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DISINHIBITION IN HUMAN VISION

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ABSTRACT

Recent electrophysiological and psychophysical data have suggested that within the human visual system there exists specialised neural units which respond maximally to specific orientations. This suggestion is based upon electrophysiological data recorded from orientation specific neurons in the cortex of the cat and monkey, and psychophysical studies of normal observers.

Following a review of this literature three psychophysical paradigms (masking, aftereffect, and dichoptic aftereffect) were utilized to investigate disinhibition of orientation analyzers in humans.

Chapter two examined the spatial selectivity of the disinhibition function with successive presentation of two masking gratings. The results indicated that, for a vertical test stimulus, disinhibition was maximal when the orientations of M1 and M2 were similar and was minimal when the orientational difference was greater than 15 deg.

Chapter three investigated disinhibition in the orientation aftereffect, following both successive and simultaneous presentation of two adaptation gratings. The results showed that regardless of the temporal sequencing the addition of a second grating could either disinhibit or summate the magnitude of the aftereffect. Generally, interaction was maximal when when the orientation difference between the gratings was 15 deg.

Dichoptic presentation of stimuli (chapter four) demonstrated that orientation disinhibition may be a high level effect at least parallel to that of binocular rivalry. The results indicated firstly that disinhibition and summation were maximal when the orientation difference between the gratings was 15 deg and secondly that these functions could not be disrupted by binocular rivalry.

The results of this thesis are in keeping with a lateral inhibition explanation of orientation disinhibition. This lateral inhibition system is consistent with a general feature detection model of visual perception which is known to exist in humans.

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1.0.0 Physiological strategies for studying vision.

An important step in developing and testing theories of visual phenomena often involves determining the mechanisms of neural processes underlying visual phenomena. However in the case of human vision direct access to the nervous system is not possible so it is necessary to resort to more indirect techniques and strategies, and rely on generalization from physiological data obtained from animals. This type of research centres on electrophysiological confirmation of neural responses to various types of visual stimuli.

The dominant theory of visual pattern analysis for the last 20 years has been a model of hierarchial feature detectors which had it's inception in the early reports of Hubel and Wiesel (1959, 1962, 1965, 1968) concerning the receptive fields of cortical cells in animals. Their major findings, using microelectrodes placed into single cells, suggested that neurons in both the cat and monkey responded preferentially or exclusively to spatially structured stimuli. Specifically, neurons seemed to have stimulus orientation preferences and seemed to respond to bars (dark) or slits (light) of specific widths or to edges of particular orientations. Numerous research from animals, for example on cats, monkeys, rabbits, pidgeons, and squirrels, has shown such orientation selectivity to be an apparent fundamental part of vertebrate vision (Levick, 1967; Maturana & Frenk, 1963; Micheal, 1972).

The possibility that our own visual system may contain similar mechanisms to those found in animals is an exciting one for the analysis of visual perception. This has produced numerous human psychophysical experiments to explore this proposition (e.g., Carpenter & Blakemore, 1973; Campbell & Kulikouski, 1966; Coltheart, 1971) as will be seen later.

Attempts to obtain direct evidence that the human visual system has mechanisms similar to those of the cat and monkey have been produced by adopting a method of measuring evoked potentials, elicited by visual stimuli from the visual cortex. For example evoked potential studies have been used to investigate orientation (Smith & Jeffreys, 1978), motion (Clarke, 1973, 1974), colour perception (Regan, 1970, 1973), and binocular rivalry (Cobb, Ettlinger & Morton, 1967).

While evoked potential recording is an excellent risk-free technique for obtaining objective data on brain function from conscious human subjects, unfortunately close correlation with conscious perception is not reliable (Regan, 1981). The technique might well provide a bridge between animal and human experiments but would usually amount to little more than a complicated and expensive alternative to psychophysical tests.

1.1.0 Psychophysical strategies for studying vision.

The study of visual perception has involved attempts to relate psychophysical functions with the direct neurophysiological function of the visual pathways. A number of psychophysical paradigms (e.g., masking, aftereffect and binocular rivalry) have been used in an attempt to relate the psychophysics of visual perception to the activity of feature detecting mechanisims in the human visual system (Weisstein, 1969, 1972; Anstis, 1975; Breitmeyer & Ganz, 1976; Breitmeyer, 1978).

The psychophysical approach has attempted to demonstrate that the selectivity (spatial and/or temporal) of neurons is reflected in perceptual data (Magnussen & Kurtenbach, 1980, 1981; Wenderoth & Tyler, 1979). Using the response characteristics of neurons determined by electrophysiological techniques (Hubel & Wiesel, 1962, 1968), the psychophysical approach argues that if neural activity is modulated by prior stimulation, and if perception is mediated by neural activity, then perception should be modulated by prior stimulation. Consequently, by determing the parameters over which perceptual response can be modified, visual processing in human beings can be studied with psychophysical techniques where electrophysiological techniques are restricted for ethical reasons.

The main aim of this thesis is to examine the spatial selectivity of the disinhibition function in the human visual system by utilizing psychophysical methods, specifically, those of masking and aftereffect.

1.1.1 Masking

Visual masking occurs when one visual stimulus interferes with the perception of another visual stimulus. The masking stimulus (MS) is that stimulus that interferes with the perception of the test stimulus (TS). The designations MS and TS are somewhat arbitrarily chosen in that the stimuli mutually interact, but it is conventional to designate as TS the stimulus upon which the observer must report (Fox, 1978).

Masking or interference in the detection of the TS depends on the spatial, temporal, and intensive characteristics of the two stimuli. For example masking is greatest when TS and MS are presented together and becomes progressively less as the temporal distance between them increases (Kolers, 1962). In the case of orientation for instance, inspection of a vertical MS renders a subsequently presented vertical TS less visible but exerts little influence on detection of a horizontal TS (Lovegrove, 1976; Sekuler, 1965; Gilinsky & Mayo, 1971). In both cases reduction in visibility of the TS is quantifiable as the amount by which the perception of the TS is raised by the MS.

With respect to measuring the time delay or temporal relationship between TS and MS two conventions are used. The first refers to the time between the first stimulus (TS or MS) offset and the onset of the second stimulus and is known as the interstimulus interval (ISI). The second called stimulus onset asynchrony (SOA) measures the difference in time between the onsets of both stimuli.

By convention positive SOA values indicate that the MS follows the TS in time, a procedure known as backward masking.

The label 'backward' results from the fact that the MS appears to operate backward (retroactively) in time upon the TS. Forward masking, accompanied with negative SOA values, occurs when the MS is presented before the TS (Breitmeyer & Ganz, 1976).

Masking when the contours of the MS and TS do not spatially overlap is referred to as paracontrast, where forward masking is used. Metacontrast which refers to backward masking is also a general term for both forward and backward masking as situations where the MS and TS stimulate adjacent but nonoverlapping retinal areas. Where the MS (and at times also the TS) is a homogeneous illumination, over a retinal area that completely contains the contours of the TS, this non-metacontrast masking is known as masking by light (Crawford, 1974). Masking by noise and masking by structure are other techniques employed in non-metacontrast masking. In the first instance the MS consist of a random array of black and white areas bearing little or no structure (Kinsbourne & Warrington, 1962), and in the second the spatially overlapping MS may be structurally related to the TS.

Like accounts of other visual processes, recent theories of visual masking, for the most part, are based either on an information processing approach (Turvey, 1973; Coltheart, 1975) or on a neurophysiological approach (Breitmeyer & Ganz, 1976; Breitmeyer, Rudd & Dunn, 1981; Weisstein, Ozog & Szoc, 1975; Bridgeman, 1971).

One influential class of theoretic formulations outlining an information processing approach are known collectively as integration theory. The central assumption is that, while there is a physical difference in time between the TS and MS, this temporal difference disappears after both stimuli have entered the nervous system. The 'integration' of integration theory refers to some kind of fusion or combination of the neural representations of TS and MS which is assumed to cause a degradation in the representation of the stimuli analogus to the effect produced by double exposure of photographic film (Felsten & Wasserman, 1980). Visual masking simply becomes a special case of temporal summation of heterogeneous stimuli, and at its extreme, integration can completely erase the effect of the TS. Perhaps the clearest psychophysical support for an integration theory of masking was reported by Schultz and Erikson (1977) who concluded that integration occurs either through "energy summation when the successive stimulations fall within the critical duration or summation interval" or through "superimposition on the sensory register of the new stimulation on the decaying trace of the previous stimulus".

The term 'interruption theory' identifies a set of theoretic formulations frequently considered to be competing alternatives to integration theories. While particular versions of the interruption theory offered by researchers differ in detail the underlying concept, that the MS acts to stop or interrupt processing of the TS by some means other than by degradation of the TS is shared (Kahneman, 1968; Turvey, 1973).

While the difference between integrative (energy dependent) and interruptive (time dependent) mechanisms is profoundly important, and while they appear to be in direct conflict, there is no intrinsic reason why both processes could not be operative under certain conditions (Spencer & Shuntich, 1970). Indeed Turvey (1973) has developed what he calls a concurrent-contingent model that incorporates concepts from both integration and interruption theories.

Integration and interruption theories do not place emphasis upon neurophysiologic phenomena but take into account only very general neurophysiologic considerations. In contrast several neurophysiological models of visual masking have been proposed (Weisstein, et al., 1975; Breitmeyer & Ganz, 1976; Matin, 1975). Perhaps the most sophisticated neural model is one developed and described be Weisstein in 1968 and subsequently modified (Weisstein, 1972; Weisstein, et al., 1975). The model is composed of a network of five hypothetical neurons with both excitatory and inhibitory outputs that operate in accord with the well defined mathematical assumption of the idealized two-factor neurons described by Rashevsky (1948) and Landahl (1967). Two of the neurons are peripheral and convey information about the target and mask respectively. Each of these peripheral neurons makes contact with one of two respective, second-order central neurons. The second-order target neuron transmits an excitatory signal to a more central third-order decision neuron, which also receives inhibitory in-put via colateral fibres of the second-order mask neuron. However, only until quite recently (Weisstein, Ozog, & Szoc, 1975), several critical assumptions on which the model rests had not found neurophysiological support.

Another major neurophysiological model has been proposed by Breitmeyer and Ganz (1976). The model assumes that a brief stimulus elicits two types of response. Firstly, a short latency, relatively brief duration response called a transient response. Secondly, a long latency, longer duration response called a sustained response. It also assumes that transient activity can inhibit sustained activity particularly when the TS - MS SOA is such that the inhibition produced by the transient activity of one stimulus is optimally superimposed in time on the excitatory sustained activity of the second stimulus. However inhibition of sustained activity-on-transient activity is by no means suggested to be unidirectional. In fact both sustained-on-transient inhibition and transient-on-sustained inhibition is suggested (Breitmeyer, Rudd, & Dunn, 1981; Breitmeyer, 1978).

It should perhaps be noted that while neural theories such as those of Weisstein (1972) and Breitmeyer and Ganz (1976) emphasize neurophysiologic phenomena, they are not neurophysiologic theories in the sense that they may be disconfirmed by direct neurophysiological investigation. Rather, like theories based on an information processing approach, they are psychophysical or behavioural theories that can be tested by behavioural experiments (Fox, 1978).

1.1.2 Aftereffect

The aftereffect paradigm differs from masking in that the observer judges the spatial properties of a suprathreshold TS immediately after inspection of an adaptation stimulus (AS). When a suprathreshold line is shown after prolonged inspection of a grating tilted in a clockwise

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direction the TS appears displaced in a counterclockwise direction (negative aftereffect). Tilt-illusion or orientation contrast describes the case when the perceived orientation of a TS is changed by an adjacent adaptation (inducing) grating (O'Toole, 1979; Tolhurst & Thompson, 1975).

This spatial distortion (aftereffect) was first reported by Gibson (1937) who termed as adaptation the phenomena that curved lines appear to straighten when viewed over a period of time. Adaptation with an accompanying aftereffect occurs with the perception of orientation, movement, brightness, colour, and the judgement of curvature. Spatial aftereffects such as those of orientation (Muir & Over, 1970; Ware & Mitchell, 1974) and direction of movement (Sekuler & Ganz, 1963; Pantle, Lehmkule & Caudill, 1978) are believed to be processed by populations of feature detecting neurons.

The direction and magnitude of tilt-aftereffect is dependent upon the duration, spatial frequency, energy levels, and particularly orientation of the AS.

While a vertical TS appears distorted counterclockwise after exposure to gratings tilted less than 45 deg in a clockwise direction, inspection of gratings tilted between 45 and 90 deg results in clockwise distortion of the TS. However judgements of the TS are not affected by exposure to an AS of 0, 45, or 90 deg orientation (Gibson, 1937).

Maximum tilt-aftereffect has been found when the orientation of the AS is between 10-20 deg (Muir & Over, 1970; Mitchell & Muir, 1976) and has been investigated under various conditions; for example, interocular transfer

(Campbell & Maffei, 1971), spatial selectivity, (Ware & Mitchell, 1974), colour and contour rivalry (Wade & Wenderoth, 1978), and disparity (Blakemore & Julesz, 1971).

Numerous theories have been proposed in an attempt to explain the psychophysical effects of aftereffect (Gibson, 1937) and more recently by extrapolation from neurophysiological data (Ganz, 1966; Weisstein, 1969; Coltheart, 1971; Blakemore & Tobin, 1972; Sillito, 1979). Gibson maintained that negative aftereffect is produced through normalization. Here, both vertical and horizontal are considered to be the 'norm' of the visual system. Consequently, when adaptation occurs to obliquely orientated lines, these lines are interpreted as the norms and subsequently presented stimuli will appear displaced in the opposite direction. There have been a number of objections to the theory with the current emphasis, based on neurophysiological developments (Hubel & Wiesel, 1965, 1968), adopting a more neural approach.

Sutherland (1961) and Coltheart (1971) interpret aftereffect in terms of a process of adaptation, satiation, or fatigue of orientation detectors. Neurons in the visual cortex are supposed gradually to decrease in sensitivity during prolonged strong stimulation by the AS. Upon viewing a vertical TS, neurons unaffected by the AS respond at their normal rate while those stimulated by the AS respond at a reduced rate because of fatigue, resulting in an interpretation that appears biased in the opposit direction.

Recent investigation based on further neurophysiological (Blakemore & Tobin, 1972; Nelson & Frost, 1978) and psychophysical studies (Blakemore & Carpenter, 1973; O'Toole, 1979; Magnussen & Kurtenbach, 1980; Kurtenbach & Magnussen, 1981) proposes tilt-aftereffect and tilt-illusion to be manifestations of lateral inhibition. Neurons specific to the orientation of a stimulus will maximally respond while those specific to different orientations respond to a lesser degree. As one neuron is stimulated it tends to inhibit maximal responding by its adjacent neighbours. Consequently a decrease in the firing rate of an orientation detector can be achieved by simultaneously stimulating the adjacent neurons.

Blakemore and Tobin (1972) in providing neurophysiological support for the existence of lateral inhibition produced a tuning curve for a complex cell in the cat's visual cortex showing inhibition occurred over a broad range of orientation. Where the tuning function peaked for a cell's maximal orientation response, a similar (but opposite) alignment also occurred for the inhibition response.

The hypothesis of orientation specific inhibition now seems generally accepted when applied to simultaneous orientation interactions,but the suggestion that orientation aftereffects are the result of inhibition rather than neural fatigue is rather more controversial.

1.1.3 Binocular and Monocular Rivalry

Typically when two stimuli are simultaneously presented, one to each eye, each stimulus competes for dominance and alternation occurs, where percepts alters from one stimulus to the other. An important phenomena of binocular rivalry is the effectiveness of suppression; even a very strong stimulus can be completely blocked from awareness for several seconds by the 'dominant' stimulus.

