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DEPENDENCE OF VISUAL SUPPRESSION ON THE AMPLITUDES OF SACCADES AND BLINKS

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Abstract—Visual suppression accompanying voluntary saccades and eyeblinks was measured for a range of amplitudes of both. Saccade amplitudes varied from 2 to 32° and blink amplitudes varied from a slight movement to a full closure of the eye. In every case, thresholds for detecting full-field luminance decrements were determined with the method of constant stimuli and a two alternative forced choice procedure. Results from three subjects show a monotonic increase in the amount of suppression produced by saccades and blinks of increasing amplitude. Data are discussed with respect to theories about the origin of visual suppression.

Human Suppression Saccades Blinks Decrement sensitivity

INTRODUCTION

It is well established that there is a partial loss of visual sensitivity accompanying voluntary saccadic (Volkmann, 1962; Latour, 1966; Zuber and Stark, 1966), involuntary microsaccadic (Beeler, 1964; Zuber and Stark, 1966), and vergence (Manning and Riggs, 1984) eye movements, and also accompanying eyeblinks (Volkmann *et al.*, 1980), an effect which has been termed Visual Suppression. The magnitude of the effect varies with the conditions of testing, but typically there is an elevation of threshold of 0.5–1.0 log unit. Suppression is most pronounced for stimuli presented at or about the onset of the oculomotor or lid activity, but it is measurable for stimuli presented as much as 50 msec before the eye or lid begins to move (cf. Volkmann *et al.*, 1968, for time-course data).

As early as 1900 Dodge pointed out that we typically do not perceive the blurred image that must accompany saccadic eye movements across complex visual scenes. He proposed several factors which might contribute to this decreased perceptibility; that there is a selective inattention to events occurring between fixations, that the blurring of the image reduces its contrast below detectable levels, that there are visual masking interactions between pre-saccadic (or post-saccadic) fixational images and the blurred images during the saccade, and that there is a partial ischemia caused by the forces that act to move the eye. In the more recent literature, special attention has focused on the factors of visual masking (Matin *et al.*, 1972; Brooks *et al.*, 1980), and of partial ischemia or interruption of visual processing due to shearing forces acting upon retinal cells (Richards, 1968, 1969). In day to day situations, any or all of these factors may contribute to the general lack of awareness of images that impinge on the retina during eye movements.

There is evidence, however, that a significant amount of visual suppression can be measured in situations designed to eliminate the above effects, suggesting the action of a central mechanism that inhibits visual function in the temporal vicinity of a saccade or blink. This mechanism may be a corrollary discharge of the kind proposed by Helmholtz (1909) to account for the apparent stability of the visual world during eye movements. Suppression persists under Ganzfeld conditions that contain no contours that might mask one another (Riggs and Manning, 1982) and under conditions of very brief stimulation that preclude blurring of the image (Volkmann *et al.*, 1968). Most such experiments employ forced choice procedures and highly practiced subjects, making attentional biases unlikely. Various control experiments have also shown an absence of visual

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suppression at the time of nonvisual acts such as finger movement (Lederberg, 1970) which should entail the same attentional effects.

The possibility of partial ischemia is harder to rule out experimentally. Although suppression is evident for stimuli presented before the onset of eye or lid movement, the retina might still be processing stimuli when the acceleration of the eyeball produces its shearing effect (Richards, 1968). If suppression is in fact produced by the forces involved in moving the eye or eyelid, then it should be proportional to that force across a range of eye movement and eye blink amplitudes. Mitrani *et al.* (1970) measured visual suppression for horizonal saccades ranging from 8.5 to 17°, and found a monotonic increase in suppression with increasing saccade amplitude. However, their yes/no task did not directly yield a measure of threshold elevation in terms of stimulus amplitude or a baseline measure of suppression for their smallest saccade amplitude. Their stimulus was a grid target flashed for 20 msec, which allows the possibility that image blur may have affected the results as well. Brooks *et al.* (1980) measured suppression for two sizes of horizontal saccade (5 and 15°) and also found greater suppression with the larger saccade. Their stimulus was a diffuse 2° spot presented for a few microseconds on a large, nonhomogeneous background. These conditions allow for the possibility that masking or image blur was responsible for the threshold elevations they obtained, and this is the conclusion they reach in their discussion.

The experiments reported here seek to test the shear hypothesis by measuring the visual suppression associated with saccades and blinks that span a range of amplitudes, from those so small that the force involved is minimal to those large enough that the force is substantial. Ganzfeld viewing conditions and full-field decrement stimuli are used to minimize the possible contributions of the other above mentioned mechanisms, and a forced choice procedure is used to obtain direct threshold estimates in all conditions.

