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Temporal Response of the Human Visual System to Suprathreshold Luminance and Opponent Colour Contrast Gratings

by

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Abstract

The goal of the present study was to characterize the temporal processing of both suprathreshold luminance and opponent-colour defined contrast in the human visual system. We used a detection task in five experiments; following a 900 Hz, 2-cycle tone, observers were presented with a sinusoidal grating stimulus. The interval separating the warning tone and the presentation of the grating was manipulated to determine the influences of attentional dwell time in a cross-modal task. This theory states that the first of two successive events will interfere with the processing of the second event. In all four luminance experiments the gratings were presented with contrast levels of .8, 16 and 64 percent contrast. In the first experiment the contrast gratings were presented following interstimulus intervals (ISIs) ranging from 100 to 1000 ms in 100 ms intervals. In Experiment 2 the ISIs were 1000 ms and 1500 ms. In the third experiment gratings were presented following ISIs ranging from 500 to 2000 ms in 500 ms intervals. In Experiment 4 gratings were presented following ISIs ranging from 250 to 1000 ms in 250 ms intervals. In the opponent-colour experiment the gratings were presented with colour contrasts of red-green (RG), blue-yellow (BY) or red-blue (RB) following ISIs of 100, 250, 500, and 750 ms. In all experiments the mean luminance of the gratings and the grey background was 10 cd/m^2. Reaction times (RTs) were used to measure the latency difference in processing these gratings. The findings demonstrated that increases in suprathreshold contrast resulted in a significant decrease in response latency. In addition, we found decreased RTs for RG as opposed to BY and RB gratings. Finally, we were able to demonstrate an attentional dwell time in a cross-modal task. The implications of the above findings were discussed in conjunction with the relevant literature.

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Table of Contents

List of Figures

Temporal Response of the Human Visual System to Suprathreshold Luminance and Opponent Colour Contrast Gratings

The human visual system presumably evolved for the detection and identification of objects in the environment (De Valois & Switkes, 1983). The study of spatial vision has included how the visual system undertakes the task of perceiving the luminance and colour defined contrasts that characterize objects and patterns present in the environment. Although it may appear trivial initially, imagine viewing any scene without the ability to perceive differences in light intensity and wavelength. The visual world would become a blur without the borders and edges that are defined by contrasts in light intensity and colour. Borders and edges defined by high contrast aid us in the distinction of figure and ground. Successful survival in terms of foraging for and obtaining food and avoiding predators is dependent on these capabilities.

The goal of the present study was to characterize the processing of both luminance and opponent-colour defined contrast in the human visual system. Psychophysics has been used extensively to investigate the underlying physiology of the visual system. Several psychophysical methods exist which share the benefit of providing quantifiable behavioural evidence without being invasive, which makes these methods ideal for studies involving humans. We used a detection task to characterize the time course of processing in the visual pathways which sub-serve the processing of suprathreshold luminance and opponent-colour signals. In addition, the role of attention in the processing of these signals was addressed as a function of its influence on response latency.

LUMINANCE EXPERIMENTS

Defining Contrast

Contrast refers to the differences in light intensity at an edge or a border. Environmental stimuli are generally quite complex and as a result the perception of contrast has been studied utilizing simplified visual stimuli such as contrast gratings. The benefit of using gratings is that variations in contrast can be specifically defined over time and space. For grating stimuli, contrast can be more specifically defined as the amplitude of the grating divided by the total intensity. The dark bars in a grating have a lower intensity relative to the light bars which have a higher intensity. As the difference between the maximum and minimum intensities between these light and dark bars increases, the amplitude of the grating increases. By adjusting the relative intensities of the light and dark bars, the contrast of a grating can be manipulated without affecting the mean intensity. In the present study, manipulating the level of contrast within a sinusoidal grating while maintaining a constant mean luminance allowed us to determine the response properties of the visual system to increases in contrast.

Several other important components of contrast gratings have been previously defined and manipulated (Goldstein, 1996). For example, gratings can be conceptualized as waveforms. A waveform describes the pattern of intensity changes across a gratings' distribution and can vary from a square-wave to a sine-wave or sinusoidal waveform. In the present study we have selected sinusoidal gratings as our stimuli. In addition, gratings can be described in terms of their spatial frequency, which is the frequency of intensity differences over a given area measured in cycles per degree of visual angle. Fine details of a stimulus correspond to high spatial frequency information whereas the gross features of a stimulus correspond to low spatial frequency information. The grating stimuli used in the present study had a spatial frequency of 2

cycles per degree, for which the pattern of intensity changes can be easily resolved by the human eye.

The present experiments examined how the processing speed of a grating was influenced by the level of contrast present in the stimulus, with the intention of establishing a stable psychophysical curve of reaction time (RT) as a function of contrast. In general, response latency to above-threshold stimuli co-varies with contrast level, such that as contrast level increases, RT decreases until the contrast becomes very high (Harwerth & Levi, 1978). This relationship exists when the contrast in the stimulus is presented above the threshold for detection. Presently, it is not clear what the assembly of cells looks like that are responsible for the perception of contrast. One possibility is that the detection of contrast is signaled by a certain firing rate of a pool of neurons tuned to contrast. Presumably when the firing rate of this pool of neurons which are tuned to respond to contrast surpasses a threshold, the contrast signal will be passed on to a conscious mechanism and result in the perception of a grating. As the firing rate of these cells increases with increases in contrast, this criterion or threshold should be met earlier. The result would be a faster response latency as contrast increases for contrast levels above the threshold for detection, until at very high contrast levels the response latency would asymptote.

Models of Contrast Perception

Investigations into the perception of contrast have accompanied discoveries about the nature of our visual system and how it processes contrast. Several theories have been proposed to explain how our visual system might undertake the task of processing intensity differences that result in the perception of contrast. Hubel and Weisel, who won a Nobel Prize in 1981 for their work on the visual system of the cat and monkey, proposed a feature detector model to illustrate how the brain processes light

intensity. According to their research, cells in area 17 of the visual cortex of the monkey and cat respond preferentially to bars and edges of particular orientations and widths (Hubel & Weisel, 1962). These cells will fire action potentials more vigorously when their receptive fields encounter stimuli they prefer. Hubel and Weisel (1962) hypothesized a hierarchical organization of neurons as one moves from the retina to the visual cortex. These neurons receive information from a particular portion of the visual field and become increasingly specialized with respect to the features of stimuli they respond to.

Optic nerve fibers and lateral geniculate nucleus (LGN) cells comprise the bottom of the proposed hierarchy and are characterized by center-surround response properties which respond optimally when a stimulus impinges on the excitatory area and not on the inhibitory area. These nerve fibers feed into simple cortical cells which have excitatory and inhibitory areas arranged side by side which respond best to bars of a particular orientation. According to the feature detector model, simple cells then feed into a network of complex cells which respond optimally to moving bars of a particular orientation but not well to stationary stimuli. Both simple and complex cells may be end-stopped cortical cells which respond best to corners, angles and bars of a particular length; however, only complex cells respond to movement in a particular direction (Hubel, 1988). The specialization of the cells in the hierarchy provides evidence for the means by which the visual system responds to and breaks down complex environmental patterns into their component features (De Valois & De Valois, 1980). The detected features are then combined and transformed into a uniform cortical representation of spatial patterns (Barlow, 1972). For the purpose of the present study, the feature detector model would suggest that the perception of a grating results from the combination of signals from several cells which "care about" or are tuned to fire to particular features of the grating. The combination and summation of these signals would result in a unified perception of the contrast grating.

However, the feature detector model cannot explain why the complex cells are less sensitive to some stimulus properties in comparison to simple cells. For example, there is a loss of sensitivity to stationary stimuli as one proceeds in the hierarchy from the simple to the complex cells. This results in a loss of specificity as the contrast signal is carried through the cortex, which must be regained before an accurate perception of the visual environment can be formed (De Valois & De Valois, 1980). It appears as though the feature detector model is not capable of accounting for all aspects of the perception of spatial stimuli, especially the stationary contrast gratings we investigated.

Another framework has been suggested to explain how the visual system may code for contrast. Rather than a hierarchical structure of feature detectors that respond to bars and edges, a spatial frequency filter model has been proposed. Campbell and Robson (1968) proposed the concept of multiple spatial frequency channels which break down the spatially variant visual stimulus into its individual spatial frequency components. Subsequently, the firing pattern of these spatial frequency cells is combined into a single percept of the pattern, in what is thought to be some form of Fourier analysis (Sekuler, 1974, as cited in De Valois & De Valois, 1980). Several researchers have provided support for this hypothesis by demonstrating that cells in various portions of the visual cortex are finely tuned to particular spatial frequencies (Blakemore & Campbell, 1969; De Valois, Albrecht, & Thorell, 1977; Movshon, Thompson, & Tolhurst, 1978).

Blakemore and Campbell (1969) performed an experimental comparison of the feature detector model and the spatial frequency filter model. The researchers recorded the visual evoked potential (VEP) which estimates the neural response to the contrast stimuli. Blakemore and Campbell (1969) adapted cells to a square-wave grating stimulus and measured responses to the same stimulus after adaptation. A decrease in sensitivity to the adapting grating should be apparent in cells which are selectively tuned

to respond to the pattern of spatial frequency present in the stimulus. The investigators found that not only was the cells' sensitivity depressed to the fundamental frequency of the grating but also to the gratings' third harmonic. The feature detector model could not account for this finding because the model would not predict the adapted cells' depressed sensitivity to the third harmonic. Similar experiments by Sullivan, Georgeson and Oatley (1972) and Campbell, Howell and Robson (1971) found that following adaptation, depression in the sensitivity of neurons to the fundamental frequency resulted in the depression of sensitivity to the harmonics of the fundamental frequency of the adapting grating. Together, these results are better predicted by a spatial frequency filter model rather than a model based on feature detection.

Other research has attempted to test the spatial frequency filter model using systematic retinotopic mapping of the striate cortex similar to that performed by Hubel and Weisel (1962). Tootell, Silverman and De Valois (1981) measured the responses of neurons in the striate cortex to a drifting sine-wave grating using a 2-deoxy-D-glucose technique developed by Sokoloff, Reivich, Kennedy, DesRosiers, Patlak, Pettigrew, Sakurada and Shinohara (1977; as cited in Tootell et al., 1981). The results of the experiment confirmed that the striate cortex was organized into columns of cells which are tuned to respond optimally to particular spatial frequencies. Although such cells respond optimally to a particular spatial frequency, they also respond to a lesser extent to a bandwidth of spatial frequencies centered around the optimal spatial frequency (Maffei & Fiorentini, 1973). In addition, researchers have also found that adjacent columns show peak responses to a similar range of spatial frequencies suggesting that cortical layers contain columns which are organized by frequency sensitivity rather than feature sensitivity (Tootell et al., 1981).

More recently, von der Heydt, Peterhans , and Dursteler (1992) investigated responses to contrast gratings in the monkey's visual cortex. The researchers were able

to isolate a collection of cells that responded optimally to gratings but slightly or not at all to bars and edges. The researchers found cells that responded best to stationary gratings with particular spatial frequencies at a particular orientation, over a range of sampled frequencies from 2 to 19 cycles per degree. The notion of cells that respond optimally to certain properties of a stimulus is consistent with Hubel and Weisel's model of specialized cells in the visual cortex. However, this research clearly supports the proposal that the response to contrast is at least in part determined by the spatial frequency of the stimulus.

Two pathways have been argued to carry the contrast signal from the retina to higher visual areas. Some researchers have argued that the simple and complex cortical cells of the hierarchical model resemble the X and Y cells respectively of the retina and lateral geniculate nucleus (LGN) (Wilson & Sherman, 1976). Previously, researchers have investigated the X and Y cells and used psychophysics to characterize their response properties (Kulowski & Tolhurst, 1973; Tolhurst, 1973; Breitmeyer & Julesz, 1975). The response properties of these cells to grating stimuli appears to support the existence of parallel spatial frequency pathways projecting to the cortex, namely the X and Y cells. The terms sustained and transient have been used to describe some of the response properties of the X and Y cells, respectively (Cleland, Dubin, & Levick, 1971). The sustained channel (X) cells appear to summate linearly over their receptive fields and demonstrate sustained responses throughout the duration of a stimulus. Research in the cat has shown that they respond optimally to high spatial frequency and low temporal frequency stimuli. Conversely, transient channel (Y) cells do not show linear summation over their receptive fields and respond optimally to low spatial frequency and high temporal frequency stimuli and are more sensitive to stimuli with rapid onset and offset (Enroth-Cugell & Robson, 1966; Cleland, Levick, & Sanderson, 1973; Breitmeyer, 1975).

Physiological evidence has emerged to support the distinction between these psychophysical pathways. The sustained and transient psychophysical channels are thought to map onto the parvocellular and magnocellular pathways of the primate visual system (Garey & Blakemore, 1977). The physiological distinction between these pathways can be seen in the size of the neurons that form the pathways and their relative conduction speeds. The large fiber magnocellular neurons of the transient channel conduct impulses more quickly from the retina to the cortex in comparison to the small parvocellular fibers of the sustained channel (Ikeda & Wright, 1974). Figure 1 provides an overview of the characteristics of the magnocellular and parvocellular pathways.

In summary, the evidence suggests that both the feature detector model and spatial frequency model can account for some aspects of the neural coding of contrast in the visual system. Spatially variant stimuli are processed by cells which break down the visual stimulus into its component spatial frequencies. Information from these cells are carried through to the cortex via the X and Y psychophysical channels of the monkey which likely map onto the magnocellular and parvocellular pathways of the human visual system. The contrast signal may be carried by either of these channels depending on some of the properties of the contrast stimulus. Responses to a stimulus with low spatial frequency and rapid onset and offset, such as the stimuli we have used, are likely carried to the cortex via the transient system. Thus, we predicted shorter response latencies relative to previous studies in which stimuli had higher spatial frequencies and other characteristics which are handled by the sustained pathway. The shorter response latencies are a result of the transient pathways' large fibers which are capable of conducting impulses more quickly.