The parameters that produce binocular rivalry correspond closely with those of feature detectors that have been discovered in mammalian visual cortex (Hubel & Wiesel, 1962, 1968). Binocular rivalry can be produced by monocular stimuli differing in orientation (Blake & Fox, 1974; Kitterle & Thomas, 1980), spatial frequency (Blakemore,1970), movement (Breese, 1899; Lehmkuhle & Fox, 1975), and colour (Wade, 1975; Helmholtz, 1925).

There is another form of rivalry also dependent upon the interaction of colour, movement, orientation, luminance levels, and spatial frequency (Wade, 1975). Known as monocular rivalry, in this situation gratings are superimposed and usually (not always; see Experiment 5) presented monocularly. For example, Breese (1899) superimposed a red grating orientated at 135 deg on a green grating of 45 deg and presented the stimulus monocularly. He reported the resulting monocular rivalry to be slower than that of binocular rivalry when the green grating was presented to one eye and the red grating was presented to the other eye simultaneously. Moreover, for monocular rivalry it was rare for one grating to disappear completely as occurred under binocular rivalry. Similar findings have also been made more recently by Kitterle and Thomas (1980), Wade and Wenderoth (1978), and Walker and Powell (1979), to name a few.

Early studies (Breese, 1899; Helmholtz, 1911, 1925) considered binocular rivalry to reflect a central selective process that took effect subsequent to the analysis of two monocular stimuli. Conversely it was more recently regarded, by some researchers, to reflect peripheral sensory mechanisms. Bishop (1973), Wade (1975), and Jung (1961) suggest that the suppressed stimulus suffered blocking at an early stage of the visual system and interpreted this as meaning the process was peripherally located.

However, Walker (1978) finds considerable support for the traditional approach of central processing, suggesting that the suppressed stimulus in binocular rivalry is in fact analyzed and through selective attention may be perceived (e.g., Blake & Overton, 1979). One specific line of evidence to support the central approach is the contribution of a suppressed stimulus to stereopsis (depth perception). Numerous studies have reported stereopsis occurring despite rivalry, indicating that the information in the suppressed stimulus is still being processed (Blake, et, al., 1980; Julesz & Miller, 1975). For stereoprocessing to occur both monocular inputs must combine to produce a fused image, because the site of this occurs centrally, rivalry is also presumed to occur centrally.

To assert that rivalry reflects central selective processes is to reaffirm that, not only does the phenomena indicate that perceptual experiences reflect processes of analysis of sensory information, but also that binocular rivalry may be useful in isolating and investigating these processes (Walker, 1978).

1.2.0 Disinhibition in Human Vision

When a second mask stimulus is introduced into a masking sequence, the introduced mask is able to reduce the masking effect (disinhibit) of the first mask (Dember & Purcell, 1968; Dember, Schwartz & Kocak, 1978; Breitmeyer, Rudd & Dunn, 1981). Recovery of a TS phenomena (disinhibition) was first described by Robinson (1966, 1968) who suggested that the second stimulus disinhibits the TS by masking the mask. Disinhibition has been frequently demonstrated under backward masking (Dember & Purcell, 1979; Lovegrove, 1976). The significance of such TS recovery resides in the implication that masking does not always erase the information imparted by the TS.

Disinhibition has also been shown to occur under aftereffect paradigms when a reduction in the magnitude of the aftereffect of an initial adaptation stimulus results following the introduction of a second adaptation stimulus (Carpenter & Blakemore, 1973).

Like masking and aftereffect, disinhibition effects are dependent upon the spatial, temporal, and energy levels of the stimuli (Long & Gribben, 1971; O'Toole, 1979; Breitmeyer, 1978). When these variables are held constant disinhibition becomes more dependent upon the interactions between visual contours within the stimulus arrays. In the case of orientation, pronounced disinhibition in masking and aftereffect occurs when the orientational difference between the distorting stimuli is less than 15 deg (Lovegrove, 1976) and between 10 and 15 deg (Magnussen & Kurtenbach, 1980) respectively.

While an apparent opposit to disinhibition, summation (an increase in the initial inhibition of one stimulus by introducing a second stimulus into the sequence) has occurred in situations where disinhibition might be expected. Specifically, in experiments investigating disinhibition, summation has resulted when an aftereffect and a simultaneous illusion of opposite signs (clockwise and counterclockwise) were paired by first adapting to a clockwise orientation and then presenting the vertical TS together with a counterclockwise inducing line, the two effects summed linearly (i.e., inhibition increased)(Magnussen & Kurtenbach, 1980; Kurtenbach & Magnussen, 1981).

Many theoretical explanations have been offered to account for disinhibition and summation taking either an information processing approach or a neurophysiological approach (see masking and aftereffect) but theories based on a neurophysiological properties of feature detecting neurons are particularly relevant when the TS and MS/AS spatial and temporal relationships determine disinhibitory and summative effects (Breitmeyer & Ganz, 1976; Weisstein, Ozog & Szoc, 1975).

The basic assumption of a neural theory of disinhibition and summation is that a neuron's activity can be modulated by prior activity and/or by the activity of neighbouring neurons. Since a period of post-excitatory suppression follows prolonged optimal stimulation a TS presented at near threshold during this time must be presented at a higher level in order to be detected. Interchannel inhibition may also modulate a neurons response but only to the extent that the channels are responsive to the same overlapping dimensions in the stimuli. This latter explanation has been offered to account for the occurrence of disinhibition and summation in aftereffect (Magnussen & Kurtenbach, 1980;

Carpenter & Blakemore, 1973) and masking (Wenderoth & Tyler, 1979). In some ways it has been the demonstration of disinhibition and summation that has led some researchers to adopt a lateral inhibition explanation of orientation detection over a neural fatigue explanation.

1.3.0 Thesis Aims and Objectives

The aim of this thesis is to utilize a number of psychophysical paradigms (masking is used in Chapter 2 and aftereffect is used in Chapters 3 and 4) to determine the orientation parameters over which disinhibition occurs.

Under each of the paradigms the subject's task differs. For example, in masking the subject's task is the detection of a threshold TS, while in aftereffect the subject's task is to judge a spatial feature of a supra-threshold TS.

One of the advantages of utilizing orientation as an independant variable in disinhibition sequences is that it allows independent evaluation of the disinhibition arising from the orientation displayed in either the masking/adaptation or disinhibiting stimulus. This assessment can be determined by interpreting the disinhibition function in terms of the well established limitations of orientational functions. Therefore in a disinhibition masking or aftereffect paradigm it is possible to separate the increased or reduced interference or distortion of the TS, arising either as a direct result of disinhibition or as the result of reduced interference or distortion by the use of extreme non-interferring orientations.

Should masking and aftereffect paradigms display similar orientation selectivity this would provide support for a common neural processing mechanism. In this thesis a lateral inhibition explanation of orientation disinhibition is proposed.

CHAPTER TWO: MASKING

2.0 Masking: Experiments 1 and 2.

The following two experiments investigate orientation selectivity of disinhibition under a masking paradigm. Microelectrode studies have revealed neural cells which are tuned to specific stimulus configurations (Hubel & Wiesel, 1962, 1968). For example there are some neurons that respond with great vigor to a line of a particular orientation while remaining relatively unresponsive to the same line after rotation through some angle.

The area of interest is the psychophysical characteristics of orientation mechanisms especially the range of orientation over which they respond. Visual masking enables the examination of the response ranges. If viewing a mask stimulus of one orientation interferes with the detection of test stimuli having some other orientation, then the extent of the interference is a measure of the degree to which perception of both orientations is mediated by common mechanisms (Houlihan & Sekuler, 1968).

In Experiment 1 and 2 subjects are required to detect the presence or absence of a test stimulus following the successive presentation of two masking stimuli (M1 and M2). Since M1 is expected to mask M2 and therefore disinhibit the test stimulus, the orientation selectivity of such a disinhibition function is suggested to be similar to a forward masking function alone. For example, if a vertical mask exhibits maximum inhibition (masking) on a vertical test stimulus, the introduction of a second vertical mask may result in maximum disinhibition (target recovery). In other words the isolation of orientation tuning ranges over which disinhibition occurs are expected to be similar to those isolated by other psychophysical techiques (Campbell & Maffei, 1970; Over, Broerse & Crassini, 1972; Sekuler, 1965).

2.1 Experiment 1: Spatial disinhibition of orientation analyzers under forward masking with ISI 1 of 1 msec.[1]

When a TS is presented within close temporal and/or spatial contiguity with a MS the mask is able to reduce the detectability of the TS. The detection threshold of the TS may be raised however, by the introduction of a second MS into the masking sequence.

Such recovery (disinhibition) which was first reported by Robinson in 1966 and later reproduced and extended by him (1968) was thought to have implications for the generality of integration theories of visual masking (Dember, Schwartz & Kocak, 1978). Using stimulus conditions similar to Robinson's (1966), Schurman & Erikson (1968) failed to obtain recovery of a masked target. However at the same time, numerous positive results concerning recovery have been reported. The results presented by Dember and Purcell(1967) showed moderate recovery and more recently, Kristofferson, Galloway & Hansen (1979) repeated Dember & Purcell's experiment and found almost complete recovery of the target. Dember, Schwartz & Kocak (1978), Schiller & Greenfield (1969) and Tenkink & Werner (1981) have also reported disinhibition using different stimulus configura-

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[1] Published as, Spatial disinhibition of orientation analyzers. Perception and Psychophysics, 1981, 29, 212-216. Appendix.

tions.

The exact parameters required to optimize the effect are not clear. The intensity of stimuli, absolute and relative stimulus size, and the configuration of stimuli have not yet been studied extensively (Tenkink & Werner, 1981). However in experiments that have reported disinhibition, the effect appears to be critically dependent upon the SOAs and the masking ability within the masks (Breitmeyer, 1978; Bryon & Banks, 1980; Long & Gribben, 1971). For disinhibition to occur, the mask must exert a moderate masking effect on the TS and provided that the SOAs are sufficient to prevent summation between the masks, then the second mask (disinhibitor) will disinhibit the TS (Long & Gribben, 1971).

As has been seen, many theoretical explanations have been offered to account for masking and disinhibition, but the neurophysiological theories are more relevant when the temporal and particularly spatial relationships of the target and masking stimuli determine masking, and therefore disinhibitory effects. The spatial limitation of the masking function obtained in feature masking has been attributed to the inhibitory interaction of neural units (Breitmeyer, 1980; Weisstein, et al., 1975). Furthermore the selectivity in the masking functions has been observed to be spatially restricted to the stimuli that have similar spatial values (Blakemore & Hague, 1972; Over, Broerse, & Crassini, 1972).

Blakemore, et al. (1970) and O'Toole (1979) have demonstrated orientation disinhibition by observing the apparent contraction or expansion of acute angles when a disinhibitory stimulus is introduced. In both these experiments the maximum disinhibitory effect occurred when the difference between the masking and disinhibitory orientations was 10-20 deg. Orientational selectivity has also been demonstrated directly from microelectrode recording (Hubel & Wiesel, 1968; Campbell & Maffei, 1970) and from psychophysical data (Gilinsky & Mayo, 1971; Over et al., 1972).

In this present experiment, it is hypothesized that the detectability of a vertical target line will vary as a function of the orientation of the masking orientations. Specifically, it is proposed that orientation disinhibition should occur only when the orientations of the mask and the disinhibitor maximally mask each other.

METHOD:

Three undergraduate students with normal or corrected-to-normal vision served as subjects.

Apparatus:

The TS was a single black vertical line, 7 deg 8 min long and 9 min wide, while the square-wave black on white gratings utilized for M1 and M2 subtended 9 min wide. All MS displays were circular and could be rotated. Four orientation values of M1 and M2 were used (0, 7, 15, and 30 deg from vertical). The space average luminance of the TS was maintained at 29.5cd/m^2 with a Michelson contrast $\left[(L_{max} - L_{min} / L_{max} \times L_{min})\right]$ of 0.80 and was 26.0cd/m^2 for M1 and M2 a contrast of 0.60. The space average luminance of the catch stimulus was maintained at

29.5 cd/m^2.

Procedure:

A forward masking-disinhibition paradigm was used. Following the presentation of a centrally located fixation point (10 sec), the stimulus sequence commenced with M1 presented for 150 msec. Interstimulus 1 (ISI1) for 1 msec, M2 for 150 msec, ISI2 for 10 msec, and then the TS (or a homogeneous blank field on catch presentations) followed. The duration of the TS was 4 msec and was the duration at which the subjects could correctly detect the TS at 50% accuracy when a vertical grating was presented beforehand. The stimuli were aligned so that the features impinged on the same retinal area when displayed in separate channels of a Scientific Prototype Tachistoscope.

In each session, the subject was given 20 minutes of practice in reporting the presence of the TS when one MS was used. During the practice session, the subjects TS threshold was determined and this value was subsequently used throughout the experiment. All orientation combinations of M1 and M2 were randomized into 16 blocks and were balanced in accord with a latin square so that all subjects received all combinations in different orders. Four further blocks of all M1 orientations without the presence of M2 (i.e., normal forward masking) were also included to serve as controls against which disinhibition could be measured. Each block consisted of 12 trials made up of six trials on which the TS was actually present, randomly interspersed with six catch trials. On the six target trials, the single vertical line was presented, while on catch trials a homogenous field of equal luminance was shown. The subject's task was to report whether the TS was present or absent (i.e., to differentiate between the target and catch trials).

Testing was conducted in a darkened room, with each subject triggering the tachistoscope. There was approximately 10 sec between trials and 1 minute between blocks.

RESULTS:

The percent correct detection of the TS was calculated for each subject under all factorial combinations of M1 and M2, and was the accuracy with which each subject could correctly detect the presence or absence of the TS. An analysis of variance was performed on these data. The percent detection varied significantly as a function of the orientation of M2 $[F(3,6)=18.65,\ p<0.01]$, while the orientation of M1 did not exert a significant influence $[F(3,6)=4.49,\ p>0.05]$. The two way interaction between these variables was significant $[F(9,18)=7.48,\ p<0.01]$ and is shown in Figure 1.

In order to directly compare disinhibition (increase in correct detection of TS) and summation (decrease in correct detection of TS) from forward masking a priori comparisons between all orientation combinations of M1 and M2 and control conditions were performed and are shown in Figure 2. Figure 2 shows the summation and disinhibition effects of M1 when the forward masking effect is controlled for. For example when a 0 deg forward masking control is removed from a 0 deg M2 the addition of a 0 and 7 deg M1 resulted in significant disinhibition ($p < 0.01$).

