (SOAs). For measurements during saccades, the contrast of the second presentation was scaled so as to be equally detectable to the first, given the variation of suppression with time after saccade onset (measured independently).

Observers made large (20 deg) horizontal rightward saccades between two fixation points. Saccades were detected by electro-oculogram. Two silver electrodes were positioned near the outer canthus of each eye, and a third earth electrode on the forehead. The potentials were suitably amplified and filtered (Kronhite, 0.01–100 Hz, 6 dB/oct), and fed into the computer analogue to digital converter. On reaching a threshold voltage (the lowest that did not give excessive false alarms), the computer initiated the display on the next frame. Given a framerate of 120 Hz, there was 8 msec variation in the actual start time of the display. Both the electro-oculogram and the stimulus presentation were displayed on an oscilloscope, observed by one of the authors. If the stimulus did not occur early in the saccade, or was erroneously triggered before the saccade, the trial was aborted. In practice it was seldom necessary to abort trials. Since completing these experiments we have acquired a more sophisticated eye monitoring system, and can estimate that the stimuli tended to occur about 15–23 msec after the beginning of each saccade. The saccades lasted about 50 msec.

Thresholds were measured using two techniques. Thresholds were first measured with a yes–no staircase, in which the observer reported whether the stimulus appeared visible on each trial, by pressing the appropriate

response button. For these measurements the Gaussian patch of grating was always centred in the middle of the screen. For observer MCM additional measurements were also made with a two-alternative forced-choice procedure, where she reported whether the stimulus appeared above or below the centre of the screen (it was in fact centred 7 deg above or below fixation, at random). Both procedures gave very similar results, although more trials were needed for a reliable estimate from the forced-choice procedure. As the pattern of results was basically similar, we plot only those for the forced-choice procedure for observer MCM, and yes–no procedure for observer DCB.

For both procedures, the contrast of the stimuli was adjusted by the adaptive QUEST algorithm (Watson & Pelli, 1983), that estimated thresholds after each trial and placed the contrast of the following trial near that estimate. The final estimate of threshold was made by fitting the frequency-of-seeing functions (percent correct versus contrast) for all trials of a given condition with a cumulative Gaussian function:

$$p(c) = \gamma + \frac{1 - \gamma}{\sigma\sqrt{2\pi}} \int_{-\infty}^c \exp\left(-\frac{(c_T - k)^2}{2\sigma^2}\right) dk \quad (1)$$

where p is proportion correct, c and k log-contrast, c_T log-contrast at threshold, γ the probability of guessing the correct response (0.5 for forced-choice, 0 for yes–no) and σ the standard deviation of the Gaussian. The two free parameters, c_T and σ were determined by minimizing the residual mean square error between data and prediction, using the simplex algorithm (Nelder & Mead, 1964).

RESULTS

Timecourse of saccadic suppression

The two-pulse technique studies the interaction between two briefly presented pulses, as a function of their separation in time. A basic requirement is that the two should be equally detectable, when presented independently. However, as they necessarily occur at different delays after the onset of the saccade, they will be subject to different amounts of suppression, and, therefore, not equally detectable independently. As the evidence suggests that saccadic suppression occurs early in visual processing (Burr *et al.*, 1994), it probably precedes the site of interaction of the pulses. We therefore scaled the second pulse in contrast to equate it for sensitivity with the first.

To determine the amount by which the second pulse should be scaled, we first measured how the suppression varied with time after saccade onset. Figure 1 shows the results, as a function of time after the onset of the saccade (yes–no procedure for DCB, forced-choice for MCM). The dashed and dotted lines show the thresholds during free viewing, for luminance and colour, respectively. As previously shown by several researchers, there was a strong suppression of luminance stimuli for about 50 msec, which steadily decreased to reach the sensitivity for free viewing after about 150 msec. For equiluminant

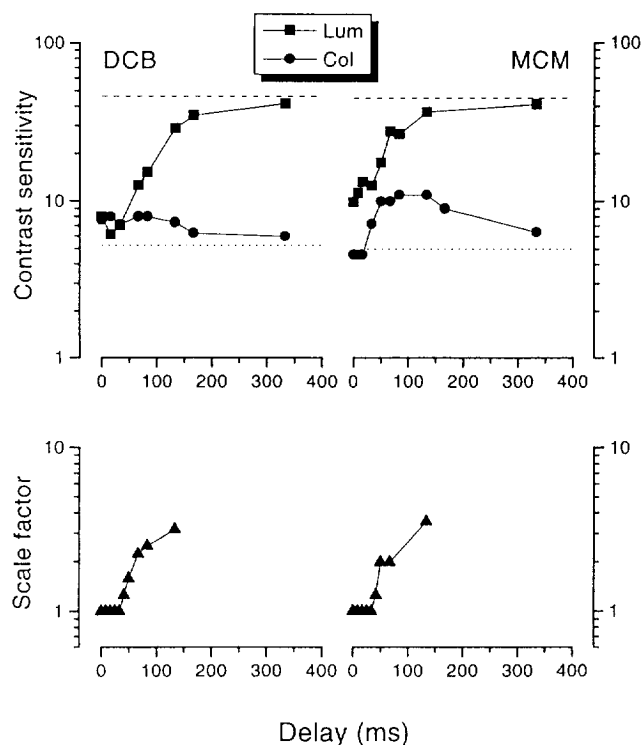


FIGURE 1. (Top) Contrast sensitivity for detecting a Gaussian-vignetted grating, as a function of duration after the onset of the saccade. For this and the following figures, squares refer to stimuli modulated in luminance, circles to equiluminant stimuli. For DCB, thresholds were measured with a yes–no procedure, for MCM with a forced-choice procedure requiring her to guess the location of the patch. Delay refers to the time after the saccade was triggered, on average 15–23 msec after the beginning of the saccade. (Bottom) The amount by which the second pulse in the summation experiments were scaled to equate for sensitivity. This was applied only for luminance modulated stimuli.

stimuli, there was no suppression during the saccade, but sensitivity was enhanced for a period after the saccade, particularly for observer MCM.