EXPERIMENT I: SACCADE AMPLITUDE

The first experiment examined the relationship between the angular size of a saccadic eye movement and the associated amount of threshold elevation.

Methods

Stimulus and recording apparatus. A detailed description of the Ganzfeld apparatus appears in Riggs *et al.* (1982). Each subject was seated comfortably in position to view the matte white inner surface of a sphere from a distance of 40 cm (Fig. 1). The surface was illuminated by three fluorescent bulbs (6 W ED3, Electronic Developments) mounted out of the subject's field of view in a symmetrical array that provided a nearly uniform illumination of the Ganzfeld surface. The bulbs' output was determined by a d.c. voltage from a regulated power supply (Iconix), which in turn was controlled by external electronics to produce a steady reference luminance of 28 ft-L. A 10 msec luminance decrement of variable amplitude served as the stimulus. The interior of the Ganzfeld was free of visible contours except for two thin vertical lines that served as fixation guides. The horizontal separation between these lines determined the size of the saccade made by the subject on a given trial. Viewing was binocular.

Eye movements were recorded using the electrooculogram (OEG) signal from electrodes mounted near the outer canthus of each eye. This signal was amplified differentially and used both to monitor eye movements and to trigger the stimulus at some fixed time after the onset of the saccade.

Procedure and threshold determination. The experiment consisted of 15 90-min sessions in which subjects repeatedly made voluntary saccades from the left fixation mark to the right fixation mark. The subject's task on each trial was to make two successive saccades on cue from the experimenter and to report whether the stimulus had occurred at the time of the first or the second. The experimenter selected a particular delay for the stimulus, enabled the stimulus on either the first or second interval (according to a predetermined random sequence), cued the subject to saccade for each interval and monitored the saccades on an oscilloscope. A two alternative forced-choice procedure and the method of constant stimuli were used to obtain psychometric functions for decrement detection. Decrements (ΔI) were imposed on the reference level (I) of Ganzfeld luminance in equal steps of $\log \Delta I/I$. Horizontal saccades of five different amplitudes (2, 4, 8, 16 and 32 deg) were used in blocks of trials randomly chosen throughout the experiment and five levels of stimulus delay (0, 20, 40, 80 and 160 msec after saccade onset) were also randomly imposed within each session on each of three subjects. Thresholds were determined from the psychometric functions by

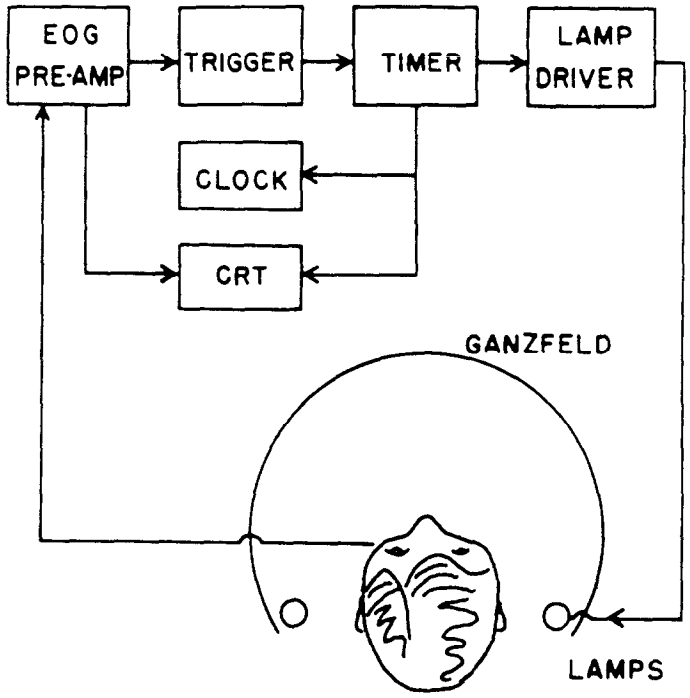

Fig. 1. Schematic diagram of the apparatus used in the saccadic suppression experiment. A Ganzfeld of radius 30 cm with a matte white interior is uniformly illuminated by three ED3 lamps (only two are shown) mounted out of view of the subject who faces the interior of the Granzfeld. Electrodes mounted on the outer canthus of each eye (only left eye lead is shown) provide an EOG signal which is amplified and fed into a trigger circuit and a CRT monitor. The trigger circuit starts a timer circuit that causes the lamp driver to produce a decrement in the lamps' output that serves as the stimulus. A millisecond clock gives a readout of the difference between saccade onset (EOG trigger) and the stimulus onset. Subjects made saccades between two movable fixation marks on the interior of the Ganzfeld.

converting the percent correct at each stimulus value to normal deviate scores, fitting a regression line to the plot thus obtained, and using this line to find the decrement value associated with 75% correct performance on the task. For comparison, a threshold for each subject was also obtained under conditions of steady fixation, and the difference in log units between this threshold and one obtained under a given experimental condition was defined as the magnitude of suppression for that condition.