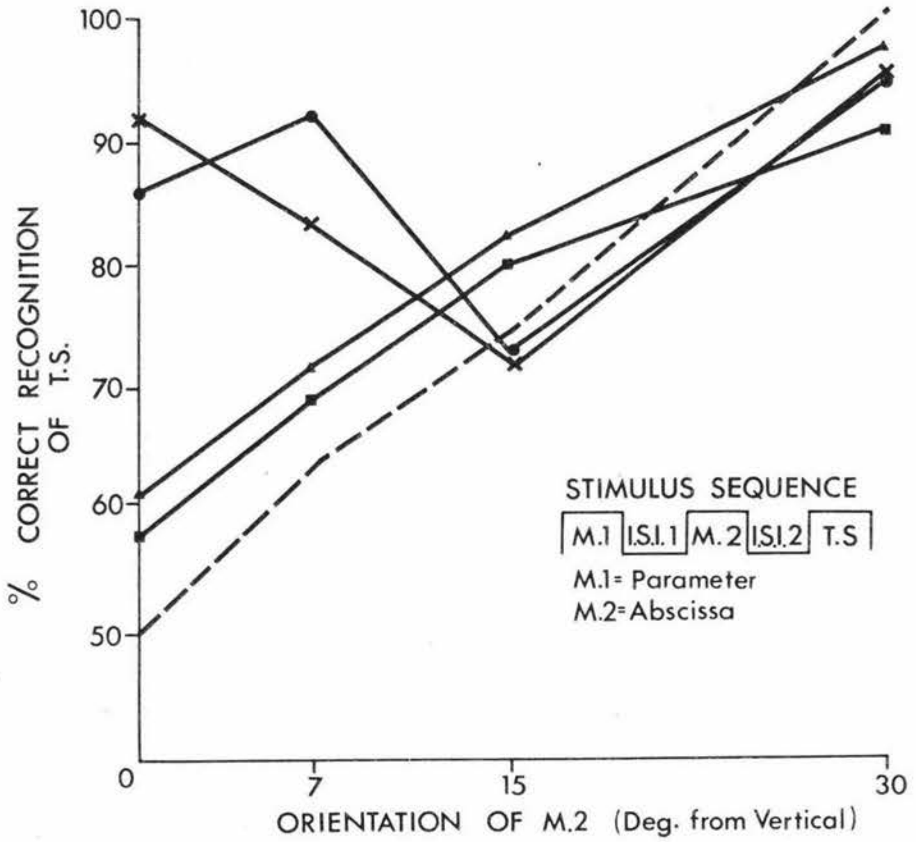

Figure 1: Percentage correct detection of TS as a function of M1 and M2 with ISI1 of 1 msec. Parameter is M1 orientation (✕——✕, 0 deg; ●——●, 7 deg; ▲——▲, 15 deg; ■——■, 30 deg) and forward masking control (-----).

Comparisons revealed that the introduction of M1 prior to M2 significantly reduced the masking effect of M2, provided the orientation of M2 was either 0 or 7 deg. Inspection of Figure 1 and Figure2 showed that disinhibition occurred when both M1 and M2 were 0 or 7 deg. If M2 was 15 or 30 deg then the introduction of a 0 or 7 deg M1 had little effect, as the function was similar to the forward masking control condition. Similarly the functions

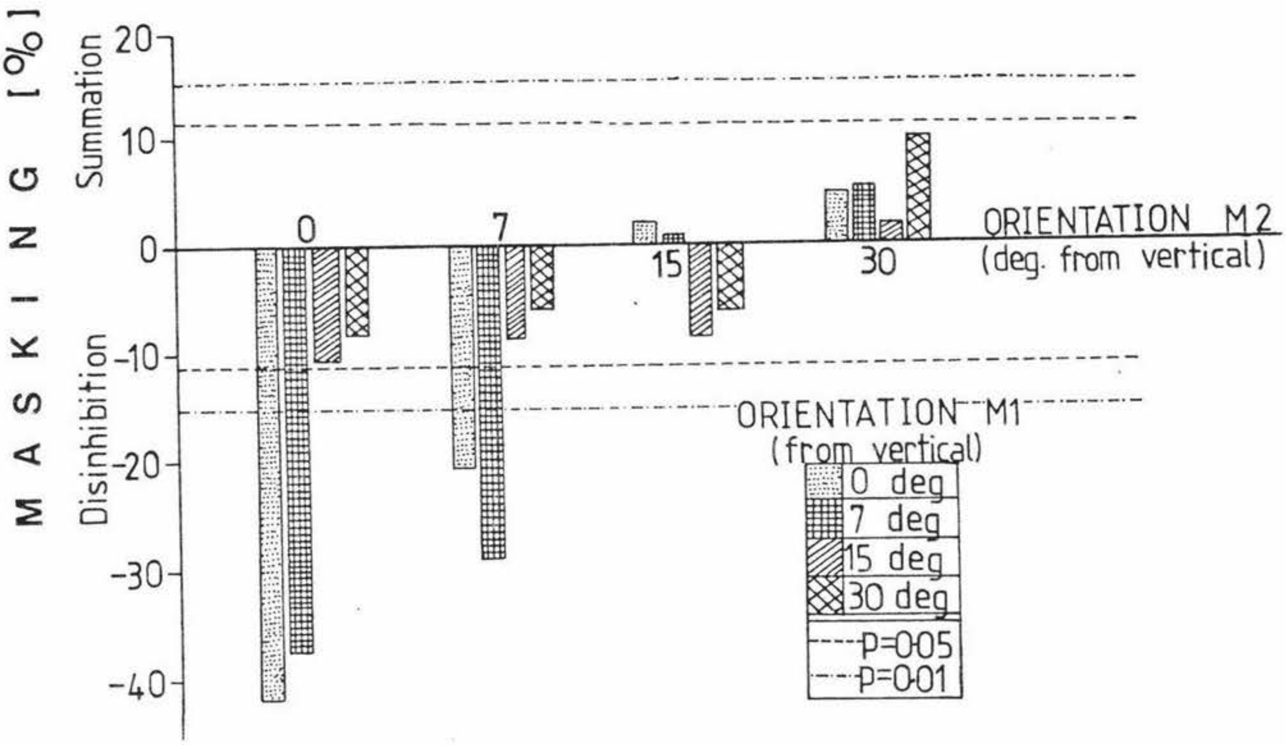

Figure 2: Percentage correct detection of TS adjusted for control orientations as a function of M1 and M2. Critical a priori F values: (----), $p = 0.05$; (-·-·-·-), $p = 0.01$.

obtained for a M1 of 15 or 30 deg at all M2 orientations were not significantly different from the forward masking control condition.

Generally it appears that if disinhibition of a vertical TS is to occur, the M1 and M2 must be processed by overlapping neural channels that are tuned to orientation values less than 15 deg to vertical.

DISCUSSION:

The results of the experiment give considerable support to the contention that the human visual system responds selectively to narrow ranges of orientation information.

Following the presentation of masking stimuli containing orientation information, disinhibition occurred when M1 and M2 were similar in orientation, and as the orientation difference between the masks increased disinhibition decreased. Orientation selectivity of disinhibition was highly specific in that disinhibition failed to occur if the orientation of the masks differed by 15 deg. The results, which suggest that M1 orientations of greater than 15 deg cannot disinhibit equal energy M2s of lesser orientations, are in partial agreement with those of Wenderoth and Tyler (1979), who reported that, in a simultaneous masking paradigm, a 0 deg (i.e., vertical) grating could also be disinhibited by orientations or 75 and 90 deg (i.e., approximately horizontal). With the exception of these latter results the orientation over which disinhibition resulted is indeed very similar to the orientation tuning ranges isolated by other psychophysical techniques (Over et el., 1972; Gilinsky & Mayo, 1971; O'Toole, 1979; Campbell & Maffei, 1970). The present data support the suggestion that disinhibition may arise by lateral inhibition in populations of feature detecting neurons. More specifically, the orientational selectivity of the effect may suggest that the disinhibition paradigm could be added to other techniques as a further method to study feature detection in the human visual system.

Breitmeyer (1980) proposed that sustained channels which exhibit a long latency, long duration response are capable of inhibiting transient channels which exhibit a short latency, rather short duration response. He and others (Dember, Schwartz, & Kocak, 1978; Weisstein et al., 1975; Breitmeyer & Ganz 1976) further suggest that sustained channels respond slowly to high spatial frequencies, and tranient channels respond rapidly to low frequencies. Since M1 and M2 utilized identical spatial frequencies the results of this present experiment can be accounted for by this theory if it is assumed that the transient channels activated by the masks are processed more rapidly than the sustained channels.

In conclusion the orientational selectivity of the disinhibition function has clearly been demonstrated. However the temporal relationship between stimuli is perhaps critical to the effectiveness of the disinhibition function. A question that needs consideration is whether the interstimuli intervals used in this present experiment are optimal for masking and disinhibition to occur.

2.2 Experiment 2: Spatial disinhibition of orientation analyzers under forward masking with ISI1 of 10 msec.

Research has shown masking effects to be most severe when the TS and MS follow one another immediately (Erikson & Hoffman, 1963; Schiller & Smith, 1965). Likewise disinhibition has been reported to be critically dependent upon the SOA with complete recovery (maximum disinhibition) being reported at SOAs of 116 msec TS-M2 and 35 msec TS-M1 (Kristofferson, et al., 1979). Tenkink and Werner (1981) examined a disinhibition condition in which a homogeneous blank flash preceded a patterned mask. The interval between Mask 1 and Mask 2 was shown to be an important parameter with optimal recovery (disinhibition) occurring when this value was between 0 and 20 msec.

As outlined previously a moderate masking effect must be exerted by the disinhibition (M1) on the mask (M2) to enable recovery of the TS, with SOAs sufficient to prevent summation between M1 and M2 (Long & Gribben, 1971). However, even at the short ISI1 of 1 msec used in Experiment 1, summation between the masks of identical orientation did not occur. Rather, the neural activity generated by M1 reduced the masking effect of M2.

In this present experiment the interstimulus intervals between M1 and M2, and M2 and TS are 10 msec and 1 msec respectively. Specifically it is suggested that since the SOA of M1-TS will be the same as experienced in Experiment 1 disinhibitory effects will not be significantly different from those obtained when ISI1 was 1 msec and ISI2 was 10 msec.

METHOD:

Five students, two graduates and three undergraduates with normal or corrected-to-normal vision served as subjects.

Apparatus:

The MS and TS in this experiment were the same as in Experiment 1.

Procedure:

As for Experiment 1 a forward masking-disinhibition paradigm was used. Following the presentation of a centrally located fixation point (10 sec), the stimulus sequence commenced with M1 being presented for 150 msec. Interstimulus 1 (ISI1) followed for 10 msec, M2 for 150 msec, ISI2 for 1 msec, and then the TS (or a homogenous blank field on catch presentations). The duration of the TS was 4 msec and was the duration at which the subjects could correctly detect the TS at 50% accuracy when a vertical grating was presented beforehand.

The remaining procedure of Experiment 2 followed strictly that of Experiment 1.

RESULTS:

The percentage correct detection of the TS was calculated for each subject under all factorial combinations or M1 and M2, and was the accuracy with which each subject could correctly detect the presence or absence of the TS. An analysis of variance was performed on these data. The percent detection varied significantly as a function of the orientation of M2 $[F(3,12)=35.30,\ p < 0.01]$ while the orientation of M1 did not exert a significant influence $[F(3,12)=0.41\ p > 0.05]$. The two way interaction between M1 and M2 was significant $[F(9,36)=5.44,\ p < 0.01]$ and is shown in Figure 3.

In order to directly compare disinhibition and summation with the forward masking control condition a priori comparisons between all orientation combinations of M1 and M2 and control conditions were performed. Figure 4 shows the disinhibition and summation effects of M1 when the forward masking effect is controlled for. This is accomplished by subracting the percent correct detection of the control orientation from the corresponding M2 orientation. For example when a 0 deg forward masking control is removed from a 0 deg M2 the addition of a 0 and 7 deg M1 resulted in significant disinhibition $(p < 0.01)$.

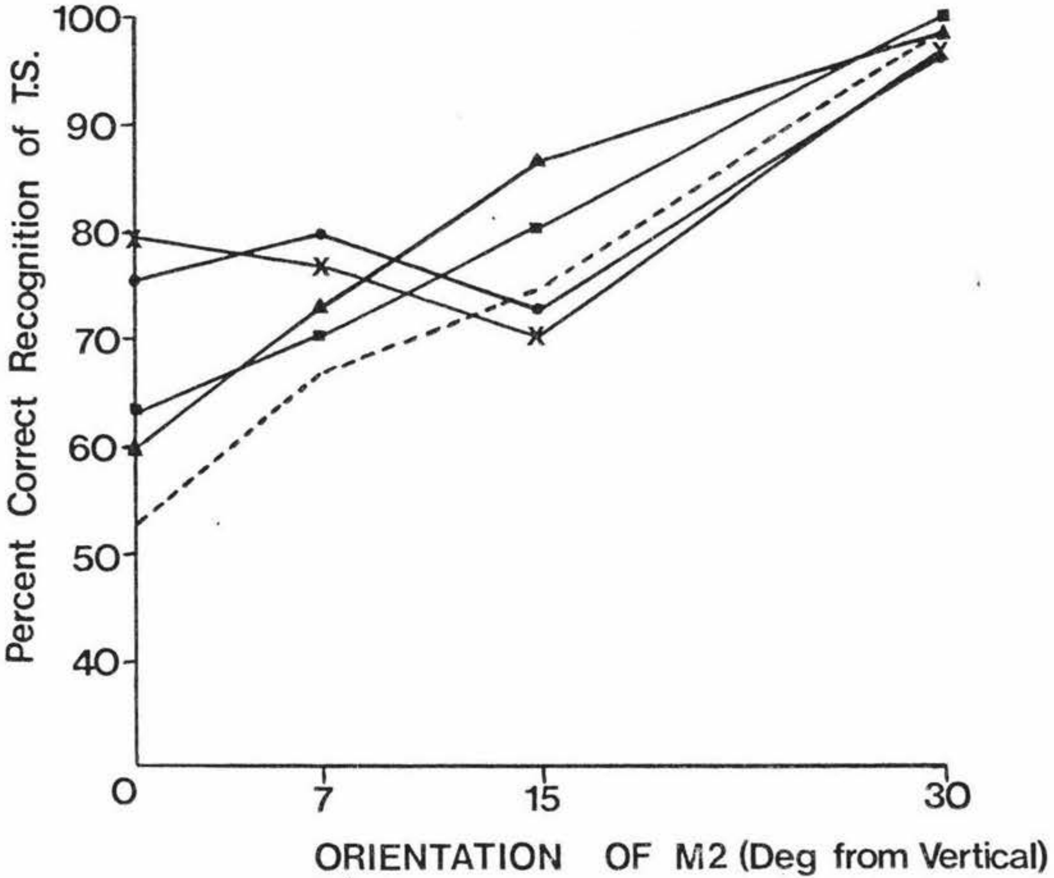

Figure 3: Percentage correct detection of TS as a function of M1 and M2 with ISI1 of 10 msec. Parameter is M1 orientation (×—×, 0 deg; ●—●, 7 deg; ▲—▲, 15 deg; ■—■, 30 deg) and forward masking control (------).

Comparisons revealed that the introduction of M1 prior to M2 significantly reduced the masking effect of M2 provided the orientation was either 0 or 7 deg. A significant decrease in masking also occurred when M1 and M2 were both 15 deg. If M2 was 15 or 30 deg, then the introduction of a 0 or 7 deg M1 had little effect.

