# A Comparison of Saccadic and Blink Suppression in Normal Observers

WILLIAM H. RIDDER III,*‡ ALAN TOMLINSON†

Recent research suggests that blink and saccadic suppression are produced by the same mechanism (Volkmann, 1986; Uchikawa & Sato, 1995; Ridder & Tomlinson, 1993, 1995). These studies demonstrated that blink and saccadic suppression have the same effect on various visual functions. However, none of these studies made a comparison of blink and saccadic suppression in the same individual. The purpose of this study was to compare the effects of blink and saccadic suppression on contrast sensitivity functions in the same subject. The effect of saccadic suppression on the contrast sensitivity function in three normal observers was determined. Employing a two-alternative, forced-choice technique, thresholds were measured for seven spatial frequencies. At each spatial frequency, the threshold was determined immediately following detection of a voluntary saccade. The magnitude of suppression was taken as the log ratio of the contrast sensitivities obtained while foveating the stimulus and those obtained during saccades. The magnitude of saccadic suppression was found to increase as the saccade amplitude increased and to be spatial-frequency dependent. Low spatial frequencies were suppressed more than high spatial frequencies. The blink suppression data have been measured previously (Ridder & Tomlinson, 1993). Saccadic and blink suppression were qualitatively similar. A vertical shift of the data brought the saccadic and blink suppression data into register. These results suggest that blink and saccadic suppression are produced by the same or similar mechanisms. © 1997 Elsevier Science Ltd

Blink suppression    Saccadic suppression    Contrast sensitivity

## INTRODUCTION

Volkmann (1986) defined visual suppression as the inability to perceive a visual stimulus under certain viewing conditions. She suggested that normal subjects demonstrate visual suppression as a means of selecting relevant information in a given scene. This implies that the mechanism of suppression serves to remove unnecessary or distracting visual information.

Suppression of vision has been demonstrated to be associated with several oculomotor activities. For example, visual suppression is observed with saccades, eyelid blinks, vergence movements, and the fast phase of nystagmus (Volkmann, 1986). If Volkmann's (1986) hypothesis is correct, then the form of suppression observed during these oculomotor activities can yield insights into the types of information the visual system considers relevant. In addition, information about any mechanism employed to produce suppression would be obtained.

Several investigators suggested, on the basis of similarities in the form of suppression, that the mechanism of suppression may be the same for eyelid blinks and saccades (Volkmann, 1986; Ridder & Tomlinson, 1993). These similarities include: (1) the magnitudes of blink and saccadic suppression are similar under appropriate viewing conditions (Volkmann, 1986; Stevenson et al., 1986); (2) the magnitudes of both blink and saccadic suppression increase as the amplitude of the movement increases (Mitrani et al., 1970; Stevenson et al., 1986); (3) suppression begins before these movements start (Beeler, 1967; Brooks & Fuchs, 1975; Volkmann et al., 1980; Manning et al., 1983; Manning, 1986; Volkmann, 1986); and (4) the effect of stimulus spatial frequency on blink and saccadic suppression is similar (Volkmann et al., 1978; Burr et al., 1982; Ridder & Tomlinson, 1993). Thus, several studies indicate that blink and saccadic suppression have similar characteristics which suggest that they may result from a single mechanism.

However, none of the above studies have measured blink and saccadic suppression in the same individual. This would allow for direct comparisons between blink and saccadic suppression to be made. The purpose of the present study was to determine if the form of suppression observed with saccades was similar to that produced by eyelid blinks in the same subjects.

*Southern California College of Optometry, 2575 Yorba Linda Blvd, Fullerton, CA 92831, U.S.A.
†Department of Vision Sciences, Glasgow Caledonian University, Glasgow, Scotland, U.K.
‡To whom all correspondence should be addressed [Tel (714) 449-7494; Fax (714) 879-9834; Email wridder@scco.edu].

