HUMAN VISUAL SUPPRESSION
FRANCES C. VOLKMANN
Department of Psychology, Smith College, Northampton, MA 01063, U.S.A.

INTRODUCTION
The history of research on visual systems, as abundantly illustrated in this Silver Jubilee Issue, is a history of the rejection of the naive realist's view that "we see the world as it is" (Holt, 1912). The selectivity of vision has emerged as a primary outcome of the evolutionary process. Human visual perception as we understand it is based upon mechanisms that create for us an information-laden visual world, a world that is not to be described by the characteristics of the stimulus environment alone. Our visual systems filter input based upon wavelength and spatial frequency in highly selective ways. Different mechanisms respond selectively to stimulus luminance and to the movement of contours across the retina. Enormous amounts of potential information are discarded in the adaptive interest of creating a perceptual world of objects, identifiable by their sizes, shapes, and hues, which may move through the larger visual environment in relation to our own movements of body, head, and eyes.

The phenomenon of visual suppression may appropriately be regarded as one means by which the visual system selects information. Stimuli which are perceived under many normal conditions are not perceived under certain conditions related to the temporal sequence of stimulation, the retinal areas stimulated, the form and luminance characteristics of the stimuli, and the oculomotor behavior of the perceiver.

Under this general definition we may include principally the decrease of vision associated with various oculomotor behaviors, some of which has been discussed also in the previous two articles. These include saccades, the brief, ballistic movements made by the eyes as we glance from one object to another in the visual scene; the fast phase of nystagmus, in which the eye follows a moving object by a series of relatively slow tracking movements interspersed by fast saccade-like return flicks; eyblinks of a pre-programmed, voluntary or reflex nature; and vergence movements, the slow disjunctive movements that align the two foveas to fixate objects at various distances. Such a definition of visual suppression may also include the decrease of vision in the fixating eye that occurs when the perception of a stimulus is masked by the presentation of another stimulus. Finally, it may include the phenomenon of rivalry, in which, in its principal form, vision is decreased in one eye when disparate images which cannot be fused are presented to the two eyes.

A more restrictive definition of visual suppression that is often used or implied in the literature limits the term to extraretinal neural events which act to decrease vision during saccades and other oculomotor behaviors (see E. Matin, 1974, 1982; Volkmann, 1962; Zuber and Stark, 1966). Such a definition excludes masking and other phenomena of visual impairment which result solely from the configuration and timing of stimulus events on the retina. The present paper adopts this latter definition to a limited degree. It reviews some of the major research that permits us to delineate the respective roles that retinal and extraretinal events play in the impairment of vision that accompanies a range of oculomotor behaviors. It, therefore, does not include suppression due to rivalry, and it includes only a specific subset of the literature on visual masking. Further, partly because of the enormous body of literature in the field, the paper concentrates on psycho-physical investigations of visual suppression using human observers. Readers interested in physiological investigations in other species may wish to consult, as a first step, the useful recent book, Visual Masking: An Integrative Approach, by Bruno Breitmeyer (1984).

SACCADE SUPPRESSION
Observations and theories prior to 1960
Almost a century ago, Erdmann and Dodge
FRANCES C. VOLKMAN (1898) reported that in a reading task, letters which reached an observer’s eye only during the brief saccadic jumps made by the eye as it moved along a line of print were not seen, and that all visual information from the printed line was acquired during the fixational pauses between saccades. There followed a series of experiments and observations by several investigators which showed that, typically, the eye is “functionally blind” during saccades, although given adequate liminance, stimuli presented only during saccades might be seen (Dodge, 1900, 1905; Holt, 1903, 1906; Woodworth, 1906; see E. Matin, 1974 and Volkmann, 1976 for reviews). Except under unusual circumstances (i.e. when the eye moves at the same speed as a bright stimulus exposed by a stroboscope), the stimulus, if seen, appears dim and blurred.

While the loss of vision during a saccadic eye movement was accepted by all of these early investigators, they disagreed as to the mechanism(s) responsible for it. Variations on the models which they proposed to account for suppression have in large measure set the framework for research in the field ever since.

Holt (1903, 1906) believed that vision was “blanked out” centrally in the brain during saccades by an “anesthesia” which originated in the neural impulses from the extraocular muscles. He believed the “anesthesia” to be essentially complete, and held that when an observer reports having seen a stimulus that appeared only during a saccade he is actually seeing an afterimage of the stimulus, which persists after the saccade has ended.

Dodge (1900, 1905) contended that both a central inhibitory process and peripheral, retinally originating processes contribute to visual suppression during saccades. He viewed the central effect in terms of “apperceptive predisposition and attention” (Dodge, 1900, p. 464) which causes the observer to ignore the dim blurred image on the retina during saccades. In addition, he postulated an equally important peripheral factor, which “consists in the inhibitive action of the new stimulation at each new point of regard” (Dodge, 1905, p. 197). As E. Matin (1974) has emphasized, this notion anticipates more recent attributions of saccadic suppression to phenomena of visual masking (see below).

Woodworth (1906, 1938) added his own experiments, criticized those of Holt and Dodge, and offered the most parsimonious model, which attributes saccadic suppression entirely to differences in retinal stimulation of the saccading and the fixating eye. “Vision with the rapidly moving eye,” he wrote, “does not differ essentially from vision with the resting eye, or with the eye which is making a ‘pursuit movement’—given only the same retinal stimulation in the three cases” (Woodworth, 1906, p. 69).

And there the matter stood for approximately half a century. The basic questions were framed, but the answers had to await the advances in quantitative methods and instrumentation that occurred many years later, primarily in the physical sciences and engineering.