In addition to the time course data for positive stimulus delays, functions were obtained for saccades of two amplitudes (4 and 32 deg) at both positive and negative (i.e. stimulus presented before saccade) delays in one subject (A.G.E.). The procedure for these sessions was modified somewhat from the above in order to achieve these negative values of delay. The subject was again told to make two successive saccades, on cue from the experimenter, but this time the decrement was presented with a variable delay after the cue; i.e. during or after the reaction time of the subject in executing the saccade. The EOG was used as a signal of saccade onset, but not to trigger the stimulus. The delay between the stimulus and the saccade onset was read from a digital millisecond clock that was started by either the stimulus onset (for negative delays) or the saccade onset (for positive delays), whichever came first, and was stopped by whichever of these events came second. These delays ranged from 87.5 msec of negative delay to 87.5 msec of positive delay and, for the purposes of analysis, were grouped into 25 msec wide intervals. Thresholds were determined as before from the psychometric functions and suppression was again found by comparison to a baseline (steady fixation) threshold.

Results

The results of the saccade amplitude experiments with positive delays are shown in Fig. 2 for all three subjects averaged together. Figure 2 shows visual suppression plotted against time after saccade onset for the five amplitudes of saccade. Suppression increases monotonically

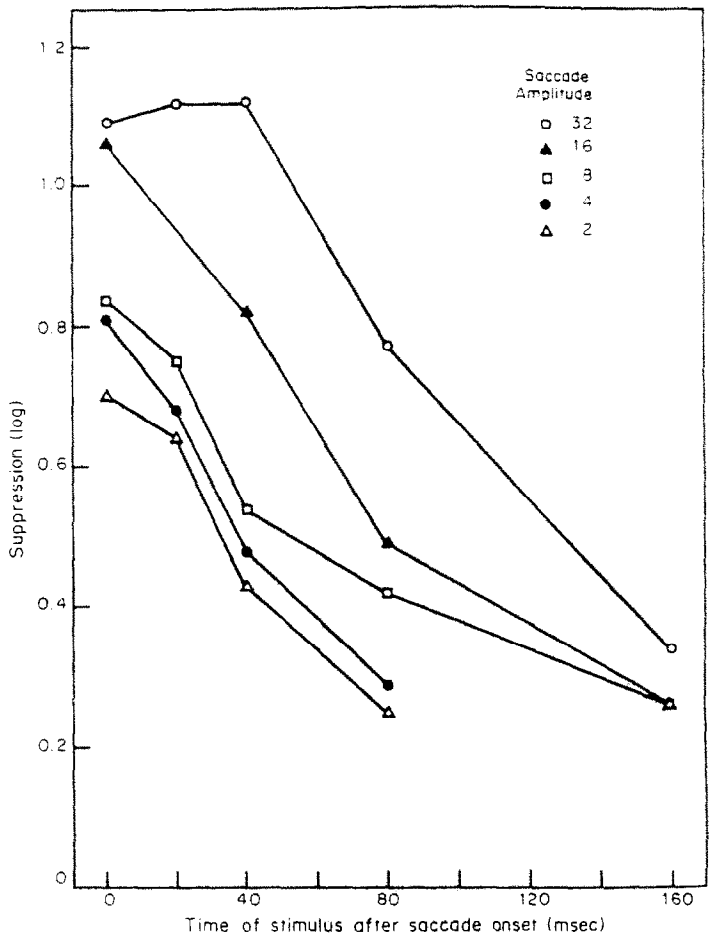

Fig. 2. Visual suppression as a function of stimulus delay for saccades of five amplitudes. All data points are the average of three subjects' results. Visual suppression is the difference between the decrement threshold in a particular saccade condition and the decrement threshold in a steady eye condition, both in units of $\log(\Delta I/I)$. Stimulus delay is the time in milliseconds between the onset of a saccade, determined from an EOG signal, and the onset of the stimulus decrement. Stimulus delays were determined here by adjustment of a timer circuit and were all positive in this case. Saccade amplitudes were determined by placement of two fixation guides on the interior of the Ganzfeld. Figures 2–5 are plotted with GRAPH (Hayes, 1981).