Suprathreshold Contrast Sensitivity

Presently, our concern is to describe the temporal response to variations in above-threshold contrast. In the past, researchers have used various techniques to study the perception of above-threshold contrast in human and non-human visual systems, including the measurement of psychophysical responses (De Valois & De Valois, 1980). Psychophysicists have typically studied contrast threshold by measuring the smallest intensity difference between the light and dark bars of a grating which results in detection. An observer's contrast sensitivity is the reciprocal of their threshold and can be calculated as 1/contrast threshold. A contrast sensitivity function (CSF) can then be generated by plotting an observer's contrast sensitivity to gratings of varying spatial frequency. For most observers, the CSF indicates the highest sensitivity for gratings with spatial frequencies ranging between 2 and 4 cycles per degree. Gratings with spatial frequencies higher or lower than this range require the contrast present in the grating to be increased in order for the grating to be detected. A comparison of human and non-human CSFs reveals a similar sensitivity distribution; however, the peak sensitivity is shifted depending on the species being investigated. Blake (1988) found the cats' CSF was almost identical in form to the human CSF; however, the cats' peak sensitivity is at a lower spatial frequency than the human contrast sensitivity distribution.

Environmental stimuli are rarely at threshold levels and investigations into the processing of suprathreshold level contrast have provided information about how we process the easily detected stimuli we are more likely to encounter in our visual environment. Researchers have established that the CSF at threshold levels of contrast does not necessarily predict contrast sensitivity at suprathreshold levels (Swanson, Georgeson, & Wilson, 1988). The term suprathreshold MTF or modulation transfer function is used to describe the contrast sensitivity function at higher contrast levels. The suprathreshold MTF is relatively flat except for extremely low and very high spatial

frequencies (Levy, 1970; Georgeson & Sullivan, 1975). The MTF indicates that the visual system perceives all spatial frequencies within the standard spatial frequency range with high contrast almost equally as well. As mentioned, the exception is for very low spatial frequencies which are not perceived well and extremely high spatial frequencies in which the grating cannot be seen even with maximum contrast (Felipe, Buades, & Artigas, 1993). In the present study, the use of suprathreshold contrast stimuli with spatial frequency of 2 cycles per degree falls well within the range of spatial frequencies perceivable with high sensitivity. However, the differences in the speed with which these suprathreshold gratings are perceived is of interest.

Detection Studies

Psychophysicists have used RT as a tool for understanding the response latencies in the visual system since as early as the 1800's. James Cattell undertook one of the first studies looking at the effect of varying the intensity of light on simple RT (Cattell, 1886). The author reported that the mean RT decreased with increases in light intensity. Since this time, many researchers have used RT to study the processing of a variety of spatial stimuli and the response latencies generated by the visual system.

RT in a simple detection task is the combination of a perceptual response and a motor response. Perception time refers to the amount of time that passes before a stimulus is detected by the visual system. The motor time refers to the amount of time that passes between the point when the stimulus is detected and a motor response such as a key press is produced (Gish, Shulman, Sheehy, & Leibowitz, 1985). The perception time is dependent on the properties of the stimulus whereas the motor time is independent of the stimulus properties such as contrast (Wiener, Oram, & Richmond, 1998). For our purposes, the perception time is of interest, as the motor time is not influenced by stimulus properties such as contrast.

One stimulus variable that has been shown to influence RT in a number of studies is spatial frequency (i.e. Breitmeyer, 1975; Tolhurst, 1975). Gish et al. (1985) presented observers with a sinusoidal grating pattern at 1, 4 and 10 cycles per degree and measured the RT at four levels of contrast above the threshold for detection. The data indicated that with increasing spatial frequency, RTs were longer for a collection of contrast levels ranging from those well above the threshold for detection to those near threshold values. The authors argued the results were evidence for increased perceptual latency with increases in spatial frequency. We decided to maintain a constant spatial frequency to isolate the influence of changes in above-threshold contrast on perceptual latency.

RT has also been used as a means of characterizing the temporal response properties of the sustained and transient channels. Harwerth and Levi (1978) investigated the detection of suprathreshold grating stimuli using RT measures. The authors presented observers with vertical sinusoidal gratings with contrast ranging from threshold to 44 percent and spatial frequencies ranging from 0.5 to 12 cycles per degree. The authors confirmed previous findings of a decrease in RT with increases in grating contrast. In addition, the authors reported that a break occurred in the response time curve for gratings with 10 percent contrast for spatial frequencies ranging from 2 to 6 cycles per degree. However, this break was not as apparent in the 0.5, 1, 8, and 12 cycle per degree data. The break in the curve at 10 percent contrast resulted in a faster rate of decrease in RTs for gratings with more than 10 percent contrast.

The authors argued the biphasic contrast versus RT function represents the presence of two perceptual mechanisms specialized for processing different stimulus properties. The high contrast gratings with spatial frequencies between 1 and 8 cycles per degree were thought to be detected by one mechanism whereas lower contrast levels appeared to be detected by another mechanism, with a longer response latency.

The authors hypothesized that the mechanisms were the magnocellular and parvocellular pathways which have different temporal response properties. As discussed earlier, these are respectively the physiological pathways that the psychophysical sustained and transient pathways are believed to map onto.

Mitov, Vassilev and Manahilov (1981) attempted to describe the transition from the transient to the sustained channel for a range of spatial frequencies independently of contrast. The authors reported that the transition between the two systems occurs for stimuli with spatial frequency ranging between 5 and 8 cycles per degree as evidenced by a discontinuity in the slope of the RTs. However, the authors performed the experiments with only two contrast levels, 0.2 and 0.6 percent contrast, and therefore were only able to generalize their findings to a small range of stimulus properties. We have limited the spatial frequency to one level in order to sample a broader range of contrast levels.

Felipe et al. (1993) investigated RT to a grating stimulus as a function of the contrast and spatial frequency of the grating. The authors attempted to discern the point of transition between the transient system with its shorter response latency and the sustained channel with its longer response latency as a function of contrast and spatial frequency. The authors noted the transition from the sustained to the transient channel had occurred at different frequencies and contrast levels in previous research due to experimental differences such as field width, retinal location and stimulus duration. These factors influence RT independently of contrast and spatial frequency.

The results of Felipe et al. (1993) support the previous findings of Harwerth and Levi (1978). RT decreased with increases in contrast, across all spatial frequencies. The transition from the sustained to the transient channel was clearly demonstrated in a curve of RT as a function of spatial frequency for stimuli with contrast from threshold levels to levels of contrast approaching 100 percent. The transition is easily seen

because the suprathreshold MTF is nearly flat at all spatial frequencies except for very low ones and the effect on RT due to contrast level is equal for all spatial frequencies in the transition zone.

In addition, the authors found a discontinuity in the RT versus contrast curve for stimuli with approximately 10 percent contrast which was consistent with the findings of Harwerth and Levi (1978). However, the break was only apparent within the range of spatial frequencies from 6 to 8 cycles per degree which was a smaller range than proposed by previous researchers (Mitov et al.,1981; Harwerth and Levi,1978). Felipe et al. (1993) concluded that the MTF or suprathreshold contrast sensitivity function was the most influential determinant of RT across all spatial frequencies. The exception was for a small interval between 6 and 8 cycles per degree where the transition from the transient to the sustained channel became more influential in determining RT. Figure 2 shows the relationship between suprathreshold contrast, RT, and spatial frequency based on the findings of Harwerth and Levi (1978), Mitov et al. (1981) and Felipe et al. (1993). We anticipated that it would be difficult to visualize the break in the RT curve with our stimuli, as 2 cycles per degree falls outside the range of frequencies in which the break is normally apparent.

An important variable that must be considered in detection studies of contrast, is the effect of monocular versus binocular viewing conditions on RT. We have chosen binocular viewing conditions which might differentiate our experimental results from previous studies in which monocular viewing conditions were used. In addition to the spatial frequency of our stimuli, we anticipated that the break in the RT curve would not be evident due to the benefit binocular viewing has over monocular viewing conditions. Binocular viewing allows for information to be integrated from both eyes and thus results in enhanced performance over monocular viewing on some tasks (Anzai, Bearse, Freedman, & Cai, 1995). Binocular summation is the interaction between two

independent and equally sensitive pathways (Smith & Harwerth, 1979) and was first introduced by Pirenne (1943). The probability of detecting a stimulus is therefore predicted from the summation of two monocular probabilities. This neural summation would enhance the RTs we are measuring in our detection task.

However, research has shown that the probability of detecting a stimulus is not as elementary as previously thought and often binocular detection exceeds what is predicted on the basis of probability summation (Legge, 1984). Some researchers have shown that binocular summation does not reflect the simple addition of monocular sensitivities but rather is due to a neural summation (Thorn & Boynton, 1974; as cited in Legge & Rubin, 1981). Predicting the effects of binocular viewing is further confounded by the influence of stimulus properties such as the level of contrast present in the stimulus from threshold levels to very high levels of contrast (Legge & Rubin, 1981). In addition, the effect of the binocular interaction can also be influenced by the nature of the cells involved in the response and can include facilitation, inhibition or summation (Ohzawa & Freeman, 1986).

Anzai et al. (1994) investigated the CSF of cells in the striate cortex of cats to determine the influence of binocular versus monocular viewing. The researchers took extracellular recordings from cells in area 17 of the cats' visual cortex while the animal viewed drifting sinusoidal gratings of various contrast levels. Although the investigators did not examine RTs, they found that binocular viewing had three advantages over monocular viewing. First, the contrast sensitivity of individual cells was higher when they were stimulated binocularly. The second advantage was that cells were more sensitive to changes in contrast near threshold levels when the viewing conditions were binocular. Although this research was not conducted with humans, presumably the advantages of binocular over monocular viewing would be similar in a detection task with human participants. This may result in the break in the RT curve appearing closer to threshold

levels of contrast as cells become more sensitive to gratings with lower contrast. The final advantage of binocular stimulation was the finding that more cells contributed to processing and ultimately the detection of contrast. Again if these findings can be extended to humans, these three factors may combine to result in overall faster RTs in detection tasks in which contrast gratings are viewed binocularly.

Blake, Martens and Di Giafilippo (1980) measured monocular and binocular RTs of human observers to a series of sinusoidal grating patterns with varied contrast. The results indicated that binocular RTs were consistently faster than monocular RTs. The facilitating effect of binocular viewing was found for all contrast levels even at high levels where RT tended to reach asymptotic levels. In addition, the effect of binocular viewing was greater than that predicted by probability summation for observers with good stereopsis and equal to that predicted by probability summation for individuals with deficient stereopsis (Blake et al., 1980).

A similar investigation by Smith and Harwerth (1979) involved presenting vertical sinusoidal contrast gratings to observers both binocularly and monocularly. The authors reported binocular summation for contrast levels approaching threshold. However, as the contrast increased above the threshold for detection, the degree of binocular facilitation (i.e. more than that predicted by summation) increased until it was quite substantial for high contrast levels. The authors concluded that the high degree of binocular interaction at suprathreshold levels of contrast was due to underlying facilitating neural interactions that resulted in faster responses than what would be expected from the sum of the individual monocular responses.

Harwerth, Smith and Levi (1980) used a detection paradigm to study the effect of monocular versus binocular presentation of suprathreshold grating stimuli. The authors reported that the mean RTs for low contrast levels were shorter for binocular viewing for all observers. However, at higher contrast levels the relationship between RT and

viewing condition varied depending on the observer. Some observers showed equivalent RTs at mid-range contrast levels for both viewing conditions and some observers had shorter RTs at the higher contrast levels for monocular viewing indicating binocular inhibition rather than summation or facilitation at high contrast levels. The authors concluded that their data showed that binocular interactions cannot be predicted on the basis of probability and must represent some underlying physiological interaction between cells that get input from both eyes. The findings of Blake et al. (1980), Smith and Harwerth (1979) and Harwerth et al. (1980) agree with our prediction that the use of binocular viewing conditions will differentiate our RTs and response curves from previous studies which used monocular viewing conditions. More specifically, we anticipate that our RTs will generally be faster than those produced in similar experiments using monocular viewing conditions (i.e. Harwerth & Levi, 1978).

The present study attempted to establish a stable psychophysical curve of RT as a function of suprathreshold contrast. It was hypothesized that the procedure employed presently would produce a RT curve similar to those generated in previous research (Felipe et al., 1993). The present experimental procedure most closely resembles that of Felipe et al. (1993) who used binocular viewing of above threshold gratings over a range of spatial frequencies. However, it was hypothesized that the transition region evidenced by a break in the RT curve (as observed by Harwerth & Levi, 1978), where processing of the contrast signal moves from the sustained to the transient channel, would not be generated in the present experiment. Several reasons existed for the expected inability to detect a transition. First, the grating stimuli used in the present work had a spatial frequency of 2 cycles per degree, which is below the range in which the transition from the sustained to the transient channel has been found (Felipe et al., 1993). In addition, the use of binocular viewing in the present experiment was expected to produce faster overall RTs relative to those produced in previous work (Harwerth &

Levi, 1978). Finally, the contrast levels sampled in the present study are not sufficiently fine grained to detect the transition.

We argue that the response in our detection task reflects the pooled response of a population of neurons that respond selectively to changes in contrast. We hypothesize that these neurons fire more vigorously as the contrast in our grating stimulus increases. As the firing rate of these neurons reaches the threshold level of the cell they impinge on, the contrast signal is sent further on in the visual system where the contrast stimulus is perceived. The faster this threshold level is met, the faster the stimulus will be detected. We predicted that for contrast levels above the threshold for detection, increases in contrast will drive the neural signal above the criterion level faster and will result in a shorter latency to detect the grating stimulus as the contrast is increased.