In agreement with Experiment 1 it appears that if disinhibition of a vertical TS is to occur, then M1 and M2

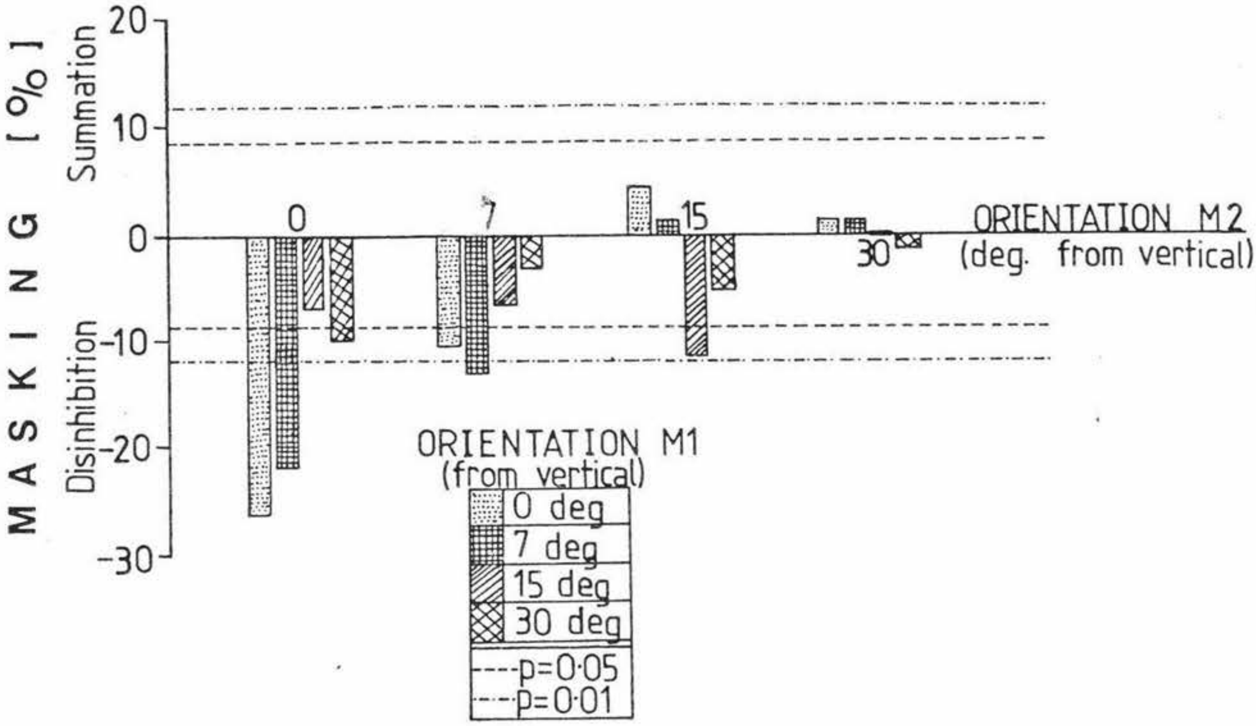

Figure 4: Percentage correct detection of TS adjusted for control orientations as a function of M1 and M2. Critical a priori F values: (-----), p = 0.05; (-·-·-·-), p = 0.01.

must be processed by overlapping neural channels that are tuned to orientation values less than 15 deg. And while this is more pronounced for orientation values less than 15 deg to vertical, disinhibition of a vertical TS by a 15 deg M1 and M2 shows it need not always be so - the overlapping neural channels being the crucial factor.

DISCUSSION:

The results show the orientational secletivity of the disinhibition function of this present study to be similar to that obtained when ISI1 and ISI2 were 1 and 10 msec respectively (i.e., Experiment 1).

While the SOAs used were greater than those demonstrated by Kristofferson, et al. (1979) to be critical to elicit complete recovery, the phenomena under investigation (orientation disinhibition) did not appear particularly dependent on such critical SOA values. The specific orientation of M1 relative to M2 appears to be a more critical parameter, with maximum disinhibition occurring when M1 and M2 are similar in orientation and failing to occur as the orientation differences between the masks increases.

2.3 Masking Summary and Conclusions:

The orientation selectivity of the disinhibition function has been clearly demonstrated lending further support to a lateral inhibition explanation consistent with a general feature detection model of visual perception.

Maximum recovery of the TS following the presentation of masking stimuli occurred when M1 and M2 were similar in orientation irrespective of whether ISI1 and ISI2 were 1 msec and 10 msec or 10 msec and 1 msec respectively. Disinhibition was highly orientation specific and did not usually occur in situations where the difference in orientation between the masks was more than 15 deg.

The present experiments differ in several aspects from previous studies since forward masking-disinhibition has been used, where as backward masking-disinhibition paradigms have almost universally been utilised in the past. The forward masking paradigm was adopted to maximize the masking effect of M1 and M2 (Wenderoth & Tyler, 1979).

Any discrepancy between findings of Experiment 1 and 2 may be accounted for by an increased inhibitory influence exerted by M2 on the TS. Since, as seen earlier, masking effects are optimal when the MS and TS follow one another immediately (Schiller & Smith, 1965). An increase in the interstimulus interval between M1 and M2 may also have had some influence. However, as the interval examined was within the range determined by Tenkink and Werner (1981) to be optimal for disinhibition, such influence may be considered as minimal.

To conclude this chapter on disinhibition in a masking paradigm, it should be noted that the findings of these experiments are specific to a TS of 0 deg, since there is evidence to suggest oblique orientations are signalled by channels that are less specifically tuned and less represented within the visual system than vertical and horizontal orientations (Appelle, 1972; Matin & Drivas, 1979). In order to predict the likehood of orientation disinhibition between masks and TS of various orientations the different sensitivies of the visual system to oblique orientations must be taken into account.

CHAPTER THREE: AFTEREFFECT

3.0 Aftereffect: Experiments 3 and 4.

Generally experiments in which the temporal sequencing and the spatial orientation are important are described as masking or aftereffect paradigms, while those in which simultaneous spatial parameters predominate are described as simultaneous masking or illusion. The difference between masking and aftereffect paradigms depends on whether the subject is required to judge the presence or absence of a threshold TS (masking), or to judge the spatial distortion or a suprathreshold TS (aftereffect and illusion). While the tasks required for masking and aftereffect/illusion are different, the similarities of the psychophysical functions suggest the spatial selectivity to be similar. Specifically, both masking and aftereffect/illusion are considered as manifestations of inhibition between cortical orientation detectors (Blakemore, Carpenter & Georgeson, 1970; Sekuller & Littlejohn, 1974; Magnussen & Kurtenbach, 1980).

While Experiments 1 and 2 examined the phenomena of disinhibition in a forward masking paradigm, the following experiments adopt both a simultaneous and successive aftereffect paradigm to examine the orientation selectively of the disinhibiton function by judging the distortion of a suprathreshold TS.

3.1 Experiment 3: Orientation aftereffect following successive presentation of a disinhibitory stimulus.

As seen earlier a vertical TS when viewed following an oblique grating appears tilted in the opposit direction (tilt-aftereffect). A similar effect results from viewing an oblique grating simultaneously with the TS (tilt-illusion).

There is considerable evidence that tilt-aftereffect and tilt-illusion are both caused by orientation specific lateral inhibition (Carpenter & Blakemore, 1973; Sekuler & Littlejohn, 1974; Magnussen & Kurtenbach, 1980; Kurtenbach & Magnussen, 1981).. In particular both effects are subject to disinhibtion.

Disinhibition is observed when a second adaptation stimulus is introduced into the aftereffect paradigm and its presence is able to disinhibit (reduce the distortion caused by the AS of) the TS. Carpenter and Blakemore (1973) found that for tilt-illusion the orientation error induced by a line tilted 10-20 deg clockwise away from the TS was reduced by a second clockwise adapting line. Likewise, Magnussen and Kurtenbach (1980) found that adapting to two clockwise adapting lines, one of which formed a 12 deg angle with the TS, resulted in smaller tilt-aftereffects than were obtained by adapting to the 12 deg line alone.

The findings of Experiment 1 show the disinhibitory effect to be critically dependent upon the spatial characteristics of the MS. With maximum disinhibition occurring when the orientation difference between M1 and M2 was less than 15 deg. In this present experiment the orientation selectivity of the disinhibition function is examined further, adopting an aftereffect paradigm. Like experiment 1 successive presentation of stimuli precede the TS however in this case subjects are required to judge the spatial distortion of a suprathreshold TS. Specifically it is proposed that the distortion in aftereffect and subsquent modification caused by a disinhibitory grating should be compatible with findings of tilt-aftereffect generally. That is, since maximum aftereffect occurs when the orientation of the AS is between 10 and 20 deg (Muir & Over, 1970; Gibson & Radner, 1937) and minimum aftereffect occurs when the orientation of the AS is 0 deg (i.e., vertical) then maximum disinhibition should occur when the orientation of the disinhibitory grating is vertical.

METHOD:

Three subjects with normal or corrected-to-normal vision were used. Two were graduate students of the psychology department, the third was a technician employed by the department. Each subject received up to ½ hour preliminary practice in judging the orientation of a single vertical TS following exposure of one AS presented at various orientations.

Apparatus:

The AS (S1 and S2) were two identical square-wave black on white gratings and these were used to manipulate the orientation of the TS when presented successively. S1 and S2 subtended 7 deg 8 min and each line of the gratings was 9 min wide. The space average luminance was maintained at 8.5 cd/m^2 with a Michelson contrast of 0.5. The AS displays were circular and could be rotated. Five orientation values of S1 and S2 were used (0, 7, 15, 30, and 45 deg from vertical).

The TS was a single black line 9 min wide and 7 deg 8 min long and was presented at 45 cd/m^2 with a contrast of 0.8.

Each stimulus was binocularly viewed in separate channels of a Scientific Prototype three-field tachistoscope and were aligned so that, at similar orientations, the TS aligned perfectly with a central black line of the TS.

Procedure:

Following the presentation of a centrally located fixation point (5 sec) S1 was shown for 15 sec followed by an ISI1 of 1 sec. After S2 was shown for 15 sec the second ISI (ISI2) of 500 msec was followed by the TS which was displayed for 5 msec. The observers' task on each trial was to judge whether the orientation of the TS was to the left or right of vertical. The observer was not permitted to report that the orientation of the TS was vertical. The aftereffect was measured at each orientation combination of S1 and S2 and was the orientation of TS necessary to cancel the distortion caused be the prior presentation of S1 and S2.

All orientation combinations of S1 and S2 were randomized into 25 blocks and were balanced in accord with a latin square so that all subjects received all combinations in different orders. The combinations in which S1 and S2 were the same orientation served as controls against which disinhibition and summation could be measured.

On the first trial of any block the TS was orientated at 0 deg from vertical. If the observer responded "left" the TS was presented with one degree increase clockwise on the next trial. If the observer responded "right" the next trial was presented with one degree decrease counter-clockwise. This procedure continued until six reversals in judgment occurred under each combination of S1 and S2.

Testing was conducted in a darkened room with each subject triggering the tachistoscope to begin each trial. At the beginning of each session 15 minutes was allowed for dark adaptation and the subject was given the practice trials. There were approximately 10 sec between trials and 2 minutes between blocks.

RESULTS:

The amount of aftereffect was defined as the mean of the TS orientations associated with transition responses that is shifts from left to right and visa versa.

Aftereffect scores were calculated for each subject under all factorial combinations of S1 and S2. An analysis of variance was performed on these data. The amount of

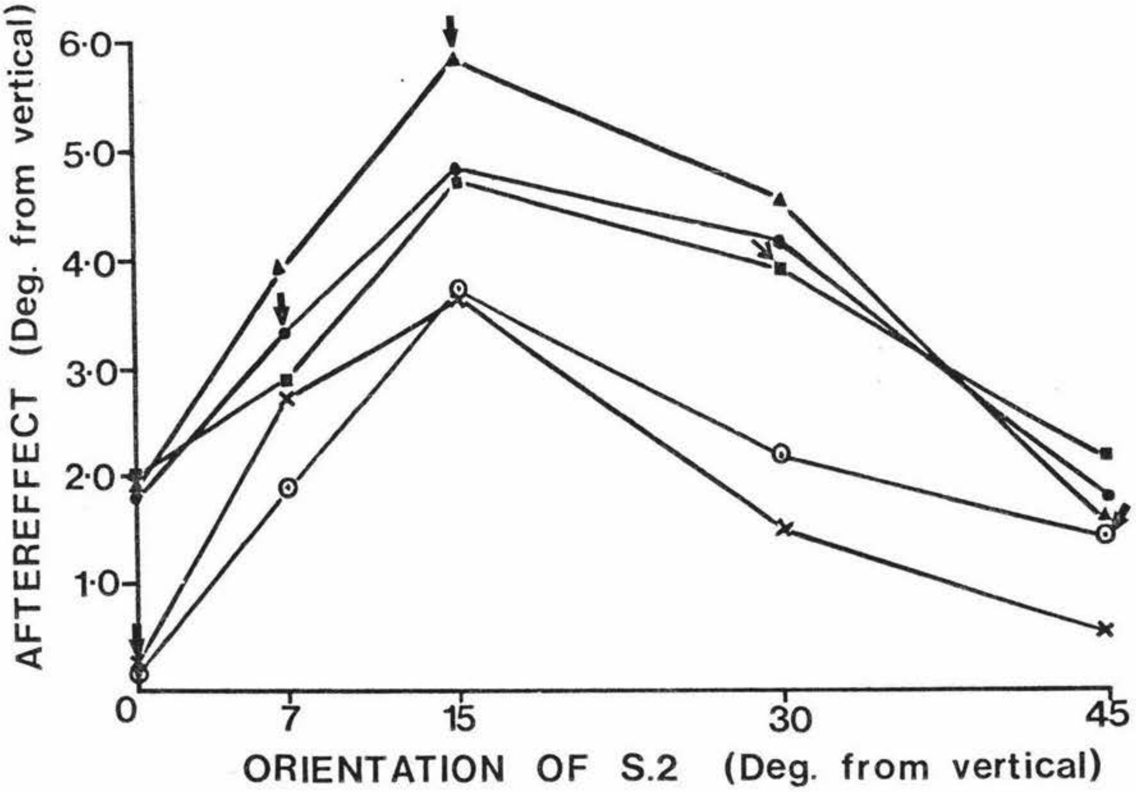

Figure 5: Mean aftereffect under successive adaptation as a function of S1 and S2. Parameter is S1 orientation (×——×, 0 deg; ●——●, 7 deg; ▲——▲, 15 deg; ■——■, 30 deg; ⊙——⊙, 45 deg). The arrows indicate control conditions where orientation of S1 and S2 is equal.

aftereffect varied significantly as a function of the orientation of S1 $[F(4,8)=31.41,\ p<0.01]$ and the orientation of S2 $[F(4,8)=45.50,\ p<0.01]$. The two way interaction between these two main effects (S1 and S2) was also significant $[F(16,32)=2.03,\ p<0.05]$ and is shown in Figure 5.

The five control conditions are identified in Figure 5 by the arrows; at these points both orientations of S1 and S2 are identical. At each orientation of S2 points below the control condition indicate disinhibition (decrease in inhibition) while points above the control condition indicate summation (increased inhibition). In order to directly compare disinhibition and summation from the appropriate control conditions a priori comparisons between all orientation combinations of S1 and S2 and control conditions were performed by subtracting the appropriate control condition from all orientation combinations of S1 and S2. Figure 6 shows the adjusted disinhibition and summation effects of S1 when the aftereffect of S2 is controlled for. For example when the control aftereffect of 0 deg (S1 0 deg and S2 0 deg) is removed from a vertical S2, the addition of a 7, 15, or 30 deg S1 results in significant summation ($p<0.01$). Figure 7, on the other hand, shows the disinhibition and summation effects of S2 when the aftereffect of S1 is controlled for.

The general formulae used for determining values in Figure 6 and 7 were, S1/S2 - S2/S2 and S1/S2 - S1/S1 respectively.