OSCILLOSCOPE

13 degrees

26 degrees

FIXATION MARKER

OCCLUDER

INFRARED EYE MONITOR

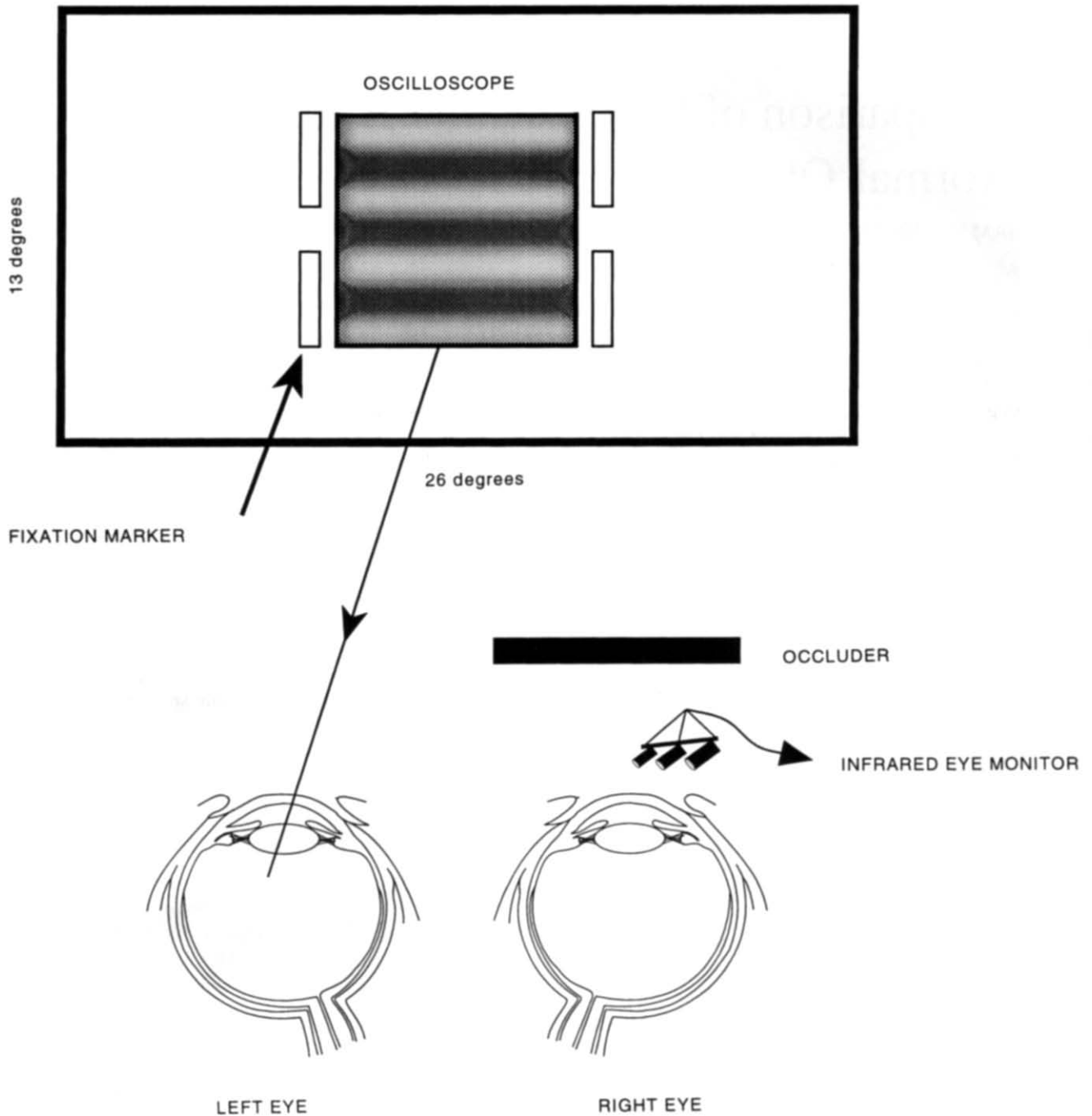LEFT EYE                                    RIGHT EYE

FIGURE 1. Experimental setup. The subject monocularly fixated the left marker before a trial began. Stimulus initiation was controlled by the subjects' saccades to the right fixation marker. The saccades were monitored by an infrared eye monitor.

## METHODS

### Subjects

Three observers were employed in this psychophysical study. They had 6/6, or better, corrected vision. Ocular health was normal for all subjects. One of the subjects was naïve with respect to the purpose of the experiment.

### Visual stimulus

A CRT Image Synthesizer (Innisfree, Picasso) produced the visual stimulus, a horizontally oriented, sine-wave grating (16.67 msec stimulus duration, square-wave onset and offset), on a Tektronix 608 monitor. The phosphor decay rate of the monitor was approximately 1 msec for a 90% contrast, square-wave grating (Ridder & Tomlinson, 1993). Since the contrast of the stimulus typically employed in this study was considerably less than 90%, the stimulus presentation time was not appreciably lengthened by the phosphor decay rate of the monitor. The Picasso was controlled by an 80386 computer. The stimulus screen subtended angles of 6.0 deg vertically by 8.0 deg horizontally at a 1.0 m viewing distance, and had a mean screen luminance of 22.3 cd/m$^2$. Surrounding the screen was a white board

(13 deg × 26 deg) with a luminance of 2.23 cd/m². The room luminance was approximately 1 cd/m².

## Technique

The subject viewed the stimulus under monocular conditions (Fig. 1). Seven spatial frequencies were used (0.5, 1.0, 2.0, 4.0, 6.0, 8.0 and 15.0 c/deg). Contrast was defined as $C = ((L_{max} - L_{min})/(L_{max} + L_{min}))$, where $L_{max}$ and $L_{min}$ are the maximum and minimum luminances of the sine-wave grating. A temporal, two-alternative, forced-choice paradigm combined with a self-paced method of limits was employed. Trials were only initiated when the experimenter had determined that the subject was fixating the center of the left fixation marker. The subject then initiated the trial by making a saccade to the center of the right fixation marker. Stimuli were presented as soon as the saccade was detected or during central viewing of the oscilloscope. During a single run the subject was required to correctly identify the time interval that contained the stimulus. Stimulus contrasts were increased by 0.1 log unit for incorrect responses and decreased by 0.1 log unit for two consecutive correct responses. The procedure continued for 11 reversals of stimulus contrast and the last nine reversals were averaged to give a threshold and standard deviation.

An Eye Trac Model 200 monitored the limbal position of the nonviewing eye. Processing times by the eye monitor and the computer were determined by feeding the eye monitor signal into a Tektronix model 5441 dual channel, storage oscilloscope. The signal to the Tektronix 608 oscilloscope from the computer was fed into the second channel of the storage oscilloscope. The time difference between the two signals was taken as the processing time. An average of ten trials gave a processing time of 20.2 msec (SD = 8.52). Thus, the stimulus was presented approximately 20 msec after the saccade was detected. Thresholds were obtained for saccades of 6, 12, 18, and 24 deg amplitudes. Different saccade amplitudes were obtained by moving the fixation targets to the appropriate distance while always keeping the oscilloscope centered.