ATTENTIONAL MECHANISMS

Thus far, we have looked at the processing of luminance contrast from a stimulus driven perspective. However, when using psychophysics to investigate the systems responsible for the processing of these stimuli, the influences of higher-level cognitive settings or top-down mechanisms must be considered. Attention becomes a significant top-down contributor, especially in psychophysical experiments involving hundreds of trials. The attentional setting of the observer, in conjunction with the demands of the paradigm, is certain to influence the behavioural data. We have found what appear to be attentional effects in a pilot experiment and will describe the results here briefly.

In this pilot study, we discovered an interesting effect when we varied the interval between an alerting cue and the presentation of a contrast grating stimulus. In a trial, a centrally presented auditory cue was followed by a variable interval which we refer to as the inter-stimulus interval (ISI), after which a central grating appeared on a monitor positioned directly in front and along the midline of the observers' body. Figure 3 depicts a timing diagram for experimental trials. The observer's task was to make a manual key

press response, as quickly as possible, when the stimulus was detected on the computer screen. The auditory cue informed the observer that the stimulus would appear at some point during the following 2500 ms interval. Observers were informed of the exact location of the stimulus presentation and were instructed to fixate on this area which was marked on the center of the grey screen. The results indicated that when the ISI was 1000 ms, RT was significantly slower than when the ISI was 2000 ms. This difference was observed for all stimuli, regardless of the contrast level present in the grating. Differences in RT of approximately 10 ms were reported between the two ISI conditions. (see Figure 4)

We looked to previous attentional studies to determine if there was a theory which could account for the slowed RTs observed in the pilot study. Attention directed towards serial stimulus events has been shown to impede processing of the second of two successive events (e.g. Duncan, Ward, & Shapiro, 1994; Potter, Chun, Banks, & Muckenhoupt, 1998). This disruption in the processing of the second stimulus is thought to be the result of an attentional dwell time (Duncan et al., 1994) or an attentional blink (Raymond, Shapiro, & Arnell, 1992). Both of these terms have been used to describe the capacity limits of our attentional resources in tasks that require the processing of serial stimulus events. According to these theories, delayed RTs in the pilot experiment could be the result of overloading the capacity of the attentional system, where it may not be possible to effectively divide attention between the auditory signal and the visual target without repercussions in response latencies. Previously, two basic approaches have been used to investigate this phenomenon: The 'Two-Target" method and Rapid Serial Visual Presentation (RSVP).

The two-target method (Visser, Zuvic, Bischof, & Di Lollo, 1999) has been used to investigate interference caused by processing successive events by Duncan and his colleagues (e.g. Duncan, et al., 1994; Duncan, Martens, & Ward, 1997). In a typical two-

target procedure, visual stimuli are presented at two different spatial locations on a display and each item is followed by a masking stimulus. The target stimuli which are separated by blank intervals, appear at either location and there are no intervening distractor stimuli between target items. The length of the blank interval between presentations of the target stimuli is manipulated to determine the impact of identification of the first target (T1) on identification of the second target (T2). Duncan et al. (1994) have used the term attentional dwell time to refer to the interference that processing the T1 has on identifying T2, in this two-target task.

Duncan et al., (1994) examined the time course of attentional demand, to determine how long one item can continue to interfere with a subsequent item. The authors hypothesized that attention is not a high-speed mechanism but rather a sustained state, which will result in interference when a novel item has attentional demands. The investigators measured the attentional dwell time or how long one item can occupy the capacity of attention, in two visual search tasks. In the first task, subjects were presented with one of two numbers for 45-60 ms followed by a variable interval, after which they were presented with one of two letters for 45-60 ms. The observers' task was to either identify the first, second or both alphanumeric targets. In the second task, the subjects were required to detect the pre-specified target amongst non-targets presented for 40-104 ms in sequence, separated by a variable interval. Interference was determined by the percentage of correct responses for each interval used.

Duncan and colleagues (1994) found that when the first stimulus could be ignored, there was no interference. However, when both stimuli were attended, there was interference and a graded decrease in the amount of interference as the interval extended from 0 to 450 ms. For the visual search task in target present trials, a preceding non-target item significantly impaired target detection up to 300 ms and

approached significance for intervals up to 450 ms. The authors suggested that this evidence supported limited capacity models of attention rather than high-speed serial processing models. In this sense, attention can be thought of as a sustained state with a dwell time, which makes objects available for responding over a period of time. The sustained state or dwell time of attention was argued to be over several hundreds of milliseconds.

Duncan et al., (1997) studied the ability of the first of two stimuli to interfere with a second stimulus when the stimuli were presented within the auditory and visual modalities. To test for interference in the auditory modality, the investigators presented subjects with two simultaneous auditory streams, one spoken in a high voice and the other in a low voice. The spoken streams contained repetitive nonsense syllables with intervening target syllables at particular intervals. To test for interference in the visual modality, subjects were simultaneously presented with a visual stream containing non-target X's with intervening target letters following specified intervals. Within each modality, participants were required to attend to one stream and identify targets detected within that stream or to attend to both streams and identify targets appearing in each stream. Within both the auditory and visual modalities, the results indicated that when participants were required to attend to only one stream, there was no interference in processing the target. However, when attention was divided between the simultaneous streams of targets in the same modality, identification of a target in one stream significantly interfered with the later identification of the second target in the other stream. The results were the same for targets within the auditory and visual modalities. The results are consistent with the notion that there is a dwell time of attention for auditory, as well as, visual stimuli.

In the RSVP method, a sequence of stimuli appears at the same display location and each new stimulus replaces the preceding item (Raymond et al., 1992). Target

stimuli are placed at different temporal positions within the sequence and are separated by a range of distractor items. The number of distractor items between successive items can be manipulated to determine the temporal properties of the attentional effect. The term attentional blink has been used to describe the interference that identification of T1 has on the subsequent T2 (e.g. Chun & Potter, 1995; Jolicoeur, 1999; Volkman, Riggs & Moore, 1980).

Using RSVP, Chun and Potter (1995) characterized the pattern of interference that processing a visual T1 has on a visual T2. The results indicated a U-shaped pattern of interference, which differs from the monotonic pattern of interference demonstrated with the two-target method (Duncan et al., 1994; 1997). In this U-shaped function accuracy was high following the 100 ms SOA, dropped substantially for targets following lags of 200 ms to 500 ms and became increasingly higher as the SOA lengthened. Chun and Potter (1995) demonstrated this U-shape pattern of interference in several experiments with interference being maximal following intervals of 200-500 ms.

More recently, attempts have been made to determine whether the interference previously documented occurs only within modality or operates at a central, amodal level. Duncan et al. (1997) presented participants with concurrent streams of auditory and visual stimuli with a target embedded in each stream. The results indicated that regardless of whether attention was focused on one modality or was divided between the two, when targets were not presented in the same modality, the interval separating the target stimuli had no effect on the number of correct responses. The authors argued that these results were evidence that attentional dwell time is not amodal, but rather it is restricted to stimuli that appear in sequence within the same modality. However, Potter et al. (1998) were able to demonstrate cross-modal interference effects by using different response modes for each target.

In related work, Jolicoeur (1999) investigated the influence that processing a simple auditory event would have on the processing of a second visual event. The investigator presented observers with a rapid display of letters with a randomly placed target letter which was either an X or a Y. In addition, either a high or low frequency tone was presented concurrently with the visual display. The SOA, the interval between the tone and the subsequent presentation of the target letter, was manipulated. In one condition, subjects were required to make a speeded response to the tone indicating if it was high or low frequency and then indicated which target letter appeared in the visual display without any time pressure. In the other condition, observers were told to ignore the tone and to indicate which target letter appeared in the stream of letters without any time pressure.

Interference in processing of the visual event was examined by determining the percent of correct target letter identifications for each level of SOA. Jolicoeur (1999) reported that when the observers were instructed to ignore the tone, there was no subsequent interference in identification of the visual target. However, when observers were required to indicate the frequency of the tone (high vs. low), interference was observed in the processing of the visual target. The interference, as evidenced by low accuracy rates, was high for targets presented following very short SOAs with decreased interference as the interval lengthened. The results suggest that the capacity of attention is not merely limited within modalities but rather that the capacity of attention can be overloaded when a response must be executed for stimuli of different modalities.

Although the RSVP and two-target methods differ in some aspects of their procedure they both use accuracy to assess interference effects. With both methods identification of T2 is not a speeded response but rather the emphasis is on correctly identifying T2. However, some degree of interference may occur, even when targets are accurately identified in a task in which observers are instructed to ignore T1. Measuring

the speed with which these targets are processed is an alternative and possibly more sensitive method of determining whether there is interference in processing T2. In the present study we had observers make speeded detection responses for T2. Given that RT might be a more sensitive measure of interference it was anticipated that an interference effect would be observed even when a response to T1 was not required.

In the present study we attempted to demonstrate that the capacity of the attentional system could be exhausted when processing successive stimulus events in different modalities. We argue that the failure of previous studies to demonstrate cross-modal attentional dwell was due to the use of accuracy as a measure of dwell time. By using RT in the present study it should be possible to see the limitations of attention when an auditory cue precedes a visual event. The results of the present study were examined with respect to the predictions derived from research on attentional dwell time. Consistent with the notion of a dwell time, it was anticipated that the auditory cue would interfere with the processing of the visual grating stimulus when these were presented relatively close together in time. Accordingly, following short intervals we expected response times to be slow because processing the auditory stimulus would interfere with the subsequent processing of the visual target. As the interval between these two stimuli increased we expected to see a decrease in the amount of interference.

In summary, with respect to attention, the purpose of the present experiment was twofold. Primarily, we wanted to replicate the finding of the delayed RTs we observed in the pilot study. Secondly, we wanted to determine if the attentional dwell time theory accounted for these slowed RTs. Delayed RTs may be the result of overloading the capacity of the attentional system, where it may not be possible to rapidly shift attention between the auditory signal and the target without slowing the response to the visual stimulus. The attentional dwell time theory would predict that the closer the cue and target are together in time, the longer it will take for a response to be generated.

LUMINANCE EXPERIMENTS

Method

Participants

Individuals with normal or corrected-to-normal vision were recruited to participate in the study. All participants were strongly right-handed as determined by the administration of a modified Oldfield handedness questionnaire (Oldfield, 1971). All participants completed a minimum of three practice sessions prior to commencing experimental sessions.

Materials

All experiments took place in a darkened lab room, in which the walls and desktops were black to prevent the reflection of ambient light from the computer monitor. Stimuli were generated by a Power Macintosh 8100/80 computer [model# M1688], and presented on an Apple Multiple Scan 1705 Display monitor [model# M4436]. To ensure that the contrast in luminance in the gratings was as planned, a photometer (Minolta Chroma Meter CS-100) was used to take luminance measurements from the monitor. To compensate for the nonlinearity of the display, luminance measurements taken at 256 increments were entered into a computer program which recalibrated the display as necessary to linearize the luminance output. RT responses were recorded from the space bar on a keyboard positioned on the desktop directly in front of the observer. To maintain the observers viewing angle throughout experimental sessions, a stainless steel chin rest lined with ½ inch foam was mounted on the edge of the desk, 57 cm from the monitor.

Stationary, 2-D Gaussian circular sinusoidal vertical grating stimuli (Campbell & Green, 1965) had a spatial frequency of 2 cycles per degree and the same mean luminance as the grey background. Stimuli were presented at various contrast levels above the threshold for detection. Contrast was defined as (%) contrast = 100 X (L_{max} -

$L_{min})/(L_{max} + L_{min})$, where L_{max} and L_{min} are the maximum and minimum luminance values of the grating stimulus (Anzai et al., 1995). The mean luminance was held constant at 10 cd/m^2 for all contrast levels.

Design and Procedure

A randomized block design was used with each level of contrast and inter-stimulus interval (ISI) presented in a random sequence for each observer. Observers were seated in the lab room for 5 minutes prior to commencement of the session to allow for adjustment to the dark testing room. Sessions lasted for approximately 1 hour in all experiments. Observers viewed the computer monitor binocularly with any needed corrective lenses in place.

For a given trial, following the 2000 ms inter-trial interval (ITI) during which the screen was grey and had a mean luminance of 10 cd/m^2, a 2-cycle, 900 Hz tone, lasting 300ms from onset of the first cycle to offset of the second cycle, was presented to warn the observer that the stimulus was about to be presented. The grating appeared following a variable ISI, and responses consisted of depressing the keyboard with the right index finger as soon as the stimulus was detected (see Figure2). This resulted in the removal of the stimulus from the display monitor. RTs were recorded by the computer. RTs determined to be anticipatory (less than 150 ms) and RTs that indicated insufficient attention (greater than 2000 ms) were discarded from each participants' data set.

Experiment 1

Method

Two individuals completed 5 sessions consisting of 3 blocks of 120 trials, for a total of 1800 trials. Experiment 1 was designed to determine the range of the ISI effect observed in the pilot study using a fine-grained analysis which covered several ISI

levels. The gratings were presented with .8, 16 and 64 percent contrast. The ISIs ranged from 100 to 2000 ms in 100 ms intervals.

Results

Due to the large number of conditions the data were very noisy (see Figure 5). We excluded the first session and collapsed across contrast to reduce the variability; however, the results remained inconclusive (see Figure 6).

Experiment 2

Method

A reduced number of ISIs were used in an attempt to determine the time course of the attentional effect (~10 ms) observed in the pilot study and to determine if the RTs were slowed for ISIs between the 1000 and 2000 ms interval used in the pilot study. Three individuals completed 5 sessions consisting of 3 blocks of 120 trials, for a total of 1800 trials. The gratings were presented with .8, 16 and 64 percent contrast. The ISIs were 1000 and 1500 ms.