with increasing saccade amplitude for all delays measured, with noticable amounts of suppression still present for stimuli presented as much as 160 msec after the saccade onset for the larger saccades. Figure 3 shows the full time course data for subject A.G.E. with suppression plotted against delay for 4 and 32° saccades. These data indicate that suppression has reached a maximum for stimuli presented on or after the onset of a saccade, but that it has begun to appear for stimuli presented well before the onset, as has been previously reported (Latour, 1966; Volkmann *et al.*, 1968). Figure 4(a) shows suppression plotted against saccade amplitude for the 0 msec delay condition, in which suppression is greatest overall. This function shows nearly 0.7 log unit of suppression at the smallest saccade tested, 2° with an increase to 1.05 log units at 32°. Figure 4(b) shows the isometric force associated with a saccade plotted against saccade amplitude (Robinson, 1964) for comparison (see discussion).

EXPERIMENT II: BLINK AMPLITUDE

The second experiment examined the relationship between eye blink amplitude and the associated amount of threshold elevation. Blink amplitude (downward excursion of the upper lid) was measured indirectly with the Electroblepharogram (EBG), and a preliminary experiment was run to validate this method by correlating the EBG signal with the lid excur-

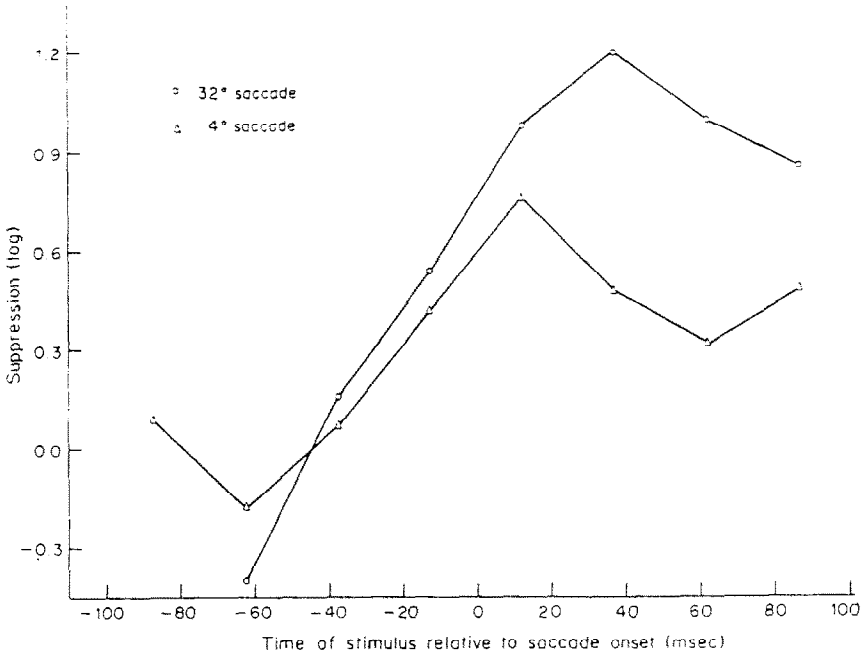

Fig. 3. Complete time-course data for one subject (A.G.E.), showing visual suppression in log units (determined as in Fig. 2) as a function of stimulus delay for a range of delays from −87.5 to +87.5 msec. Delays are determined in this case from readings on a millisecond clock which indicates the difference between saccade onset and stimulus onset, regardless of which comes first. Delays have been collected into bins 25 msec wide for analysis. Data for two saccade amplitudes (4 and 32°) are shown. The suppression vs delay function rises, broadens and shifts slightly toward positive delays with increasing saccade size.

sion as measured by direct videotaping and replay.

Procedure: measurement of lid movement and EBG

EBG calibration. Three subjects were each run through one session lasting a quarter of an hour in which eyeblinks and EBG traces were recorded simultaneously onto videotape (RCA color video camera) at a speed of 30 frames per second. The subject was seated with his head supported firmly by a bite bar and his right eye directly behind a magnifying lens. Electrodes mounted above and below the right eye provided an EBG signal which was amplified and displayed on an oscilloscope CRT. The video camera was aimed at the eye such that the magnified image filled the lower half of the monitor screen, and a mirror mounted just above the lens reflected an image of the oscilloscope into the upper half. A small piece of black tape was fixed to the upper lid to ensure that a distinct line was always visible to facilitate measurement of the position of the lid.