The experiment shown in Fig. 1 is very similar to that of our earlier report (Burr *et al.*, 1994; Fig. 2), with very similar results (except for an overall scaling factor). However, in the previous publication, the task was to *discriminate* the colour or the brightness of the flash. Here, observers were simply required to report whether the flash was seen, or to report the position of the flash (as these were the tasks used for the summation experiments). It is apparent that the detection task used here gives very similar results to the discrimination task of the previous report.

Figure 1 shows the actual values used to attenuate the second of the two pulses in the major experiment. The attenuation was applied only for the luminance condition, as it is clear that there is a rapid recovery from suppression, and that the suppression occurs early. For the first 42 msec, no correction was made, as the difference was slight, and measurements of interaction as a function of relative contrast showed maximum interaction with zero attenuation of the second pulse. For the equiluminant stimuli, there seems to be a postsaccadic

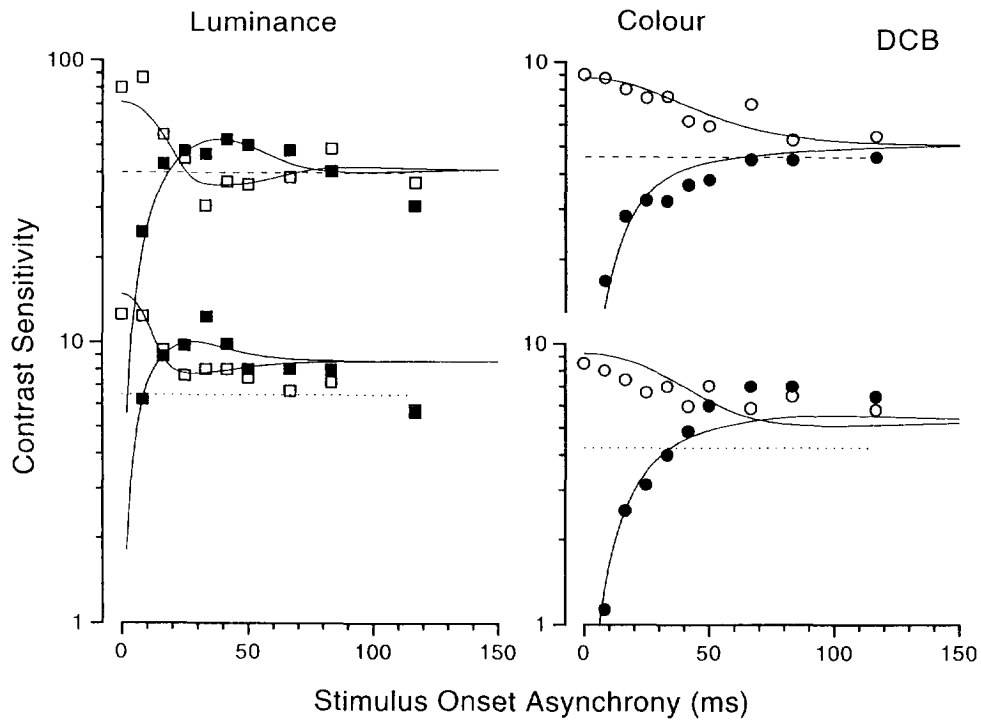


FIGURE 2. Contrast sensitivity for observer DB for detecting the double-pulse presentations as a function of stimulus-onset asynchrony (SOA), using the yes-no technique. Open symbols refer to the in-phase condition, solid symbols to the out-of-phase condition. As before, squares refer to luminance modulation, circles to chromatic modulation. The dashed and dotted lines show sensitivity for a single pulse, in normal and saccadic conditions, respectively. The continuous curves are the estimates of contrast sensitivity derived from the impulse response functions of Fig. 5.

enhancement of sensitivity, both for detection and for colour discrimination. However, because this enhancement is not yet well understood, may occur early or late in visual processing, and because of its variability in magnitude between observers, we did not introduce a

systematic attenuation of the second pulse for the major experiments. However, for observer MCM, some measurements were made with appropriate attenuation of the second pulse in the chromatic condition, to show that this did not substantially affect the results.

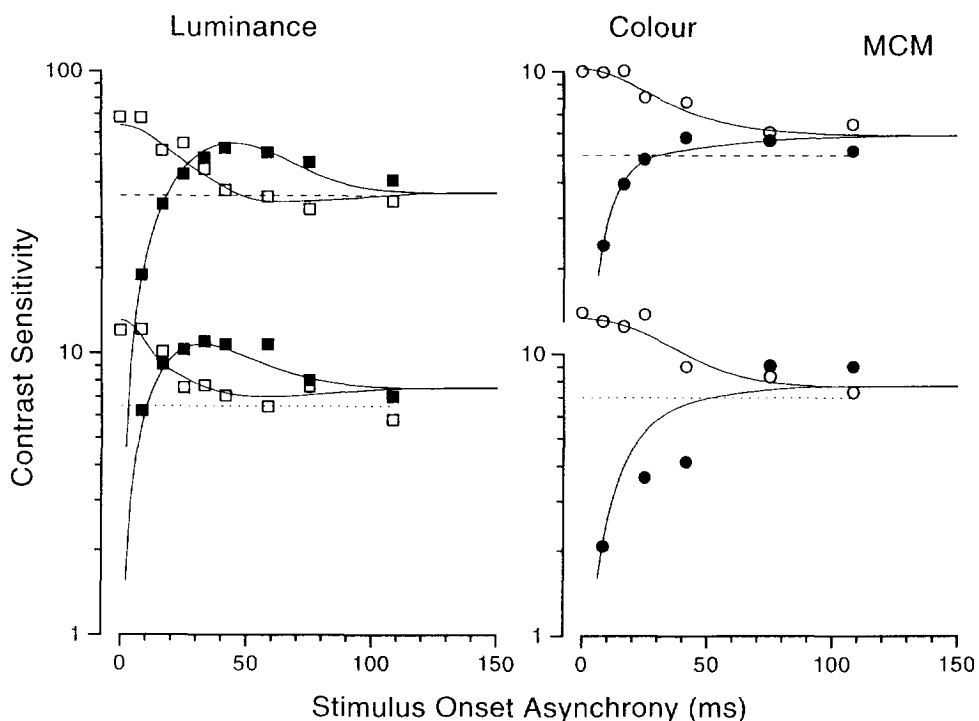


FIGURE 3. As for Fig. 2, for observer MCM, using the two-alternative forced-choice technique.