Results

Figure 7 shows the results for one observer. This pattern of results was characteristic of all observers. When the interval between the auditory cue and the visual target was 1000 ms, the RTs were approximately 15-20 ms slower than RTs following the 1500 ms interval for all contrast levels.

Experiment 3

Method

Three individuals participated in 5 sessions consisting of 3 blocks of 120 trials, for a total of 1800 trials. Experiment 3 was designed to test an extended range of ISIs, to determine the range of the effect observed previously. As in the previous experiments, the gratings were presented with .8, 16 and 64 percent contrast. The ISIs

ranged from 500 to 2000 ms in 500 ms intervals. This range of ISIs allowed us to determine the effect of ISI when the level was above and below those used in Experiment 2. In addition, Experiment 3 allowed us to replicate the parameters used in the pilot study and Experiment 2, within one experiment.

Results

All observers demonstrated the same pattern of responding (see Figure 8). The RTs for trials with a 500 ms ISI were slower than those for all other trials. In addition, there was an ordered progression of increasingly faster RTs as the interval between the cue and target lengthened.

Experiment 4

Method

Seven participants completed 8 sessions consisting of 3 blocks of 120 trials. The gratings were presented with .8, 16 and 64 percent contrast. The ISIs ranged from 250 to 1000 ms in 250 ms intervals. Again, we wanted to extend our range of ISIs to more precisely describe the time course of the attentional effect.

Results

Participants completed 8 sessions, consisting of 3 blocks of 120 trials. Trials with RTs of less than 150 ms or greater than 500 ms were removed from each observers' data set. The 5 sessions in which greater than 80% of the trials met this criterion and had the lowest mean error, were selected for analysis. A Random Block univariate ANOVA was performed on the mean RTs.

The ANOVA revealed that increases in contrast resulted in a significant decrease in RT, [$F(2,66) = 403.6$, $MS_e = .004$, $p < .001$]. A regression analysis revealed that a quadratic trend best models the relationship, $R^2 = .64$, [$F(1,81) = 20.8$, $p < .001$] (see Figure 9).

In addition, there was a significant main effect of ISI, [$F(3,66) = 11.2$, $MS_e = .0011$, $p < .001$]. (see Figure 9). Tukey's HSD revealed that RTs following the 250 ms ISI were significantly slower than RTs for all other ISIs, $p<.01$. The mean RTs for each ISI level were: '250 ms' = 289 ms, '500 ms' = 278 ms, '750 ms' = 273 ms, '1000 ms' = 274 ms. Figure 10 displays mean RT as a function of contrast and ISI for one observer.

Discussion

We conducted a series of 4 experiments to characterize the time course of the slowed RTs we observed in our pilot study. The results were in keeping with our predictions of faster RTs with increases in suprathreshold contrast. Because the stimuli were identical in size, location and spatial frequency, it is likely that the same group of neurons was responsible for the contrast signal. However, faster RTs for stimuli with higher contrast suggests that increasing the contrast in the stimulus drives the neural firing rate. Pooling of this signal from several neurons would result in the threshold for detection being surpassed more quickly. In turn, this would lead to a shorter latency to generate a response when detecting stimuli with high contrast.

In addition, we sought to determine whether the attentional dwell time theory would account for our results. The results of the present experiment support the dwell time theory of attention. Consistent with this theory, we found RTs to be inhibited when there was a short interval (i.e. 250 ms) separating the auditory and visual stimuli. The processing of the auditory stimulus interfered with the detection of the visual stimulus when the interval was 250 ms.

Duncan and his colleagues (1994) found that the capacity of the attentional system to shift between successive visual events was limited by the duration of the interval separating the stimuli. Our findings extend this previous research by demonstrating attentional dwell in a cross-modal paradigm. Although an attentional dwell time has been shown in cross-modal paradigms previously, this research had been

unable to produce inhibition unless a response was made to both stimuli in succession (Jolicoeur, 1999). In addition, by measuring RT our detection procedure provides a different means of investigating the dwell time of attention which is typically studied using accuracy rates as an indication of interference.

COLOUR EXPERIMENT

Opponent Colour Processing

The goal of this thesis was to describe the latency differences that occur in perceiving high contrast objects in our environment. Thus far we have discussed how pooling the neural responses to luminance contrast results in response latency differences. Another form of contrast that is of interest to us is opponent-colour contrast. The borders that define and distinguish objects from one another are often characterized by differences in hue. The perception of colour has significant implications for successful interaction with our environment. Accurate perception of these differences in colour tremendously improves the chances of successfully identifying and distinguishing between objects in the environment. For example, identifying red fruit against a background of leaves is enhanced by the contrast provided by the coloured fruit against the green leaves (Goldstein, 1996).

The visual system has evolved two specialized opponent mechanisms sensitive to differences in colour. These mechanisms generate opposite signals to a stimulus depending on its wavelength (Kaiser & Boynton, 1996). How and when individual colour signals are combined may lead to latency differences when stimuli are processed by the two opponent-colour systems within the visual system. Our goal is to determine the temporal response properties of the blue-yellow (BY) and red-green (RG) opponent mechanisms using a detection task similar to that used for the luminance defined contrast in Experiments 1-4. The following review of the underlying physiology of the visual system suggests that the differences in the temporal characteristics of these

opponent mechanisms should become evident in a detection task. More, specifically, it appears as though the BY opponent mechanism does not receive opponent input until later stages of cortical processing relative to the RG opponent mechanism. This physical delay in establishing opponency should be apparent in terms of a temporal delay when responding to a BY versus a RG stimulus.

Defining Colour

Colour can be broadly defined as the perception of the redness, greenness, etc. of objects and lights in our environment (Goldstein, 1996). For our purposes, colour can be thought of as the light emanating from its source and impinging directly on the retina. We use the term colour to refer to chromatic colours i.e. red, green, blue and yellow, and luminance to refer to achromatic colours i.e. white, grey, and black. Light has several physical properties, which correspond to and influence our perception of colour. The first of these properties is wavelength, of which a narrow range corresponds to the spectrum of colours or hues we perceive. The visible spectrum of light for humans extends from approximately 400 nm to 700 nm and captures our entire range of perceivable hues from violet to red.

Two other physical properties of light can influence our perception of colour. Light intensity, when manipulated is responsible for our perception of brightness. Thus, increasing the intensity of light results in an increase in our perception of the brightness of a colour. De Valois and De Valois (1993) proposed that the relative brightness of spectral colours is the result of the combination of the achromatic non-opponent signal in the parvocellular pathway and the luminance signal in the magnocellular pathway. The authors noted that evidence for the contribution of these pathways to the perception of brightness was the finding that when these two signals are summed, the resulting curve resembles the perceptual brightness function. Finally, saturation, the third physical property of colour is inversely related to the amount of white in a colour (Goldstein,

1996). For example, a less saturated colour appears pale and pastel, e.g. red becomes pink with the addition of white.

Many attempts have been made in the past to find an accurate and efficient way to describe these three dimensions of colour for humans. For example, Newton described colour space in terms of a colour circle in which the three primary colours were arranged symmetrically about the perimeter of a circle with complementary colours appearing diagonally opposite from each other (Humphrey & Servos, 1999). In the 1920's the International Commission on Illumination (CIE) met and attempted to establish a universal system of colour specification with the intention that scientific communication with regards to colour could be made precise. In addition, it was necessary to find a compromise between the imprecise use of colour names and the abstract description the spectral power distribution provided (Kaiser & Boynton, 1996). The commission devised the CIE colour space which can be described by three psychophysical units called tristimulus values: X, Y, and Z. These values correspond to the three primaries, red, green and blue, respectively. Tristimulus values were generated by colour matching experiments averaged over several observers to create the CIE standard observer. Plotting these values in CIE space allows for the specification of when two stimuli will match in colour appearance at equal luminances, for a standard observer (Kaiser & Boynton, 1996). In addition, the CIE space allowed for the determination of the dominant wavelength and purity of a stimulus which are characteristic of the hue and saturation of the stimulus, respectively (Humphrey & Servos, 1999).

Psychophysical measurements have also been used to describe the functioning of the opponent-colour mechanism. Jameson and Hurvich (1955) were able to describe the appearance of opponent-colours using a psychophysical method called hue cancellation. Their method was dependent on Hering's opponent-colours theory in that it

relied on the knowledge that the underlying signals in both the BY and RG opponent-colour systems were antagonistic. Their hue cancellation technique allowed them to determine the exact amount of red needed to cancel out the perception of green and the exact amount of blue needed to cancel out the perception of yellow and vice-versa. By presenting one light of a particular wavelength and later adding its antagonistic pair, these researchers were able to determine how much of the antagonistic colour was needed to cancel out the perception of the paired colour. In doing this, the researchers were able to determine the chromatic response function, which is a plot of how much energy is needed in the antagonistic wavelengths to cancel out the perception of the test wavelengths presented at equal energy. The peaks of these chromatic response functions correspond to pure green, red, blue and yellow. In addition, these peak wavelengths correspond to the peaks of the human opponent-colour spectral sensitivity functions (Sperling & Harwerth, 1971).

We have chosen to use these peak wavelengths to define our opponent-colour stimuli. These peak wavelengths have been used in other psychophysical studies of the opponent-colour mechanisms (Mullen, 1985). These wavelength pairs cause maximum modulation in one opponent system while causing only minimal modulation in the other opponent system (Mullen, 1985). Thus any latency differences we observe between the two systems should be mainly due to modulating the system of interest.

Models of Colour Vision

One-Stage Models

In the early 1800's, Thomas Young proposed a theory of colour vision which later became known as the trichromatic theory, in which the visual system contained three mechanisms responsible for colour vision (Goldstein, 1996). With psychophysical and physiological evidence being scarce at the time, this model lay dormant and widely unaccepted until the mid 1800's. At this point, Hermann von Hemholtz revived the

trichromatic theory and it became the popular view of the time with regards to colour vision (Goldstein, 1996). The theory developed from colour matching experiments in which observers were required to use lights of three different wavelengths, to match a single wavelength of coloured light. Researchers noted that normal observers could match any single wavelength of light by combining three other wavelengths or spectral power distributions (SPDs). However, observers were unable to make accurate colour matches when they were provided with only two other wavelengths of light. This finding resulted in the conclusion that colour vision was the result of a three-receptor system, with each receptor being responsive to a particular portion of the visible spectrum (Goldstein, 1996).

This view became known as the Young-Hemholtz theory of colour vision, in which three receptors with differing spectral sensitivities accounted for the sensation and perception of colour (Kaiser & Boynton, 1996). Accordingly, it was postulated that when light impinges on the receptors, each receptor fires differentially to a particular band of wavelengths and the spectrum is coded by the nervous system in terms of the receptors' pattern of firing. This pattern of firing was argued to result in the ability to perceive and differentiate various spectral colours.

Another theory of colour vision, originally thought to be mutually exclusive of the trichromatic theory, emerged in the 1800's. Ewald Hering, an eminent 19th century physiologist, observed that some colours appeared to be perceptually related to others (Kaiser & Boynton, 1996). He noted that although some colours could be described as the combination of two other colours, for example cyan was bluish-green, other colours never appeared in combination, for example red and green, and blue and yellow (Goldstein, 1996). Hering argued that the latter colours (red-green and blue-yellow) were perceptually paired with one another. In addition, Hering noted that after observing one of these colours for an extended period of time (e.g. blue), the afterimage generated

in the absence of the stimulus was the colour of its perceptual pair (e.g. extended exposure to blue produced a yellow afterimage). Finally, Hering observed that individuals who were colour blind were unable to perceive both colours in a perceptual pair. For example, if an individual was colour blind for green, then they were also unable to perceive red.

Based on his observations, Hering proposed the opponent-process theory of colour vision (Goldstein, 1996). The model included three basic mechanisms, which responded differentially to various wavelengths of light. The model consisted of a luminance mechanism in which a positive response was generated to white light (W+) and a negative response was generated in the absence of light or black (B-). The model also contained two other mechanisms which accounted for colour vision; an R+/G- mechanism and a B-/Y+ mechanism in which plus signs indicated a positive response, (e.g. to red and yellow light) and a minus sign indicated a negative response, (e.g. to green and blue light). Hering postulated that the positive and negative responses were the result of the accumulation and breakdown of chemicals in the retina (Goldstein, 1996).

Two-Stage Models

It became apparent that the reason for previous discrepancies between the trichromatic and opponent-processing models was that each theory was describing a different stage in the perceptual processing of colour. As a result, there was a need for a more complex model of colour processing which could incorporate both of the processing stages. The first two-stage models emerged in the late 1800's and early 1900's, and were proposed combinations of the two opposing theories of colour vision at the time (Donders, 1881; von Kries, 1905; Muller, 1930; as cited in De Valois & De Valois, 1993). However, these proposals were not taken very seriously at a time when little was known about the underlying physiology of the visual system. Jameson and

Hurvich (1955) would later be credited with generating the first widely accepted two-stage model of colour vision (De Valois & De Valois, 1993). However, it wasn't until the 1960's that evidence became available that would offer unwavering support for the two-stage model.

The ability to measure the spectral absorption of cones became available when microspectrophotometry was applied to both fish and primate retinas. Microspectrophotometry is similar to retinal densitometry except it allows for cone sensitivities to be measured in vitro (Kaiser & Boynton, 1996). Both microspectrophotomerty and retinal densitometry involve passing light through a desired receptor. Some of the light is absorbed by the receptor and a portion of the light is reflected back. A photometer is used to measure the light which is reflected back from the eye, to determine the absorption spectra of the receptor of concern. Researchers studying the human retina were able to confirm the predictions of the trichromatic theory; specifically that three distinct cone types existed, each maximally sensitive to particular bands of wavelengths of light (Brown & Wald, 1964).

