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MEASUREMENTS OF VISUAL SUPPRESSION DURING OPENING, CLOSING AND BLINKING OF THE EYES*

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Abstract—We have previously shown that the sensitivity of human vision, as measured with a stimulus that bypasses the eyelids, is briefly impaired at the time of an eyeblink. We now find that the visual loss is almost equally extensive during eye closure if the eyes then remained closed. But little impairment occurs during eye opening when the eyes then remain open. We have previously concluded that, in blinking, visual suppression is associated with an inhibitory signal sent out by the brain. We now conclude that this signal arises primarily as a corollary to the efferent discharge that closes the eyelids.

INTRODUCTION

Eyeblinks occur, on the average, 15 times per minute under normal conditions of human vision (see for examples Drew, 1951; Gregory, 1952; Moses, 1975; Peterson and Allison, 1931; Ponder and Kennedy, 1928; Poulton and Gregory, 1952; Stevens and Livermore, 1978; Zametkin *et al.*, 1979).† Though highly variable, a typical blink has a total duration of 250–450 msec, and a "blackout duration" of 40–200 msec, during which time the upper lid occludes the pupil (Doane, 1978, 1980, 1981; Gordon, 1951; Hung *et al.*, 1977; Kennard and Glaser, 1964; Lawson, 1948a, b; Lord and Wright, 1948; Moses, 1975; Slater-Hammil, 1953; Weiss, 1911). Occlusion of the pupil reduces light entering the eye by almost two log units and virtually eliminates all perception of contour or contrast (Volkmann *et al.*, 1980; see also Crawford and Marc, 1976). Thus, as we go about our daily activities our vision is severely interrupted every few seconds by eyeblinks.

It is a common observation that we do not ordinarily notice the periodic blackout produced by our blinks, even though a comparable interruption of visual stimulation produced externally catches our attention immediately (Moses, 1975; Riggs *et al.*, 1981). This observation has suggested to us that eyeblinks may be accompanied by a suppression of vision. Suppression would have the adaptive effect of diminishing the visual impact of the blackout produced by pupillary occlusion and thus would contribute to the subjective impression of continuous clear vision.

Research in our laboratory has recently been aimed at measuring visual suppression during voluntary blinks and establishing some of its characteristics (Riggs *et al.*, 1979, 1981; Volkmann *et al.*, 1979, 1980). We have also been interested in possible relations between blink-related suppression and saccadic suppression (see Matin, 1974; Volkmann *et al.*, 1978a), and in the degree to which models of saccadic suppression can describe blink-related suppression.

The evidence thus far indicates that voluntary blinks are indeed accompanied by a suppression of vision. In an experiment designed to measure visual thresholds during blinks, we bypassed the lids and illuminated the retina through a fiber optic bundle placed in the mouth. We found that sensitivity to brief decrements in this otherwise steady retinal illumination is decreased by 0.4–0.7 log unit during blinks (Riggs *et al.*, 1979; Volkmann *et al.*, 1980). In an experiment designed to measure the subjective effect of a blink, we had subjects view a homogeneously illuminated Ganzfeld and match the perception of their own blinks with that of a brief decrement in Ganzfeld luminance. We found that blinks were judged equal to Ganzfeld decrements that were substantially shorter and of smaller magnitude than the decrements produced by the actual blinks (Riggs *et al.*, 1981).

Blink-related suppression resembles saccadic suppression in both magnitude and time course. The

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†Blinking, or "winking" as used by some authors, is a temporary closure of both eyes that is under both voluntary and involuntary control. Blinks have been categorized into three types: (a) voluntary blinks, which can be executed on command, (b) spontaneous blinks, which are involuntary and centrally programmed, and (c) reflex blinks, which are produced involuntarily in response to peripheral stimulation such as an object approaching or touching the eye (see Blount, 1928; Hall, 1945; McEwen and Goodner, 1969; Moses, 1975).