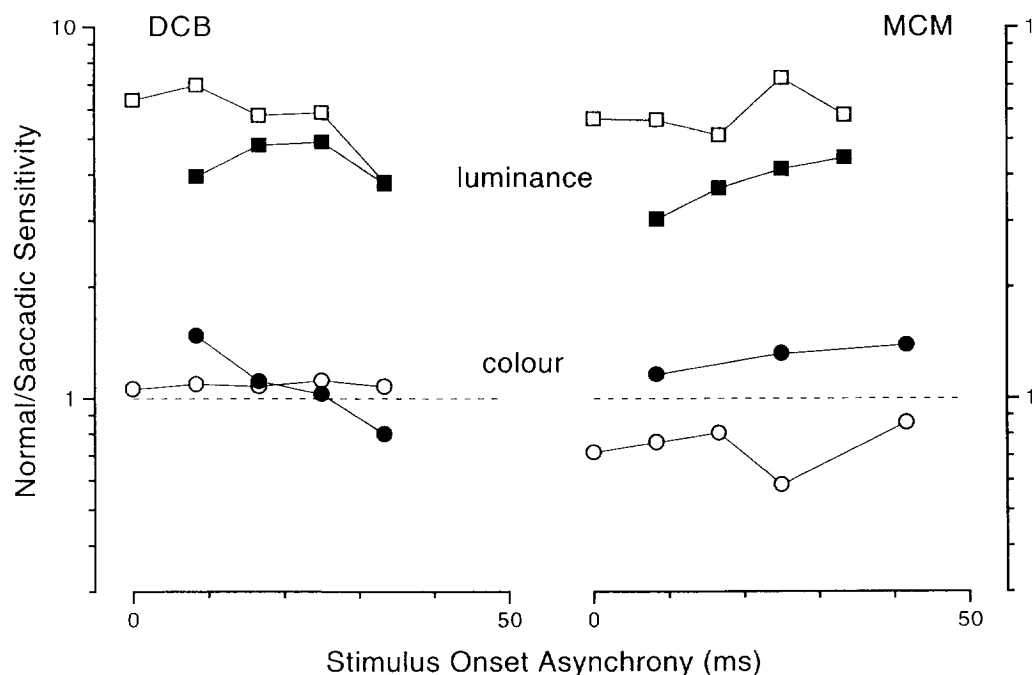


FIGURE 4. The amount of saccadic suppression, defined as the ratio of normal to saccadic sensitivity, as a function of stimulus onset asynchrony. Symbols as before: solid symbols, out-of-phase; open symbols, in-phase; squares, luminance; circles, colour.

Two-pulse summation

To estimate the impulse response, thresholds were measured for detecting pairs of briefly pulsed gratings presented successively at various stimulus–offset asynchronies. The two successive gratings were either in-phase or 180 deg out-of-phase. The observers simply reported whether the pattern was visible or not (DCB), or guessed in forced-choice whether it fell above or below the screen centre (MCM). Contrast sensitivity for the task was defined as the inverse of the contrast of the first pulse at threshold. For the luminance condition, the contrast of the second pulse was attenuated with respect to that of the first by the amount shown in Fig. 1.

Figures 2 and 3 show the results for the two observers. The left-hand curves refer to luminance stimuli and the right-hand curves to chromatic stimuli. Open squares show data from the in-phase summation condition, and solid circles for the out-of-phase condition. The upper curves show data for normal viewing, the lower curves during saccades. Note that the ordinate for the colour condition is repeated to separate sensitivities during normal and saccadic vision, as the thresholds were very similar. For the luminance modulation, however, there was strong suppression, so both results can be plotted on the same ordinate without confusion.

Consider first the data for luminance modulation. At very brief SOAs, Block's law applies, so stimuli of the same phase summate completely to yield a two-fold increase in sensitivity (compared with the single presentation). As the delay between pulse presentation was increased, summation became progressively less. For the out-of-phase stimuli, sensitivity first improved with SOA, then slowly returned to values near that for the single presentation. The results during saccades are qualitatively quite similar to those of normal viewing,

with a clear advantage for the out-of-phase condition for a range of SOAs. However, the out-of-phase curve crosses the in-phase curve earlier during saccades than in normal viewing, about 6 msec earlier for both observers. At the shortest possible SOA (8 msec, the duration of the frame), the sensitivity during saccades was about the same as for the single pulse, whereas that in normal viewing was attenuated by a factor of two (see also Fig. 4).

As reported before (Burr & Morrone, 1993), the summation results for equiluminant stimuli were quite different. For same-contrast stimuli, summation decreased gradually with SOA (more gradually than the luminance condition), reaching asymptote around 100 msec. For stimuli of opposite contrast, sensitivity increased gradually with SOA, again asymptoting around 100 msec, without the sharp peak evident in the curves for luminance stimuli. The results during saccades were very similar to those of normal viewing, both in absolute sensitivity and in the form of the curves. As mentioned earlier, most of the data were collected without attempting to equate the two pulses for visibility, compensating for the postsaccadic enhancement of equiluminant stimuli. However, a few measurements were made for observer MCM with the second pulse attenuated by a factor of two (indicated by triangles). These data were not used to calculate impulse response, but clearly do not deviate greatly from the measurements without attenuation.