Evidence for the existence of a second stage, in which the predictions of the opponent-process model were confirmed, came in the form of electrophysiological recordings from fish and primates. This research demonstrated the existence of opponent cells in the visual pathway (De Valois & De Valois, 1993). Svaetichin (1956; as cited in De Valois & De Valois) was the first to show that cells in the retina of fish showed response properties consistent with the opponent-processing model. These cells would respond positively when stimulated by light at one end of the spectrum but would respond negatively to lights at the other end of the spectrum. Following this, De Valois (1980) recorded from cells in the LGN of the rhesus monkey and was able to show that these cells demonstrated opponent properties similar to those demonstrated previously in the fish. The firing pattern of the cell increased to light from one end of the

spectrum and decreased to light from the other end of the spectrum. Both of these significant findings led to the widespread acceptance that both the trichromatic theory and opponent-process theory accurately described some aspects of the processing of colour.

It became evident that although these processes did not operate in conjunction, they both appeared to oversee the colour signal, but merely at different stages of processing. In the first stage of the two-stage model, three specialized receptor types, which are selectively sensitive to particular bands of wavelengths, receive and encode the incoming wavelengths of light. In the second stage of this model, cells receiving the colour signal demonstrate opponent response properties. These cells fire positively to light of a particular band of wavelength and negatively to light of other wavelengths. These two-stage models lay the groundwork for more complicated models of colour vision which could account more accurately for the processing of opponent-colour stimuli.

Multi-Stage Models

Although the two-stage model provided a reasonable account of the processing of the colour signal, more recent advances in technology have provided a wealth of information, some of which could not be accounted for by a simplistic two-stage model. In fact as early as the 1930's, Muller (1930) and Judd (1949) had suggested that a more complex model of colour vision was necessary (De Valois & De Valois, 1993). De Valois and De Valois (1993) responded to the need for a more comprehensive model that could account for the discrepancies between the two-stage model and recent physiological findings. The researchers proposed a multi-stage model in which discrepant research findings were identified and explained at different stages in their model. In addition, this multi-stage model has allowed us to make predictions based on physiology as to why we

might expect response latencies to differ for the opponent-colour gratings we used in our detection task.

De Valois and De Valois (1993) noted that recent research has provided a great deal of information on the anatomy of the retina and the organization of the retinal mosaic. The finding of relatively small number of S cones (5-10% of all cone receptors) in the retina, which contribute to the BY system, required consideration. The authors argued that a model was needed that can account for the perceptual balance between the RG and BY system, in spite of the large difference in the proportion of cones devoted to either system. In addition, the model was developed to overcome the discrepancies between recording data from cells in primate LGN and psychophysical evidence involving perception of short wavelength stimuli. De Valois and De Valois (1993) argued that there must be some amplification of the blue signal at the cortical level in order for the electrical firing to be representative of the perceptual experience of blue. The paucity of S cones must also be considered when investigating the latency differences between the RG and BY systems. The S cones contribute differentially to each system and leave the BY system disadvantaged relative to the RG system in terms of the relative number of cones contributing to each mechanism. The need to augment the S cone signal to balance the opponent systems perceptually might lead to latency differences between the two systems.

In addition, De Valois and De Valois argued that the random connectivity of cells in the retina must somehow lead to an organized colour signal. Any model of colour vision must include a stage, which can incorporate this random organization into a meaningful colour signal. Lastly, the authors noted that there is spatial confounding of luminance and colour signal in the wiring of LGN cells. That is, most LGN cells have inputs from different cone types which allows them to respond to both changes in chromatic and luminance variations (Weisel & Hubel, as cited in De Valois & De Valois,

1993). These cells with center inputs from one cone type and surround inputs from another cone type will have different spatial and temporal tuning characteristics for firing to either luminance or colour. This creates the necessity of a third processing stage in any model, where colour and luminance become separable.

Anatomy and Physiology of the Visual System

Retina

Colour processing begins with the absorption of light by photopigments in cone receptors selectively sensitive to particular bands of wavelengths of light (De Valois and De Valois, 1993). Smith and Pokorny (1975) have developed a widely accepted spectral sensitivity function to represent cone sensitivities and have adjusted this spectral sensitivity function to account for pre-retinal photopigment absorption, which occurs in the lens and macular pigment. Although there has been disagreement over the number of cone pigments (3 to 5 possible pigments), all photopigments are assumed to reside within three classes of receptors (Neitz, Neitz, & Jacobs, 1991, as cited in De Valois & De Valois, 1993).

The three classes of photoreceptors include: S cones which possess a selective sensitivity to short wavelengths of light, M cones which possess a selective sensitivity to medium wavelengths of light, and L cones which possess a selective sensitivity to long wavelengths of light. Recent anatomical evidence suggests that S cones account for only 3-10% of all of the cones in the retina of both primates (macaque) and humans (De Valois & De Valois, 1993). Psychophysical reports that humans can only discriminate blue and yellow gratings with spatial frequency no finer than 7-14 cycles per degree supports this assumption (Stromeyer, Kranda, & Sternheim, 1978). L cones are assumed to be approximately twice as prevalent as M cones based on physiological reports. Thus, the ratio of L:M:S cones in the retina is postulated to be 10:5:1 (De Valois & De Valois, 1993). Recently, Roorda and Williams (1999) used adaptive optics with

retinal densitometry to map the retinal mosaic in the living human eye. In addition, dark-adaptation and selective bleaching techniques were utilized to distinguish between S, M and L cones. The investigators found that there was no pattern or uniform distribution of the M and L cones between the sparse S cones. Roorda and Williams (1999) offered that perhaps the failure to observe a uniform distribution of L and M cones during neural development might be evidence that the perception of red and green is a relatively new feature in the evolution of old-world primates.

Psychophysical evidence based on response functions inferred from cone sensitivities suggests that these cones differ in their temporal response characteristics (Kelly, 1974). Psychophysicists have investigated the temporal response properties of the receptors in the human visual system. Mollon and Krauskopf (1973) argued that the different colour mechanisms of the eye, namely the cone receptors, have different response latencies. The investigators measured RTs to monochromatic stimuli presented on monochromatic backgrounds. The stimuli consisted of 430nm, 500nm, and 650 nm monochromatic discs presented on a background of 500 nm or 600 nm. The results demonstrated that the response latency to the 430 nm disc was slower than the 500 nm and the 650 nm discs. In addition, RTs to the 500 nm disc were faster than RTs to the 650 nm disc. Finally, Mollon and Krauskopf (1973) reported that for all wavelengths, RTs decreased with increases in the intensity of the background at 500 nm. The findings of this experiment highlight the differences in RTs as a function of wavelength.

Mollon and Krauskopf (1973) argued that the latency differences to various bands of wavelengths of light arises at the level of the individual receptor mechanisms; however, one cannot be certain at which level these latency differences arise using a psychophysical detection task. More recently, physiological evidence has demonstrated that all cones possess the same temporal response properties (Yeh, Lee, & Kremers,

1995). Thus latency differences in responding to coloured stimuli must develop at a later stage in the processing of the colour signal, where perhaps the weak S-cone signal must be increased (De Valois & De Valois, 1993).

Post-Retinal Pathways to the LGN

The latency differences in response to various opponent-colour gratings are of importance to us. A review of the post retinal pathways is necessary to demonstrate how the physiology of the visual pathways may be responsible for latency differences. De Valois and De Valois (1993) proposed that two possible patterns of connectivity between cones and ganglion cells existed; the first suggests that inputs to the surround arrive via horizontal cells, which show a random pattern of connectivity with neighboring cones. The horizontal cells are hypothesized to sum over input from several cone types i.e. L+M+S cones assumed to be in the ratio of 10L:5M:1S. The ganglion cells' possible responses would then consist of +L-(L+M+S), +M-(L+M+S), or +S-(L+M+S) when the direct receptor input is excitatory and -L+(L+M+S), -M+(L+M+S), or -S+(L+M+S) when the direct receptor input is inhibitory. The second possible pattern of connectivity suggests that cells with L and M cone centers have surrounds which receive opposing input from M and L cones respectively. When the pattern of connectivity is cone-type-specified, the resulting signal would then be +L-M or +M-L for cells with direct receptor excitatory input and -L+M or -M+L for cells with direct receptor inhibitory input.

De Valois and De Valois (1993) assumed the weighting of the direct input or "center" is equivalent to the input of the surround. Therefore, assuming the proportion of cones to be 10L:5M:1S allowed for the output of any cell to be determined. For example, RG cells could be modeled as receiving 16L-(10L+5M+S)= 6L-5M-S which would approximately equal L-M. The YB cell could be modeled as 16S-(10L+5M+S) which equals 15S-10L+5M or S-(L+M). This difference in the relative number of S cones

contributing to each signal may be responsible for latency differences in these signals as they travel to the cortex.

Visual Cortex

Perceptual colour opponency is thought to arise at a cortical level. De Valois and De Valois (1993) argued that the perceptual colour axis is represented in the parvocellular layer of the LGN and is formed by cells with L and M cone center input. De Valois and De Valois argue that in the retino-geniculate pathway there exists a single colour axis. This axis was proposed to be near an orange-cyan chromatic axis. The hypothesized function of the S cone system is to rotate the axis to form the RG and YB axes. The contribution of the S cones in rotating this single colour axis is thought to occur when the colour signal arrives in the cortex. The following is a review of the process by which the two opponent colour axes are generated within the cortex.

Six cell types are assumed to exist in the LGN [**+Lo** = +L-(L+M+S), **+Mo** = +M-(L+M+S), **+So** = +S-(L+M+S), **-Lo** = -L+(L+M+S), **-Mo** = -M+(L+M+S), **-So** = -S+(L+M+S)]. (The subscript **o** is used to describe the cells' opponent properties). De Valois and De Valois (1993) proposed that these cells respond to variations in both luminance and colour but by means of differing receptive fields. The receptive field for colour was presumed to be in the form of center-surround while the receptive field for luminance was thought to be uniform across the entire receptive field, resulting in either a positive or negative response to any particular stimulus.

The investigators proposed that when inputs from two of these six cells are combined at a cortical level, the resulting simple cell loses either the luminance or the colour signal (De Valois & De Valois, 1993). For example, +Lo with -Mo results in the luminance signal canceling out and the output represents variations in colour. However, combining the output of +Lo with +Mo results in a luminance signal with colour canceled out. The combination of three of the six cells results in a luminance signal with

+Lo+Mo+So responding to white light and -Lo-Mo-So resulting in responses to the absence of light. Figure 11 describes how combinations of these six cells result in the perception of colour and luminance.

De Valois and De Valois (1993) suggested that when +So is added to +Lo-Mo, the output would be red, however when -So is added to +Lo-Mo, the output would be yellow. Likewise, when -So is added to +Mo-Lo, the output would be green and when +So is added to +Mo-Lo, the output would be blue. The authors contended that the M and L cones provide the major contribution to the colour signal and the contribution of the S cone system is to rotate the axis into the RG and YB axes. This process is hypothesized to take place beyond the LGN, at a cortical level. These cortical cells under appropriate stimulus conditions would typically demonstrate single or double opponency (Jacobs, 1986). To differentiate between these two cells, single-opponency refers to spectral opponency whereas double-opponent cells are both spatially and spectrally opponent. Thus, the double-opponent cell is best suited for detecting coloured spatial patterns as opposed to large uniformly coloured stimuli (Jacobs, 1986). This is the type of cell we are interested in with our colour gratings which are spatially and spectrally opponent.

Complex cortical cells have large receptive fields, which encompass large numbers of receptors and are very responsive to chromatic stimuli (De Valois & De Valois, 1993). De Valois and De Valois (1975) proposed that these complex cells are used to convey information about the spatial pattern of colour. Researchers have shown that large proportions of cells in area V1 respond well to isoluminant colour variant stimuli (Gouras & Kruger, 1979). Investigators have attempted to confirm the existence of these cells and determine their location in the human visual cortex. Engel, Zhang and Wandell (1997) have used functional magnetic resonance imaging (fMRI) to investigate colour processing in cortical areas V1 and V2. Colour reversing checkerboards were

used to measure cortical colour tuning for both the RG and BY chromatic pathways. A strong response was elicited in both V1 and V2 for RG stimuli. The response was best for stimuli presented at a temporal frequency of 4 Hz, and the signal for isoluminant colour contrast was 4 times as strong as the signal produced for luminance contrast. A robust signal was also achieved for stimuli in the BY plane in both V1 and V2. However, for the BY axis, as the temporal frequency of the stimulus increased, the response to the colour stimulus decreased relative to the luminance stimulus. These findings confirm the existence of cells in V1 and V2 that are capable of responding to isoluminant, spatially variant, colour patterns.

Temporal properties of RG and BY Mechanisms

Psychophysical investigations which have attempted to characterize the spatio-temporal properties of the colour system have found that the S cone driven system appears to generate a sluggish response relative to the L and M cone driven system (Kelly, 1974). However, several synapses occur from the retina through the geniculo-striate pathway and to the cortex, thus it is difficult to determine at what stage the S cone system becomes slowed using psychophysical methods. Three or more possible sites exist for this slowed temporal responding; the response properties of the cone receptors, the relative populations of the three cone types and their multiple inputs to ganglion cells leading to the LGN, or the integration of signals in the cortical cells.

As discussed previously, the retina has been investigated as the source of the sluggish S cone response. Yeh et al. (1995) used single cell recording techniques to compare the temporal response properties of macaque ganglion cells with inputs from S, M, or L cones. Using a method of silent substitution each cone type was modulated individually and recordings were taken from cells in the parvocellular pathway. Silent substitution refers to a method in which two wavelengths are selected for which one cone type demonstrates equal sensitivity when the wavelengths are presented at equal

radiances. However, these same two wavelengths generate very unique response in other cone types, thus one cone type can be silenced while another is modulated (Kaiser & Boynton, 1996). Magnocellular pathway recordings for cells with M and L cone input were taken for comparison. The recording data indicated that the temporal properties of the parvocellular ganglion cell with inputs from the three cone types were similar. The only difference in temporal dynamics existed in the magnocellular pathway where M cone input to the ganglion cell resulted in faster responses than L cone input. The authors concluded that previous findings of sluggish S cone pathway in psychophysical studies were the result of post-retinal filtering.