When the subject was aligned on the bite bar and the video camera was focused, he was instructed to fixate steadily forward and make 10 each of small, medium and large blinks at about one second intervals. The video tape was later replayed frame by frame and on each frame in which the upper lid reached its maximum excursion downward, the distance it had travelled was recorded along with the deflection of the EBG signal. In nearly every case, the lid paused long enough before opening that it appeared stationary in one or two frames of the video.

EGB calibration results. The results of the EBG calibration experiment are shown in Fig. 5. For all four subjects it was found that the EBG deflection correlated very well with lid excursion under conditions of steady fixation. Inspection of the video recording also revealed that the subjects were quite good at controlling their blinks, such that there was good agreement between the instruction given and the size of blink executed. For "small blinks", the upper lid generally dropped down as far as the upper margin of the iris, or between the iris and the pupil, but rarely covered any part of the pupil. For "medium blinks", the lid covered most or all of the pupil without reaching the lower lid, and for "large blinks" the lid reached all the way down to the lower lid such that the eye was

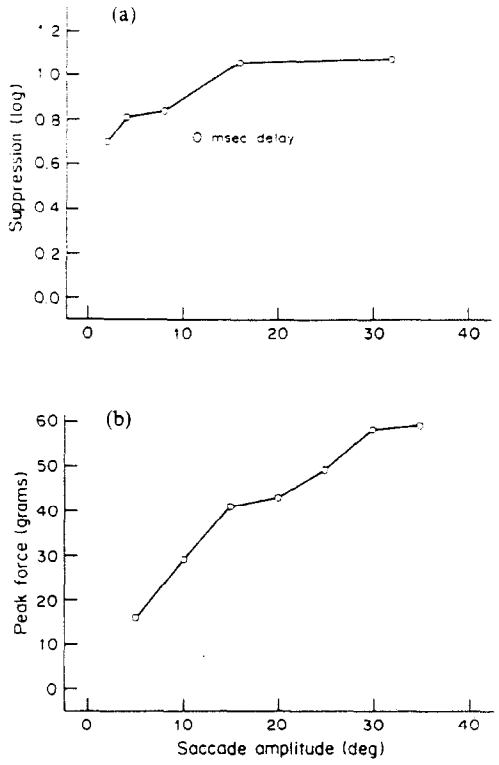

Fig. 4. (a) Visual suppression as a function of saccade amplitude for the zero delay condition. Data are replotted from Fig. 2. Visual suppression ranges from 0.7 log unit for a 2 deg saccade to 1.08 log unit for a 32 deg saccade and rises monotonically with increasing saccade amplitude. (b) Isometric force measurements for saccades of various amplitudes. Peak force in grams has been plotted against the saccade amplitude in degrees for seven saccade amplitudes. See Discussion. (Data replotted from Robinson, 1964, with permission of the author.)

completely closed. These categories are necessarily general and somewhat vague given the nature of eyeblinks, which are not so easily controlled as saccades.

Methods

Stimulus and recording apparatus. The apparatus used in the blink suppression experiment is shown schematically in Fig. 6. Light from a tungsten source passed through a collimating lens onto a mirror whose position was controlled by a galvanometer. Depending on the position of the mirror, the light then passed either through a neutral filter of density 0.6 in one channel of a bifurcated light pipe (Ealing), or through an inconel wedge in the other channel. The normal position of the mirror reflected the light through the neutral density filter, and a brief deflection of the mirror caused it to pass through the wedge channel to produce a decrement of light at the output end of the light pipe. The amplitude of the decrement thus produced could be varied by adjusting the wedge to density values greater than 0.6. The output end of the light pipe was directed at the roof of the subject's mouth and was firmly attached to the subject's bite bar. The subject wore opaque goggles, so that the only illumination to his retina was via the roof of his mouth, thus bypassing the lids and any attentuation that a blink might produce in the light reaching the retina. The light level thus produced was in the mesopic range.

Electroblepharograms were measured as described above. The differentially amplified EBG signal was used in three ways: it was displayed on a Cathode Ray Oscilloscope, so that the experimenter could monitor the eyeblinks during the session; it was sampled by a computer (Digital Equipment Corp. MINC, not shown) through an A–D converter, for on-line and later processing of the blink amplitude; and it was fed into a triggering circuit that produced the mirror deflection at blink onset on experimental (blinking) trials. For control (no-blink) trials, the deflection could also be triggered by the press of a button or by a signal from the MINC. A push-button input to the MINC was used to allow the experimenter to reject a trial if necessary. Three additional pushbuttons allowed the subject to initiate trials when ready and respond after the trial to indicate which of the two intervals had contained the stimulus decrement.