To compare the perceptual effects of stimuli presented to the fixating and the saccading eye under conditions of equivalent retinal stimulation (i.e. comparable degrees of smear) required the development of accurate techniques for recording saccades in human observers, such as the techniques of corneal reflection, the electro-oculogram, and limbus, pupil, and eyelid tracking (Young and Sheena, 1975). It required the development of techniques of stimulus presentation, timing, measurement and control, so that stimuli reaching the saccading and the fixating eye could be equated, the precise time of arrival of a stimulus in relation to a saccade measured, and an appropriate independent variable such as stimulus luminance specified and varied. It required, finally, the development of appropriate psychophysical techniques for determining and evaluating the observer’s perceptual response (Green and Swets, 1966). In general, the recent work that has contributed most to the field is that which has moved the analysis toward the precise and systematic.

The last 25 years

The first quantitative comparison of visual thresholds during saccades and during fixation (Volkmann, 1962) and the first measurement of the time-course of visual suppression during saccades (Latour, 1962) were both reported in the same year, the latter in the second volume of Vision Research. My work, conducted in Lorrin Riggs’ active laboratory at Brown University, showed that under conditions of equivalent stimulation, a stimulus to the saccading eye had to have about three times the luminance of a stimulus to the fixating eye to produce a threshold response, a difference of about 0.5 log unit. But three times the luminance didn’t seem very impressive in light of the enormous range of luminances encountered in the visual world.
Latour's paper showed that suppression began prior to the onset of a saccade and lasted beyond its conclusion. It looked as if we had and extraretinally originating inhibition of vision, but that it must play a relatively minor role in the overall elevation of threshold that occurs during saccades in normal viewing.

Ahead lay the principal work of investigating the magnitude and the time-course of saccadic suppression using a variety of dependent variables and a host of independent variables related to the characteristics of stimuli and viewing fields, of eye movements, and of observer behavior. Ahead also lay the task of attempting to sort out and identify the retinal and extraretinal sources of suppression, based upon the findings of these investigations.

**Principal dependent variables.** In the human observer, the magnitude and time-course of saccadic suppression have been measured primarily using psychophysical threshold techniques. Many experiments have asked observers to indicate whether or not a briefly presented stimulus was seen when it was presented during saccades or during fixation. Others have employed a more sophisticated forced choice technique in which observers must judge which of two saccades or two periods of steady fixation was accompanied by the presentation of a stimulus. A number of experiments have used variants of these techniques to measure other dependent variables such as suppression of suprathreshold stimuli and several have investigated saccadic suppression of image displacement.

Objective techniques (Riggs, 1976), including measurement of the visual evoked response and the pupillary light reflex have also provided measures of suppression.

**Principal independent variables.** Four major classes of independent variables have received attention: (1) characteristics of the background field of view, including field luminance and the degree of homogeneity or pattern in the field; (2) characteristics of the stimuli to be discriminated, including luminance increments or decrements, the structure or pattern of the stimulus, spatial frequency, wavelength, retinal location, and displacement or smear of the image on the retina; (3) characteristics of the eye movements executed by the observer, including their velocity, amplitude and their voluntary/involuntary or active/passive nature; and (4) characteristics of the observer's attentional state or response criteria.

**Magnitude of suppression.** The luminance level of a homogeneous viewing field (Ganzfeld) determines importantly the magnitude of suppression (Brooks et al., 1980a; Brooks and Fuchs, 1975; Riggs et al., 1982b); the higher the luminance level, the larger the suppression. The Riggs et al. paper, for example, found threshold elevations during saccades of about 0.85 log unit at a field luminance of 30 ft-L and 0.40 log unit at 0.03 ft-L, using full-field decremental stimuli. Using incremental flashes under somewhat similar conditions, Brooks and Fuchs (1975) found threshold differences ranging from about 1.3 log units at high field luminances to about 0.1 log unit in darkness.

The question of whether saccadic suppression occurs in darkness has received special attention because of its importance in separating out retinally originating from extraretinally originating components of suppression. Many experiments have measured suppression in relative darkness (Brooks and Fuchs, 1975; Brooks et al., 1980a; Krauskopf et al., 1966; Latour, 1962, 1966; E. Matin et al., 1972; Mitrani et al., 1971; Pearce and Porter, 1970; Richards, 1969; Zuber et al., 1964; Zuber and Stark, 1966). Under these conditions several investigators have found no significant threshold elevations during saccades (Brooks and Fuchs, 1975; Brooks et al., 1980a; Mitrani et al., 1971; Richards, 1969). On the other hand, Riggs et al. (1974), using as stimuli electrically produced visual phosphenes in conditions of total darkness, found saccadic thresholds to be elevated by the equivalent of about 0.4 log unit of relative luminance.

The degree of homogeneity or contour in the background field is an important determinant of the magnitude of suppression. Further, there is an interaction between the characteristics of the background field and the characteristics of the stimulus to be detected. Contour in the background field raises saccadic thresholds substantially to punctate stimuli, while having less effect on thresholds to diffuse stimuli (Brooks and Fuchs, 1975; Brooks et al., 1980a; Mitrani et al., 1971; Richards, 1969). For example, Brooks and Fuchs (1975) found saccadic thresholds for spot stimuli on contoured backgrounds to be raised by more than 2 log units, as compared with about 0.4 log unit on a noncontoured background. Full field flashes produced a smaller effect of contour: threshold elevations were about 1.75 log units on contoured backgrounds and 1.4 log units on a noncontoured one. These investigators concluded that saccadic thresholds to diffuse stimuli are more regulated by field luminance while those to
punctate stimuli are more affected by field contour, with variations occurring as a function of stimulus size and the crispness of edges (see also Brooks and Impelman, 1981; Mitriani et al., 1971; Wolf et al., 1978; Zuber et al., 1966).

Some investigators have questioned whether, if saccadic suppression is attributable primarily to masking effects (see below), any suppression exists in conditions of genuine homogeneity of the background field. Even under carefully controlled Ganzfeld conditions (Volkmann et al., 1978a; Volkmann et al., 1978b), it is difficult to achieve a truly uniform field, and an observer may receive some small degree of stimulation from the defocused edges of the nose and orbits. To address this issue, Riggs and Manning (1982) employed translucent goggles to achieve a condition of complete "whiteout," and compared suppression of diffuse light decrements under these conditions with that measured in a more conventional Ganzfeld. They found comparable magnitudes of suppression in the two cases, with thresholds elevated by 0.7 to 1.1 log units during saccades.