Chichilinsky and Baylor (1999) addressed the plausibility of poor temporal responding of the S cone system arising as a result of post-retinal filtering. The authors used multi-electrode recordings from ganglion cells in the macaque retina. The authors found the temporal response properties of the blue ON signal, +S, was similar to that of the yellow OFF signal, -(L+M). They reasoned that this was evidence that neither post-retinal filtering nor a sluggish S cone receptor response was responsible for the overall delay in the S cone system. Chichilinsky and Baylor (1999) suggested that the delay might instead arise at a cortical level.

Using single cell recordings, Cottaris and De Valois (1998) investigated the possibility that the sluggish S cone response was the result of additional processing at a cortical level. The authors hypothesized that because S cones are relatively rare, the signal arriving at the cortex must be amplified prior to being integrated with opponent signals from cells with L and M cone input. The authors presented brief flashes (30 ms) of uniformly coloured stimuli and analyzed neuronal responses. They found cells in V1 which responded with a short latency (68-98 ms) which corresponded to cells with L and M cone opponent inputs. In addition, they found cells with longer latencies (96-135 ms) in V1 which corresponded to cells with S cone opponent inputs. The authors also

reported individual cells which responded with latency differences of 20-30 ms to different chromatic regions. The longer latency was attributed to S cone opponent input whereas the shorter latency was attributed to L and M opponent input. In addition, for both single-peaked and double peaked neurons, L and M cone inputs contributed more to the early portion of the time to peak and the S cone input made its largest contribution to the late portion of the time to peak. Consistent with this, was the finding that most late peaking neurons are tuned to the S cone axis.

Cottaris and De Valois (1998) suggested that their results were evidence for the sluggish response of the S cone system being generated in the cortex. The authors proposed that because of the rarity of the S cone in the retinal mosaic, a relatively weak S cone signal arrives at the cortex. This signal must then be augmented by a specialized mechanism prior to integration with opponent L and M cone signals. The mechanism proposed to augment the S cone signal is a recurrent excitatory loop in which the signal from the striate cell repeatedly re-enters the cortical neuron and is summed with new signals. This hypothesis fits well with the doubling of the S cone signal proposed to occur in the De Valois and De Valois (1993) multi stage model discussed earlier.

The purpose of the present study is to characterize the time course of the RG and BY systems in the human visual system using psychophysics. It was anticipated that detection of BY colour gratings would be slow relative to RG colour gratings due to the necessity of augmenting the S cone signal. According to the multi-stage model discussed earlier, the primary contribution to the red and green signal comes from L cones and the primary contribution to the blue signal comes from L cones. Because there is less S cone contribution, the S cone signal will not require as much time to be augmented. This should result in a smaller temporal delay when these L, M and S cone signals must be combined (De Valois & De Valois, 1993). In addition to testing

opponent-colour gratings we included a RB non-opponent grating. We predicted that the response latency to this grating should be slower than the RG grating, due to the additional S cone information. However, the latency to respond should be somewhat shorter than response to the BY grating.

In addition, we investigated the role attentional dwell time has on RTs to colour defined contrast gratings. We anticipated that the dwell time of attention would cause interference in the processing of the opponent-colour gratings when the interval separating the presentation of the auditory cue and the grating is short. This result would be consistent with our previous findings of attentional dwell for visual stimuli with luminance defined contrast. However, we did not anticipate any interaction between colour and ISI, because the timing effect appears to be an attentional effect. We believe this effect influences responding after the colour processing has been completed and therefore influences each colour system in the same manner. This would be consistent with the results we reported for the luminance experiments, in which the attentional effect was independent of the luminance present in the stimulus.

Experiment 5

Method

Participants

Seven Wilfrid Laurier students, with normal or corrected to normal vision were recruited to participate in the study. All participants had normal trichromatic colour vision as determined by the Ishihara colour plate test and were right-handed, as determined by the modified Oldfield handedness questionnaire (Oldfield, 1971). Observers were paid for their participation with the exception of the experimenter.

Materials

All sessions took place in a darkened lab room, in which the walls and desktops were black to prevent the reflection of ambient light from the computer monitor. Stimuli

were generated by a Power Macintosh 8100/80 computer [model# M1688] and presented on an Apple Multiple Scan 1705 Display monitor [model# M4436]. To ensure the CRT output was consistent with the colour and luminance specifications for the gratings a photometer (Minolta Chroma Meter CS-100) was used to take measurements from the monitor. The display was recalibrated as necessary to ensure RGB values were as planned. RTs were recorded from the space bar on a keyboard positioned on the desktop directly in front of the observer. To maintain the observers viewing angle throughout experimental sessions, a stainless steel chin rest lined with ½ inch foam was mounted on the edge of the desk, 57 cm from the monitor.

Stimuli

Stationary, 2-D sinusoidal isoluminant RG, BY and RB vertical grating stimuli had spatial frequency held constant at 2 cycles per degree and had the same mean luminance as the grey background. Although the peak of the contrast sensitivity curve as a function of spatial frequency for either the RG or BY opponent systems does not fall at 2 cycles per degree, both the RG and BY systems demonstrate good sensitivity at this frequency and neither are disadvantaged relative to the other system (Rovamo, Kankaanpaa & Kukkonen, 1999). The mean luminance was held constant at 10 cd/m^2 for all stimuli.

Peak wavelengths that maximally stimulate one opponent system and cause the least amount of stimulation in the remaining opponent system were selected based on previous research (Mullen, 1985). Peak wavelength values of 602 and 526 nm were selected for the red and green bars of the RG grating, respectively and peak wavelength values of 470 and 577 nm were chosen for the blue and yellow bars of the BY grating, respectively. The peak wavelength selected for the red of the RG grating and the blue of the BY grating were chosen for the RB grating. The wavelength values were then converted to CIE coordinates with a program written in MATLAB which used the Smith

and Pokorny (1975) cone fundamentals which are based on the Judd modified CIE (1931) matching functions. These CIE coordinates were transformed into the RGB system of the colour monitor. The RGB phosphors of the monitor form the corners of a triangle within the CIE space, i.e. the colour gamut of the monitor. Combining the three phosphors results in a constant luminance Y and two chromaticity coordinates x (x = X / X+Y+Z) and y (y = Y / X+Y+Z) which represent hue and saturation (Kaiser & Boynton, 1996).

CIE coordinates corresponding to a plane of constant luminance (Y = 10) were used to generate the gratings. CIE values for the RG grating were taken in increments from a line of constant hue from saturated red (x = .585, y = .339) to the white point (x = .297, y = .302) and another line of constant hue from the white point to saturated green (x = .306, y = .523). CIE values for the BY grating were taken in increments from a line of constant hue from saturated blue (x = .148, y = .063) to the white point (x = .297, y = .302) and another line of constant hue from the white point to saturated yellow (x = .400, y = .459). Similarly, CIE values for the RB grating were taken in increments from a line of constant hue from saturated red (x = .585, y = .339) to the white point (x = .297, y = .302) and another line of constant hue from the white point to saturated blue (x = .148, y = .063). Saturated values correspond to the peak of the sinusoid and the white point corresponds to the trough of the sinusoid. These saturated values were the maximum we were able to produce within the gamut of our monitor with the luminance held constant at 10 cd/m^2.

Design and Procedure

A randomized block design was used, in which RTs were recorded for RG, BY and RB colour gratings randomly presented following four ISI levels of 100 ms, 250 ms, 500 ms and 750 ms. All participants had completed a minimum of three practice sessions consisting of 3 blocks of 120 trials prior to running experimental sessions. Data

from 5 experimental sessions, consisting of 3 blocks of 120 trials were analyzed from each observer. Observers were seated in the lab room for 5 minutes prior to commencement of the session to allow for adjustment to the dark testing room. Observers viewed the display binocularly with any needed corrective lenses in place.

For a given trial, following the 2000 ms inter-trial interval (ITI) a 300 ms, 2-cycle, 900 Hz tone was presented to warn the observer that the stimulus was about to be presented. The grating appeared following a variable ISI ranging from 100 ms to 750 ms, to minimize anticipatory responses and to determine the influences of attentional dwell time. Responses consisted of depressing the keyboard with the right index finger as soon as the stimulus was detected and resulted in the removal of the stimulus from the display monitor. Response times were recorded by the computer. In addition to manipulating colour as opposed to luminance, we also sampled a lower range of ISIs than in the previous luminance experiments. By sampling a lower range of ISIs we could more closely compare our results with attentional dwell time studies.

Analysis

For all experiments, RTs below 150 ms were discarded because we considered them to be anticipatory and RTs above 2000 ms were discarded because they indicated insufficient attention to the task. The mean RTs were calculated for each condition for each participant.

Results

A Random Block univariate ANOVA was performed on the mean RTs. The ANOVA revealed that the colour of the grating significantly influenced RT, [$F(2, 66) = 13.74$, $MS_e = .00038$, $p < .001$]. Tukey's HSD revealed that RTs to the RG grating were significantly faster than RTs to the BY and RB gratings, $p < .01$. There were no significant differences between the RTs for the BY and RB gratings. The mean RTs for

the gratings were: RG = 258 ms, BY = 265 ms and RB = 263 ms. (See Figure 12). The interaction between colour and ISI was not significant.

In addition, there was a significant main effect of ISI, [$F(3,66) = 11.45$, $MS_e = .00032$, $p < .001$]. (see Figure 13). Tukey's HSD revealed that RTs following the 100 ms ISI were significantly slower than RTs for all other ISIs, $p < .01$. There were no significant differences between the other ISIs, however there was a pattern of faster RT as the ISI lengthened. The mean RTs for each ISI level were: '100 ms' = 268 ms, '250 ms' = 262 ms, '500 ms' = 259 ms, '750 ms' = 259 ms. Figure 14 displays mean RT as a function of contrast and ISI for one observer.

Discussion

Our results showed that responses to the RG gratings were significantly faster than responses to BY gratings, as we predicted. In addition, RTs to RG gratings were also significantly faster than RTs to RB gratings. This result confirms the advantage RG opponent-colours have over other spectral colour contrasts with respect to processing speed. As mentioned earlier, this advantage may have evolved to aid in foraging for food (Goldstein, 1996). In addition, responses to the RB grating were faster than responses to the BY grating, however, this latency difference was not significant. This finding highlights the lag the large S cone contribution creates in the BY opponent-colour system. De Valois and De Valois (1993) contended that the M and L cones provide the major contribution to the colour signal and the contribution of the S cone system is to rotate the axis into the RG and YB axes. According to the multi-stage model discussed earlier, the primary contribution to the red and green signal comes from L cones and the primary contribution to the blue signal comes from M cones. Because there is less S cone contribution, the S cone signal does not require as much time to be augmented. This results in a smaller temporal delay when these L, M and S cone signals must be combined (De Valois & De Valois, 1993).

Our results would indicate that the delay that results from augmenting the S cone signal is approximately 7 ms. However, this delay is likely longer than the delay we have demonstrated, as our stimuli did not modulate each opponent colour mechanism without causing some modulation in the other opponent mechanism. Had we been able to modulate each opponent mechanism in isolation we would have expected a larger latency difference between the responses to the RG and BY gratings. This larger latency difference would presumably be a better estimate of the timing delay caused by the underlying augmentation of the S cone signal.

The finding of longer delays following a 100 ms interval as opposed to longer intervals is in keeping with the predictions we had developed on the basis of the attentional dwell time theory. Processing the auditory tone interfered with responding to the visual target, resulting in longer RTs when the interval separating the auditory and visual stimulus was short. This finding has typically been difficult to produce in other paradigms which have used accuracy as opposed to RT as their measure of interference (e.g. Duncan et al., 1997).

GENERAL DISCUSSION

The goal of the present study was to characterize the processing of both luminance and opponent-colour defined contrast in the human visual system. Psychophysics has been adopted extensively to investigate the underlying physiology of the visual system. We used a detection task to characterize the time course of processing in the visual pathways which sub-serve the processing of suprathreshold luminance and opponent-colour signals. In addition, the role of attention in the processing of these signals was addressed as a function of its influence on response latency.

In the contrast study we attempted to establish a stable psychophysical curve of RT as a function of suprathreshold contrast. It was hypothesized that the procedure we

used would produce a RT curve similar to those generated in previous research (Felipe et al., 1993). The present experimental procedure most closely resembles that of Felipe et al. (1993) who used binocular viewing of above threshold gratings over a range of spatial frequencies. We believe that the response in our detection task reflects the pooled response of a population of neurons that respond selectively to changes in contrast. We hypothesized that these neurons fire more vigorously as the contrast in our grating stimulus increases. As the firing rate of these neurons reaches some threshold level, the contrast signal is then sent further on in the visual system where the contrast stimulus is perceived. The faster this threshold level is met, the faster the stimulus will be detected. We had predicted that even for contrast above the threshold for detection, increases in contrast would drive the neural signal above the cells' criterion level faster and would result in a shorter latency to detect the grating stimulus. Our results showed that increases in contrast above the threshold for detection did result in faster response times to the contrast gratings.

However, we hypothesized that the transition region evidenced by a break in the RT curve (as observed by Harwerth & Levi, 1978), where processing of the contrast signal moves from the sustained to the transient channel, would not be generated in the present experiment. The results of our luminance experiments were consistent with our predictions. We were not able to detect a break in the RT curve as the contrast in the grating increased. We have acknowledged several reasons why we would not be able to detect the transition of the contrast from the sustained to the transient pathway. First, the grating stimuli used presently had spatial frequency of 2 cycles per degree, which is below the range in which the transition from the sustained to the transient channel had been found (Felipe et al., 1993). In addition, we used binocular viewing conditions in the present experiment which we expected to produce faster overall RTs relative to those produced in previous work (Harwerth & Levi, 1978). Finally, in the present study we

sampled only three contrast levels which is not sufficiently fine grained to detect the transition.