Figure 4 plots the first few data points of Figs 2 and 3, as the ratio of normal to saccadic sensitivity, for the in-phase and out-of-phase conditions. For all these data points, both pulses occurred early during the saccade so no attenuation was applied to the second pulse. For the luminance condition (squares), there was strong suppres-

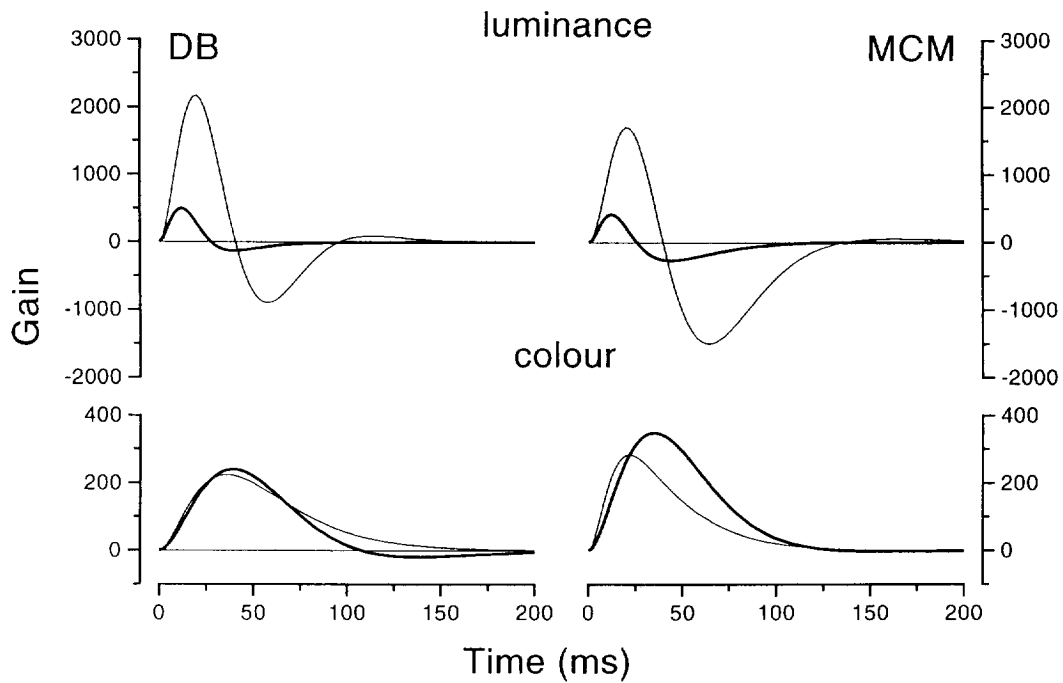


FIGURE 5. Impulse response functions derived from the sensitivity data of Figs 2 and 3, using the procedure described in the text. Top panel shows functions for luminance, bottom panel shows functions for colour. Thin curves show the results for normal viewing, thick curves during saccades.

sion for both conditions, but more for the in-phase than out-of-phase condition, particularly at the shorter SOA. Greater suppression for the in-phase than the out-of-phase condition during saccades means that the response of the system becomes less sustained. For the equiluminant gratings, there was very little suppression at all.

Impulse response functions

The data of Figs 2 and 3 can be used to derive estimates of impulse response during normal and saccadic viewing. For this, some simplifying assumptions are necessary. We assume small signal linearity, probability summation of the response over time, and that the impulse response

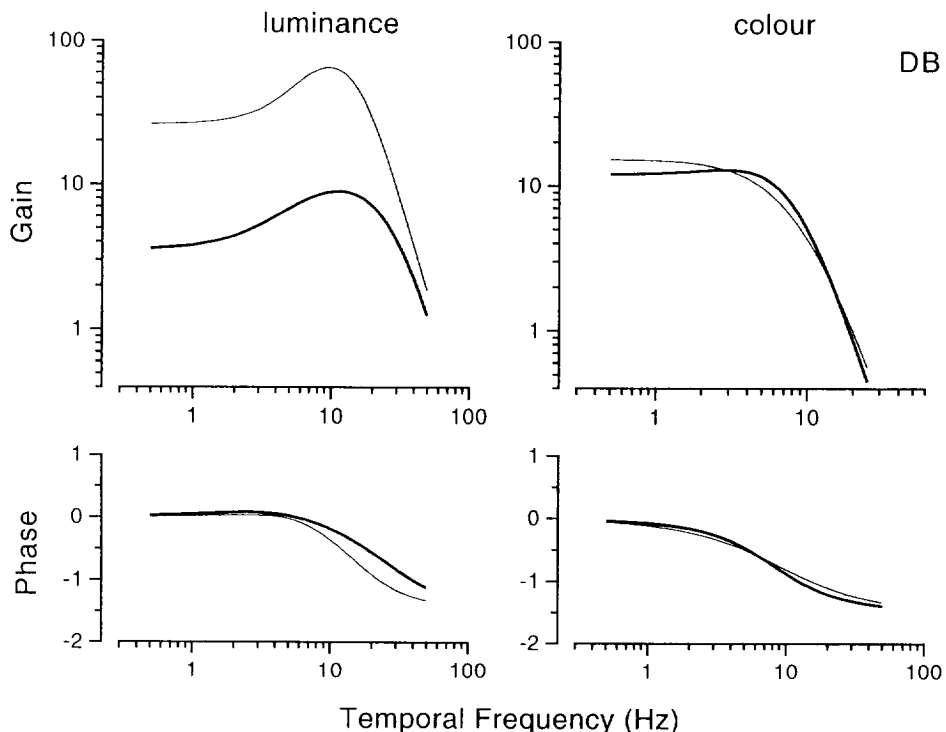


FIGURE 6. Temporal tuning functions during normal viewing (thin curves) and saccades (thick curves), obtained from Fourier transform of the impulse responses of Fig. 5, for subject DB.