former reaches a maximum value of 0.4–0.8 log unit of suppression just before the descending upper lid begins to cover the pupil, and the latter typically reaches a similar magnitude just before or at the time of saccade onset, depending on luminance conditions and saccade amplitude (Volkmann *et al.*, 1979; Volkmann *et al.*, 1981). Nevertheless, there is no evidence that the process of blinking involves saccadic eye movements (Doane, 1978, 1980, 1981; Ginsborg, 1952; Ginsborg and Maurice, 1959; Volkmann *et al.*, 1979) (subjects are able to execute a saccade while blinking, but the two are not necessarily locked together). Rather, movements of the eyes during a blink appear to be small downward and nasalward movements resulting from the pressure of the upper and lower lids on the eyeball. These passive movements vary somewhat with the direction of gaze (Doane, 1980; Ginsborg and Maurice, 1959; Hung *et al.*, 1977; Miller, 1967; see also Kennard and Glaser, 1964; Kennard and Smyth, 1963). Doane (1980) also reports a globe retraction of about 1.5 mm during lid closing, and a return during lid opening. Contrary to earlier reports (Miles, 1931), recent work shows no evidence of Bell's phenomenon during blinks (Doane, 1980). Blink-related suppression, therefore, cannot be attributed to saccadic suppression.

Blink-related suppression may arise from mechanisms that are the same or similar to those underlying saccadic suppression. Our evidence supports the concept of a centrally originating inhibitory process in the brain which feeds forward to suppress vision as it commands the appropriate muscles to execute a blink (Sperry, 1950; von Holst and Mittelstaedt, 1950; see also Borchers and Ewert, 1978). Blink-related suppression is almost surely not produced in substantial degree by any of the other mechanisms which have been widely invoked to account for saccadic suppression, namely smear of the stimulus image on the retina, masking effects produced by contour shifts on the retina, or retinal noise produced by shearing forces set up in the retinal layers by saccadic accelerations (for examples of this literature, see Breitmeyer and Ganz, 1976; Bridgeman, 1977; Brooks and Fuchs, 1975, 1977; Brooks *et al.*, 1980a; Brooks *et al.*, 1980b; Campbell and Wurtz, 1978; Matin, 1974; Richards, 1969; Riggs *et al.*, 1974; Volkmann *et al.*, 1978a; Volkmann *et al.*, 1978b; Zuber and Stark, 1966). We have found that blink-related suppression occurs under conditions of pupillary occlusion in which image smear and contour shifts on the retina are impossible. It occurs under conditions of diffuse retinal illumination of the dark adapted eye and homogeneous contour-free illumination of the light adapted eye—conditions which minimize possible effects of masking stimuli present before and after the blink (see also Holland and Tarlow, 1972; Malmstrom *et al.*, 1977; Wegmann and Weber, 1973). Finally blink-related suppression occurs under conditions in which the saccades necessary to produce retinal shearing are absent.

A number of other mechanisms have also been evaluated as determinants of saccadic suppression, and would presumably also be relevant to blink-related suppression: shifts in the subject's operating characteristic during the motor event (see Green and Swets, 1966; Pearce and Porter, 1970), increased uncertainty regarding the spatial or temporal location of a test stimulus that is presented during the event (Greenhouse *et al.*, 1977; Greenhouse and Cohn, 1980), or generalized shifts in attention produced by the motor event (see Lederberg, 1970). Possible changes in the operating characteristic can be obviated by the use of criterion free forced choice psychophysical procedures; these procedures yield substantial amounts of saccadic suppression (Pearce and Porter, 1970; Volkmann, Riggs, White and Moore, 1978b). Possible increases in uncertainty during saccades are attributed importantly to the process of recalibration of the visual spatial coordinates, a process which is not required during blinks. Nevertheless, additional data on the roles of attention and uncertainty in saccadic and blink-related suppression would be useful. We provide data here which assess these roles with respct to blinks.

Problem

In the present research we ask the question: how does the visual suppression that accompanies blinks relate to the phases of lid motion that constitute a blink? Knowledge of the relative amounts of suppression associated with the opening and closing phases of the blink may aid in discriminating further among possible mechanisms of suppression.