## Blink suppression

The blink suppression data are taken from Ridder & Tomlinson (1993). The magnitude of blink suppression was taken as the difference between the contrast sensitivity data acquired at zero and 400 msec after detection of the blink. The 400 msec data were used because the suppression resulting from the blink had dissipated by this time. For this study, the sine-wave gratings were oriented vertically. Horizontal gratings were used with the saccades to minimize the effects of masking (minimal with horizontal saccades) and to more readily compare these data with previous studies of saccade suppression that used horizontal gratings. This difference in grating orientation should not have an effect on the results for two reasons. First, the control and experimental data are obtained with the same grating orientation for both blinks and saccades. Thus, we are
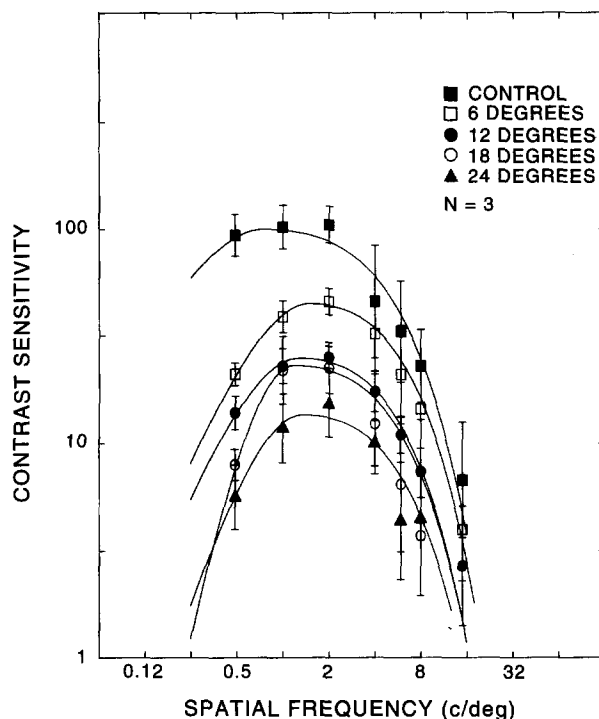


FIGURE 2. Contrast sensitivity functions obtained while foveating the stimulus and during saccades of various amplitudes. The mean and standard error is plotted for all the subjects. The solid curves drawn through the data are the best fitting functions derived from an iterative fitting routine. See text for further details and Table 1 for the results of the curve fits. Saccades resulted in a decrease in sensitivity that was dependent on the saccade amplitude and the stimulus spatial frequency.

comparing magnitudes of suppression which are independent of grating orientation and absolute contrast sensitivity. Second, contrast sensitivity for vertical and horizontal gratings are comparable so the grating orientation should have little effect (Campbell et al., 1966; Berkeley et al., 1975; Camisa et al., 1977; Williams et al., 1981). Thus, the difference in grating orientation for the blinks and the saccades should have a minimal effect on the results.

## RESULTS

The contrast sensitivity functions (mean ± SE) for the three subjects are displayed in Fig. 2. Spatial frequency is plotted on the horizontal axis and contrast sensitivity on the vertical axis. The control data (filled squares) were obtained with the subjects centrally fixating the oscilloscope screen. The contrast sensitivity functions for the four saccade amplitudes are also plotted (open squares = 6 deg saccades, filled circles = 12 deg saccades, open circles = 18 deg saccades, and filled triangles = 24 deg saccades). Overall, the contrast sensitivity decreases as the saccade amplitude increases. This is consistent at all the spatial frequencies investigated. For all four saccade amplitudes, the contrast sensitivity is decreased the greatest at the low, relative to the high, spatial frequencies. Similar functions have been presented

TABLE 1. The parameters derived from the contrast sensitivity function curve fitting routine

| Condition | Peak CS | Peak SF | High slope | Low slope | Cut-off |
|-----------|---------|---------|------------|-----------|---------|
| No saccade | 100(F) | 0.74 | 2.22 | 1.25 | 20.3 |
| 6 deg | 44.8 | 1.48 | 2.22 | 1.82 | 20.2 |
| 12 deg | 25.0 | 1.26 | 2.34 | 1.85 | 16.5 |
| 18 deg | 23.0 | 1.16 | 2.22(F) | 3.92 | 16.5 |
| 24 deg | 13.6 | 1.33 | 2.22(F) | 2.39 | 14.8 |
| Blink | 39.3 | 1.21 | 1.85 | 2.07 | 21.7 |

The data with an (F) indicate that these points had to be fixed during the iterative routine to obtain an optimum fit. Results are shown for the control condition and the different saccade amplitudes for the entire group of subjects. The results are also given for the blink data. The curves are displayed in Fig. 2. Peak CS = peak contrast sensitivity, Peak SF = peak spatial frequency, High slope = high spatial frequency slope, Low slope = low spatial frequency slope, Cut-off = high spatial frequency cut-off or resolution in c/deg.
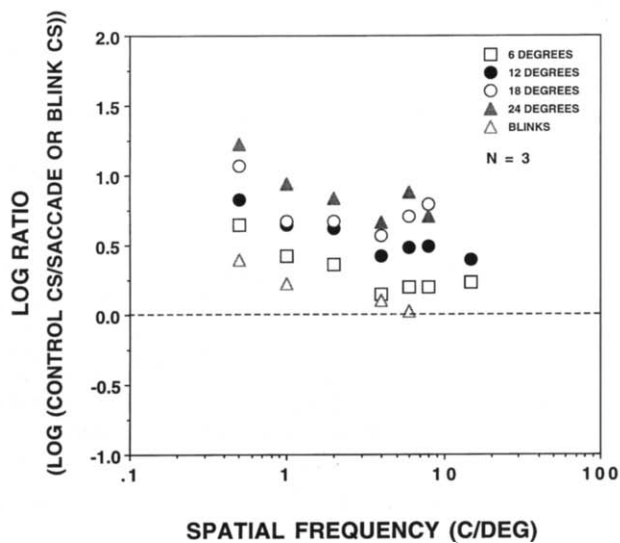