Procedure and threshold determination. The experiment consisted of 5 or 6 sessions of about 90 min each, including a 20-min dark adaptation period. There were four types of trial; small, medium, large or no blink. Thirty of each type were run in a session for a total of 120 trials per session. Thresholds were determined separately for each type using a 2-alternative forced choice procedure and the method of constant stimuli. All the stimuli were delivered at 0 msec delay, at the onset of the EBG signal. The stimulus duration was 17 msec for subjects J.P.K. and S.B.S. and 34 msec for subject L.A.R. (to compensate for his lower overall sensitivity to the decrements). At the beginning of a trial, the wedge was set to a particular value and the subject was informed as to what type of blink to make. The subject indicated readiness and was cued by the computer to blink for each interval. After a trial, the experimenter had the option of rejecting it if the subject made two blinks during an interval or if the triggering did

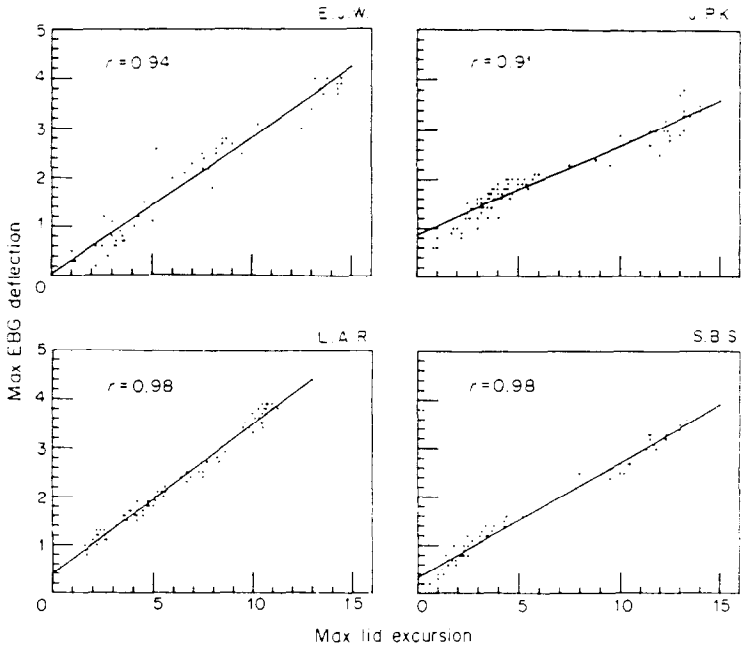

Fig. 5. Correlation and regression functions for EBG amplitude and actual upper lid excursions for four adult male subjects. Each subject made at least 30 blinks, ranging from very small movements of the lid to full closure of the eye. EGB traces were displayed on an Oscilloscope CRT and videotaped simultaneously with a magnified image of the eye. The videotape was replayed frame by frame and both EBG deflection and lid excursion were measured on a monitor. One unit of EBG deflection corresponds to 100 μV (200 for J.P.K.) and one unit of lid excursion corresponds to 0.7 mm. All correlations are above 0.9, demonstrating the validity of the EBG as a measure of lid excursion.