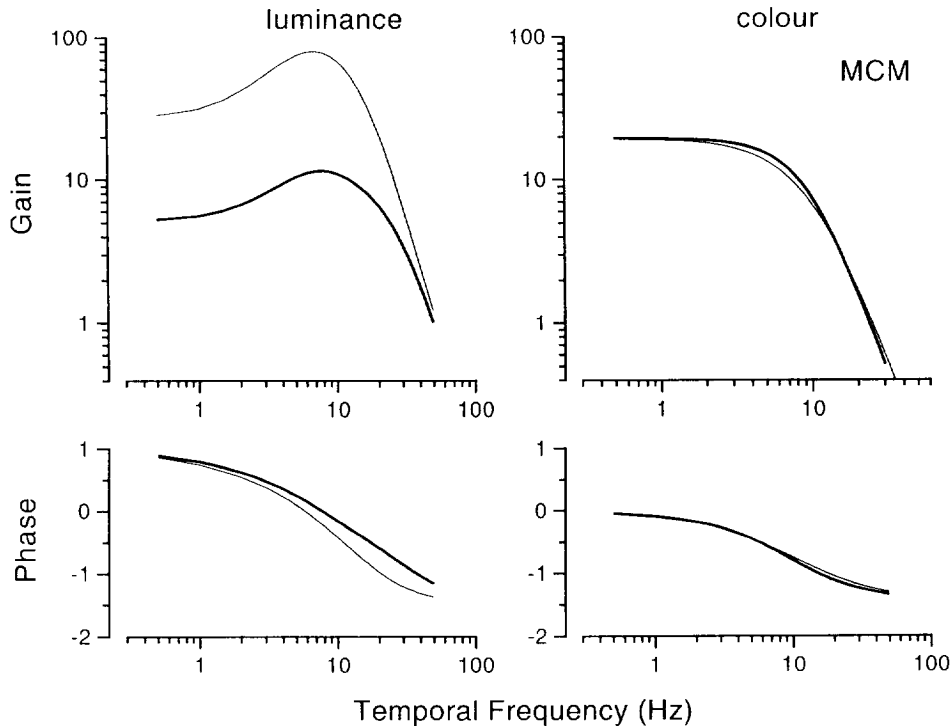


FIGURE 7. Temporal tuning functions during normal viewing (thin curves) and saccades (thick curves), obtained from Fourier transform of the impulse responses of Fig. 5 for subject MCM.

$I(t)$ can be well approximated by an exponentially damped, frequency modulated sinusoid, governed by four free parameters:

$$I(t) = a_0 H(t) t \sin\{2\pi[a_1 t(t+1)^{-a_2}]\} \exp(-a_3 t) \quad (2)$$

where t is time (in seconds). All parameters a_j were positive: a_0 governs the overall gain of the function, a_1 the fundamental frequency of oscillation, a_2 the modulation of frequency over time and a_3 the steepness of the exponential decay. $H(t)$ is the Heaviside function:

$$H(t) = 0, t < 0$$

$$H(t) = 1, t \geq 0$$

Put simply, equation (2) describes a function that commences at zero, oscillates over time with decreasing (or constant) frequency, while being progressively damped to zero. It is multiplied by t to ensure continuity of the function and its first derivative at $t=0$. With four free parameters, the function can take on a variety of forms, corresponding to many reasonably stable filter responses (see Burr & Morrone, 1993 for further details). From the assumption of small signal linearity, the visual response $R(t, \tau)$ to two stimuli of equal contrast presented briefly with temporal offset t will be given by the sum of the two impulse responses I :

$$R(t, \tau) = k[I(t) + sI(t + \tau)] \quad (3)$$

where $s = \pm 1$, depending on whether the gratings were in phase or not.

From the probability summation assumption, sensitivity $S(\tau)$ at SOA τ is determined by raising the absolute value of the function $R(t, \tau)$ to the power β , integrating over time, and raising the result to the power $1/\beta$, with β

taken as 3.5, consistent with measurements in the literature (see Pelli, 1985) and with those in this study.

$$S(\tau) = \left[\int |R(t, \tau)|^\beta dt \right]^{1/\beta} \quad (4)$$

As the integral of equation (4) is not easily solved analytically, we calculated the parameters for the impulse response functions with an iterative computer procedure (simplex: Nelder & Mead, 1964) that minimized the least squares error between data and predictions. The average deviation from the data (given by the square root of the average squared residual) was less than 1 dB (<0.05 log-units). The continuous curves of Figs 2 and 3 show the thresholds predicted from the impulse response. In all cases the curves follow the data reasonably well.

Figure 5 shows the hypothetical impulse response functions that produced the best fit of the data of Figs 2 and 3. The thin curves refer to normal viewing, the thick curves to saccades. For both normal and saccadic viewing, the luminance impulse response was biphasic, with a clear negative lobe following the initial positive response. However, the response during saccades is faster, with a time-to-peak of 12 msec rather than 20 msec in normal viewing (for both observers). The impulse response for chromatic contrast is monophasic in both normal and saccadic viewing, and very similar in form.