FIGURE 3. Loss in contrast sensitivity during saccades and blinks (data for blinks taken from Ridder & Tomlinson, 1993). The log ratio of the contrast sensitivity obtained under control conditions and during the saccades or blinks is plotted. The greater the saccade amplitude, the greater the suppression obtained. Additionally, saccadic suppression is the greatest at low spatial frequencies, regardless of the saccade amplitude. The form of blink suppression across spatial frequency is similar to that of saccadic suppression. The magnitude of blink suppression is less than that obtained with a 6 deg saccade.
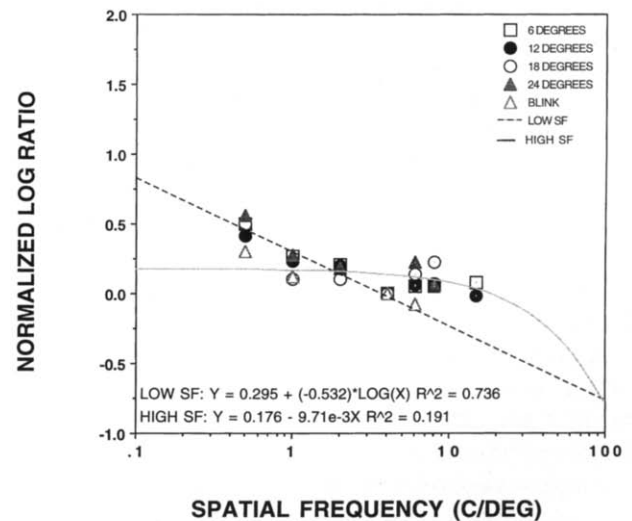


FIGURE 4. Normalized log ratio for the four different saccade amplitudes and blinks. See text for normalization procedure. The normalization procedure decreased the variability between the data for different saccade amplitudes. The magnitude of saccadic suppression decreased up to 4.0 c/deg and then leveled off. The normalized data could be modeled with two equations; one for low and one for high spatial frequencies. This suggests that there may be two separate mechanisms producing the loss in sensitivity observed with saccades. The blink suppression data were not significantly different from the saccadic suppression data ($P = 0.57$).

previously for saccadic and blink suppression (Volkmann et al., 1978; Ridder & Tomlinson, 1993; Burr et al., 1994).

The data were fit with a function that had four floating variables (peak contrast sensitivity, peak spatial frequency, high spatial frequency slope, and low spatial frequency slope) (Harwerth et al., 1990, for a discussion of the curve fitting routine). The curves drawn through the data are the best fit based on this function (Fig. 2). Table 1 contains the four floating variables determined for each fit. There are several important features of the curve fits. First, the peak spatial frequency of the fit to the control data is 0.74 c/deg, whereas, for all the saccade data the peak spatial frequency is greater than 1.0 c/deg. Second, the low spatial frequency slopes for the saccades are greater than for the control condition. Thus, the saccades result in a decrease in contrast sensitivity for

low spatial frequencies. This changes the shape of the contrast sensitivity function from low pass to band pass. Third, the high spatial frequency slopes for all of the data are similar. And lastly, the changes in peak spatial frequency and peak contrast sensitivity with increasing saccade amplitude produce spatial frequency cut-offs (c/deg) that are similar for all the conditions (i.e., spatial resolutions ranging from 20/30 to 20/40). The variables obtained from the curve fits to the blink suppression data are similar to the saccade suppression data.

The effect of stimulus spatial frequency on the magnitude of suppression can be displayed more clearly by plotting the log ratio of the control data and the saccade or blink data (Fig. 3). Spatial frequency is plotted on the horizontal axis and the log ratio of the control data and saccade or blink data (i.e., Log (Control Contrast Sensitivity/Saccade or Blink Contrast Sensitivity)) on the

vertical axis. For all conditions, the low spatial frequencies exhibit the greatest magnitude of suppression. As spatial frequency is increased up to approximately 4 c/deg, the magnitude of suppression decreases. Above 4 c/deg, there is a flattening of the function. This suggests that the mechanism of suppression changes near 4.0 c/deg. The magnitude of suppression also increases as the saccade amplitude increases. The magnitude of suppression obtained with the blinks is somewhat less than that obtained with the 6 deg amplitude saccade but the effect of spatial frequency is qualitatively the same for both the blink and saccade data.

To determine whether a simple vertical shift would bring the blink and saccade suppression data into register, all the data were normalized (Fig. 4). Spatial frequency is plotted on the horizontal axis and the normalized log ratio on the vertical axis. The magnitude of suppression was set to zero at 4.0 c/deg and the other spatial frequencies were adjusted accordingly. Four cycles per degree was chosen for two reasons. First, previous studies have suggested that little or no neural suppression is observed at higher spatial frequencies (Volkmann et al., 1978; Burr et al., 1982; Ridder & Tomlinson, 1993). Examination of our Fig. 3 also indicates that above 4.0 c/deg there is a flattening of the function. This implies that at or near 4.0 c/deg there is a fundamental change in the mechanism or mechanisms that produce suppression. We wanted to normalize the data at a spatial frequency near where this mechanism changed. And secondly, an objective method of least squares was used to determine where two lines fit to the data (one for high and one for low spatial frequencies) would intercept (Bogartz, 1968). For a discussion of the methodology see Bogartz (1968). The non-normalized data (Fig. 3) for each saccade amplitude were fit by this method. For the 6 and 12 deg saccade amplitudes, the intercept was determined to be between 2 and 4 c/deg. No intercept could be determined for the 18 and 24 deg saccade amplitude data. The intercept for the blink suppression data was between 1.0 and 4.0 c/deg. Thus, based on previous qualitative impressions of the data, as well as an objective mathematical fitting routine, 4.0 c/deg appears to be the best spatial frequency to use for normalization of the data.

By making this vertical translation of data, the variability in the magnitude of suppression for the different saccade amplitudes was decreased. At low spatial frequencies, the data for the four different saccade amplitudes now overlap. Above 4 c/deg, the normalization process also decreased the variability in the data, but not as well as at the low spatial frequencies.