Focusing on the characteristics of the stimuli to be discriminated, the magnitude of suppression has been found to be influenced by a number of features in addition to size, crispness of edges, and relative "diffuseness," as described above. Using sinusoidal grating stimuli superposed upon a background of equal space average luminance, Volkmann et al. (1978b) compared contrast sensitivity during saccades and during fixation using horizontal gratings which varied in spatial frequency. They found that the magnitude of suppression varied with the spatial frequency of the grating, with maximum suppression at low spatial frequencies where the least contour and the least effect of retinal image smear occur. A number of investigators have compared acuity thresholds for foveally flashed targets during saccades and steady fixation (Volkmann, 1962; Krauskopf et al., 1966), with findings of relatively small threshold elevations during saccades. Similar results have come from experiments measuring recognition of words or letters (Uttal and Smith, 1968; Volkmann, 1962).

Saccadic suppression of retinal image displacement has received considerable attention (Beeler, 1967; Bridgeman et al., 1975; Bridgeman et al., 1979; Bridgeman and Stark, 1979; Brooks et al., 1980; Lennie and Sidwell, 1978; Mack, 1970; Mack et al., 1978; Mackay, 1970c; Stark et al., 1976; Wallach and Lewis, 1965). Bridgeman et al. (1979), using stimuli of sufficient luminance to be visible during a saccade, showed that under optimal timing conditions, target displacements are not detected if the saccade exceeds about three times the extent of the target displacement, and the displacements of up to 4 deg arc are suppressed if they occur during a large enough saccade. Likewise, a number of investigators have shown that a brief target stimulus presented just before or during a saccade cannot be localized accurately in space (Mateeff, 1978; L. Matin, 1972, 1982; L. Matin et al., 1969; L. Matin et al., 1970; L. Matin and Pearce, 1965; Sperling and Speelman, 1966). This finding has important implications for theories regarding the determinants of suppression, to be discussed below (see also Hallett and Lightstone, 1976a, 1976b).

Saccadic suppression has been demonstrated with foveal stimuli (Beeler, 1967; Lederberg, 1970; Mitriani et al., 1970b; Richards, 1968; Uttal and Smith, 1968, Volkmann, 1962; Volkmann et al., 1978b) and with peripheral stimuli (Brooks and Impelman, 1981; Brooks and Fuchs, 1975; Latour, 1962, 1966; Pearce and Porter, 1970; Zuber and Stark, 1966). Returning to the interaction between stimulus and background field characteristics, Brooks and Impelman (1981) have found that a patterned background field significantly elevates thresholds during saccades for foveal stimuli but produces inconsequential elevations for stimuli presented at a retinal location 5 deg arc eccentric to the fovea (see also Mitriani et al., 1975).

Most of the experiments discussed above have been conducted under conditions designed to eliminate or minimize smear of the retinal image of the stimulus. This is important, of course, in order to equate stimulation of the saccading and the fixating eye (see E. Matin, 1974, pp. 904–905), and is most often achieved by using very brief (microsec duration) stimulus flashes or stimulus configurations in which saccades cannot produce significant image smear (see Volkmann, 1976). It is possible, however, to evaluate independently the loss of vision attributable to image smear and that attributable to other sources (Mitriani et al., 1970a, 1971; Volkmann et al., 1978a). It is obvious that image smear plays an important role in suppression of stimuli that arrive during saccades in normal photopic vision in a structured environment. As well, it is clear that saccadic suppression is not eliminated under conditions in which image smear does not occur.
The characteristics of the saccades during which suppression is measured are, as might be expected, important determinants of the magnitude of suppression. Suppression increases as a function of amplitude for voluntary saccades (Bridgeman et al., 1975; Brooks et al., 1980a; Latour, 1966; Mitrani et al., 1970; Stevenson et al., 1986; Volkmann et al., 1981). In the latter experiment, suppression ranged from about 0.7 log unit for 2 deg arc saccades to about 1.05 log unit for 32 deg arc saccades under the same viewing conditions. There has been some disagreement about whether suppression also accompanies the small involuntary ficks of the eye that occur during normal fixation (see Steinman et al., 1973). Krauskopf et al. (1966) report no suppression, while Beeler (1967). Ditchburn (1955), Ebberts (1965), and Zuber and Stark (1966) report evidence of suppression. Quantitatively, Beeler’s results indicate a magnitude of suppression of approx. 0.5 log unit of relative luminance during ficks of an amplitude of about 30' arc or smaller. Finally, suppression has been shown to accompany the fast phase of optokinetic nystagmus (Latour, 1966), vestibular nystagmus (Zuber and Stark, 1966), and voluntary nystagmus (Nagle et al., 1980). Voluntary nystagmus has been shown to be essentially saccadic in nature (Shunts et al., 1977), and it seems reasonable to believe that the other types of nystagmus are saccadic also in the fast phase (see Bahill et al., 1975). Quantitatively, Nagle et al. (1980) found average threshold elevations of 0.53 log unit of relative luminance for stimuli presented during the fast phase of voluntary nystagmus.

Several investigators have measured the magnitude of suppression as affected by the observer’s direction of attention or by his or her criteria of responding. Lederberg (1970), for example, addressed the question of whether the elevation of saccadic over fixating eye thresholds might be due in part to the observer’s attending to executing the voluntary saccade rather than to the stimulus to be discriminated. She substituted a voluntary hand-movement for the saccade and found no elevation of visual threshold (see also Greenhouse et al., 1977; Latour, 1966; Mitrani et al., 1973). Pearce and Porter (1970) addressed the possible effect of changes in the observer’s response criteria. They found a somewhat larger magnitude of suppression with bias-free forced choice psychophysical procedures than with yes-no procedures. While a wide variety of psychophysical procedures are applicable in this field, one cannot fail to note in re-reading the literature that there has been an insufficient attention to using sound psychophysical procedures and to evaluating experimental results in terms of the procedures used.