Temporal frequency tuning

For a linear system, the temporal frequency tuning function is directly related to the impulse response by means of the Fourier transform. As we have assumed an approximation of linearity near threshold, hypothetical

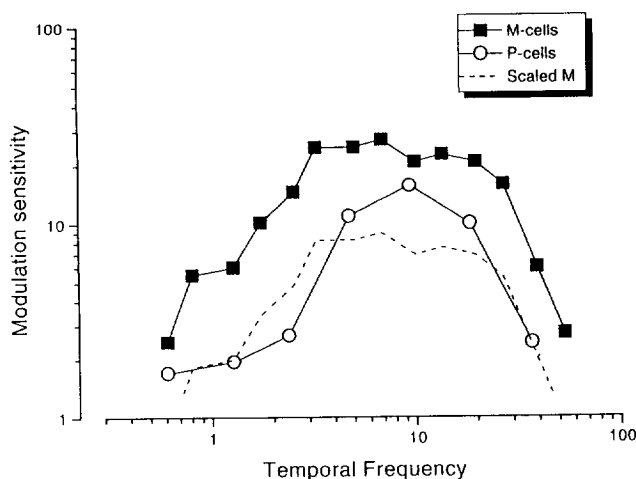


FIGURE 8. Modulation sensitivity to full-field luminance modulation at 200 Td for M-cells (squares) and P-cells (circles) of the macaque retina (modified with permission from Lee *et al.*, 1990, Fig. 3). The dashed line is the M-cell response scaled by a factor of 3 to equate for overall sensitivity. After scaling, the temporal sensitivity functions of the two classes of cells is very similar.

tuning functions for the luminance and colour visual systems can be obtained by taking the Fourier transform of the impulse response of Fig. 5. The results are shown in Figs 6 and 7. The amplitude curves for the luminance condition are band-pass functions for both saccadic and normal viewing. Although the overall gain is less during saccades than in normal viewing, the difference is progressively less at higher temporal frequencies. The phase spectra are also altered during the saccades, showing less decrease with temporal frequency (for luminance).

DISCUSSION

The major result of this paper is that during saccades, the temporal impulse response function to luminance modulated stimuli of low spatial frequency maintains its biphasic form, and becomes slightly faster than in normal viewing. The impulse response for equiluminant patterns remains fairly similar during saccades, both in amplitude and shape.

The calculation of the impulse response functions of Fig. 5, and their associated frequency response functions (Figs 6 and 7) required a few simplifying assumptions. However, the assumptions were not unreasonable, and are probably not crucial for the overall pattern of results. Small signal linearity is generally assumed in vision research, and probability summation has been well validated, both theoretically and empirically (e.g., Graham, 1977; Pelli, 1985). The particular formula of the impulse response [equation (2)] is somewhat arbitrary, but has sufficient free parameters to embrace a wide range of stable impulse responses. Indeed it is less constrictive than the more standard assumption of minimum phase (e.g., Swanson *et al.*, 1987). In any event, for normal viewing, the impulse responses predicted from equation (2) do not differ greatly from those assuming minimum phase (Burr & Morrone, 1993).

Furthermore, the previous work showed that impulse responses obtained from equation (2) predict well steady-state contrast sensitivity functions in normal viewing.

While the impulse response provides a complete description of the temporal characteristics during saccades, the fact that the saccadic suppression is less for high than for low temporal frequencies is actually clear from the raw summation data. Figure 4 shows that the suppression for the out-of-phase pulses is less than that for the in-phase pulses. Here, both pulses occur early in the saccade, so there is no need to scale the contrast of the second pulse to equate the two in visibility. These and the other data points of the figure, alone, provide clear and direct evidence that counterphased stimuli, with high temporal frequency content, are less suppressed during saccades than stationary stimuli, although the difference is, in fact, small for these types of stimuli.

The result for luminance modulated stimuli is perhaps counterintuitive, given the evidence for selective suppression of motion mechanisms during saccades (Burr *et al.*, 1982; Shiori & Cavanagh, 1989; Ilg & Hoffmann, 1993) and for selective suppression of the magnocellular pathway (Burr *et al.*, 1994). Both these lines of evidence might suggest that vision during saccades should be more sustained rather than more transient. Motion mechanisms presumably require a transient response (see, for example, Burr *et al.*, 1986), and magnocells (often called "phasic" cells) usually have more transient responses than parvo (or "tonic") cells (e.g., Derrington & Lennie, 1984). However, closer consideration shows that the two sets of results are not necessarily incompatible.

Although the temporal response of P-cells to gratings of optimal spatial frequency is slower than that to M-cells (e.g., Derrington & Lennie, 1984), consistent with behavioural measures of contrast sensitivity after selective magnocellular lesions (Merigan & Maunsell, 1993), the response of P-cells to luminance modulation of large uniform fields can be quite transient (e.g., Lee *et al.*, 1989, 1990). Figure 8 shows examples of the average contrast sensitivity of a sample of P- and M-cells of macaque monkey, as a function of temporal frequency. It is apparent that the threshold temporal response to luminance modulation of the two classes of cells is very similar, except for a difference in overall sensitivity (indicated by the dashed curve, showing the M-cell response scaled by a factor of 3). As the large flickering fields used by Lee *et al.* approximate well the very low frequencies used in this study, it is possible that under the conditions of this study, the response of the P-pathway could be even faster than that of the M-pathway.

An alternative explanation (that we favour) for the accelerated response during saccades is that detectors preferring low spatial frequencies are not totally suppressed, but continue to respond to low spatial frequency patterns with reduced sensitivity (Burr *et al.*, 1996). If this is the case, then the impulse response measured during saccades would reflect the response of the desensitized M-cells, leading to an interesting