Examination of Fig. 4 suggests that the data can be modeled with two different functions, one for low and one for high spatial frequencies. The low spatial frequencies, 0.5, 1, and 2 c/deg, are best fit with the equation: $y = 0.295 + (-0.532)*LOG(X)$. The $R^2$ for this fit to the data is 0.736. The 4 c/deg data were not used in the fit since it was the normalization point. The high spatial frequencies (6, 8, and 15 c/deg) displayed greater variability but the best fit was: $y = 0.176 - 9.7101e - 3X$,

$R^2 = 0.191$. The two equations have a crossover point which is near 2.0 c/deg. This observation is consistent with the notion that there is a fundamental difference between the forms of suppression that occur above and below 2.0–4.0 c/deg.

The vertical shift of the data decreased the discrepancy between the blink and saccade data. The blink suppression data now lie just below the saccade data at 0.5 c/deg and overlay the saccade data at 1.0 c/deg. Since it has been reported that the blink suppression data approach zero at about 4.0 c/deg (Volkmann et al., 1978; Ridder & Tomlinson, 1993), we wanted to see if the blink and saccade suppression data were significantly different at these low spatial frequencies. A repeated measures ANOVA was performed to determine if the blink suppression data were significantly different from the saccadic suppression data (6, 12, 18 and 24 deg data) at 0.5 and 1.0 c/deg. The results indicate that there is no significant difference between the blink and saccadic suppression data ($P = 0.57$). A post-hoc, pairwise comparison with the Bonferroni multiple comparisons test did not yield any significant results ($P > 0.05$).

In addition to the above analysis, a repeated measures ANOVA was run on the data at 0.5, 1.0 and 6.0 c/deg. The 4.0 c/deg data were not used because this was the spatial frequency that was set to zero in the normalization procedure. Included in the ANOVA were the 6, 12, 18 and 24 deg saccade data, as well as the blink data for each subject (similar to the previous analysis). Again, there was no significant difference found between blink and saccade suppression ($P = 0.43$). A post-hoc, pairwise comparison with the Bonferroni multiple comparisons test did not yield any significant results between the different saccade amplitudes and the blink suppression data ($P > 0.05$).

## DISCUSSION

Saccades produce a suppression of visual information that is spatial-frequency selective (Figs 2–3). The form of this suppression is independent of the saccade amplitude (Fig. 4). The normalized saccadic suppression data can be adequately modeled with two separate functions consistent with the concept that a minimum of two mechanisms are responsible for saccadic suppression (Fig. 4). Blinks produce suppression of visual information that is also spatial-frequency specific (Fig. 3). When blink and saccadic suppression data are normalized, the magnitudes of suppression across spatial frequency are indistinguishable (Fig. 4). This indicates that blink and saccadic suppression result from the same mechanism.

Several investigators suggested that the suppression associated with blinks has a neural origin (Volkmann, 1986; Ridder & Tomlinson, 1993, 1995). Blinks only result in suppression of low spatial frequency information (Fig. 3; see also Ridder & Tomlinson, 1993). This indicates that neural suppression only affects low spatial frequencies. During saccades, suppression is observed for high and low spatial frequencies, which indicates that an additional mechanism of suppression must be present.

*Low spatial frequency suppression associated with saccades and blinks*

Previous research suggested that the suppression at low spatial frequencies during blinks and saccades is specific to the magnocellular visual pathway (Volkmann *et al.*, 1978; Burr *et al.*, 1982; Ridder & Tomlinson, 1993; Burr *et al.*, 1994). The magnocellular visual pathway carries information for low spatial frequency, high temporal frequency, low contrast, achromatic stimuli. A parallel pathway, the parvocellular pathway, carries visual information for high spatial frequency, low temporal frequency, chromatic stimuli (Merigan & Maunsell, 1990, 1993). Thus, the visual stimulus employed can be manipulated to bias detection towards either the magnocellular or parvocellular pathway.

Uchikawa & Sato (1995) and Ridder & Tomlinson (1995) have used luminance and color stimuli to bias detection towards either the magnocellular or parvocellular pathway during blinks and saccades. In both studies, the luminance channel was suppressed more than the opponent-color channel, which indicated that the magnocellular pathway was being suppressed. Other aspects of the stimulus can be manipulated to bias detection to either the magnocellular or parvocellular pathway.

For example, if a low spatial-frequency stimulus with a contrast just above threshold is presented for a brief period of time (i.e., at a high temporal frequency), then it would preferentially be detected by the magnocellular pathway. The stimuli that we employed were only presented for 16.67 msec (nominally a temporal frequency of 30 Hz) and had contrasts near threshold. The low pass function that was observed with the control condition (Fig. 2) resembles previous contrast sensitivity functions obtained with high temporal frequency stimuli (Kelly, 1979, 1983, 1984). Thus, we employed a high temporal frequency stimulus that should have biased detection towards the magnocellular pathway.

The change in the shape of the contrast sensitivity function from a low pass (control condition) to a band pass function (during saccades) suggests that the magnocellular pathway is being suppressed and now detection is mediated by the parvocellular pathway. This change in shape of the contrast sensitivity function can occur by either suppressing the entire magnocellular pathway relative to the parvocellular pathway or by suppressing the low spatial frequency channels of the magnocellular pathway.