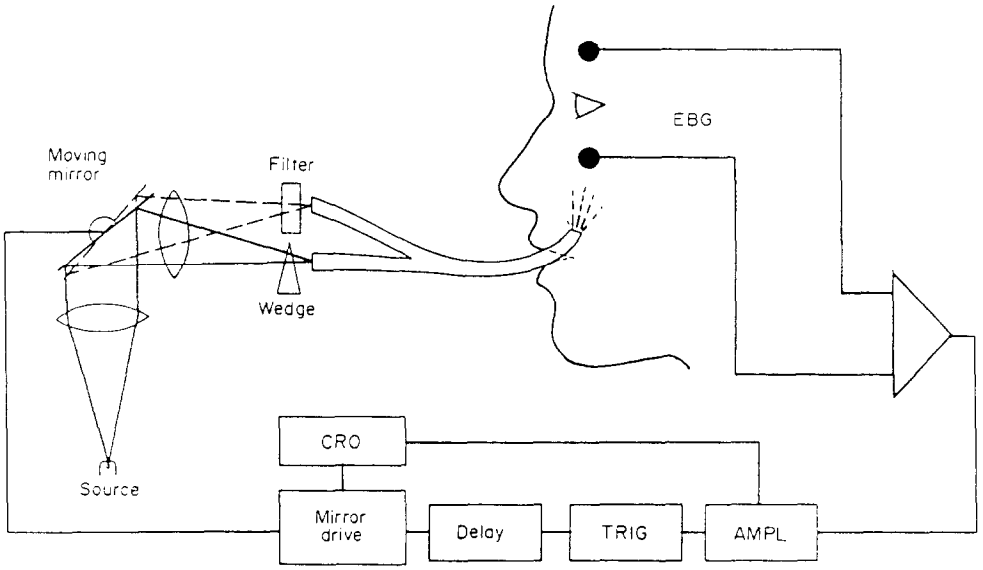

Fig. 6. Schematic diagram of apparatus used in the blink suppression experiment. Subject's right eye is illuminated through the roof of the mouth by a two channel bifurcated light pipe. Light from a tungsten source is collimated and reflected in one channel through a neutral filter of density 0.6 or in the other channel through an inconel wedge of adjustable density, depending on the position of a moving mirror. Facial electrodes provide an EBG signal that is amplified and used to trigger the mirror driver to produce a brief (17 msec) deflection of the mirror. A Cathode Ray Oscilloscope displayed both the EBG and the mirror driver pulse for monitoring during the experiment. Decrement stimulus values were set by adjustment of the wedge to densities greater than 0.6.

not occur properly. Rejected trials were repeated immediately. The experimenter also gave the subject feedback on the blink size if it was inappropriate.

The computer analyzed each blink as it occurred and generated a display that indicated the amplitude of the blink, regardless of what instruction had been given to the subject. Blink amplitude was determined by finding the point of maximum deflection in the EBG and subtracting it from a pre-blink baseline, and trials were sorted for analysis based on the amplitude so measured, regardless of the instruction given for that trial. The responses obtained across wedge settings for the four different conditions gave psychometric functions which yielded thresholds according to the same procedure used in the saccade experiment.

Results

In all three subjects, suppression rises monotonically with blink size. In two out of the three subjects there is a considerable amount of suppression for even the smallest blinks, and in the third, the suppression effect is uniformly small.

Figure 7 shows the thresholds determined for all three subjects in the four conditions. Threshold is expressed as the log of the Weber fraction. The figure is plotted as a histogram due to the fact that each size of blink represents a range of actual lid excursions. Visual suppression in each of the blink conditions is found by comparison to the unblinking condition. For subjects J.P.K. and S.B.S. the suppression ranges from about 0.5 to 0.8 log units of threshold elevation from the smallest to the largest blinks. Subject L.A.R. shows a considerably smaller range of from 0.05 to 0.25 log units of suppression.

DISCUSSION

The results from both experiments show that visual suppression increases with increasing saccade or blink amplitude, but in nearly every case [see Figs 4(a) and 7)], even the smallest movements produce a visual suppression on the order of 0.5 log unit of stimulus amplitude. This is consistent with the finding by Beeler (1967) that microsaccadic "flicks" show up to 0.5 log unit of suppression, though his conditions were quite different. The time course data from Figs 2 and 3 show that our measured amounts of suppression are at or near maximum values, because the peak of the suppression effect occurs when the test stimulus is triggered with zero delay from the onset of the saccade. This peak does not shift radically with increasing saccade size. Instead, the entire function becomes generally broader and higher. It appears that the

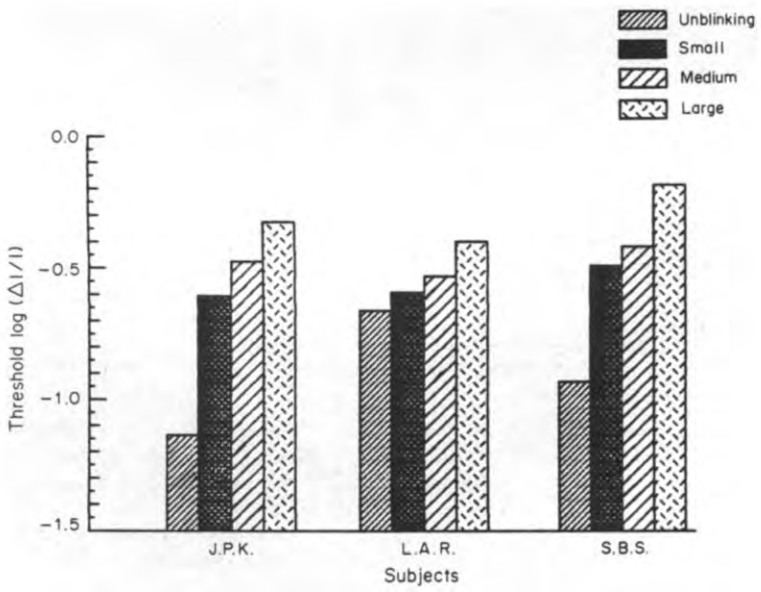

Fig. 7. Decrement thresholds for three subjects as a function of blink amplitude. Thresholds are given in units of $\log(\Delta I/I)$ of a full-field decrement in light level. Blink amplitudes are expressed in three categories (see text for description of categories), along with a no-blink control. Visual suppression is the difference between the no-blink control and the blinking conditions, and rises monotonically with blink amplitude.