Maximum aftereffects were generated for all S1 orientations when S2 was 15 deg and reducing S2 by 8 deg or

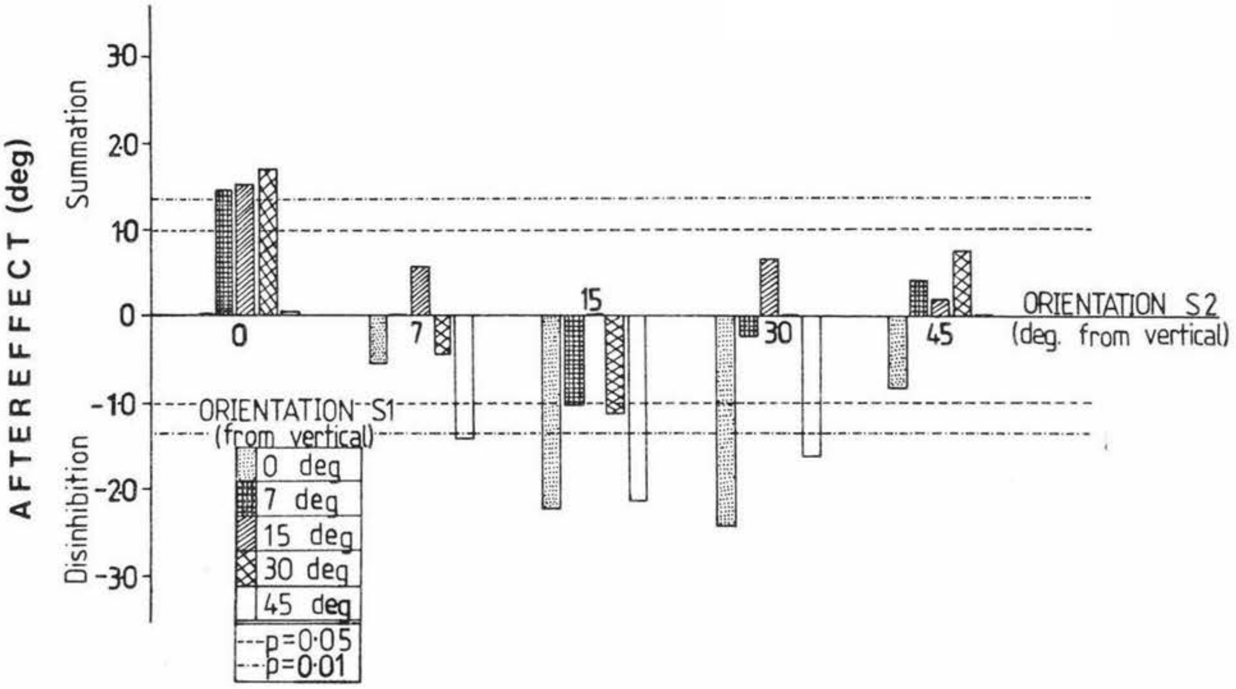

Figure 6: Mean aftereffect adjusted for control conditions of S2 under successive adaptation as a function of the orientation of S1 and S2. Critical a priori F values: (------), p = 0.05; (-·-·-·-), p = 0.01.

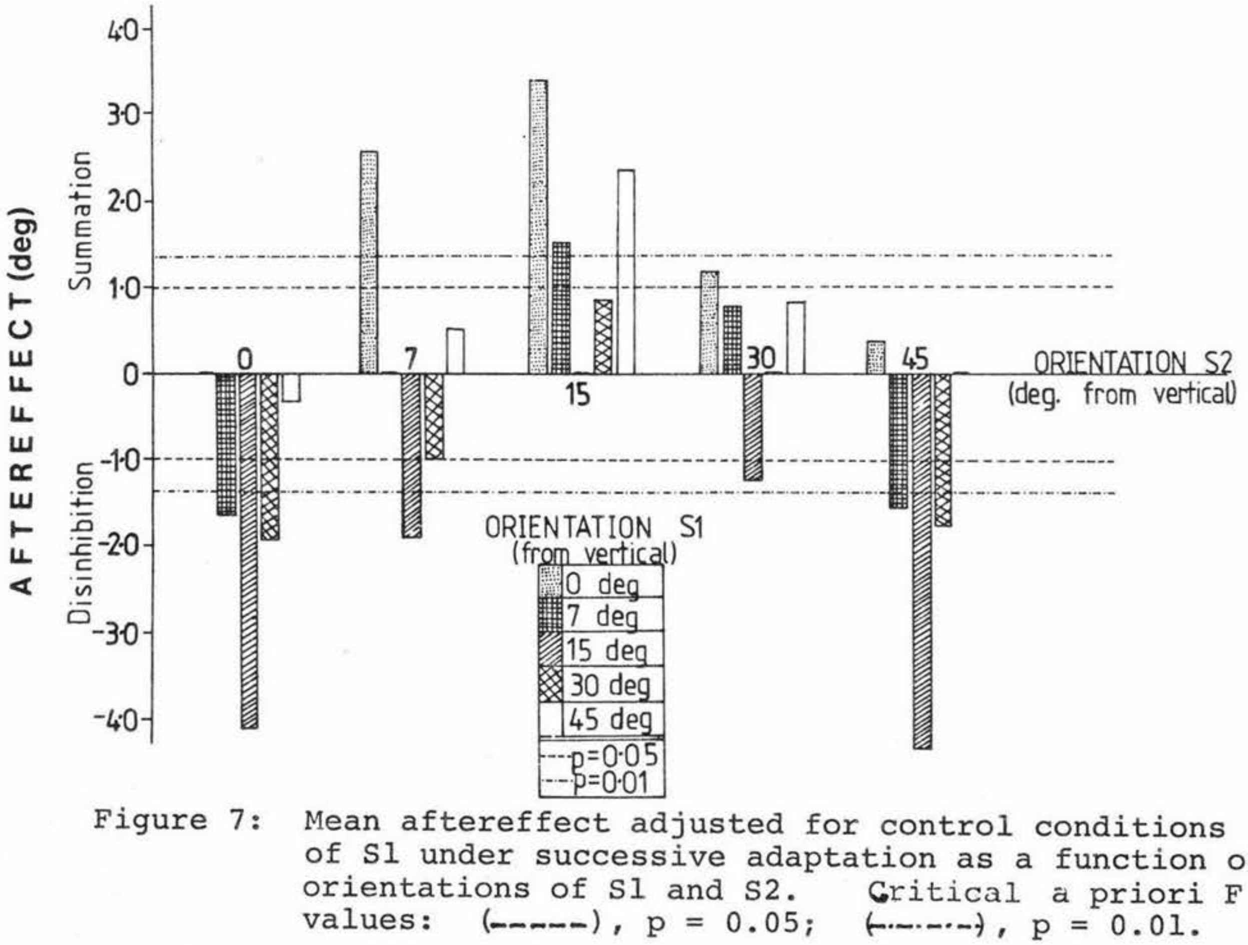

Figure 7: Mean aftereffect adjusted for control conditions of S1 under successive adaptation as a function of orientations of S1 and S2. Critical a priori F values: (------), p = 0.05; (-·-·-·-), p = 0.01.

increasing S2 by 15 deg resulted in significant reduction in aftereffect. A priori comparisons of means, where the aftereffect of S2 was controlled for (Figure 6), showed that a significant increase in aftereffect (summation) occurred for a vertical S2 when preceded by S1s of 7, 15, and 30 deg. Significant disinhibition occurred when a 7 deg S2 was preceded by a 45 deg S1 and when a 15 deg S2 was preceded by a 0, 7, 30, and 45 deg S1. Likewise a 30 deg S2 was disinhibited by a preceding S1 of 0 and 45 deg.

In Figure 7 where the aftereffect of S1 is controlled for and various orientations of S2 are introduced, a different pattern of disinhibition and summation is exhibited. For these comparisons the introduction of a vertical S2 after adaptation to a 7, 15, or 30 deg S1 results in significant disinhibition. Significant disinhibition also occurs when a 15, and 30 deg S1 is presented before a 7 deg S2, and when a 7, 15, and 30, deg S1 is presented prior to a 45 deg S2. Summation, on the other hand, results when a vertical S1 precedes a 7, or 30 deg S2 and when a 0, 7, and 45 deg S1 is presented before a 15 deg S2.

While Figures 6 and 7 show apparently different effects of various orientations of S1 and S2 (in the first instance the effect of S1 on the aftereffect of S2 is shown, and in the second the effect of S2 on the aftereffect of S1 is shown) the interaction between S1 and S2 is maintained. Essentially Figure 6 and 7 are complimentary as disinhibition at any orientation by one AS is usually accompanied by summation in the other AS. The pattern of disinhibitory and summative effects have been determined by convention, what is critical in determining the orientational selectivity of the function is the temporal order of presentation of S1 and S2 as well as the orientational difference of the two stimuli.

DISCUSSION:

The orientational selectivity of the disinhibtion function obtained with successive presentation of AS in this present experiment is similar to that obtained when the adaptation, disinhibition and test stimuli are single lines. (Kurtenbach & Magnussen, 1981; Magnussen & Kurtenbach, 1980; Carpenter & Blakemore, 1973) The results confirm the presence of disinhibition and summation in the orientation domain, but also that the magnitude of the effect is similar.

The range of orientations over which maximum disinhibition occurred for a vertical TS (i.e., ±15-20 deg) is generally in agreement with that obtained for masking (Experiment 1 & 2), aftereffect (Muir & Over, 1970; Magnussen & Kurtenbach, 1980), and illusion (O'Toole, 1979). In other words, while maximum inhibition (aftereffect) resulted from adaptation to a 15 deg orientation, inhibition of a vertical TS could be most effectively reduced (disinhibited) by the introduction of a grating whose orientation was within plus or minus 15-20 deg of the inhibitory grating. Specifically a 0 deg grating in this present study.

The data support the suggestion that disinhibition may arise by lateral inhibition, however, attempts to explain summation solely in terms of inhibitory mechanisms may appear a little confusing. However, the situation is by now means unique (Magnussen & Kurtenbach, 1980; Kurtenbach & Magnussen, 1981) and the proposal of a short versus long term inhibition (which is discussed elsewhere) may explain these findings. Most simply, it may be assumed that following prolonged excitation a neuron continues to send inhibitory signals to its neighbours after the stimulus is removed and this 'inhibitory noise' is indistinguishable from the normal inhibition from on going stimulation. The occurrence is also difficult to reconcile with Coltheart's (1971) alternative neural explanation of orientation aftereffects based on satiation and fatigue. A suggestion that both processes might be operating cannot be ruled out (Klein & Stromeyer, 1980).

The temporal presentation of stimuli must also be considered. Clearly an S2 of 0 deg exhibits considerably less inhibition on a vertical TS than a 15 deg S2 (Muir & Over, 1970; Mitchell & Muir, 1976; Gibson, 1937). Removal of such a temporal bias enables a better examination of orientation interaction and disinhibition of aftereffect.

3.2 Experiment 4: Orientation aftereffect following simultaneous presentation of a disinhibitory stimulus.

The interaction that results, known as tilt-illusion, wherein the perceived orientation of a TS is altered by the presence of adjacent gratings differing in orientation, is ascribed to a different mechanism than tilt-aftereffect, wherein the perceived orientation of a TS is changed after prolonged inspection of a preceding orientation grating Coltheart, 1971). However evidence seems to favour the hypothesis of Blakemore, et al., (1970) that both tilt-aftereffect and tilt-illusion result from a common mechanism of lateral inhibition.

Since successive introduction of a disinhibitory AS into an aftereffect paradigm exhibited maximum disinhibition when a 0 deg grating followed a 15 deg grating, should a different mechanisms be operating for successive and simultanious aftereffect, then a similar interaction may not be expected when 0 and 15 deg gratings are presented simultaneously.

In this present experiment simultaneous presentation of stimuli precede a suprathreshold TS. Specifically, it is proposed that the distortion in perception of a vertical TS and subsequent reduction of inhibition by a second AS should be similar to distortion and disinhibition occurring with successive presentation of AS (Experiment 3). Findings should also be compatible with findings of tilt-aftereffect generally (Gibson & Radner, 1937; Muir & Over, 1970; Mitchell & Muir; 1976).

METHOD:

Three graduate psychology students with normal or corrected-to-normal vision were used. Each subject received up to ½ hour preliminary practice in judging the orientation of a single vertical TS following exposure of the AS.

Apparatus:

The AS (G1 and G2) was two identical square wave black on white gratings with a greater space-to-line ratio, which were optically superimposed, was used to manipulate the orientation of the TS. The AS subtended 7 deg 8 min and each black line of the gratings subtended 8 min while the white spaces subtended 50 min. This greater space-to-line ratio minimized distracting interference patterns between the simultaneously presented gratings and while it altered the spatial frequency the phenomena under investigation, i.e., orientation, was not adversely affected. The space average luminance of AS was maintained at 9cd/m^2 with a Michelson contrast of 0.7. Five orientation values of G1 and G2 were used (0, 7, 15, 30 and 45 deg. clockwise from vertical).

The TS was a single black line 9 min wide and 7 deg 8 min long and was presented at 45cd/m^2 with a contrast of 0.8.

Each stimulus was binocularly viewed in separate channels of a Scientific Prototype three-field tachistoscope and were aligned so that at similar orientations, the TS aligned perfectly with a central black line of G1 and G2. Prior to the presentation of the stimulus sequence each subject viewed a single fixation point which was centrally located.

Procedure:

On each trial the AS (G1 with G2 superimposed) was shown for 15 sec followed by an ISI of 500 msec and then the TS for 5 msec.

As for Experiment 3 the observer's task on each trial was to judge whether the orientation of the TS was to the left or right of vertical. The observer was not permitted to report that the orientation was vertical. The after-effect was measured for all AS at each orientation combination of G1 and G2 and was the orientation of TS necessary to cancel the distortion caused by the prior presentation of the AS.

The AS with all orientation combinations of G1 and G2 were randomized into 25 blocks and were balanced in accord with a Latin square so that all subjects received all combinations in different orders. The combinations in which G1 and G2 were the same orientation (resulting in a single grating) served as controls against which disinhibition could be measured.

The procedure used for measuring the aftereffect was the same as in Experiment 3. On the first trial of any block the TS was orientated at 0 deg from vertical. If the observer responded "left" the TS was presented with one deg increase clockwise on the next trial; if the observer responded "right" the next trial was presented with one degree decrease counterclockwise. This procedure continued until six reversals in judgment occurred under each combination of G1 and G2.

Testing was conducted in a darkened room with each subject triggering the tachistoscope to begin each trial. At the beginning to each session 15 mins was allowed for dark adaptation and then the subject was given the practice trials. There were approximately 10 sec between trials and 2 mins between blocks.

RESULTS:

As outlined in Experiment 3 aftereffect was defined as the mean of the TS orientations associated with transition responses. Aftereffect scores were calculated for each subject under all factorial combinations of G1 and G2 and an analysis of variance was performed on these data. The aftereffect varied significantly as a function of the orientation of G1 $[F(4,8)=45.83,\ p<0.01]$ and G2 $[F(4,8)=49.44,\ p<0.01]$. The two-way interaction between the orientations of G1 and G2 was also significant $[F(16,32)=3.01,\ p<0.01]$ and is shown in Figure 8.