Several investigators have described movement-sensitive and pattern-sensitive systems (also referred to as transient and sustained channels) that appear to correlate with visual processing by the magnocellular and parvocellular pathways, respectively (Keesey, 1972; Kulikowski & Tolhurst, 1973; Harwerth *et al.*, 1980). These channels have been shown to each consist of several distinct subsystems or subchannels (Pantle & Sekuler, 1968; Tolhurst, 1973; Wilson *et al.*, 1983). It is possible that instead of suppressing the entire magnocellular pathway, the neural suppression that occurs only affects a portion of its channels (e.g., those tuned to
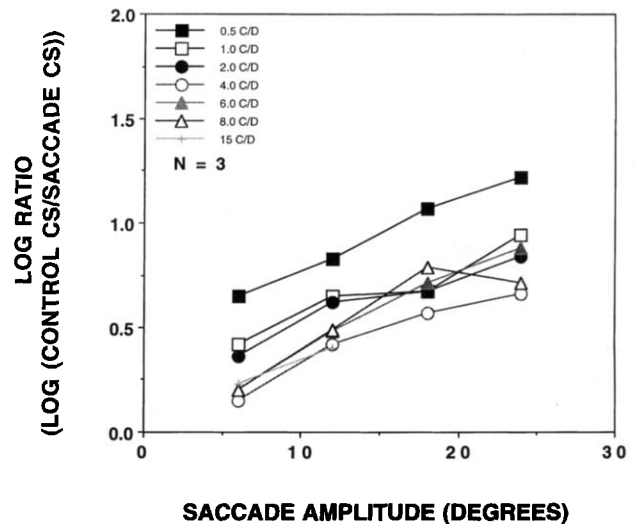


FIGURE 5. Effect of saccade amplitude on the magnitude of saccadic suppression for the different spatial frequencies investigated. The magnitude of suppression increases with increasing saccade amplitude. The functions for 4.0, 6.0, 8.0, and 15.0 cycles per degree overlap, indicating that suppression does not change at spatial frequencies above 4.0 c/deg.

spatial frequencies below 4.0 c/deg). This would require varying degrees of suppression with channels tuned to the low spatial frequencies being suppressed the greatest. Unfortunately, our data cannot discriminate between these two distinct hypotheses. Either mechanism would result in a band pass contrast sensitivity function with the peak spatial frequency gradually increasing as the magnitude of suppression increased. However, the simplest model of suppression would be one in which the entire motion-sensitive system was suppressed. This not only explains our data adequately, but would also not require varying degrees of suppression for the different channels.

*High spatial frequency suppression associated with saccades*

Saccades also produce a decrease in sensitivity for high spatial frequency information that is dependent on the saccade amplitude (Fig. 5). Saccade amplitude is plotted on the horizontal axis and the log ratio (i.e., log (control contrast sensitivity/saccade contrast sensitivity)) on the vertical axis. Data for all seven spatial frequencies are displayed. The magnitude of suppression decreases up to about 4.0 c/deg and then remains constant. A similar observation was made with the data in Fig. 4 for the normalized data. Thus, the normalization process had no effect on this observation. Since saccades, but not blinks, produce this high spatial-frequency decrease in sensitivity, there must be additional factors, other than neural suppression, associated with saccadic suppression.

What are the differences between blinks and saccades that produce this high spatial-frequency discrepancy in suppression? Volkmann (1986) reviewed the major differences between blinks and saccades that are likely to cause the discrepancy. She cited several retinal

mechanisms, such as: masking, retinal smear, errors of accommodation, or retinal shear. Masking typically has its greatest effect at high spatial frequencies where the greatest amount of contour is found in the visual field. In our experimental setup, small vertical drifts in the saccade could result in masking. Retinal smear would also have its greatest effect at high spatial frequencies. Again, small vertical drifts in the saccades could produce retinal smear of the horizontally oriented sine wave stimulus. Errors of accommodation would cause retinal blur which would decrease sensitivity at high spatial frequencies. Lastly, retinal shear (i.e., the shearing forces produced in the retina when the eye rapidly rotates around its center during a saccade) would increase as the saccade amplitude increases. This would tend to increase the background noise and cause the sensitivity to decrease, regardless of stimulus spatial frequency. Thus, masking, retinal smear, and errors of accommodation could result in the decreased sensitivity at high spatial frequencies observed with saccades. The effects of retinal smear and retinal shear would be expected to increase as saccade amplitude increases. Since retinal shear is minimal during blinks, this may cause the overall difference in sensitivity between blinks and saccades. Thus, all of these factors probably play a role in the differences in suppression observed with blinks and saccades.

The high spatial frequency loss in contrast sensitivity with saccades did not significantly alter the cut-off spatial frequencies (i.e., spatial resolution ranged from 20/30 to 20/40) determined from the curve fits to the data (Table 1). The average cut-off spatial frequency for the four saccade amplitudes was 17.0 $\pm$ 2.28 c/deg (mean $\pm$ SD), while that for the control condition was 20.3 c/deg. These values were also not different from the value obtained for the blinks (21.7 c/deg). These extrapolated cut-offs were not different because as the high spatial-frequency contrast sensitivity decreased, the peak spatial frequency of the fitted function increased. Thus, the extrapolated cut-off frequencies remained relatively constant. Little or no change in spatial resolution or acuity agrees with previous literature on saccadic suppression (Volkmann, 1962; Krauskopf et al., 1966).

The data in Fig. 5 are fit well with linear equations (Table 2). By extrapolating these functions to a saccade amplitude of zero, we can make a more direct comparison between blink and saccadic suppression. Theoretically, suppression at a saccade amplitude of zero should be free of the retinal causes of suppression that were discussed above and only neural suppression should remain. Thus, there should be a good correlation between the magnitudes of suppression at zero saccade amplitude and during blinks. The average magnitude of blink suppression across spatial frequency for the three subjects was; 0.40, 0.22, 0.10, and 0.02 (0.5, 1.0, 4.0, and 6.0 c/deg, respectively). The extrapolated saccadic suppression values were; 0.455, 0.275, 0.030, and 0. A statistical comparison of these data is not possible, although, the two sets of data do appear to be similar.