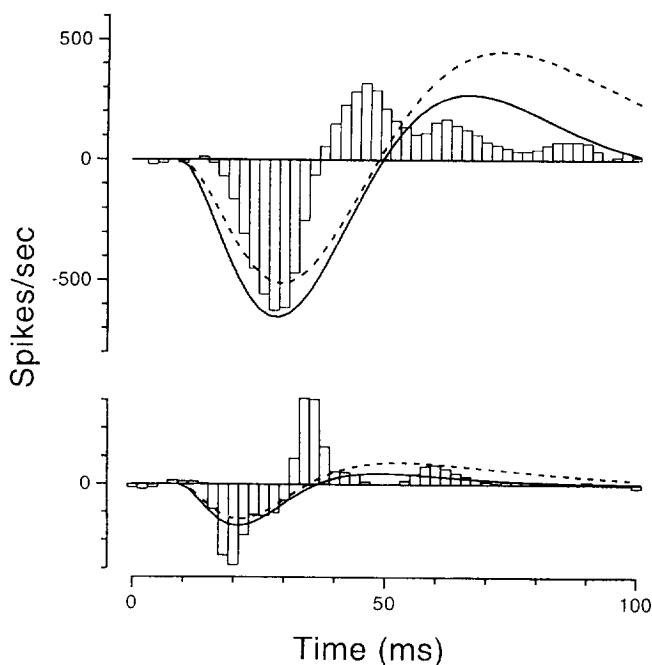


FIGURE 9. The lower histogram shows the response of an M-cell to stimulation by an 8 msec pulse of 100% contrast. The upper histogram is a prediction from its response to a 2 msec pulse of 50% contrast, assuming linearity (adapted with permission from Lee *et al.*, 1994, Fig. 3). It is clear that the response to the stronger stimulus is faster and of lower amplitude than the linear prediction. The continuous and dashed lines are the impulse response functions for DCB and MCM, respectively, shifted by an arbitrary 9 msec to align them with the monkey data (as the psychophysical impulse response estimates do not estimate absolute latency). There is a reasonable correspondence with time-to-peak estimates, consistent with the idea that the faster response during saccades results from the operation of gain mechanisms in the M-pathway. The second lobes of the functions do not coincide well, possibly because the monkey data were taken at much higher levels of illuminance in the monkey study, or possibly because the retinal functions do not predict well the shape of the psychophysical functions.

possibility: that saccadic suppression is achieved through gain control mechanisms.

At all levels of early vision, from the retina through to the cortex, many visual neurones have gain control that automatically decreases the response with increasing contrast, thereby increasing the dynamic range of the cell (eg Shapley & Victor, 1981; Ohzawa *et al.*, 1982; Schlar *et al.*, 1989). Interestingly, in the macaque retina and LGN, M-cells, but not P-cells show gain control (Purpura *et al.*, 1988; Bernadette *et al.*, 1992). All studies of gain control, in both cat and monkey (and invertebrates), have shown that the change in gain has a characteristic signature: attenuation is greatest at low temporal frequencies, leading to an acceleration of the impulse response (see Shapley & Victor, 1981 for a thorough discussion). Thus, if saccadic suppression in humans shared similar mechanisms to those regulating gain control, one would expect the parvocellular system to be spared from suppression (as observed previously), and that the residual response of the magnocellular system should be accelerated (as observed in this study).

Estimates of the effect of changing contrast by a factor

of eight (the amount we observe here for saccadic suppression) predict a decrease in time to peak of the temporal impulse response of M-cells by about 5–7 msec (Bernadette, 1994), slightly less than we observe here. However, this analysis is based on only the linear component of the contrast gain control (Shapley & Victor, 1981). We therefore compare our results with a more recent study of impulse response of M-cells, by Lee *et al.* (1994), that uses short pulsed stimuli, similar to ours. Figure 9 compares the impulse responses estimated in this study with those of a monkey M-cell. The lower histogram is the response to an 8 msec flash of 100% contrast. The upper histogram is that predicted from the response to a 2 msec flash of 50% contrast. If Bloch's law holds within this brief duration, then one stimulus has 8 times the energy of the other, corresponding to the difference in contrast of the flash under the conditions reported here. For comparison, the two psychophysical impulse response functions have been superimposed on those of the M-cell response, with an arbitrary displacement of 9 msec along the abscissa (as the psychophysical technique does not estimate absolute delay). The two sets of impulse responses are not dissimilar, particularly in the position of the first peak. Our results are also quantitatively consistent with the extensive data of gain changes in M-cells of Bernadette (1994). It is, therefore, quantitatively plausible that saccadic suppression is achieved by regulation of contrast gain. This would certainly be a very elegant and economical solution to the problem of saccadic suppression, making use of mechanisms already in place for other functions.

REFERENCES

- Bernadette, E. A. (1994). Functional dynamics of primate retinal ganglion cells. Ph.D. thesis, The Rockefeller University, New York.
- Bernadette, E. A., Kaplan, E. & Knight, B. W. (1992). Contrast gain control in the primate retina: P-cells are not X-like, some M cells are. *Visual Neuroscience*, 8, 483–486.
- Bridgeman, B. & Macknik, S. L. (1995). Saccadic suppression relies on luminance information. *Psychological Research*, in press.
- Burr, D. C., Baldassi, S., Marconi, B. & Morrone, M. C. (1996). Spatial frequency selectivity during saccadic eye movements revealed by masking. *Investigative Ophthalmology and Visual Science* (Suppl.) in press.
- Burr, D. C., Holt, J., Johnstone, J. R. & Ross, J. (1982). Selective depression of motion selectivity during saccades. *Journal of Physiology (London)*, 333, 1–15.
- Burr, D. C. & Morrone, M. C. (1993). Impulse response functions for chromatic and achromatic stimuli. *Journal of the Optical Society of America A*, 10, 1706–1713.
- Burr, D. C., Morrone, M. C. & Ross, J. (1994). Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature*, 371, 511–513.
- Burr, D. C. & Ross, J. (1982). Contrast sensitivity at high velocities. *Vision Research*, 23, 3567–3569.
- Burr, D. C., Ross, J. & Morrone, M. C. (1986). Seeing objects in motion. *Proceedings of the Royal Society (London)*, B227, 249–265.
- DeLange, H. (1952). Experiments on flicker and some calculations on an electrical analogue of the foveal systems. *Physica*, 18, 935–950.
- 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.
- Eskew, R. T., Stromeyer, C. F. & Kronauer, R. E. (1994). Temporal