Time-course of suppression. Most experiments conducted to map the time-course of saccadic suppression have used a frequency of seeing technique in which a single value of stimulus luminance that is just always visible to the fixating eye is delivered on many trials in various temporal relations to the onset of a saccade, and the observer reports after each trial whether or not he detected the stimulus (Beeler, 1967; Brooks et al., 1980a; Brooks and Fuchs, 1975; Latour, 1962, 1966; Lederberg, 1970; Mitrani et al., 1970b; Pearce and Porter, 1970; Richards, 1969; Volkmann et al., 1968; Zuber and Stark, 1966). The time-course of suppression has also been assessed using suprathreshold stimuli and a psychophysical matching procedure (Riggs et al., 1982b), and by measurements of forced choice psychophysical thresholds for stimuli of varying contrast, delivered at a range of times in relation to saccades (Volkmann and Moore, 1978; Volkmann et al., 1978a). In addition to psychophysical methods of assessment, several experiments have used the visual evoked response (a method to be described in the next section of this issue) to estimate the time-course of suppression (Brooks, 1977; Chase and Kalil, 1972; Duffy and Lombroso, 1968; Gross et al., 1967; Michael and Stark, 1976; Starr et al., 1969; Vaughan, 1973).

By whatever measures used, results show that saccadic suppression begins to appear for stimuli delivered prior to the onset of the saccade. It reaches a maximum (i.e. a minimum frequency of seeing) for stimuli delivered during the saccade, and gradually dissipates over several tens of milliseconds after the saccade has ended [see Fig. 1(A)]. In describing the time-course in these terms, it is important to remember that we are relating the perceptual response to the time of arrival of a stimulus to the eye in relation to the onset of a saccade. If suppression is in fact a central neural event, the specification of its actual time course would require knowledge of the transmission times for the neural response to the stimulus to reach the site of suppression. The precise time course depends importantly, as one would expect, upon the characteristics of the background field, the adaptation of the eye, the characteristics of the stimulus, the location
Fig. 1. Examples of the time-course of suppression associated with a variety of oculomotor and ocular events. (A) Suppression of vision of brief flashes of light presented in temporal proximity to 6 deg voluntary saccades under photopic viewing conditions for three observers (replotted from Volkmann, 1962); (B) suppression of vision of brief flashes of light presented in temporal proximity to involuntary flicks of the eye under scotopic viewing conditions for two observers (replotted from Beirer, 1967); (C) suppression of vision of brief flashes of light presented in temporal proximity to the fast phase of postrotary vestibular nystagmus (replotted from Zuber and Stark, 1966); (D) suppression of vision of brief light decrements presented in temporal proximity to reflex eyeblinks elicited by an air puff to the cornea (replotted from Manning et al., 1983); (E) suppression of vision (circles) and of the pupillary response (triangles) to brief light flashes presented in temporal proximity to 6 deg voluntary saccades. Though superposed in this figure for comparative purposes the pupillary responses is actually delayed (replotted from Zuber et al., 1966); (F) suppression of vision of a briefly flashed target presented to the fixating eye in temporal proximity to a saccade-like movement of a background field (replotted from MacKay, 1970a).

In all examples except (D), the dependent variable is the percentage of trials on which a stimulus is seen; a single value of stimulus luminance is chosen which is just above threshold for the fixating eye. In example D, quantitative measurements of sensitivity have been derived using a forced choice psychophysical procedure. The independent variable in all examples is the time of occurrence of the stimulus in relation to the onset of the eye movement, eyeblink, or displacement of the background field.

of the stimulus on the retina, and the amplitude of the saccade.

The luminance of the background field appears to be an important determinant of time-course. While the magnitude of suppression decreases at low luminance levels, its time-course becomes broader. Using a suprathreshold matching technique, for example, Riggs et al. (1982b) found that at a field luminance of 30 ft-L the time-course of suppression to a full-field decrement was quite steep, with a maximum at 0–10 msec after saccade onset. At a field luminance of 0.03 ft-L, the time-course was much broader, showing an earlier onset of suppression and a broad maximum from about 20 msec before to about 30 msec after the beginning of the saccade. Saccade duration was approx. 40 msec. Volkmann et al. (1968) have argued that peripheral stimuli or stimuli delivered to the eye under conditions of dark adaptation should require a longer processing and transmission time than foveal stimuli that are viewed under conditions...
of light adaptation. If one assumes that suppression is mediated by a central or extraretinal inhibitory effect, the time-course of suppression should appear to begin earlier prior to saccade onset in the scotopic situation.

Various characteristics of the stimulus that are important determiners of the time-course of suppression include luminance, retinal location, size and contour, and wavelength. Zuber and Stark (1966) noted that in the dark adapted eye, the duration of suppression is inversely related to the intensity of the stimulus, with suppression to dim stimuli beginning earlier in relation to saccade onset, showing longer and broader maxima, and declining in about the same temporal relation to the saccade as suppression to brighter stimuli. Brooks and Fuchs (1975) also found broader suppression curves with dimmer stimuli, but their experiment also showed slower recovery from suppression under these conditions. Mitrani et al. (1970b) found that the time-course of suppression is different for stimuli falling on different retinal locations, but the precise relations must depend on the adaptation level of the eye and the size and contour of the stimuli (see also Latour, 1966). Lederberg (1970), using a wavelength discrimination task, found that the time-course of suppression varies with the wavelength of the test stimulus, with maximum suppression occurring for red and green stimuli presented during saccades and for blue stimuli presented 40–80 msec after saccade onset (see also Richards, 1968).

The time-course of suppression varies as a function of saccade amplitude (Mitrani et al., 1970; Brooks et al., 1980a; Stevenson et al., 1986; Volkmann et al., 1981). Stevenson et al. (1986) found that the onset of suppression prior to saccades of 2 and 32 deg arc followed a similar time course, but for the large saccade maximum suppression lasted somewhat longer and the recovery of sensitivity was slower. It is clear, however, that neither the magnitude nor the time-course of suppression is tightly linked to saccade amplitude; as Beeler (1967) has shown, substantial amounts of suppression accompany microsaccades, and the period of time around the saccade during which there is some loss of sensitivity may be as long as 100–200 msec [see Fig. 1(B)].