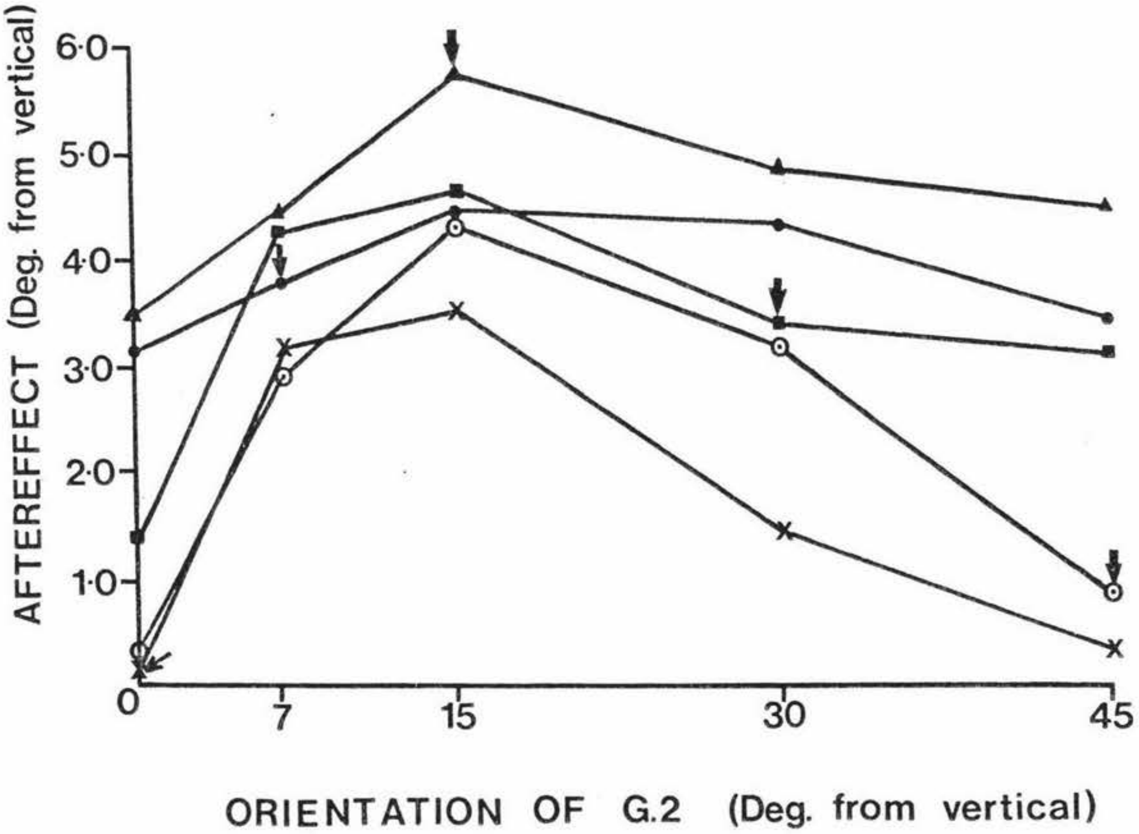

Figure 8: Mean aftereffect under simultaneous adaptation as a function of G1 and G2. The parameter is G2 orientation (×——× , 0 deg; ●——● , 7 deg; ▲——▲ , 15 deg; ■——■ , 30 deg; ⊙——⊙ , 45 deg). The arrows indicate control conditions where both G1 and G2 are at the same orientation (resulting in a single grating).

The five control conditions are identified in Figure 8 by arrows, and at these points G1 and G2 result in a single grating. At each orientation of G2 (abscissa) points below the control conditions indicate disinhibition while points above indicate summation. A priori comparisons between all orientation combinations of Gl and G2 and control conditions were performed by subtracting the appropriate control from all orientation conbinations of Gl and G2. Consequently when the control aftereffect of 0 deg (i.e., the aftereffect resulting from a single grating, due to the superimposition of Gl on G2, orientated at 0 deg) is removed for a vertical G2, the effect of superimposing a Gl grating at 7, 15, 30, and 45 deg can be seen. The formula used to adjust the values was Gl/G2 - G2/G2 and the adjusted aftereffect values are shown in Figure 9.

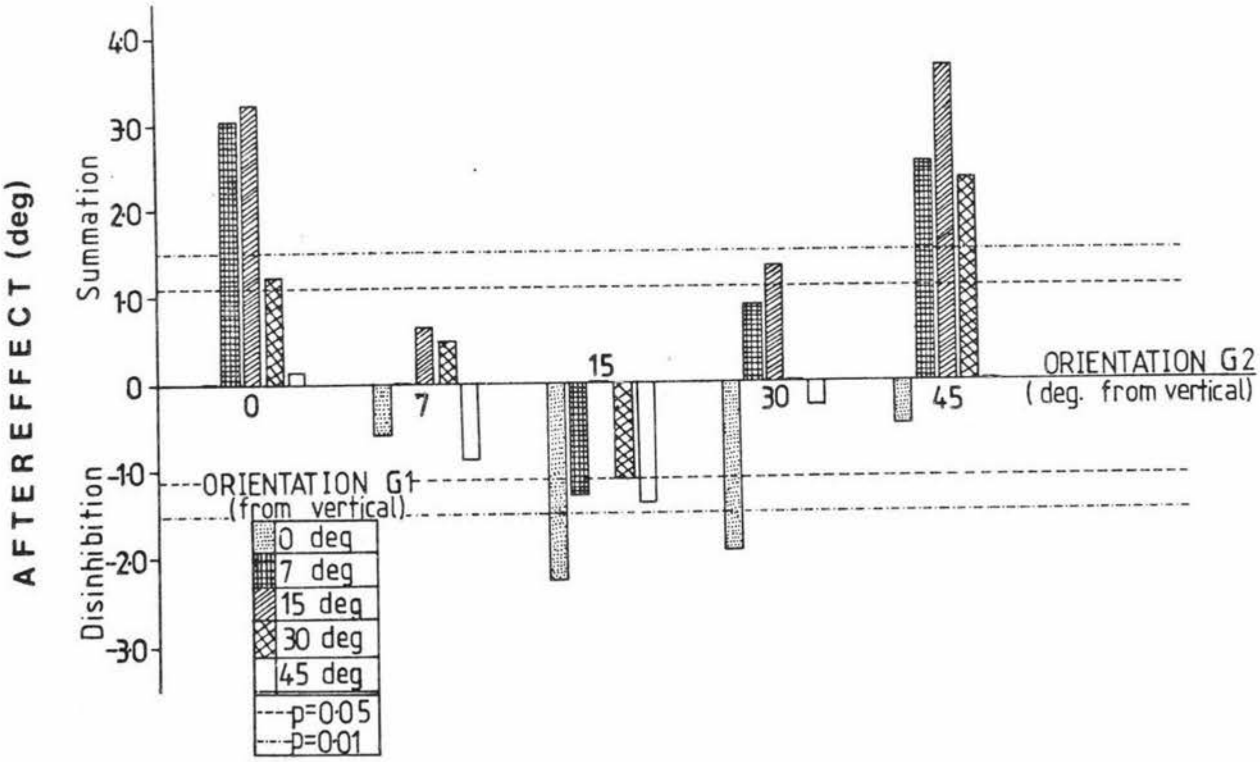

Figure 9: Mean aftereffect adjusted for control conditions of G2 under simultaneous adaptation as a function of Gl and G2. Critical a priori F values: (------), p = 0.05; (-·-·-·-), p = 0.01.

When a 7, 15, or 30 deg G1 was simultaneously presented with a vertical or 45 deg G2 significant summation resulted. Similar summation occurred when a 15 deg G1 and 30 deg G2 were paired. Significant disinhibition occurred when a 0, 7, 30, or 45 deg G1 was superimposed on a 15 deg G2 and when a 0 deg G1 was simultaneously presented with a 30 deg G2.

The pattern of disinhibition and summation is like that obtained in Experiment 3 with Figures 6 and 7 being similar. As G1 and G2 were superimposed, i.e., not temporally separated, the effect of G1 on the aftereffect of G2 must be identical to the effect of G2 on the aftereffect of G1 and therefore it is not necessary to adjust for the control condition of G1.

DISCUSSION:

The results show the orientation selectivity to the simultaneous aftereffect to be similar to that of successive aftereffect, in some aspects perhaps even identical. When a 0 deg orientation is presented simultaneously with a 15 deg orientation the vertical grating maximally inhibits the distortion caused by the 15 deg orientation alone.

The aftereffect and disinhibition data, which suggest the orientations of 15 deg exhibit maximum inhibition and orientations of 0 deg exhibit no inhibition are in agreement with those of Gibson (1937), Muir and Over (1970), and Mitchell and Muir (1976), irrespective of whether AS gratings were presented successively or simultaneously.

While the spatial frequency of this present experiment was not identical to that of Experiments 1, 2, and 3 the increase in space-to-mark ratio was not observed to have an adverse effect since control orientations in Experiments 3 and 4 were very similar.

3.3 Aftereffect Summary and Conclusions:

The results of Experiments 3 and 4 are consistent with the suggestion that aftereffects of successive and simultaneous adaptation are generated by a common neural mechanism. The most common neural mechanism believed to underlie orientation aftereffect, as seen earlier, is based on lateral inhibition between neural cells sensitive to specific orientations (Carpenter & Blakemore, 1973; Sekuler & Littlejohn, 1974; Magnussen & Kurtenbach, 1980).

A suggestion that has been proposed to account for both inhibition and disinhibition of direction in movement aftereffect (Levinson & Sekuler, 1975) could be generalized to explain the occurrence of orientation disinhibition and summation. The suggestion is that the visual system signals any discrete orientation by a balance of inhibition and excitation and that either increasing or decreasing excitation (inhibition) could result in summation. Consequently, at anytime the magnitude of the aftereffect depends upon the amount of excitation and inhibition received by neurons.

In order to account for temporal sequences of adaptation stimuli, short and long term inhibitory mechanisms are suggested for the successive and simultaneous paradigms respectively (Kurtenbach & Magnussen, 1981). A suggestion not too unlike the proposal of transient and sustained channels in masking suggested by Breitmeyer and Ganz (1976).

While some researchers ascribe different mechanisms to simultaneous contrast as compared with tilt-aftereffect (i.e., lateral inhibition -vs- fatigue; Blakemore, et al., 1971; Coltheart, 1971) successive masking and aftereffect demonstrate tuning functions similar in form to that of simultaneous masking and aftereffect, suggesting near parallel functions (Wenderoth & Tyler, 1979). Therefore there is no need to invoke different mechanisms to account for them.

Since the neural fatigue theory encounters difficulty in explaining simultaneous contrast (illusion), and hence simultaneous aftereffect, the hypothesis of Blakemore, et al., (1971) that tilt-aftereffect and simultaneous contrast are both manifestations of lateral inhibition is more in evidence, given the present experiments and those of others (Tolhurst & Thompson, 1975; Sekuler & Littlejohn, 1974). Indeed the critical test of the mechanisms underlying the various simultaneous and successive tilt-aftereffect, tilt-illusion, and masking phenomena probably will require direct physiological observation of the kind which are already beginning to be reported (e.g., Blakemore & Tobin, 1972; Nelson & Frost, 1978; Vautin & Berkly, 1977).

CHAPTER FOUR: DICHOPTIC AFTEREFFECT

4.0 Dichoptic Aftereffect: Experiment 5.

The robust nature of disinhibition has now been shown in successive and simultaneous aftereffect, and successive masking. While orientational selectivity of disinhibition remains a pertinent characteristic of the function, determining the level (i.e., level of the cortex -vs- level of the retina) of the phenomena is difficult (Long, 1979). However the data obtained in Experiments 1, 2, 3, and 4 suggest that orientation disinhibition may be a high level effect, and therefore interocular disinhibition for orientation analyzers may be able to be demonstrated. Indeed microelectrode data support this contention (Hubel & Wiesel, 1968). However, as argued by Long (1979) presence or absence of interocular transfer may not be evidence of high level processing. To avoid this dilemma Experiment 5 adopts dichoptic presentation of AS to determine whether or not the disinhibition function can be disrupted by binocular rivalry.

4.1 Experiment 5: Disinhibition and summation with dichoptic presentation of AS.

When two gratings of different orientation are superimposed and presented monocularly, one orientation may appear dominant while the other appears attenuated. With further observation dominance and attenuation may alternate and at other times the orientations may appear as a composite. This monocular rivalry or monocular pattern alternation occurs when the orientational difference between orientations is a least 15 deg (Georgeson & Phillips, 1980; Kitterle & Thomas, 1980; and Campbell & Howell, 1972).

Under dichoptic masking or aftereffect when two orientations are simultaneously presented one to each eye binocular rivalry or alternation between orientations also occurs. Like monocular rivalry, binocular rivalry is more pronounced when the orientational difference between orientations is greater than 15 deg and increases as the orientational difference increases (Kitterle & Thomas, 1980).

While the phenomena appear similar, evidence indicates that they may be mediated by different mechanisms. For example, binocular rivalry is relatively insensitive to changes in colour or spatial frequency (Kitterle & Thomas, 1980) and the number of alternations between orientations being considerably reduced under the monocular rivalry condition (Wade, 1975). However further research has shown that binocular rivalry exerts no influence on a number of visual effects. For example it has been shown that binocular rivalry does not disrupt the McCollough effect (White et al., 1978), motion aftereffect (Lehmkuhle & Fox, 1975), or interocular transfer (Blake & Overton, 1979; O'Shea & Crassini, 1981).

Disinhibition is observed when a stimulus is introduced into a masking or aftereffect paradigm and it's presence inhibits the inhibitory effect of a masking or adaptation stimulus respectively (Chapter two & Chapter three; Dember & Purcell, 1968; Blakemore, Carpenter & Georgeson, 1970; Magnussen & Kurtenbach, 1980; 1981). Evidence suggests that orientation disinhibition may be a high level effect and therefore able to be demonstrated with dichoptic aftereffect. Microelectrode data support this contention since a large number of orientation specific cells in the monkey's visual cortex are binocularly driven (Hubel & Wiesel, 1968). Presenting an AS to separate eyes simultaneously is one technique for inferring the stage in the visual system where the inhibition and subsequent disinhibition interaction occurs. If it is found under dichoptic conditions there are grounds for asserting that at least one mechanism underlying disinhibition is located no earlier than the stage where information from the two eyes is combined.

Experiments 3 and 4 considered disinhibition and summation with both successive and simultaneous presentation of AS and found the extent of inhibition between the two conditions to be very similar. Should disinhibition be able to be demonstrated dichoptically, further similarities would be expected between the findings of this present study and those of successive and simultaneous aftereffect. While confounding by binocular rivalry may certainly be a possibility, effects similar to those of successive aftereffect, where no rivalry is possible, would dispel these. Further, inhibition of aftereffect due to binocular rivalry would appear more pronounced where orientational differences between orientations was greatest.

Specifically it is proposed that the distortion of aftereffect and subsequent reduction in inhibition caused by a disinhibitory orientation will be maximum for 15 deg and vertical orientations respectively.

METHOD:

Four psychology students, three undergraduate, one graduate, with normal or corrected-to-normal vision were used as subjects. Each subject received up to ½ hour preliminary practice in judging the orientation of a single vertical TS following exposure of an AS presented binocularly to both ways at various orientations.

Apparatus:

The AS (RES and LES) were two identical square-wave gratings and these were used to manipulate the orientation of the TS when presented simultaneously (dichoptically). RES and LES were circular and subtended 7 deg 8 min wide, while the space-average luminance was maintained at 8.5cd/m^2 with a Michelson contrast of 0.6. Four orientation values of RES and LES were used (0, 7, 15 and 30 deg clockwise from vertical).

The TS was a single black line 9 min wide and 7 deg 8 min long and was presented at 45.0cd/m^2 with a contrast of 0.8. Photographic copies of each stimulus were mounted on circular discs which were able to be rotated.

RES and LES were dichoptically presented one to the right eye and one to the left eye respectively in separate channels of a Scientific Prototype Threefield Tachistoscope. The AS were aligned so that, at similar orientations the TS, which was presented to both eyes, aligned perfectly with a central black line of the AS. Prior to presentation of the stimulus sequence each subject viewed a single fixation point which was centrally located.

Procedure:

On each trial, following the binocular viewing of the fixation point, RES was shown to the right eye and LES was shown to the left eye simultaneously for 15 sec. Immediately after an ISI of 500 msec the TS was displayed for 5 msec to both eyes.

The observer's task on each trial was to judge whether the orientation of the TS was to the left or right of vertical. The observer was not permitted to report that the TS was vertical. The aftereffect was measured at each orientation combination of RES and LES and was the orientation of TS necessary to cancel the distortion caused by the prior presentation of RES and LES.

All orientation combinations of RES and LES were randomized into 16 blocks and were balanced in accord with a Latin square so that all subjects received all combinations in different orders. The combinations in which RES and LES were the same orientation served as controls against which disinhibition could be measured.