METHODS

Apparatus

The experiment required a system for stimulating the retina in such a way that light reaching the receptors would be independent of lid position. It required systems for triggering the stimuli to occur during lid closing, lid opening, or blinking and for presenting the stimuli manually to the steadily open or closed eye. Finally, it required systems for monitoring eyelid behavior and the temporal occurrence of the stimulus in relation to the various components of the blink. A portion of the technique has been described previously (Volkmann *et al.*, 1980); it is diagrammed schematically in Fig. 1.

Illumination of the retina. As Fig. 1 shows, steady light was brought to the retina through an optical system that directed it into one Y-arm (the upper arm on Fig. 1) of a bifurcated fiber optic bundle that terminated in the subject's mouth. The end of the bundle in the mouth was covered with a snugly fitting glass test tube for hygienic reasons. It was adjusted by each subject to contact the roof of the mouth at a favorable position for sending the light to the back of the right eye. It was then clamped tightly in relation to the subject's bite board, so that light struck the same position in the mouth throughout the experiment. Light

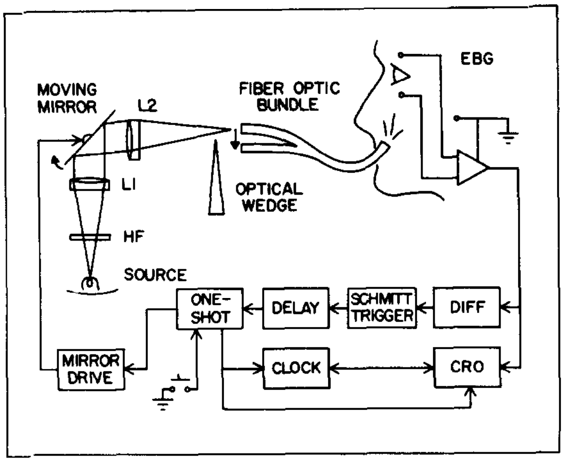

Fig. 1. Schematic diagram of apparatus. Light from a 50 W d.c. operated tungsten-halogen source passed through a heat filter HF, achromats L1 and L2, and entered one of two paths of a bifurcated fiber optic bundle. The other end of the bundle terminated in the subject's mouth, and light through this pathway provided steady illumination of the retina through the roof of the mouth and the intervening tissues. The stimulus was a brief decrement in this steady illumination, produced by a clockwise deflection of a galvanometer mirror located between L1 and L2 in the collimated portion of the light path. This deflection directed the light momentarily through a circular Inconel wedge and into the second arm of the fiber optic bundle, thus producing a decrement of variable magnitude. The decrement could be triggered by the onset of the electroblepharogram (EBG), recorded differentially by electrodes placed above and below the eye, with a reference electrode on the earlobe. The amplified EBG was fed into circuits which could be adjusted to trigger the mirror deflection with zero delay after detection of the onset of eye closing, opening, or blinking. The deflection could also be initiated manually by the experimenter. The EBG and the stimulus decrement were displayed on each trial on a cathode ray oscilloscope, and the time of occurrence of the stimulus in relation to EBG detection was displayed on a digital msec clock.

from the fiber optic bundle passed through the intervening tissues until a small fraction of it finally reached the lower nasal retina of the right eye. To the dark adapted subject, the light appeared as a large diffuse cloud of colorless light localized in the upper temporal visual field. The subject wore opaque goggles and a black felt headband to eliminate all other sources of light.

In order to specify the approximate level of the diffuse cloud of light seen by each subject, we measured absolute thresholds. To do this, we brought the level of light from the bundle down to the threshold range by interposing neutral density filters of known value into the fiber optic path. Under conditions of total darkness, we presented 100 msec exposures of this light in 0.1 log unit steps and determined thresholds for the steadily closed eye using a constant stimulus method of presentation and a forced choice psychophysical procedure. Our measurements showed that the level of steady light used in the actual experiment was 2.15 log unit above threshold for subject L.A.R., 1.5 log unit for D.J.U., and 1.35 log unit for A.G.E.