Lorber et al. (1975) have reported suppression of the pupillary light reflex during saccades, with a time-course similar to that determined psychophysically. An example of their results is shown in Fig. 1(E).

**VISUAL SUPPRESSION DURING NONSACCADIC EYE MOVEMENTS**

Several experiments have investigated visual suppression during types of eye movements other than saccades. While suppression does not appear to accompany smooth pursuit eye movements (Starr et al., 1969), it has been shown to accompany passive eye movements and the eye movements of vergence.

Richards (1968) reported small but similar elevations in threshold during voluntary saccades and during passive movements of the eye produced by tapping the eyeball near the outer canthus (see also Helmholtz, 1963). Suppression thus appears to exist in the absence of a possible centrally originating corollary discharge that might accompany the neural signal for a saccade (see below).

Manning and Riggs (1984) have now extended the investigation of visual suppression to vergence movements. Using full-field luminance decrements as stimuli in a photopically illuminated Ganzfeld, they found thresholds to be elevated over those for steady fixation by about 0.5 log unit when the stimuli were presented near the beginning of a 2–3 deg convergent or divergent eye movement. They suggest that "saccadic suppression may be only one example of a more generally occurring phenomenon of visual suppression associated with eye movement initiation" (Manning and Riggs 1984, p. 524).

**VISUAL SUPPRESSION DURING EYEBLINKS**

Eyeblinks, like saccades, produce momentary interruptions of vision at least every few seconds. Moreover, while a typical mid-sized saccade lasts only about 30 msec, the time during which the pupil is occluded and vision thereby interrupted during a normal blink is 100–150 msec. Yet we are seldom aware of this blackout due to blinks. This observation has led to several investigations of visual suppression during eyeblinks. Volkmann et al. (1980) used a technique to bypass the eyelids and deliver comparable stimuli to the retina during fixation and during voluntary eyeblinks. They found thresholds to brief full-field decrements in otherwise steady retinal illumination to be increased by 0.4–0.7 log unit during voluntary blinks (see also Riggs et al., 1984). Although certain deflections of the eye may accompany blinks (Collewijn et al., 1985), the threshold elevation seems unlikely to be attributable to such eye movements.
Riggs et al. (1981) used a suprathreshold matching procedure to estimate the visual effects of a blink and to compare the effects of real blinks with those of simulated blinks produced by light decrements in a Ganzfeld. Blink-related visual suppression was evaluated by comparing the decrements under the two conditions when the observer judged them to be equal. Magnitudes of suppression ranged from 0.5 to 1.0 log unit at a photopic Ganzfeld luminance and from 0.3 to 0.7 log unit at a scotopic Ganzfeld luminance. Thus, the magnitude of suppression during voluntary eyeblinks is similar to that often reported during saccades. As well, it shows a similar variation with the level of background illumination. Riggs et al. (1982) showed a suppression of the pupillary response using a similar procedure. In a further analysis, Volkmann et al. (1982) measured the magnitude of suppression during each of the major activities performed by the eyelids during blinking. They found suppression to be primarily related to lid-closing, and insignificantly related to lid-opening.

Visual suppression accompanies spontaneous and reflex blinks as well as voluntary blinks (Manning et al., 1983a,b). The magnitude of suppression is similar in the two cases; for reflex blinks it is about 0.2–0.5 log unit, using the technique of bypassing the eyelids developed by Volkmann et al. (1980) and eliciting blinks by means of an airpuff to the cornea.

Visual suppression during eyeblinks follows a time-course similar to that of suppression accompanying saccades (Volkmann et al., 1979; White et al., 1984), although this comparison is very general since, as shown above, the precise time-course of saccadic suppression varies with experimental conditions. Investigations to date have not sampled sensitivity at intervals spaced sufficiently close to map the fine structure of the time-course of suppression, but the general form of the curves can be seen in Fig. 1(D). Suppression begins for test stimuli presented prior to blink onset, and may even reach a maximum value by 30–40 msec before the upper lid begins to cover the pupil. This very early onset of suppression measured psychophysically implies a long latency for the neural response to the weak test stimuli to arrive at the site of suppression in the brain. Recovery from suppression is gradual over a period of 100–200 msec after blink onset. Since, as noted above, blinks tend to be of substantially longer duration than saccades, the similar time-course of visual suppression in the two cases must mean that the eye has regained its sensitivity sooner after the completion of a blink than after the completion of a saccade.

**VISUAL MASKING**

Eye movements, blinks, and movements of the head and body continuously translate even constant physical stimuli into a series of transient retinal stimuli (Matin, 1975). An understanding of the visual effects of transients is therefore basic to our understanding of visual processing, and a large body of research has developed in this field, much of it in the last 25 years. This research can be characterized as measuring changes in the response to a briefly presented target stimulus as a function of another stimulus that is also presented briefly in some specified temporal and spatial relation to the target. The term visual masking refers to the destructive interaction or interference that is typically measured in experiments of this kind. It is beyond the scope of this paper to attempt a summary of results in this complex field, but a number of excellent reviews are available (Breitmeyer, 1980, 1984; Breitmeyer and Ganz, 1976; Fox, 1978; E. Matin, 1975).

**Metacontrast**

Visual interference that is produced with respect to a target stimulus by a masking stimulus which follows it in time and which stimulates a non-overlapping retinal location is termed metacontrast. This particular form of backward masking has received a great deal of attention in the literature (for reviews, see, in addition to those cited above, Alpern, 1953; Bridgeman, 1971; Lefton, 1973; Weisstein, 1972). In addition to being an interesting field of investigation in its own right, metacontrast is of special interest because of its relation to research on saccadic suppression (Alpern, 1969; E. Matin, 1974; see also Dodge, 1900). According to the metacontrast paradigm, when the eye executes a saccade, conditions are set up by which the image of the object of fixation at the end of the saccade may interfere with perception of the blurred streak that might otherwise be visible during the saccade. Ethel Matin explicitly raised the possibility “that the lateral masking ordinarily studied in the laboratory is only a weak case of a much more powerful phenomenon and that we must look at the image generated on the retina by the saccading eye for the optimal
stimulus for masking” (Matin, 1974, p. 907).