On the first trial of any block the TS was orientated at 0 deg from vertical. If the observer responded "left" the TS was presented with one degree increase clockwise on the next trial; if the observer responds "right" the next trial was presented with one degree decrease counter-clockwise. This procedure continued until six reversals in judgment occurred under each combination of RES and LES.

Testing was conducted in a darkened room with each subject triggering the tachistoscope to begin each trial.

There was approximately 10 sec between trials and 2 minutes between blocks.

RESULTS:

The amount of aftereffect was defined as the mean of the TS orientations associated with transition responses (i.e., shifts from left to right or visa versa).

Aftereffect scores were calculated for each subject under all factorial combinations of RES and LES and an analysis of variance was performed on these data. The magnitude of aftereffect varied significantly as a function of the orientation of RES $[F(3,9)=25.28,\ p<0.01)]$ and LES $[(F3,9)=22.97,\ p<0.01)]$. The two-way interaction between the orientations of RES and LES was also significant $[(F9,27)=5.44,\ p<0.01)]$ and is shown in Figure 10.

The four control conditions are identified in Figure 10 by arrows and at these points both orientations of RES and LES are identical. At each orientation of RES points above the control conditions indicate summation or increased inhibition, and points below the control conditions indicate disinhibition or decreased inhibition.

In order to directly compare disinhibition and summation from ordinary aftereffect, a priori comparisons between all orientation combinations of RES and LES, and control conditions were performed by subtracting the appropriate RES control condition from all orientation combinations of RES and LES. Thus when the control aftereffect due to RES is removed the effect of presenting RES simultaneously with LES is seen. The formula used to adjust the values was LES/RES - RES/RES and the adjusted aftereffect values are shown in Figure 11.

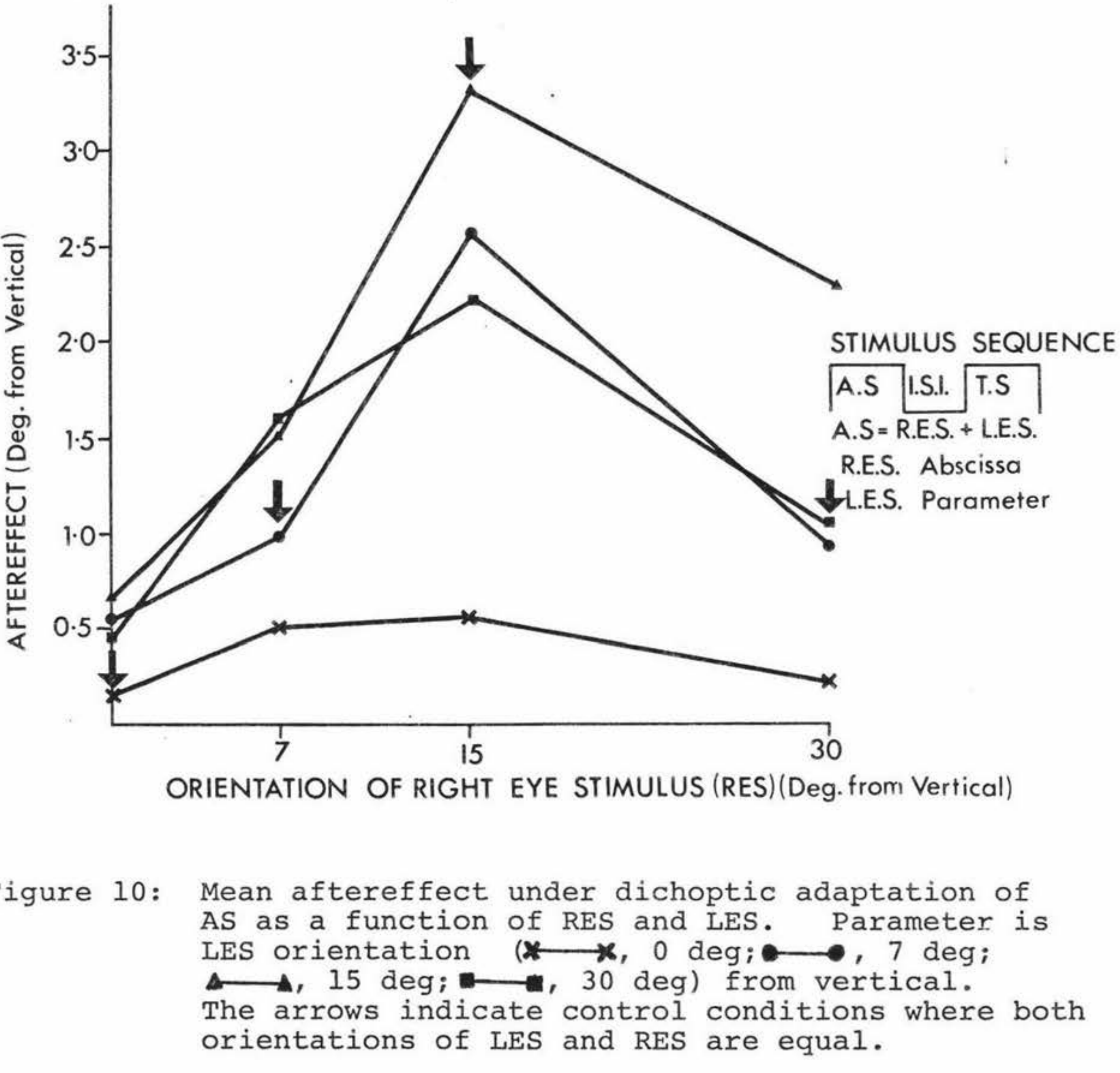

Figure 10: Mean aftereffect under dichoptic adaptation of AS as a function of RES and LES. Parameter is LES orientation (×——×, 0 deg; ●——●, 7 deg; ▲——▲, 15 deg; ■——■, 30 deg) from vertical. The arrows indicate control conditions where both orientations of LES and RES are equal.

Maximum aftereffects were generated for all LES orientations when RES was 15 deg and as Figure 11 shows, reducing the orientation of LES 8 and 15 deg or increasing it by 15 deg resulted in significant disinhibition. Similar disinhibition also occurred when LES 0 deg was presented with RES of 30 deg. While an LES of 15 deg and an

RES of 0, 7, or 30 deg resulted in summation a significant increase in inhibition only occurred when RES was 30 deg. Summation also resulted when a 7 deg RES was presented with a 30 deg LES.

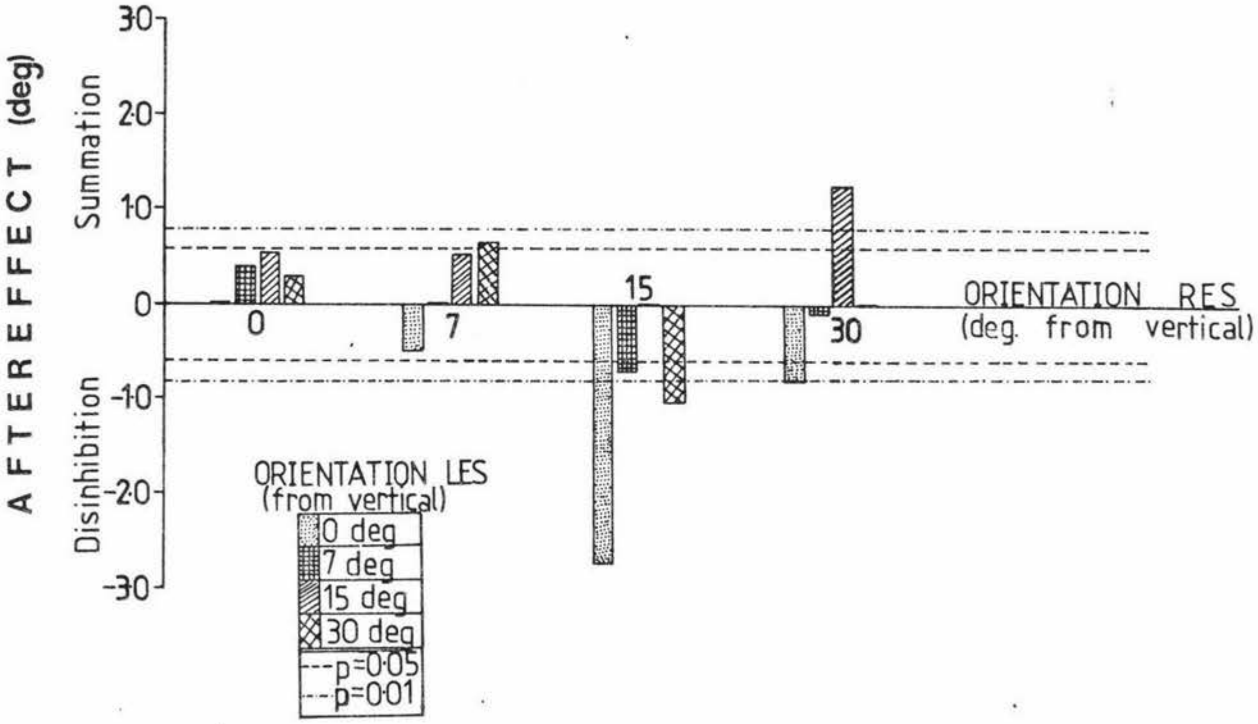

Figure 11: Mean aftereffect adjusted for control conditions of RES under dichoptic adaptation of AS as a function of RES and LES. Critical a priori F values: (-·-·-·-), p = 0.01; (------), p= 0.05.

Generally the results indicate strong inhibitory effects exerted by the 15 deg orientation and disinhibitory effects exerted by the vertical orientation. No evidence could be found to suggest that inhibition due to binocular rivalry had occurred as this would have been exhibited by a significant decrease in aftereffect where orientational differences between orientations were greatest for example when vertical and 30 deg orientations were presented together.

DISCUSSION:

The orientation selectivity of the disinhibition functions in this experiment are consistent with those obtained in a successive or simultaneous aftereffect condition (Experiment 1 and 2). One notable difference between the monocular and dichoptic conditions is the overall reduction in magnitude of aftereffect with dichoptic presentation of AS. However the range of maximum orientation disinhibition for a vertical TS is in agreement with that obtained for the successive and simultaneous aftereffect (Magnussen & Kurtenbach, 1980) and for masking (Experiments 1 & 2; Wenderoth & Tyler, 1979).

The results of this experiment, like those of aftereffect and masking, lend further support to the lateral inhibition explanation of disinhibition. Neurons optimally sensitive to one orientation inhibit neurons optimally sensitive to other orientations and since disinhibition has occurred dichoptically, inhibition by binocular neurons can be inferred.

Binocular rivalry has not been shown to disrupt tilt aftereffect (Wade & Wenderoth, 1978) or motion aftereffect (Lehmkuhle & Fox, 1978) and since there is considerable evidence both neurophysiological and psychological which suggests that the site of these aftereffects and rivalry is cortical (Hubel & Wiesel, 1968), the site of orientation disinhibition may also be cortical since disinhibition was not disrupted by a binocular rivalry paradigm. O'Shea and Crassini (1981) argue against the contention that the motion aftereffect mechanism is a lower level effect and suggest possible parallel processing of motion aftereffect and binocular rivalry. The present findings would support this contention further suggesting that orientation disinhibition engages processing at least parallel to that of binocular rivalry and assert that at least one mechanism underlying disinhibition is located no earlier than the stage where information form the two eyes is combined (Weisstein, 1972).

4.2 Dichoptic Aftereffect: Discussion and Conclusions

Several studies have attempted to isolate the locus of the disinhibitory function by utilizing dichoptic masking (Robinson, 1968; Turvey, 1973). However interpretation of these results is difficult since identification of the locus of an interaction on the basis of the presence or absence of interocular effects is insufficient (Long, 1979). By avoiding the question of interoccular transfer, Experiment 5 has demonstrated the disinhibition effect may be cortical. Indeed, orientation disinhibition in masking and aftereffect suggest the function to be a high level effect but an apparent inability of binocular rivalry to disrupt disinhibition reinforces these findings.

While these general points may be valid a few specific points are perhaps worth mentioning. Firstly, while findings of disinhibition in simultaneous aftereffect and dichoptic aftereffect emphasize the similarities between the two phenomena a suggestion of mediation by a similar mechanism can not be made. The mere fact that overall magnitude of aftereffect between the two phenomena was not identical needs consideration. It is necessary to establish more fully the parts played by binocular and monocular neurons in orientation disinhibition under dichoptic aftereffect and binocular rivalry.

Secondly, although not in any clear evidence in this present experiment, inhibition due to rivalry suppression may have been operative during dichoptic aftereffect. Indeed the duration of adaptation was long enough for suppression to have occurred. Perhaps dichoptic masking as a means of further determining disinhibition as a high level effect is not unwarranted since the inhibition due to rivalry may not be generated rapidly enough to influence the brief stimulus presentation characteristic of masking.

CHAPTER FIVE:

GENERAL SUMMARY AND CONCLUSIONS

5.0 General Summary and Conclusions

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Feature detection explanation of masking and aftereffect assume that the likelihood of detection of a TS (masking) and the distortion of a TS (aftereffect results from activity within populations of feature detecting neurons in the human visual system. Masking assumes that the detection of a threshold TS is reduced by prior presentation of a mask. During masking the overall activity of the feature detecting population signally the TS is suppressed (masked) by the mask. Therefore, for detection of the TS to occur, either an increase in the energy level of the TS, or introduction of a second mask into the masking sequence to inhibit suppression caused by the mask is required.

The latter has been demonstrated in Experiments 1 and 2 to be highly orientation specific, with maximum disinhibition occurring when the orientation of M1 and M2 are similar, and is absent when the orientation difference between M1 and M2 is greater than 15 deg.

On the other hand, aftereffect paradigms require the judgement of a suprathreshold TS, following exposure to an adaptation stimulus. The neural activity of the suprathreshold stimulus is not suppressed by the AS so as to change its detectability, but the overall neural activity of the TS is distorted by the neural activity of the AS. Reduction of TS distortion has been shown (Experiments 3 and 4) with the introduction of a second orientation stimulus into an aftereffect sequence. Maximum disinhibition resulting when the orientation of the AS approximated the orientation of the TS. That is, for a vertical TS, when the orientation of one of the AS was also vertical.

The question of the site of disinhibtion between orientation detectors was considered in Experiment 5. Although it cannot be categorically stated that the effect is cortical, it has been demonstrated to be at least parallel to that of binocular rivalry since the function was not disrupted by the phenomena, and therefore at least one mechanism underlining disinhibition may be cortical.

The experiments outlined lend considerable support for a lateral inhibition explanation of orientation disinhibition with a general feature detection model of visual perception. Indeed the feature detection theory has been now generally accepted, however two aspects of the theory have been questioned. Firstly, whether the cells early in the system can best be described as feature detectors or as spatial frequency filters. Secondly, whether the physiological and anatomical organization is in fact as hierarchial as initially postulated. A suggestion by Campbell & Robson (1968) that there may be multiple spatial frequency channels has had quite an impact because it leads to an entirely different concept of the way in which the visual system might function in dealing with spatial stimuli (DeValois & DeValois, 1980). Perhaps, as they suggest, rather than specifically detecting such features as bars and edges the system breaks down complex stimuli into their individual spatial frequency components in a kind of Fourier analysis. However, while the correctness of this particular model may be beyond the relms of this thesis it emphasizes the many ways in which the visual system could analyse the world.

The interpretation of human physiological functioning, in terms of physiological data obtained from animals, must be done with great caution. A response from a single neuron obtained from a paralyzed cat with immobile eyes is a datum not easily related to the behavioural response of a conscious human observer. However, it is only through such physiological data, and psychophysical investigation (as seen in this thesis) and the colaboration of these two, that we may gain insight into the elusive mechanisms of human vision.