Stimuli. The stimulus, a brief decrement in the steady illumination of the retina, was produced by the rotation of a galvanometer mirror (General Scanning Co.) placed in the optical pathway (see Fig. 1). The mirror rotation deflected the light from its location on the upper Y-arm of the fiber optic bundle, and directed if through a neutral density wedge and into the lower Y-arm of the bundle. The adjustment of the wedge determined the magnitude of the decrement. The wedge was calibrated to produce 0.1 log unit steps of log $\Delta I/I$, where I is the steady light reaching the retina, and ΔI is the decrement produced by deflecting the light through the wedge. The duration of the decrement was determined by the scanning galvanometer; it was adjusted to achieve a range of decrements appropriate for threshold measurements for each subject. The durations were 20 msec for subjects L.A.R. and D.J.U. and 30 msec for A.G.E.

Systems for triggering stimulus decrements and monitoring eyelid behavior. In a previous experiment we used high speed photography to measure the behavior of the lids during a blink (see Volkmann *et al.*, 1980, Fig. 1). Prior to the present experiment we measured the behavior of the lids during eye closing and opening as well as blinking in two subjects. The photographic records showed that the rate of lid motion during eye closing is very similar to that of the downward phase of the blink; during eye opening, which may be somewhat slower, the lids behave similarly to the opening phase of the blink. The waveforms of the electroblepharogram (EBG) were similar enough in the various conditions of lid closing, opening, or blinking to serve as an appropriate signal to trigger the stimulus decrement (see Fig. 1). The EBG, amplified and differentiated, was fed into a Schmitt trigger which was adjusted to initiate the decrement early in the waveform of the desired response. Specifically, during blinking or lid closing, the onset of the decrement occurred slightly before the descending upper lid began to cover the pupil. During lid opening, the decrement occurred before the ascending lid began to uncover the pupil. These temporal relations were used because our earlier work on blinking had indicated that maximum suppression occurs very early in the motor event (Volkmann *et al.*, 1980).

To present the stimulus decrement to the steadily fixating eye, the experimenter initiated the decrement manually. Throughout the experiment, the EBG and the time of occurrence of the stimulus decrement in relation to the EBG were monitored by means of a CRO display and a digital msec clock, as shown on Fig. 1.

Procedure

Three adult subjects served in the experiment. One, L.A.R., was highly practiced. The others were new to the experiment but had served in other psychophysical experiments in our laboratory.

The experiment required 6–8 sessions for each subject. The subject was dark adapted for 30 min prior to each session, which lasted for approximately 2 hr, including brief rest periods. The first three sessions were practice sessions designed to familiarize the subject with the unusual source of stimulation and with the experimental conditions. Five conditions of lid position were used: (1) steady open eye, (2) steady closed eye, (3) closing eye, (4) opening eye, and (5) blinking eye. In each session the steady closed condition was run as a control along with two other conditions; each condition was run on at least three days.

For each experimental condition we chose 4 or 5 values of stimulus decrement to permit measurement of a threshold value of decrement using a constant stimulus method of presentation. On each trial, the subject performed a pair of the appropriate motor events (a pair of blinks, a pair of lid openings, etc.) spaced about 2 sec apart on signals from the experimenter. A decrement accompanied one event of the pair, and the subject judged in a two alternative forced choice procedure whether the decrement occurred with the first or the second event. In this way we obtained 35–60 judgments at each of four or five values of decrement under each condition.