Investigations of masking in relation to saccadic suppression have taken several forms. In a relatively early experiment, E. Matin et al. (1972) stimulated the horizontally saccading eye with a vertical slit of light at luminances high enough to be visible in the dark, and varied the duration of stimulation. They found that when stimulation ended prior to the conclusion of the saccade, the observer reported having seen a blurred streak of light and could estimate its length by means of a comparison stimulus. With longer stimulus exposures which extended into the period after the saccade, the streak appeared shorter and dimmer until, with sufficiently long presentations, the observer saw no streak at all but only the sharply defined light slit. The clear, relatively brighter (on any given photoreceptor) slit visible at the end of the saccade thus appeared to mask the blurred streak during the saccade; this streak would otherwise have been visible. In a similar experiment, Campbell and Wurtz (1978) illuminated a contoured visual scene for various durations of time before, during and after saccades and found evidence of both forward masking and metacontrast. They suggest that the term “saccadic omission” is more descriptive of these effects than the term “saccadic suppression.” Corfield et al. (1978) went on to simulate with the fixating eye the retinal events associated with saccades by presenting a blank field of short but variable duration bracketed in time by vertical gratings of space average luminance equal to that of the blank. They found that with high spatial frequency gratings, blank field durations as long as 350 msec may not be perceived.

A substantial number of experiments have demonstrated that saccadic suppression can be simulated by presenting to the fixating eye a target stimulus in close temporal proximity to a rapid displacement of a background field. Both the magnitude and the time-course of the masking effects produced with this paradigm are within the range of those measured for saccadic suppression (Brooks and Fuchs, 1975; Brooks and Impelman, 1981). The characteristics of the background fields used have been quite varied. Brooks and Fuchs (1975) and Brooks et al. (1980a) included in their studies large background fields which were uniform except, sometimes, for fixation points, and which were varied in luminance. Their results showed similar elevations of threshold whether the eye moved across the background in a saccade or the background was displaced in a saccadic fashion across the retina of the fixating eye. Thresholds increased as a function of field luminance, and the increase was larger for large or full-field test stimuli than for small stimuli. Brooks et al. (1980a) found similar threshold elevations when the background was momentarily brightened rather than displaced. As an example of the threshold elevations measured, Brook and Fuchs (1975) found, under comparable conditions for two subjects, elevations of 0.80 and 0.95 log unit of luminance for diffuse stimuli presented during saccades, and 0.79 and 0.88 log unit for the same stimuli presented to the fixating eye during displacement of the background field.

A number of studies have used contoured or patterned background fields. The contour may be provided only by the edges of the field (Mackay, 1970a) or may be introduced in the form of gratings (Breitmeyer and Valberg, 1979; Brooks and Fuchs, 1975; Brooks and Impelman, 1981; Mateeff et al., 1976) or other patterns (Brooks and Fuchs, 1975; Mitrani et al., 1971) located in the periphery of the visual field. Results show a pronounced elevation of threshold as a function of the movement of contours across the retina of the fixating eye. In a comparison experiment, for example, Brooks and Fuchs (1975) found that detection threshold for a stripe stimulus presented on a striped background increased by 2.15 log units when the stimulus was delivered during a saccade, and by 2.27 log units when the stimulus was delivered to the fixating eye during displacement of the background.

Lateral masking effects are typically considered to operate over a maximum distance on the retina of 2–3 deg separation between the target and the mask (Breitmeyer, 1984). The type of peripheral stimulation provided by the background contours in many of the above experiments, however, produces a substantial elevation of threshold for foveal stimuli, even though the contours may lie in a remote retinal location (Breitmeyer and Valberg, 1979). This effect,
termed the "far-out jerk effect" by Breitmeyer and Valberg, is found only in the fovea. It may well be an important determinant of threshold elevations measured for stimuli delivered during saccades across highly contoured visual fields under photopic conditions of vision.

The time-course for masking, like that for saccadic suppression, varies with intensity of the test stimulus (Brooks and Fuchs, 1975), with the angular displacement of the background contour (Brooks et al., 1980b; Mateeff et al., 1976), and with the luminance of the background field (Brooks and Fuchs, 1975; Brooks et al., 1980a). In the case of fields consisting of gratings, it varies as well with the spatial frequency of the gratings (Corfield et al., 1978; Mitrani et al., 1975; Mateeff et al., 1976).

**DETERMINANTS OF VISUAL SUPPRESSION**

The research of the last 25 years has both clarified and complicated the theoretical issues raised by the early investigators. With respect to saccadic suppression, we are much better able to delineate the conditions under which threshold elevations associated with saccades may be attributable to events originating in the retina and events originating extraretinally or centrally in the brain: I think that most investigators are moving away from the type of dichotomous thinking that attempts to account for all of the findings with one mechanism. At the same time, the extension of research on saccadic suppression to nonsaccadic eye movements and to eyeblinks has complicated the matter considerably. On the one hand, one cannot help but note the remarkable similarity in both magnitude and time course between saccadic suppression and suppression accompanying these other quite different activities. This similarity might lead one to suspect that all of these types of suppression are mediated by common mechanisms. On the other hand, some of the mechanisms that seem to offer considerable explanatory power for describing saccadic suppression, such as some of the afferent mechanisms elaborated below, do not work well for explaining other forms of suppression. We do not yet know to what degree common mechanisms may mediate the various forms of suppression. It is therefore productive to see how well the major mechanisms proposed to account for saccadic suppression also account for the other forms.