TABLE 2. The linear equations fit to the data in Fig. 5

| Spatial frequency | N | Equation | $R^2$ |
|---|---|---|---|
| 0.5 c/deg | 3 | $y = 0.455 + 0.0325x$ | 0.993 |
| 1.0 c/deg | 3 | $y = 0.275 + 0.0263x$ | 0.919 |
| 2.0 c/deg | 3 | $y = 0.250 + 0.0248x$ | 0.937 |
| 4.0 c/deg | 3 | $y = 0.030 + 0.0280x$ | 0.945 |
| 6.0 c/deg | 3 | $y = 0.000 + 0.0378x$ | 0.988 |
| 8.0 c/deg | 3 | $y = 0.090 + 0.0305x$ | 0.800 |
| 15.0 c/deg | 3 | $y = 0.060 + 0.0283x$ | 1.000 |

These data can be manipulated so that a statistical analysis can be made. If for each spatial frequency, we subtract the magnitude of blink suppression from saccade suppression we can again produce a graph like Fig. 5. If a linear fit to the data at each spatial frequency goes through the origin, then there is no difference between blink and saccadic suppression at that spatial frequency. An analysis of covariance (ANCOVA) was used to estimate the regression line and determine if it intercepted the origin. For 0.5, 1.0, and 4.0 c/deg, the ANCOVA indicated that the regression lines intercepted the origin ($P = 0.106$, $P = 0.094$, $P = 0.804$ for 0.5, 1.0, and 4.0 c/deg, respectively). The test for the 6.0 c/deg regression line indicated that it may not intercept the origin ($P < 0.00005$), indicating again that above 4.0 c/deg blink and saccadic suppression are different. This analysis indicates that for low spatial frequencies blink and saccadic suppression are similar. Furthermore, it provides additional evidence that retinal mechanisms associated with the saccade are responsible for the differences in suppression between blinks and saccades.

## Masking effects

A common question in studies of blink and saccadic suppression is, "How much of the suppression is due to masking?". This question is addressed quite well by Volkmann (1986). She concludes that masking does play a role in these forms of suppression but under appropriate viewing conditions masking is not the primary cause of suppression. In the past, as in this study, masking has been minimized by presenting very brief stimuli (<20 msec, Volkmann et al., 1978). This results in the least amount of image spread over the retina with saccadic eye movements. Image spread was negligible with the paradigm that was employed with the blinks (Ridder & Tomlinson, 1993). Another technique employed to minimize masking is to orient the stimulus along the axis of the eye movement. Thus, image spread would not disrupt the sine-wave pattern. A third way to minimize masking is to use an homogeneous field of view that reduces contour in the field. Some studies have employed a Ganzfeld presentation to achieve this effect. In our study, we used an homogeneous field of 13 deg (V) $\times$ 26 deg (H) surrounding the screen. To determine if this smaller background could have resulted in some masking of our stimulus, we performed a control experiment. We placed a back illuminated, translucent screen around the oscilloscope. The dimensions were
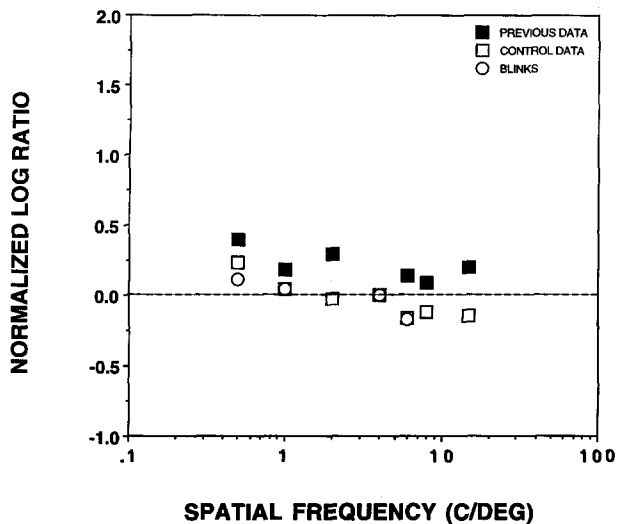
**SPATIAL FREQUENCY (C/DEG)**

FIGURE 6. Effects of a larger background field on the magnitude of saccadic suppression. The background (65 deg (V) × 70 deg (H)) was matched in luminance to the stimulus. The saccade amplitude was 12 deg. The larger background resulted in the magnitude of suppression dropping by approximately 0.2 log units and more closely resembling the blink suppression data.

65 deg (V) × 70 deg (H) at a viewing distance of 20 cm and the luminance of the surround was matched to the oscilloscope. At 20 cm, the oscilloscope dimensions were 28 deg (V) × 35 deg (H). The saccade amplitude was 12 deg. Figure 6 displays these control data compared with the previous data for this subject. Spatial frequency is plotted on the horizontal axis and the normalized log ratio is plotted on the vertical axis. Overall, the magnitude of suppression was about 0.2 log units less with the larger background and stimulus screen. The general shape of the function, across spatial frequency, has not changed (i.e., the greatest suppression is obtained at the low spatial frequencies). Furthermore, these data now overlie the blink suppression data at 1.0 and 6.0 c/deg, whereas the previous data did not. Thus, by using a larger background, the difference between the blink and saccade data is decreased. Thus, masking may have had an effect on the magnitude of suppression observed, but it did not affect the shape of the function.

## CONCLUSION

This investigation demonstrates that blink and saccadic suppression measured in the same individuals result in qualitatively similar functions. When the data are normalized by a vertical shift, the functions become quantitatively indistinguishable. To date, this is the most convincing evidence that blinks and saccades invoke the same mechanism to suppress visual information.