The second goal of this thesis was to characterize the time course of detecting borders that are defined by differences in colour, independent of luminance. The visual system has evolved two specialized opponent mechanisms sensitive to differences in colour. These mechanisms generate opposite signals to a stimulus depending on its wavelength (Kaiser & Boynton, 1996). More specifically, we attempted to determine the temporal response properties of the BY and RG opponent mechanisms using simple RT. It appears as though the BY opponent mechanism does not receive opponent input until later stages of cortical processing relative to the RG opponent mechanism. This physical delay in establishing opponency should be apparent in terms of a temporal delay when responding to a BY versus a RG stimulus.

We anticipated that responses to a RG grating would be faster than responses to a BY grating based on the underlying physiology of these two opponent systems. Consistent with Cottaris and De Valois (1998) we expected latency differences to arise due to the need to augment the weak S cone signal. This S-cone signal is thought to rotate the colour axis into the BY and RG opponent axes. However, because of the scarcity of S cones relative to L and M cones, S cone signals must be enhanced at some point to reflect the perceptual equality of the RG and BY mechanisms (Cottaris & De Valois, 1998).

Our results showed that responses to the RG gratings were significantly faster than responses to BY gratings, as we predicted. In addition, RTs to RG gratings were also significantly faster than RTs to RB gratings. This result confirms the advantage in latency terms RG opponent-colours have over other spectral colour contrasts. As mentioned earlier, this advantage may have evolved to aid in foraging for food (Goldstein, 1996). Although the differences in RT were small, we were anticipating this

because we were not completely isolating each opponent mechanism. Although the peak wavelengths that we chose for our grating stimuli maximally stimulated the appropriate colour signal there was likely some modulation of other colour signals (Mullen, 1985). Had we been able to completely isolate each opponent mechanism we would have expected a larger gap in the latency differences between each opponent-colour system.

Finally, there was a trend for responses to the RB grating to be faster than responses to the BY grating, however this latency difference was not significant. This finding highlights the lag the large S cone contribution creates when responding to BY opponent-colour contrast. De Valois and De Valois (1993) contended that the M and L cones provide the major contribution to the colour signal and the contribution of the S cone system is to rotate the axis into the RG and YB axes. This process is hypothesized to take place beyond the LGN, at a cortical level. According to the multi-stage model discussed earlier, the primary contribution to the red and green signal comes from L cones and the primary contribution to the blue signal comes from M cones. Because there is less S cone contribution, the S cone signal will not require as much time to be augmented. This will result in less of a temporal delay when these L, M and S cone signals must be combined (De Valois & De Valois, 1993). The mechanism proposed to augment the S cone signal is a recurrent excitatory loop in which the signal from the striate cell repeatedly re-enters the cortical neuron and is summed with new signals.

One alternative explanation for the underlying cause of the latency differences between the RG and BY opponent mechanisms is a sampling bias. The relative number of cones contributing to each opponent system may have affected RTs to opponent-colour gratings in addition to the presumed latency difference arising as a result of the manner in which these cone signals are combined later on in the visual system. The neural summation of signals from the more prevalent L and M cones may have

increased the speed with which these signals were processed relative to the scarce S cones. Analogous summation effects have been observed for binocular detection tasks, relative to monocular detection tasks (Blake et al., 1980, Harwerth & Smith, 1985).

Further investigation of the relative contribution of opponent-colour and luminance contrast is needed. It would be interesting to determine whether these two forms of contrast would facilitate each other in detecting a grating which contained both luminance and opponent-colour contrast, in a psychophysical detection task like ours. Because the luminance signal is largely carried by the faster magnocellular fibers, the luminance signal may mask the benefits of opponent-colour in terms of response latency. However, the possibility exists that these systems may act together to produce a faster response latency than what would be predicted based on the functioning of each system in isolation. Recent physiological work has shown that there appears to be interactions between the luminance and chromatic pathways (Victor, Purpura & Conte, 1998). More specifically, it appears as though colour contrast facilitates processing luminance contrast.

Finally, in our investigations of both colour and luminance contrast we were interested in determining the influence of attention on response latency. From previous investigations, it has been established that the capacity of the attentional system to shift between successive events is limited by the dwell time of attention and thus by the duration of the interval separating successive stimuli (Duncan et al., 1994). The results of the present experiments supported the dwell time account of sustained attention. Consistent with this account, we found RTs to be slower when there was a short interval separating the auditory and visual stimuli. The processing of the auditory stimulus interfered with the detection of the visual stimulus when the interval separating these events was short (i.e. 100 ms). However, as the interval between the stimuli lengthened, attention was able to shift efficiently to the next stimulus and the amount of interference

was diminished. Duncan and his colleagues (1994) found the capacity of the attentional system to shift between successive visual events was limited by the duration of the interval separating the stimuli. Our findings extend this previous research by demonstrating attentional dwell in a cross-modal paradigm. We have demonstrated that the ability of attention to shift efficiently from one item to the next is restricted in cross-modal tasks, contrary to previous research (Duncan et al., 1997).

The procedure used in the present study departs from attentional dwell time studies in several ways. First, in our procedure observers were informed that the auditory signal signified that the visual stimulus would appear within a specified window of time. However, our subjects were not required to make an overt response to the tone and were asked to maintain fixation at the target location throughout the experiment. This differs from previous studies in which observers were required to make a response, usually an identification of the first of the two successive stimulus events, in addition to responding to the T2 (Duncan et al., 1994, 1997; Jolicoeur, 1999). Typically, this type of procedure has produced some evidence of interference, but not always in cross-modal tasks (Duncan et al., 1994, 1997). However, several researchers have been unable to demonstrate this interference when the first of two stimuli was ignored (Duncan et al., 1994, 1997; Jolicoeur, 1999).

The second way in which our procedure differed is that typically the interference that processing one stimulus has on processing of subsequent stimuli is measured by the percent of correct identifications of the second stimulus. Thus, the greater the number of errors, the greater the underlying interference. We argue that RT may be a more sensitive measure of the underlying interference, as we have been able to repeatedly demonstrate small (~10-30 ms) but significant increases in RT as the interval between targets decreased. We suggest that perhaps the failure to detect interference in previous cross-modal tasks requiring one response was due to the use of accuracy

which is possibly a less sensitive measure of interference. Another difference between our task and those used previously is with regards to the stimuli themselves. Previous studies have used letter, digits, symbols and syllables as targets, all of which posses some semantic meaning. Our simple tone and grating stimulus have no semantic meaning and therefore may be able to tap into a purely sensory form of interference. This difference in stimulus attributes may contribute to our ability to generate cross-modal interference where other attempts have failed.

Other procedural differences may explain the incongruent results produced using different procedures. Typically, the presentation rates of stimuli are approximately 100 ms (Chun & Potter, 1995), however the range of stimulus durations has extended from 40 to 104 ms in some experiments (Duncan et al., 1994). In our procedure, the auditory stimulus is present for 300 ms and the visual target is present until a response is made (generally 150 ms to 500 ms). This difference in presentation rates may be a factor that has led to our ability to produce cross-modal interference. In addition, in our procedure stimuli are separated by blank intervals, we did not use distractors as in the RSVP procedure or masking stimuli as in the two-target method. A monotonic pattern of interference has been repeatedly produced in investigations using the two-target method (Duncan, et al., 1994; 1997), which is consistent with our results. However, the RSVP procedure typically produces U-shaped patterns of interference (Chun & Potter, 1995; Potter, et al., 1998). Thus, it appears that using distractors or blank intervals to separate successive targets may play a role in the pattern of interference produced.

Others have argued that the pattern of interference is dependent on the task demands for each target (Potter et al., 1998). These authors have argued that the monotonic interference effect produced in attentional dwell time studies represents interference as a result of task switching and is independent of the interference termed attentional blink. Potter et al. (1998) argued that interference arising from changing the

target search characteristics produces a monotonic interference effect. The attentional dwell time effect is argued to be amodal and operates at a central level and attentional blink is argued to be purely a visual phenomenon and thus operates at a local level. Duncan et al's (1997) finding of interference when a similar response was made to both auditory targets is evidence that a task switch was not necessary and disputes the claim that attentional blink is limited to the visual modality. Secondly, our finding of interference in a task that requires only one response and therefore no task switch, to a single stream of stimuli supports the conclusion that interference can be produced in cross-modal tasks with one stream of stimuli. However, we do acknowledge that the warning tone in our task does at least cause the subject to orient to the task. This orientation must have some attentional requirements that liken it to a first response in a two-response task.

Although attentional dwell has been shown in cross-modal paradigms previously (i.e. Jolicoeur, 1999), this research had been unable to produce interference as we have shown, unless a response was made to both stimuli in succession. By measuring RT, our detection procedure is a possibly more sensitive means of investigating the dwell time of attention, which is typically studied using accuracy rates as an indication of interference. The findings of attentional dwell time in a multi-modal task were not surprising when we considered an older body of literature which was devoted to studying the influence of attention in tasks with serial stimuli.

The psychological refractory period theory received a lot of interest and research in the 1950s and 1960s (Smith, 1967). The more recent research which terms the interference in responding to the second stimulus event attentional dwell or attentional blink has focused on accuracy as opposed to the RTs investigated in the psychological refractory period literature. The findings of the attentional dwell time and psychological refractory period research are similar as they appear to be investigating the same

underlying limited capacity attentional mechanism. The psychological refractory period theory holds that when two stimuli are presented in close succession (e.g. short ISIs), typically the response to the second stimulus is prolonged (Smith, 1967). This delay in responding has been said to arise as a result of a psychological refractory period.

Several competing theories have been postulated to account for this psychological refractory period. The most accepted and supported theory is the single-channel theory which holds that there exists a mechanism with limited capacity which may become overburdened when two responses are needed within a short period of time. As such, this limited capacity mechanism is argued to be the source of the delay in responding in serial response tasks. This single-channel theory pre-dates the attentional dwell time theory and confirms what we have shown with regards to producing delays in cross-modal serial detection tasks.

The locus of the limited capacity mechanism is thought to occur at the response selection stage where two responses can not be generated simultaneously. Smith (1967) has described several mechanisms in this single channel system which explain how the delay in responding develops. First, each sensory system has a sensory input mechanism capable of storing sensory information for a short period of time. Secondly, there are several effector mechanisms which are capable of carrying out the appropriate response to the sensory information. There is a decision mechanism of limited capacity which forms a single channel between the sensory input and the response generator. This single channel is limited in the amount of stimulus information it can process at any given time. While this mechanism is processing sensory information, newly arriving sensory input is accumulated and must be held in store until the decision mechanism is free. In addition, the decision mechanism is responsible for selecting the appropriate response for the effector mechanisms which may be in the process of receiving proprioceptive information from previous responses.

This single channel system is thought to function in the following way; Kristofferson (1965) argues that the limited capacity decision mechanism has an attentional gate with stimulus information arriving via separate channels. Attention is assumed to be limited to one channel and the gate controls which channel attention will be allocated towards. The gate is argued to have a fixed periodicity which determines the delay when attention must be shifted to one of the sensory input channels. Thus, RT to the second of two stimuli will be delayed until the attentional gate is opened to that channel. It is not clear whether the gate is redirected towards the novel stimulus after the response selection has been made or after proprioceptive information from the first response has been attended to. If the latter case were true, longer delays in the second response would be expected when the first stimulus required a response than in the case when a response is not required to the first stimulus. This may explain why the delays in RTs we have reported here are not as long as those reported in some two response tasks (Smith, 1967).

Perhaps the question of whether attentional dwell time or attentional blink are amodal phenomena, which operate at a central level can be resolved by referring back to the body of research devoted to the psychological refractory period. This literature lends support to our contention that RT is a more sensitive measure of interference than accuracy. As such, it may be difficult to detect cross-modal interference in any task that uses accuracy as a measure of the interference. The use of RT in the two-target and RSVP methods may result in the ability to produce cross- modal attentional dwell or attentional blink.

In summary, presently we have characterized the processing of both luminance and opponent-colour defined contrast in the human visual system using psychophysics. We used a detection task to characterize the time course of processing in the visual pathways which sub-serve the processing of suprathreshold luminance and opponent-

colour signals. These signals aid in the detection of borders which define the world around us. In addition, the role of attention in processing these signals was addressed as a function of its influence on response latency. Attention has proven to be a significant contributor to the RT to contrast defined by luminance and opponent-colour and certainly warrants consideration in any study focusing on the temporal response properties of the visual system.

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Figure 1. Characteristics of the Magnocellular and Parvocellular Pathways.