**Retinal mechanisms**

**Masking.** The similarity in both magnitude and time-course of threshold elevation produced by masking and by saccadic suppression has led a number of investigators to conclude that saccadic suppression can be accounted for largely or entirely in terms of events that originate in the retina (Brooks and Fuchs, 1975; Brooks and Impelman, 1981; Brooks et al., 1980a; Campbell and Wurtz, 1978; Corfield et al., 1978; Mitrani et al., 1971; Mitrani et al., 1975).

It is clear that the rapid movement of luminance gradients or contours across the retina, whether produced by saccades or by displacement of the visual field, results in comparable changes in perception. As well, stimuli reaching the stationary eye just after the conclusion of a saccade may interfere with perception of stimuli which might otherwise have been visible during the saccade. Masking effects, therefore, undoubtedly play a primary role in threshold elevations which accompany saccades in lighted, contoured environments. It is equally clear, however, that saccadic suppression can be shown to exist under experimental conditions in which masking effects are minimized, such as in lighted Ganzfeld where no abrupt luminance changes occur (Riggs and Manning, 1982; Volkmann et al., 1978b) or in total darkness (Riggs et al., 1974). Further, masking would be expected to have little effect during microsaccades, slow convergence or divergence movements, or eyeblinks made in darkness. Masking effects, important as they are, may thus account for visual suppression only under a limited range of conditions. Breitmeyer (1984) has proposed a neurophysiological model for masking that is based upon inhibitory effects mutually exerted by transient and sustained neural channels. He views these afferent effects as working in conjunction with a central or efferent corollary discharge to produce the threshold elevations that we call saccadic suppression (see Breitmeyer, 1984, pp. 324-335).

**Effects of rapid retinal image motion.** The rapid sweep of the image of a stimulus across the retina during a saccade may act in two obvious ways to decrease vision of the stimulus. First, unless the stimulus is presented very briefly, its image is smeared across the retina so as to be substantially unidentifiable. Second, the saccade has the effect of decreasing the duration of stimulation on each retinal receptor. For brief durations of stimulation, time and inten-
Human visual suppression

sity are reciprocally related for a given photo-
chemical effect; therefore, decreasing the dur-
ation of stimulation decreases the effective
stimulation at the receptor (Bloch's law). Thus,
under normal conditions of viewing, a stimulus
may not be noticed during a saccade both
because it is smeared and because its effective
brightness is reduced.

Saccadic suppression, however, is not elimin-
ated by the use of very brief test flashes or
other stimulus arrangements which minimize
the effects of the rapid eye movement (Mitrani
et al., 1970a; Volkmann, 1962; Volkmann et al.,
1978a). Smear or reduced photochemical effects
could also not account for the elevation of
threshold that precedes and follows saccades or
for the elevation of threshold accompanying
vergence movements or eyeblinks.

Shearing forces in the retina. A model of
saccadic suppression that has been often cited
but little investigated is that of Richards (1968,
1969). He suggested that a saccade has an
effect on the eyeball similar to rapidly rotating
a bowl of jelly; different intraocular materials,
including different layers of the retina, might be
expected to accelerate and decelerate at different
relative velocities. Thus mechanical shearing
forces are set up which may disrupt the process-
ing of neural signals. More specifically, under
conditions of light adaptation these forces could
raise the level of background noise in the retina
at times during and near a saccade, and could
thus interfere with perception of a test stimulus.

Results of experiments which show an increase
in the magnitude and duration of suppression
with an increase in saccade amplitude are to
some degree consistent with Richards' model.
Shear, however, would be expected to be deter-
mined by acceleration, and the magnitude of
suppression does not vary linearly with accelera-
tion. Further, Richards' model would not pre-
dict threshold elevations to stimuli presented
during microsaccades [see Fig. 1(B)] or during
saccades in total darkness, and does not seem
relevant to experiments showing suppression
during vergence movements or eyeblinks.

Extraretinal mechanisms

Retinal mechanisms of suppression are best
investigated by presenting to the fixating eye
stimulus situations in which the effects of condi-
tions such as masking the retinal smear can be
evaluated separately from any central
efferent effects. Conversely, extraretinal
mechanisms are best illuminated by presenting
to the moving or blinking eye stimulus
situations in which these retinal effects are
minimized or eliminated. Unfortunately, many
experiments have confounded the delineation of
extraretinal mechanisms by measuring
suppression under conditions in which these
mechanisms cannot be separated from retinally
originating mechanisms.

As reviewed above, the results of carefully
controlled experiments which minimize or
eliminate the effects of afferent mechanisms
show significant suppression of vision during
saccades, vergence movements and blinks. Such
results have typically been interpreted as
supportive of the notion of an extraretinally
originating neural inhibitory mechanism which
acts to decrease visual sensitivity during these
behaviors.

Holt (1903; see also Sherrington, 1918)
attributed this neural suppression to signals
originating in the extraocular muscles; this
model has since come to be known as "feed-
back" or "inflow" theory. Without additional
reliance upon afferent mechanisms such as
masking, inflow theory is not supported by
evidence regrading the temporal characteristics
of suppression, particularly the onset of sup-
pression prior to the onset of activity in the
extraocular muscles. Inflow from the extra-
ocular muscles may, however, provide informa-
tion regarding eye position that is used in the
maintenance of visual stability (E. Matin, 1974,
1982; see also Shebilski, 1977).

The general model of neural inhibition that
describes many of the experimental results has
come to be referred to as an "efferent,"
"outflow" or "feedforward" theory, in which a
signal originating in the brain and associated
with the central command to the extraocular
muscles feeds forward to inhibit visual
perception at some central site in the visual
system. The "outflow" theory is based upon
Helmholtz's "effort of will" (Helmholtz, 1963),
von Holst and Mittelstaedt's "Efferenzkopie"
(von Holst and Mittelstaedt, 1950; von Holst,
1954), and Sperry's "corollary discharge" (CD)
(Sperry, 1950). One form of the theory is dia-
agrammed in Fig. 2. Here, the oculomotor com-
mand signal gives rise to an "efference copy" or
corollary discharge of equal and opposite sign
to the "reafference" signal arising from changes
in retinal stimulation that occur as a result of
the saccade; the two signals combine to cancel
the effects of the changes, all at the unconscious
level. Thus the "efference copy" or "corollary
discharge" may in general be envisioned as an extraretinal signal that informs the visual system of the intended position of the eye (Bridgeman and Fishman, 1985; Skavenski, 1972; Skavenski et al., 1972; Stark, 1983; Schiller, this issue).