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APPENDIX

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Spatial disinhibition of orientation analyzers

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Following the successive presentation of two masking gratings (M1 and M2), subjects were required to detect the presence or absence of a single vertical line (TS). When the orientations of the two masks were optimal, M1 was able to reduce the masking effect of M2 on the TS. For a vertical TS, disinhibition was maximal when the orientations of M1 and M2 were similar and was minimal when the orientational difference was greater than 15 deg. It is suggested that the spatial selectivity of the disinhibition function reflects the activity of neurons tuned to orientation, and that the disinhibition masking paradigm may be a useful psychophysical technique to measure tuning functions of other feature detectors.

When a visual target stimulus (TS) is presented within close temporal and/or spatial contiguity with a masking stimulus, the masking stimulus is able to reduce the detectability of the TS. If a second mask is introduced into the masking sequence, the introduced mask is able to disinhibit (reduce the masking effect of) the first mask (Dember & Purcell, 1968; Dember, Schwartz, & Kocak, 1978; Kristofferson, Galloway, & Hanson, 1979; Robinson, 1966). In these studies the TS was often a single uppercase letter, while the first mask (M1) and the second mask (M2) were a disk and either a larger disk or ring, respectively. Maximum disinhibition has been reported at stimulus onset asynchronies (SOAs) of 116 msec (TS − M2) and 35 msec (TS − M1) (Kristofferson et al., 1979). In the experiments that have reported disinhibition, the effect is critically dependent upon the SOAs, the masking ability and the energy levels within the masks (Breitmeyer, 1978; Bryon & Banks, 1980; Long & Gribben, 1971). Other experiments that have varied stimulus size, configuration, luminance, and the forced-choice procedure have failed to report disinhibition (Barry & Dick, 1972; Prager & Matteson, 1978; Schurman & Eriksen, 1969). For disinhibition to occur, M1 must exert a moderate masking effect on TS and, provided that the SOAs are sufficient to prevent summation between the masks, then M2 will disinhibit M1 (Long & Gribben, 1971).

Many theoretical explanations have been offered to account for masking and disinhibition (e.g., interruption, integration, and overtake), but theories based on neurophysiological properties of feature detecting neurons are obviously relevant when the TS and MS temporal and spatial relationships determine masking effects (Breitmeyer, 1980; Breitmeyer & Ganz, 1976; Weisstein, Ozog, & Szoc, 1975). The basic assumption of a neural theory of disinhibition is that the activity of a neuron can be modulated by prior activity and/or by the activity of neighboring units. Following prolonged optimal stimulation, a neuron undergoes a period of postexcitatory suppression. If a near-threshold TS is presented during this period, it must be presented at a higher energy level for detection. Also, interchannel inhibition may modify a neuron's response, but only to the extent that the channels are responsive to the same or overlapping spatial dimensions in the stimuli. This latter explanation has been offered to account for the occurrence of disinhibition in orientation illusion (Blakemore, Carpenter, & Georgeson, 1970; O'Toole, 1979), aftereffect (Magnussen & Kurtenbach, 1980), and masking (Wenderoth & Tyler, 1979).

Barry and Dick (1972) and Purcell and Dember (1968) have suggested that disinhibition in Robinson's (1966) paradigm may arise as successive brightness contrast or brightness reversal. Implicit in this explanation is that disinhibition arises within populations of neurons that are maximally responsive to luminance properties of M1 and M2. More powerful support for a feature detection explanation is evidenced by the spatial selectivity of motion disinhibition observed when the direction of a moving grating is varied (Levinson & Sekuler, 1975). Using the direction-specific properties of motion detectors, Levinson and Sekuler (1975) determined the threshold of a rightward moving test grating (i.e., for this moving grating, the inhibitory component moved leftwards). Subsequent preadaptation to a leftward moving grating disinhibited the inhibitory component of the rightward moving grating with a subsequent reduction in the threshold of the test grating. Similar spatial restrictions of disinhibition when lines and bars have been utilized have been reported (Breitmeyer, 1978; Rentschler & Hilz, 1976). Breitmeyer reported that the masking effect of briefly presented bars on the detection of a vernier

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target was reduced when two disinhibiting bars were presented, and that the reduction was dependent on the spatial configuration of the stimuli. For example, when the disinhibiting bars were laterally separated by 20 minarc from the mask, there was a substantial increase in masking. These spatial restrictions on the magnitude of disinhibition suggest that the effect is likely to occur at a high level in the visual system.

Several studies have attempted to isolate the locus of the disinhibitory effect by utilizing dichoptic masking (Robinson, 1968; Turvey, 1973). However, interpretation of these results is difficult since identification of the locus of the interaction on the basis of the presence or absence of interocular effects is insufficient (see Long, 1979). If disinhibition arises as the direct result of an interchannel inhibitory process within feature detecting neurons, then the effect should be spatially restricted to the known receptive field properties (e.g., tuning ranges) of the neurons. The importance of this additional requirement is that it implies a central locus for the effect, as there is strong evidence that suggests that spatial selectivity is a major property of neurons in the visual cortex (Hubel & Wiesel, 1968; Maffei & Fiorentini, 1973; Poggio & Fischer, 1977).

The spatial limitation of the masking functions obtained in feature masking has been attributed to the inhibitory interaction of neural units (Breitmeyer, 1980; Weisstein et al., 1975). Furthermore, the selectivity observed in the masking functions is spatially restricted to the stimulus features that have similar spatial values (Blakemore & Hague, 1972; Blakemore, Nachmias, & Sutton, 1970; Over, Broerse, & Crassini, 1972).

Blakemore et al. (1970) and O'Toole (1979) have demonstrated orientation disinhibition by observing the apparent contraction or expansion of acute angles when a third disinhibitory line is introduced. In both of these experiments, the maximum disinhibitory effect occurred when the difference between the masking and disinhibiting orientations was 10-20 deg. In the present study, a neural explanation of visual masking is offered to account for spatial disinhibition observed in orientation illusion and masking. Orientational selectivity has been demonstrated directly from microelectrode recording from neurons in the monkey cortex (Hubel & Wiesel, 1968), visually evoked cortical potentials from humans (Campbell & Maffei, 1970), and from other human psychophysical data (Gilinsky & Mayo, 1971; Over et al., 1972). There are theoretical problems associated with the linking of electrophysiological data based on the activity of single neurons and psychophysical data (Sekuler, 1974; Wenderoth & Latimer, 1979). However, the aim is not to infer equivalence of neural functioning, but to offer support for the psychophysical data when the further restraint of physiological data is considered (Breitmeyer, 1980). In this study, it is hypothesized that the detectability of a vertical target line will vary as a function of the orientation of the masking gratings. Specifically, it is proposed that orientation disinhibition should occur only when the orientations of M1 and M2 maximally mask each other.

METHOD

Subjects

Three undergraduate students with normal or corrected-to-normal vision served as subjects.

Procedure

A forward masking-disinhibition paradigm was used. Following the presentation of a centrally located fixation spot (10 sec), the stimulus sequence commenced with M1 presented for 150 msec. Interstimulus 1 (ISI1) for 1 msec, M2 for 150 msec, ISI2 for 10 msec, and then the TS (or homogeneous blank field on catch presentations). The duration of the TS was 4 msec and was the duration at which the subjects could correctly detect the TS at 75% accuracy and when a homogeneous MS of 26.0 cd/m² was displayed beforehand. A homogeneous rather than a grating MS was used to ensure that any subsequent change in the detectability of the TS was due to the presence of oriented features within the mask. The stimuli were aligned so that the features impinged on the same retinal area when displayed in separate channels of a Scientific Prototype tachistoscope.

The TS was a single black vertical line, 7 deg 8 min long and 9 min wide, while the square-wave gratings utilized for M1 and M2 subtended 7 deg 8 min, and each line of the grating subtended 9 min wide. All MS displays were circular and could be rotated. Four orientation values of M1 and M2 were used (0, 7, 15, and 30 deg from vertical). The space average luminance of the TS (or catch stimulus) was maintained at 29.5 cd/m² and was 26.0 cd/m² for M1 and M2.

In each session, the subject was given 30 min of practice in reporting the presence of the TS when one MS was used. During the practice session, the subject's TS threshold was determined, and this value was subsequently used throughout the experiment. All orientation combinations of M1 and M2 were randomized into 16 blocks and were balanced in accord with a Latin square so that all subjects received all combinations in different orders. Four further blocks of all M1 orientations without the presence of M2 (i.e., normal forward masking condition) were also included to serve as controls against which disinhibition could be measured. Each block consisted of 12 trials made up of six trials on which the TS was actually present, randomly interspersed with six catch trials. On the six target trials, the single vertical line was presented, while on the catch trials, a homogeneous field of equal luminance was shown. The subject's task was to report whether the TS was present or absent (i.e., to differentiate between the target and catch trials). Testing was conducted in a dark room, with each subject triggering the tachistoscope. There was approximately 10 sec between trials and 1 min between blocks.

RESULTS

The percent correct detection of the TS was calculated for each subject under all factorial combinations of M1 and M2, and was the accuracy with which each subject could correctly detect the presence or absence of the TS. An anlysis of variance was performed on these data. The percent detection varied significantly as a function of the orientation

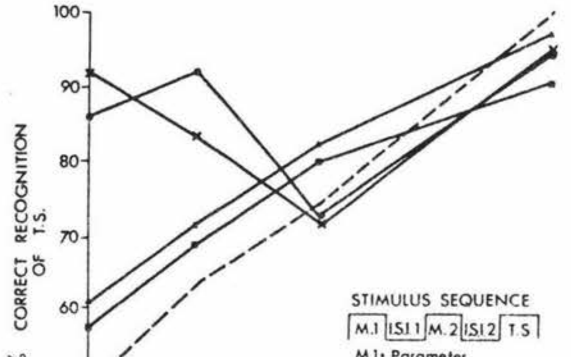

Figure 1. Percentage correct detection of TS as a function of the orientations of M1 and M2. Parameter is M1 orientation (×——×, 0 deg; ●——●, 7 deg; ▲——▲, 15 deg; ■——■, 30 deg) and forward masking control (- - -).

of M2 [F(3,6) = 18.65, p < .01], while the orientation of M1 did not exert a significant influence [F(3,6) = 4.49, p > .05]. The two-way interaction between these variables was significant [F(9,18) = 7.48, p < .01] and is shown in Figure 1.

In order to directly compare the disinhibition and the forward masking control condition, the percent correct detection scores from the disinhibition data were pooled over M1 orientations and subjected to a further analysis of variance. While the orientation of M2 exerted a significant effect on the percent correct detection of the TS [F(3,6) = 20.46, p < .01], there was no significant difference between the disinhibition and forward masking control conditions [F(1,2) = 11.46, p > .05]. The two-way interaction between these variables was significant [F(3,6) = 106.16, p < .01]. Multiple comparisons of means using the Newman-Keuls method of comparison revealed that the introduction of M1 prior to M2 significantly reduced the masking effect of M2, provided the orientation of M2 was either 0 or 7 deg. Inspection of Figure 1 showed that disinhibition occurred when both M1 and M2 were 0 or 7 deg. If M2 was 15 or 30 deg, then the introduction of a 0- or 7-deg M1 had little effect, as the function was similar to the forward masking control condition. Similarly, the functions obtained by M1s of 15 and 30 deg at all M2 orientations resembled the forward masking control condition. Generally, it appears that if disinhibition of vertical TS is to occur, then M1 and M2 must be processed by overlapping neural channels that are tuned to orientation values less than 15 deg to vertical.

DISCUSSION

The results of the present experiment give considerable support to the contention that the human visual system responds selectively to narrow ranges of orientation information. Following the presentation of masking stimuli containing orientation information, disinhibition occurred when M1 and M2 were similar in orientation, and disinhibition declined as the orientation difference between the masks increased. Orientation disinhibition was highly specific in that disinhibition failed to occur if the orientation of the masks differed by 15 deg.

The findings of this experiment are specific to a TS of 0 deg, since there is considerable evidence that suggests that oblique orientations are signaled by channels that are less specifically tuned and less represented within the visual system than vertical and horizontal orientations (Appelle, 1972; Matin & Drivas, 1979). In order to predict the likelihood of orientation disinhibition between masks of various orientations, the different sensitivities of the visual system to oblique orientations must be taken into account. The current results, which suggest that M1 orientations of greater than 15 deg cannot disinhibit equal energy M2s of lesser orientations, are in partial agreement with those of Wenderoth and Tyler (1979), who reported that, in a simultaneous masking paradigm, a 0-deg (i.e., vertical) grating could also be disinhibited by orientations of 75 and 90 deg (i.e., approximately horizontal). With the exception of these latter results, the orientation over which disinhibition resulted is extremely similar to the orientation tuning ranges isolated by other psychophysical techniques (Campbell & Maffei, 1970; Fidell, 1972; Gilinsky & Mayo, 1971; O'Toole, 1979; Over et al., 1972). The present data support the suggestion that disinhibition may arise by lateral inhibition in populations of feature detecting neurons. Furthermore, the orientational selectivity of the effect suggests that the disinhibition paradigm could be added to other psychophysical techniques as a further method to study feature detection in the human visual system.

The magnitude of disinhibition at optimal orientation values between M1 and M2 is relatively large, and this finds support with the strong recovery effects reported by Dember et al. (1978), Kristofferson et al. (1979), and Wenderoth and Tyler (1979). The present experiment differs in several aspects from previous studies since forward disinhibition has been used, whereas backward disinhibition paradigms have almost universally been utilized in the past. The forward masking paradigm is utilized to maximize the masking effect of M1 on M2 (Wenderoth & Tyler, 1979). Surprisingly, at the short ISI1 used in the present experiment, summation between the masks of identical orientation did not occur, but rather the neural activity generated by M1 reduced the masking effect of M2.

Two major theoretical accounts have been offered for disinhibition. Kristofferson et al. (1979) have proposed a recognition model based on the probability of detecting a target when the masking effect of the second mask on the target is zero. While this explanation is adequate for evaluating the detection likelihoods of combinations of stimuli, it has difficulty in accounting for the orientational selectivity obtained in the current data. Dember et al. (1978) have utilized Breitmeyer and Ganz (1976) and Weisstein et al.'s (1975) models to explain masking in terms of interchannel inhibition. In these models, sustained channels respond slowly to high spatial frequencies, and transient channels respond rapidly to low frequencies. Backward masking results from the transient units stimulated by the mask's overtaking and inhibiting the sustained units stimulated by the target. While this mechanism could account for backward masking, it had difficulty in explaining forward masking. This difficulty has been overcome by the proposal that sustained channels are also capable of inhibiting transient channels (Breitmeyer, 1980). Since the present experiment utilized stimuli with identical spatial frequencies, the results can be accounted for by this theory if it is assumed that the transient channels activated by the masks are processed more rapidly than the sustained channels.

In conclusion, a brief comment should be made on the absence of interocular disinhibition (Robinson, 1968). Long (1979) has argued that the presence or absence of interocular transfer is insufficient evidence on its own to indicate that the locus of ocular interaction is central or peripheral. In order to determine a central locus, spatial selectivity of the interaction must also be demonstrated. The failure of Robinson (1968) to demonstrate disinhibition suggests that brightness detectors are not binocularly driven or else that the effect is processed at a low level within the visual system. The present data suggest that orientation disinhibition may be a high level effect, and therefore interocular disinhibition for orientation analyzers should be able to be demonstrated. Microelectrode data support this contention, since a large number of orientation specific cells in the monkey's visual cortex are binocularly driven (Hubel & Wiesel, 1968).

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