largest saccades show more suppression than the largest blinks. However, it should be noted that luminance levels were more than three log units higher in the saccade experiment than in the blink experiment. Previous work has indicated that suppression increases with overall luminance (Richards, 1969; Brooks *et al.*, 1980). The difference in results for subject L.A.R. in the blink experiment relative to the other two subjects could be due to the age of that subject, who was 73 (the other two subjects were both aged 26). Older subjects have a reduced visual sensitivity and possibly a diminished capacity for neural suppression. It would also seem possible that the longer duration of the stimulus decrement used for L.A.R. (34 rather than 17 msec) to compensate partly for his reduced sensitivity may have allowed for more of the stimulus to extend into the time after peak suppression. Other than these differences, the results for the two conditions are quite similar.

In the case of saccades, these results can be compared directly to data gathered by Robinson (1964) on the force acting on the eyeball during saccadic eye movements of various amplitudes. Figure 4(b) replots his data, showing the peak force acting on the eye for various saccade amplitudes. (These data may overestimate the peak force transmitted to the receptors if damping occurs.) It is clear that the force acting on the eye approaches 0 at the smallest saccade amplitudes. This is in contrast to the data from Fig. 4(a) which show considerable suppression even at the smallest amplitudes. If suppression is caused by the force acting on the retina, for example through shearing of the various layers, as Richards (1968) has suggested, it would be expected that small saccades would produce correspondingly small suppression effects. Note also that scarcely any increase of suppression occurs with an increase of saccade amplitude from 16 to 32°, even though the force on the eyeball has gone up from about 42 to 58 g.

In the case of blinks, comparable data on the forces involved are not available. It is logical to assume, however, that our category of "small" blinks, in which the upper lid reaches no farther than to the upper margin of the pupil, must produce only a small deformation of the eye and a small increase in intra-ocular pressure when compared to the "large" blinks, in which the upper lid comes fully down to meet the lower lid. Based on this assumption, it once again seems unlikely that the force itself is acting to interrupt processing to the extent necessary to produce the suppression effect we have found. Because blinks are often accompanied by a small rotation and a retraction of the eyeball (Evinger *et al.*, 1984; Collewijn *et al.*, 1985; Riggs *et al.*, 1986), it is probable that the extraocular muscles exert a force on the eyeball apart from the action of the lid. However, the Collewijn *et al.* (1985) and the Riggs *et al.* (1986) studies show that eye rotations accompanying blinks are slower than saccades and are smallest when fixation is near the primary direction, as was the case in our study, being on the order of 1°. They further indicate that this activity is proportional to blink amplitude, so the same argument should apply.

Additional arguments against the shear hypothesis can be made from a comparison of saccade and blink related suppression. The time courses of suppression are very similar for the two cases (Volkmann *et al.*, 1968, 1980), while the time courses of the oculomotor events, and presumably the forces produced, are quite different. The nature of the forces produced must be quite different as well. Blinks produce predominantly compressive forces, while saccades produce predominantly angular, or shear forces on the globe and retina. It seems unlikely that such different physical events could produce a visual suppression that is so similar.

Other proposed mechanisms of suppression would also appear to be precluded by the procedures used. An explanation of suppression based on masking or retinal smearing phenomena depends upon the interaction of visible contours, and both experiments reported here were done under conditions of diffuse, homogeneous illumination. The saccades were executed against a Ganzfeld background, and the blinks were executed against a diffuse field projected onto the back of the eye through several cm of tissue.

The results of these experiments point to an as yet unidentified source of suppression that accompanies the efferent signals causing the eye to move or blink. A reasonable mechanism for this is that the same central process that initiates the efferent signal to move the muscles also feeds forward an inhibition within visual sensory areas of the brain. The increase in suppression that is observed with increasing saccade and blink amplitude can be viewed as an increase in the strength of this inhibition. This "corollary discharge" model applies strictly to situations in which peripheral mech-

anisms have been ruled out, as in the present Ganzfeld or light pipe experiments.

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