It is possible to study situations in which a mismatch exists between the CD and the afferent signals from the retina. Helmholtz (1963) pointed out that patients with oculomotor paralysis reported a shift in the location of visual images when they tried unsuccessfully to move their eyes. Further study by L. Matin et al. (1982, 1983) with subjects under the effects of systemic D-tubocurarine showed that the effect of CD depended on the conditions of visual stimulation. They instructed observers to try to fixate with the paralyzed eye a display of illuminated points located at a constant offset from the primary position, producing a constant CD (or "effort of will"). Under these conditions, perception of straight ahead was normal as long as a structured visual field was present; the extraretinal signal was superseded by the visual field stimuli arriving at the retina. When structure was removed from the field, however, the illuminated points appeared to the subject to drift in the direction of the deviated CD; the CD became the predominant factor in determining the perception of location.

Another manipulation which has been used to induce a mismatch between CD and eye position is the eyepress. Subjects are asked to monocularly fixate a target, and then the eye is moved passively by pressing upon the outer canthus or lower lid. The extra innervation required to maintain fixation reflects an increase in CD. The eyepress produces a perception of target movement, which can be attributed to the mismatch between the CD and the retinal signals. If the subject's other eye is occluded, a deviation in the occluded eye can be recorded as the result of the binocular change in innervation to the oculomotor muscles to counter the effect of the eyepress (see Bridgeman, 1979; Bridgeman and Delgado, 1984; Bridgeman and Fishman, 1985; Post et al., 1984; Skavenski et al., 1972; Stark and Bridgeman, 1983).

Since classical CD theory postulates that the perception of stability in the visual world is based upon a match between the CD and the afferent signals generated by the shift in the retinal image during a saccade, it cannot adequately explain the findings that displacement of a target stimulus that occurs during a saccade is not perceived. MacKay (1972, 1973) has proposed a modified form of the theory, in which the extraretinal signal simply informs the system of an eye movement, and any resulting image movement which is roughly consistent with the extraretinal signal is interpreted as a movement of the eye rather than as a movement of the visual world.

Bridgeman and his collaborators have recently questioned all theories which treat visual stability as a single vector, and have presented data to support the hypothesis that stability is determined by cognitive, attentional variables rather than by oculomotor properties (Bridgeman, 1981; Bridgeman et al., 1979).

A commonly held view is that one of the means by which CD maintains visual stability and direction constancy is saccadic suppression. E. Matin (1974, 1976, 1982) has proposed a dual mechanism theory of direction constancy in which the first mechanism is a saccade-contingent compensatory shift produced by an
extraretinal signal in the perceived direction (or directional local sign) of a stimulus. Imperfections exist in this system, however, and the time-course of the shift does not follow precisely the time-course of the saccade (see Shebilske, 1976, 1977). Yet the visual world appears stable. Matin envisions saccadic suppression as the second mechanism, contributing to visual stability by preventing the perception of stimuli received during the transient period just before, during and after a saccade, when the mismatch between the compensatory shift and the retinal stimulation would otherwise destabilize perception of an objectively stable world. She supports the notion that an extraretinal signal provides a portion of the basis for saccadic suppression, but explicitly leaves open the question of whether this signal might be the same signal as that which produces the compensatory shift in local sign.

Matin suggests that the results of Nagle et al. (1980), which show both suppression and oscillopsia during voluntary nystagmus, may indicate that the two extraretinal factors are in fact different (E. Matin, 1982). An alternative explanation is possible, based upon the hypothesis that (a) there is a loose rather than a tight linkage between the CD and the eye movement and (b) the duration of suppression exceeds the intersaccade interval for voluntary nystagmus. Under these conditions, a stimulus sufficiently bright to be seen during nystagmus might well be expected to be perceived as jumping back and forth.

The linkage between suppression and the CD clearly seems to be loose rather than tight. Such a notion is supported by the results of experiments which show that the magnitude and time course of suppression do not increase linearly with increases in saccade amplitude. As well, it is supported by the findings of comparable magnitude and time-course of suppression during oculomotor behaviours of quite diverse durations, namely saccades, vergence movements, and blinks (see Fig. 1).

CONCLUSIONS

The perception of a stable visual world requires a system that discriminates between image motion on the retina that is produced by movements of the eyes and image motion that is produced by movements of external objects. The perception of a clear and continuous visual world requires a system that ignores blurred images produced by retinal motion and momentary interruptions of vision produced by eye-blucks. To meet these requirements, the human perceptual system has evolved both afferent and efferent selective mechanisms, including mechanisms of visual suppression of stimuli which would otherwise interrupt or destabilize perception. These mechanisms, taken together, operate over the entire dynamic range of vision and in every possible stimulus environment with the effect of selectively discarding information that might lead to maladaptive responses. They operate with every blink, with every change in fixation from a near to a far object or the reverse, and with every glance from one object to another in the visual scene.

We know more about the retinal mechanisms than we do about the extraretinal ones, and more about their perceptual consequences than about their physiological foundations. Undoubtedly, in the next 25 years the precise relations among the mechanisms and the different levels of analyses of the systems will be illuminated much further.

Those of us who have worked in this field over the last 25 years have experienced the rewards of solving small pieces of an enormously complex puzzle, and of imagining how our pieces fit with others into a coherent whole. For myself, perhaps the greatest reward has been to learn about a beautiful and intricate adaptive system and to come to appreciate increasingly the evolutionary processes through which it evolved.

REFERENCES