Volkmann (1986) suggested that suppression blocks unnecessary or distracting information from being perceived. Our results suggest that during saccades retinal factors decrease sensitivity to high spatial frequency information and neural suppression decreases sensitivity to low spatial frequency information. Thus,

suppression during a saccade decreases sensitivity to all incoming visual information which could disorient the individual. However, suppression during blinks only affects low spatial frequencies. It was suggested that this mechanism serves to minimize the percept of the eyelid (a low spatial frequency stimulus) occluding the pupil during a blink (Riggs et al., 1981). Why high spatial frequency information is not suppressed during the blink remains to be determined.

## REFERENCES

Beeler, G. (1967). Visual threshold changes resulting from spontaneous saccadic eye movements. Vision Research, 7, 769–775.
Berkeley, M. A., Kitterle, F. & Watkins, D. W. (1975). Grating orientation and retinal eccentricity. Vision Research, 15, 239–244.
Bogartz, R. S. (1968). A least squares method for fitting intercepting line segments to a set of data points. Psychological Bulletin, 70, 749–755.
Brooks, B. A. & Fuchs, A. F. (1975). Influence of stimulus parameters on visual sensitivity during saccadic eye movements. Vision Research, 15, 1389–1398.
Burr, D. C., Holt, J., Johnstone, J. R. & Ross, J. (1982). Selective depression of motion sensitivity during saccades. Journal of Physiology (London), 333, 1–15.
Burr, D. C., Morrone, M. C. & Ross, J. (1994). Selective suppression of the magnocellular visual pathway during saccadic eye movements. Nature, 371, 511–513.
Camisa, J. M., Blake, R. & Lema, S. (1977). The effects of temporal modulation on the oblique effect in humans. Perception, 6, 165–171.
Campbell, F. W., Kulikowski, J. J. & Levinson, J. (1966). The effect of orientation on the visual resolution of gratings. Journal of Physiology, 187, 427–436.
Harwerth, R. S., Boltz, R. L. & Smith, E. L.III (1980). Psychophysical evidence for sustained and transient channels in the monkey visual system. Vision Research, 20, 15–22.
Harwerth, R. S., Smith, E. L.III, Crawford, M. L. J. & von Noorden, G. K. (1990). Behavioral studies of the sensitive periods of development of visual functions in monkeys. Behavioral Brain Research, 41, 179–198.
Keesey, U. T. (1972). Flicker and pattern detection: a comparison of thresholds. Journal of the Optical Society of America, 62, 446–448.
Kelly, D. H. (1979). Motion and vision. II. Stabilized spatio-temporal threshold surface. Journal of the Optical Society of America, 69, 1340–1349.
Kelly, D. H. (1983). Spatiotemporal variation of chromatic and achromatic contrast thresholds. Journal of the Optical Society of America, 73, 742–750.
Kelly, D. H. (1984). Retinal inhomogeneity. I. Spatiotemporal contrast sensitivity. Journal of the Optical Society of America, 1, 107–113.
Krauskopf, J., Graf, V. & Gaarder, K. (1966). Lack of inhibition during involuntary saccades. American Journal of Psychology, 79, 73–81.
Kulikowski, J. J. & Tolhurst, D. J. (1973). Psychophysical evidence for sustained and transient detectors in human vision. Journal of Physiology (London), 232, 149–162.
Manning, K. A. (1986). Eye-movement-dependent loss in vision and its time course during vergence. Journal of Neuroscience, 6, 1976–1982.
Manning, K. A., Riggs, L. A. & Komenda, J. K. (1983). Reflex eyeblinks and visual suppression. Perception and Psychophysics, 34, 250–256.
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.
Mitrani, L., Mateeff, S. & Yakimoff, N. (1970). Dependence of visual

suppression on the angular size of voluntary saccadic eye movements. *Vision Research, 10*, 411–416.

Pantle, A. & Sekuler, R. (1968). Size-detecting mechanisms in human vision. *Science, 162*, 1146–1148.

Ridder, W. H. III, Tomlinson, A. (1993). Suppression of contrast sensitivity during eyelid blinks. *Vision Research, 33*, 1795–1802.

Ridder, W. H. III, Tomlinson, A. (1995). Spectral characteristics of blink suppression in normal observers. *Vision Research, 35*, 2569–2578.

Riggs, L. A., Volkmann, F. C. & Moore, R. K. (1981). Suppression of the blackout due to blinks. *Vision Research, 21*, 1075–1079.

Stevenson, S. B., Volkmann, F. C., Kelly, J. P. & Riggs, L. A. (1986). Dependence of visual suppression on the amplitudes of saccades and blinks. *Vision Research, 26*, 1815–1824.

Tolhurst, D. J. (1973). Separate channels for the analysis of the shape and the movement of a moving visual stimulus. *Journal of Physiology (London), 231*, 385–402.

Uchikawa, K. & Sato, M. (1995). Saccadic suppression of achromatic and chromatic responses measured by increment-threshold spectral sensitivity. *Journal of the Optical Society of America A, 12*, 661–666.

Volkmann, F. C. (1962). Vision during voluntary saccadic eye movements. *Journal of the Optical Society of America, 52*, 571–578.

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

Volkmann, F. C., Riggs, L. A. & Moore, R. K. (1980). Eyeblinks and visual suppression. *Science, 207*, 900–902.

Volkmann, F. C., Riggs, L. A., White, K. D. & Moore, R. K. (1978). Contrast sensitivity during saccadic eye movements. *Vision Research, 18*, 1193–1199.

Williams, R. A., Boothe, R. G., Kiorpes, L. & Teller, D. (1981). Oblique effects in normally reared monkeys (*Macaca nemenstrina*): meridional variations in contrast sensitivity measured with operant techniques. *Vision Research, 21*, 1253–1266.

Wilson, H. R., McFarlane, D. K. & Phillips, G. C. (1983). Spatial frequency tuning of orientation selective units estimated by oblique masking. *Vision Research, 23*, 873–882.