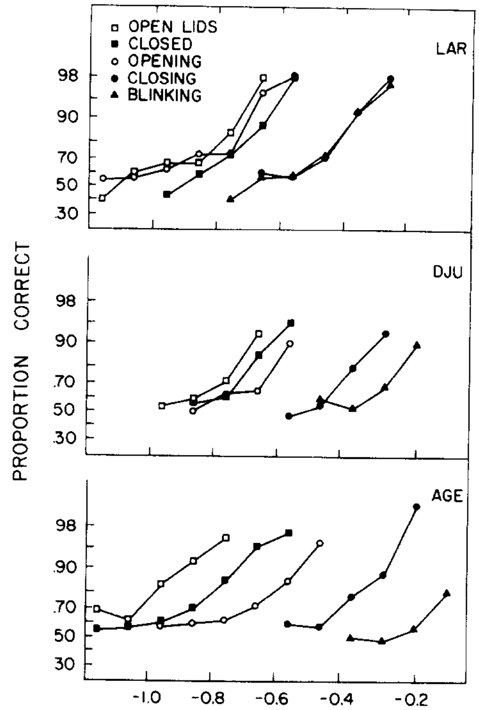

Fig. 2. Psychophysical functions showing proportions of correct detection of stimulus decrements of variable magnitude. Results are shown from five experimental conditions: presentation of the stimulus during eye opening, closing, or blinking, or to the steady open or closed eye. Detection was assessed using a two-alternative forced choice procedure; the ordinate thus shows a probability scale ranging from 50% (chance) to near 100% correct. The abscissa shows stimulus magnitude (Log $\Delta I/I$), where I is the steady level of light reaching the retina through the fiber optic bundle and ΔI is the decrement from this steady level. Results are shown for three subjects, L.A.R., D.J.U. and A.G.E.

RESULTS

Psychophysical functions

Figure 2 shows the psychophysical results for each subject, plotted as proportion of judgments correct, on a probability scale, as a function of log $\Delta I/I$. The log $\Delta I/I$ values indicate the *relative* amounts of decrements required for correct judgments for each subject; absolute amounts of decrement are not strictly comparable, since the level of I and the duration of ΔI varied from one subject to another (see Methods).

The relative positions of the various functions are clearly related to the corresponding experimental conditions. All subjects are most sensititive when the decrement is presented to the steady open eye. Although the subjects differ somewhat in the relative amounts of decrement they required to perform correctly in the steady open, steady closed and opening conditions, all subjects required substantially larger decrements to perform correctly when the stimulus was presented during lid closing and blinking. There is no overlap in the functions resulting from these latter two conditions and the former three conditions.

Magnitude of suppression

We performed linear regression analyses on the data of Fig. 2, and determined a threshold value of decrement for each of the five experimental conditions.* We defined threshold as the magnitude of decrement associated with the 75% point on the fitted functions (that is, halfway between chance and 100%). Figure 3 shows these thresholds, plotted relative to the threshold for the steady open eye. The height of each bar in the histogram indicates the magnitude of decrement that had to be added to the threshold decrement for the steady open eye in order for threshold

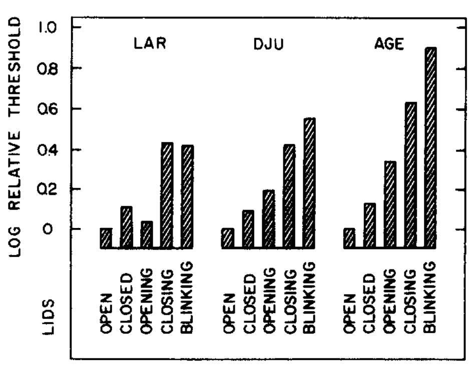

Fig. 3. Visual suppression during the eye opening, closing, blinking, or steady-eye conditions. For each of the three subjects the threshold with the steady open eye is used as a reference (Log $\Delta I/I = 0$) against which to plot the relative magnitudes of the other thresholds.

*Each linear function was fitted to data falling between the highest value of log $\Delta I/I$ at which a subject performed at chance and the lowest value at which the subject performed at 100%. All 15 of the r^2 values obtained with these analyses were above 0.84 and 10 were above 0.95.

accuracy to be achieved in each of the other conditions. Thus, the histogram shows relative suppression of vision in each condition.

Suppression is largest for the conditions of blinking, where the threshold is elevated by 0.42, 0.55 and 0.90 log unit for the three subjects, and lid closing, where elevations are 0.43, 0.425 and 0.63 log unit. Two subjects show a lesser amount of suppression during eye opening (0.19 log unit for D.J.U. and 0.34 log unit for A.G.E.); the third (L.A.R.) shows none. All subjects show a slight threshold elevation to decrements presented when the eye is steadily closed in comparison to when it is steadily open.† Using the steadily closed eye as a reference, suppression during blinks is 0.32, 0.46 and 0.65 log unit, respectively, for the three subjects.