- properties of the red-green chromatic mechanism. *Vision Research*, *34*, 3127–3137.
- Field, D. J. (1987). Relations between the statistics of natural images and the response properties of cortical cells. *Journal of the Optical Society of America*, *A4*, 2379–2394.
- Graham, N. (1977). Visual detection of aperiodic stimuli by probability summation among narrow band channels. *Vision Research*, *17*, 637–652.
- Holt, E. B. (1903). Eye movements and central anaesthesia. *Psychological Review*, *4*, 3–45.
- Ikeda, M. (1965). Temporal summation of positive and negative flashes in the visual system. *Journal of the Optical Society of America*, *55*, 1527–1534.
- Ikeda, M. (1986). Temporal impulse response. *Vision Research*, *26*, 1431–1440.
- Ilg, U. J. & Hoffmann, K. -P. (1993). Motion perception during saccades. *Vision Research*, *33*, 211–220.
- Latour, P. L. (1962). Visual threshold during eye movements. *Vision Research*, *2*, 261–262.
- Lee, B. B., Martin, P. R. & Valberg, A. (1989). Amplitude and phase of responses of macaque retinal ganglion cells to flickering stimuli. *Journal of Physiology (London)*, *414*, 245–263.
- Lee, B. B., Pokorny, J., Smith, V. & Kremers, J. (1994). Responses to pulses and sinusoids in macaque ganglion cells. *Vision Research*, *34*, 3081–3096.
- Lee, B. B., Pokorny, J., Smith, V., Martin, P. R. & Valberg, A. (1990). Luminance and chromatic modulation sensitivity of macaque ganglion cells and human observers. *Journal of the Optical Society of America*, *A7*, 2223–2236.
- Maunsell, J. H. R., Nearnly, T. A. & DePriest, D. D. (1990). Magnocellular and parvocellular contributions in the middle temporal visual area (MT) of the macaque monkey. *Journal of Neuroscience*, *10*, 3323–3334.
- Merigan, W. H. (1989). Chromatic and achromatic vision of macaques: role of the P pathway. *Journal of Neuroscience*, *9*, 776–783.
- Merigan, W. H. (1991). P & M pathway specialization in the macaque. In Valberg, A. & Lee, B. B. (Eds), *From pigments to perception*. New York: Plenum Press.
- Merigan, W. H. & Maunsell, J. H. R. (1990). Macaque vision after magnocellular lateral geniculate lesions. *Visual Neuroscience*, *5*, 347–352.
- Merigan, W. H. & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369–402.
- Nelder, J. A. & Mead, R. (1964). A simplex method for function minimization. *Computer Journal*, *7*, 308–313.
- Ohzawa, I., Schlar, G. & Freeman, R. D. (1982). Contrast gain control in the cat's visual cortex. *Nature*, *298*, 5871–5873.
- Pelli, D. G. (1985). On the relation between summation and facilitation. *Vision Research*, *27*, 119–123.
- Purpura, K., Kaplan, E. & Shapley, R. M. (1988). Background light and the contrast gain of primate P and M retinal ganglion cells. *Proceedings of the National Academy of Science USA*, *85*, 4534–4537.
- Ridder, W. H. & Tomlinson, A. (1995). Spectral characteristics of blink suppression in normal observers. *Vision Research*, *35*, 2569–2578.
- Robson, J. G. (1966). Spatial and temporal contrast sensitivity function of the visual system. *Journal of the Optical Society of America*, *56*, 1141–1142.
- Roufs, J. A. J. (1972). Dynamic properties of vision—II. Theoretical relationships between flicker and flash thresholds. *Vision Research*, *12*, 279–292.
- Schlar, G., Maunsell, J. H. R. & DePriest, D. D. (1989). Contrast adaptation in striate cortex of macaque. *Vision Research*, *29*, 747–755.
- Shapley, R. (1990). Visual sensitivity and parallel retinocortical channels. *Annual Review of Psychology*, *41*, 635–658.
- Shapley, R. M. & Victor, J. D. (1981). How the contrast gain control modifies the frequency responses of cat retinal ganglion cells. *Journal of Physiology (London)*, *318*, 161–179.
- Shiori, S. & Cavanagh, P. (1989). Saccadic suppression of low-level motion. *Vision Research*, *29*, 915–928.
- Swanson, W. H., Uneno, T., Smith, V. C. & Pokorny, J. (1987). Temporal modulation sensitivity and pulse-duration thresholds for chromatic and luminance perturbations. *Journal of the Optical Society of America*, *A4*, 1992–2005.
- Tyler, C. W. (1992). Psychophysical derivation of the impulse response through generation of ultrabrief responses: Complex inverse estimation without minimum-phase assumptions. *Journal of the Optical Society of America*, *A9*, 1025–1040.
- Uchikawa, K. & Ikeda, I. (1986). Temporal integration of chromatic double pulses for detection of equal-luminance wavelength changes. *Journal of the Optical Society of America*, *A3*, 2109–2115.
- Uchikawa, K. & Sato, M. (1995). Saccadic suppression to achromatic and chromatic responses measured by increment-threshold spectral sensitivity. *Journal of the Optical Society of America A*, *12*, 661–666.
- Volkman, F. (1962). Vision during voluntary saccadic eye movements. *Journal of the Optical Society of America*, *52*, 571–578.
- Watson, A. B. & Nachmias, J. (1977). Patterns of temporal interaction in the detection of gratings. *Vision Research*, *17*, 893–902.
- Watson, A. B. & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception and Psychophysics*, *33*, 113–120.
- Zuber, B. & Stark, L. (1966). Saccadic suppression: Elevation of visual threshold associated with saccadic eye movements. *Exploratory Neurology*, *16*, 65–79.

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