DISCUSSION

The present results confirm and extend the results of our previous work on visual suppression during voluntary eyeblinks (Riggs *et al.*, 1978; Volkmann *et al.*, 1980). One subject, L.A.R., served in both experiments and showed the same amount of suppression (0.4 log unit) in each. The other three subjects, W.J.D. from the previous experiment and D.J.U. and A.G.E. from the present one, all showed larger amounts of suppression of 0.7, 0.55 and 0.9 log unit. Thus we may conclude that perception of the decremental stimulus due to blinks is typically reduced by about 0.6–0.7 log unit. This means that the decrement has to be about 5 times stronger during a blink than during steady fixation if it is to be visible.

The principal finding of the present experiment, that suppression is systematically more pronounced when the stimulus decrement is presented during blinking and lid closing than when it is presented during lid opening or steady fixation, is of theoretical interest. It is difficult to imagine how such a finding could be explained adequately by models of masking or of retinal shear. Masking effects should be essentially identical during the opening and closing conditions, since the stimulus arriving at the retina through the fiber optic bundle is the same. Retinal shear should be expected to be minimal in all conditions, based on the characteristics of eye motions that occur in blinking (see Introduction). Any residual increase in retinal noise, however, would be expected to be very similar for the opening and closing conditions, where we find systematic differences of 0.4, 0.36 and 0.56 log unit of decrement at threshold for the three subjects (Fig. 3). Our findings also argue against an explanation of suppression based upon increased uncertainty or shifts of attention during blinks. Such explanations clearly could not account for the systematic differences we have found between the opening condition and the closing and blinking conditions; uncertainty in these two conditions would be expected to be similar, as would the attentional demands of the tasks.

Certainly afferent effects such as masking or retinal noise, or central effects such as uncertainty, may play significant roles in saccadic suppression under certain stimulus conditions. The role of these mechanisms in blink-related suppression under conditions of normal vision is yet to be determined. The conditions of our experiments minimize the effects of these variables. We have concluded that under our conditions the parsimonious model for blink-related suppression, as well as for saccadic suppression, is that of a central neural inhibition of vision. It now appears that the blink-related neural inhibition is linked primarily to the efferent discharge to close the eye. We have shown previously that by the time the pupil is being uncovered again during the blink, suppression is substantially diminished (Riggs *et al.*, 1978; Volkmann *et al.*, 1980); our present finding that little effect on vision is measured when the lids open from a steady closed position is consistent with this previous result.

Viewed as an adaptive mechanism, blink-related suppression may be supposed to diminish the subjective impact of the blackout produced by occlusion of the pupil by the lids. The present results, by linking suppression primarily to lid closing, suggest a mechanism that not only minimizes the blackout but also enables rapid recapture of the visual scene as the eyes reopen.

†We have considered whether some small amount of the steady light from the fiber optic bundle might be emerging through the tissues at the front of the globe and entering the eye through the normal optical path in the open eye condition. We took pains to eliminate all forms of stray light such as this; the subjects wore both snugly fitting opaque swim goggles and black felt masks. In the apparatus, they could report no difference in the appearance of the stimulus with eyes open or closed. Nevertheless, the threshold difference persisted. Some subjects reported that keeping their eyes closed during the stimulus presentations seemed unnatural and required some effort. This might conceivably account for the slightly higher thresholds obtained with the eyes closed. If there were any light leakage from the fiber optic bundle into the front of the eye, it would affect the dynamic conditions of the experiment as well as the static ones. Specifically, it would slightly improve performance in the blinking and closing conditions (where the stimulus arrived prior to occlusion of the pupil by the descending lid) relative to the opening condition (where the stimulus arrived prior to the uncovering of the pupil by the ascending lid). Evidence from the two static conditions indicates that such an effect would be almost negligibly small, but would result in slightly larger amounts of suppression for the blinking and closing conditions than we have reported.

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