Magnocellular Pathway	Parvocellular Pathway
• Corresponds to the Y cells of the retina and LGN (Wilson & Sherman, 1976)	• Corresponds to the X cells of the retina and LGN (Wilson & Sherman, 1976).
• Responds optimally to stimuli with low spatial frequency, rapid onset and rapid offset (Enroth-Cugell & Robson, 1966)	• Responds optimally to stimuli with high spatial frequency and low temporal frequency (Enroth-Cugell & Robson, 1966)
• Larger fiber neurons conduct impulses quickly (Ikeda & Wright, 1974)	• Small fiber neurons conduct impulses slowly (Ikeda & Wright, 1974)
• Process achromatic, luminance information (Kaiser & Boynton, 1996)	• Process signals resulting in the perception of colour (Kaiser & Boynton, 1996) and some brightness information (De Valois & De Valois, 1993)
• Large increases in neural response with increasing contrast (Livingstone & Hubel, 1988)	• Small increases in neural response with increasing contrast (Livingstone & Hubel, 1988)

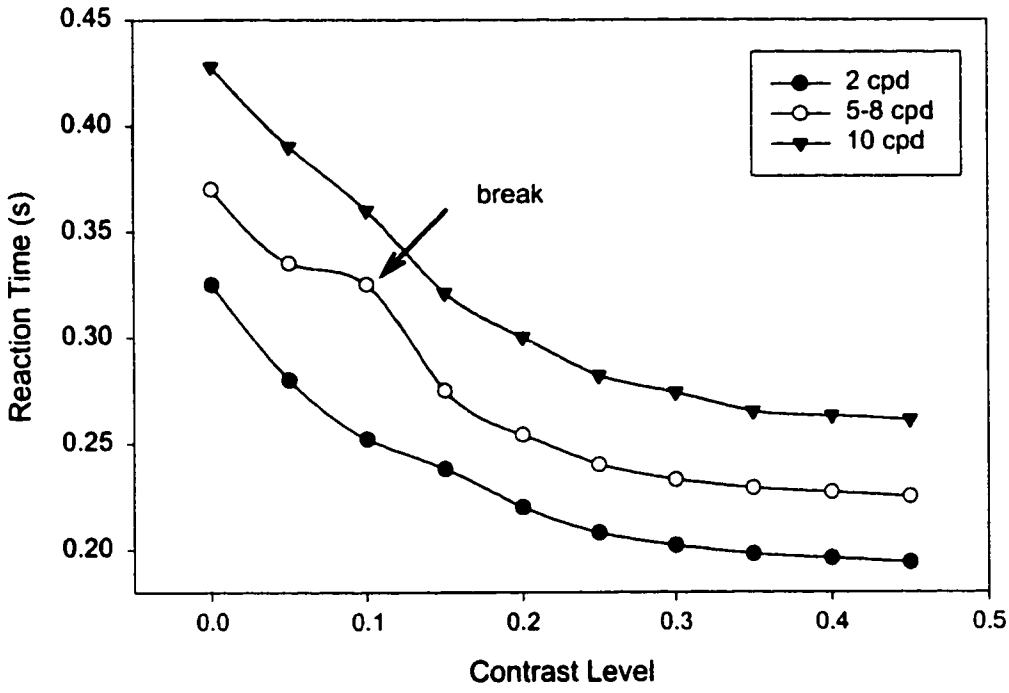

Figure 2. The Relationship between RT, contrast and spatial frequency based on the findings of Harwerth and Levi (1978), Mitov et al. (1981) and Felipe et al. (1993).

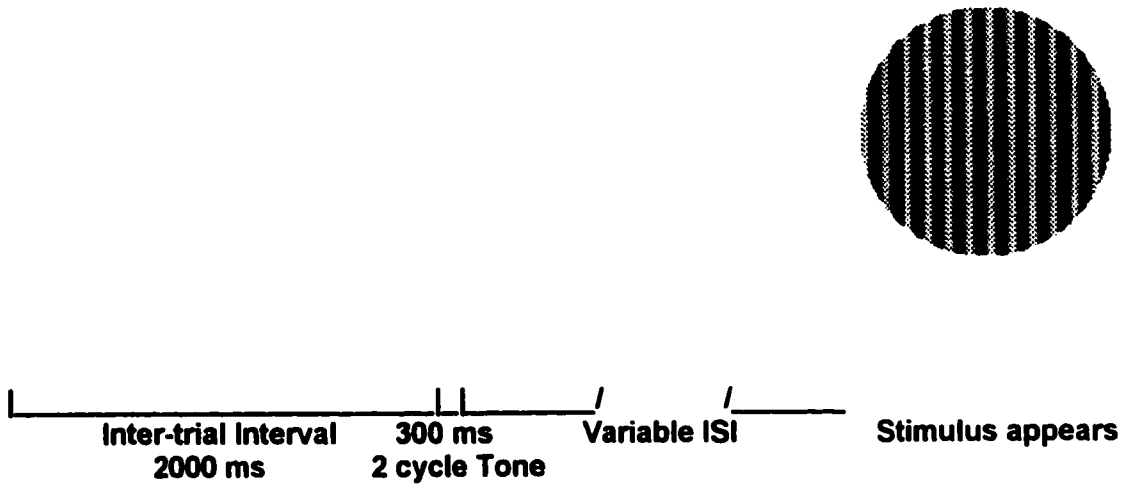

Figure 3. Timing diagram for experimental trials. The ISI levels were varied depending on the experiment.

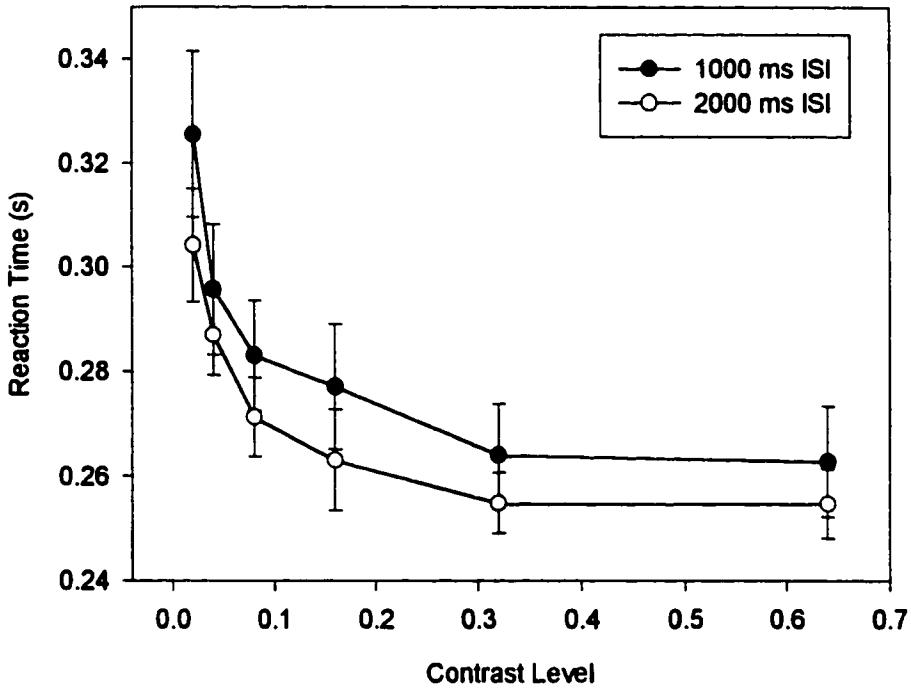

Figure 4. Group data from pilot study, depicting RT as a function of contrast and ISI. Note the slower RTs for trials with targets following the 1000 ms ISI.

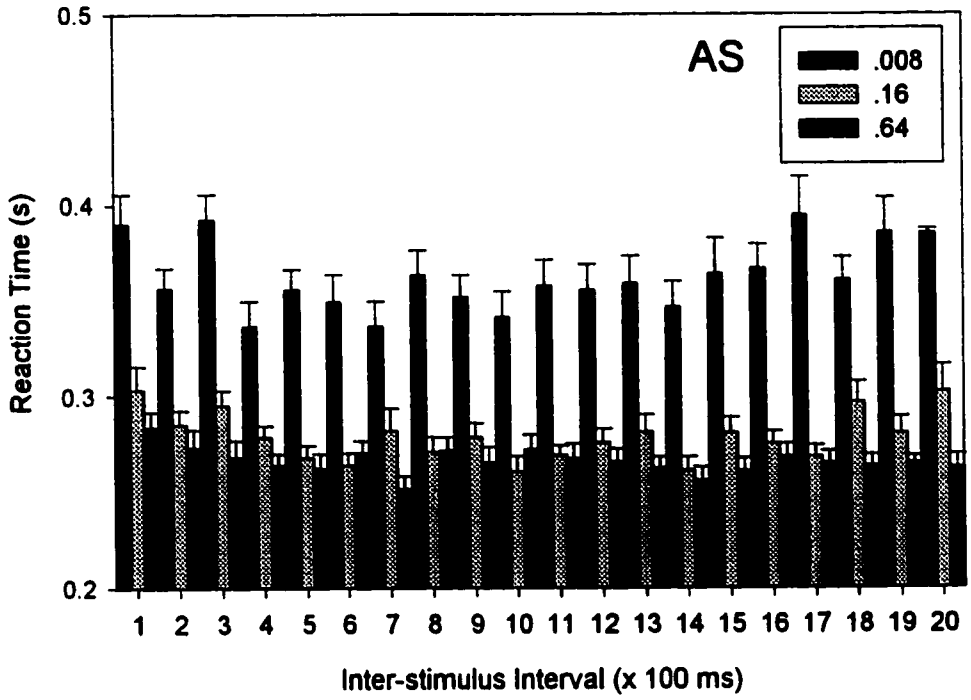

Figure 5. Results for one observer in Experiment 1. RTs were plotted for each level of ISI and contrast.

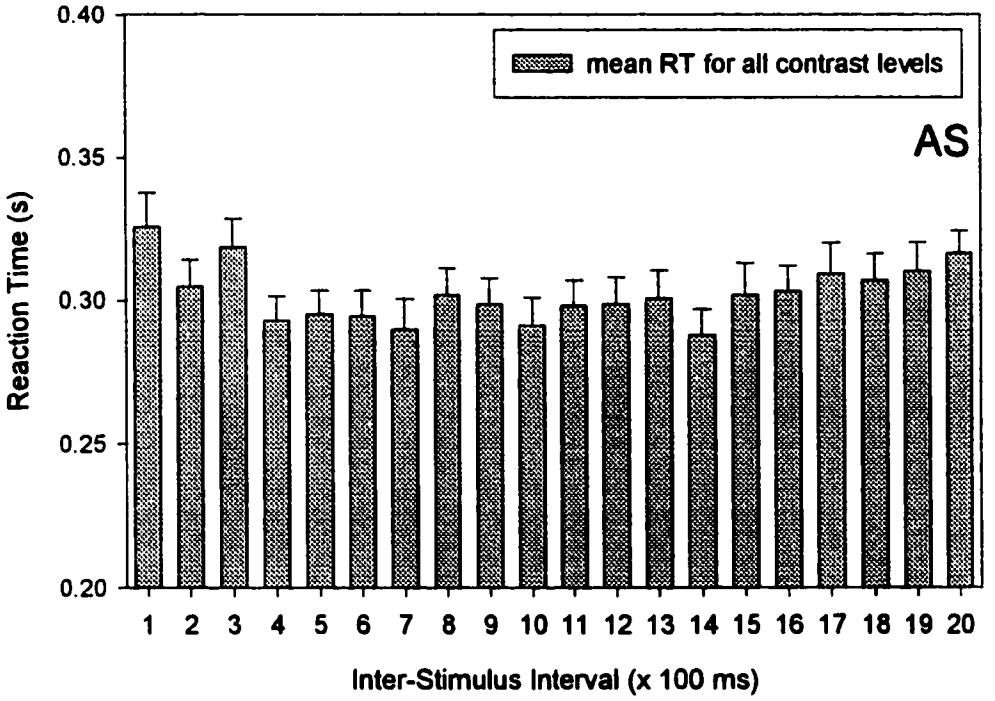

Figure 6. Results for one observer in Experiment 1. RTs were collapsed across contrast levels and plotted for each level of ISI.

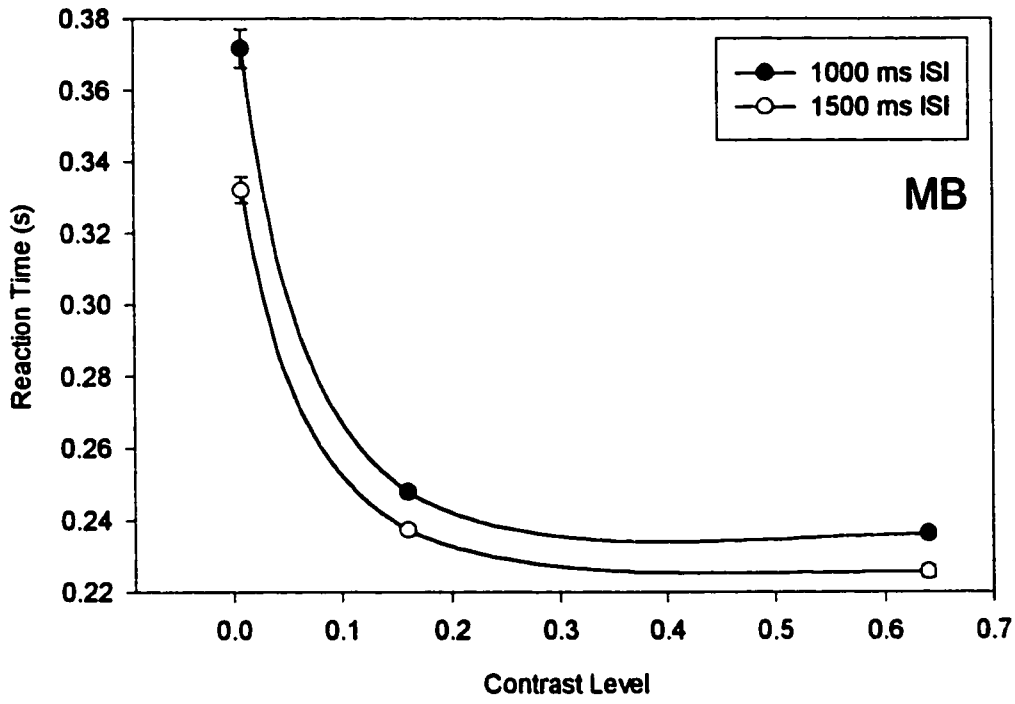

Figure 7. Data for one observer in Experiment 2, depicting RT as a function of contrast and ISI. Note the slower RTs for trials with a 1000 ms ISI.

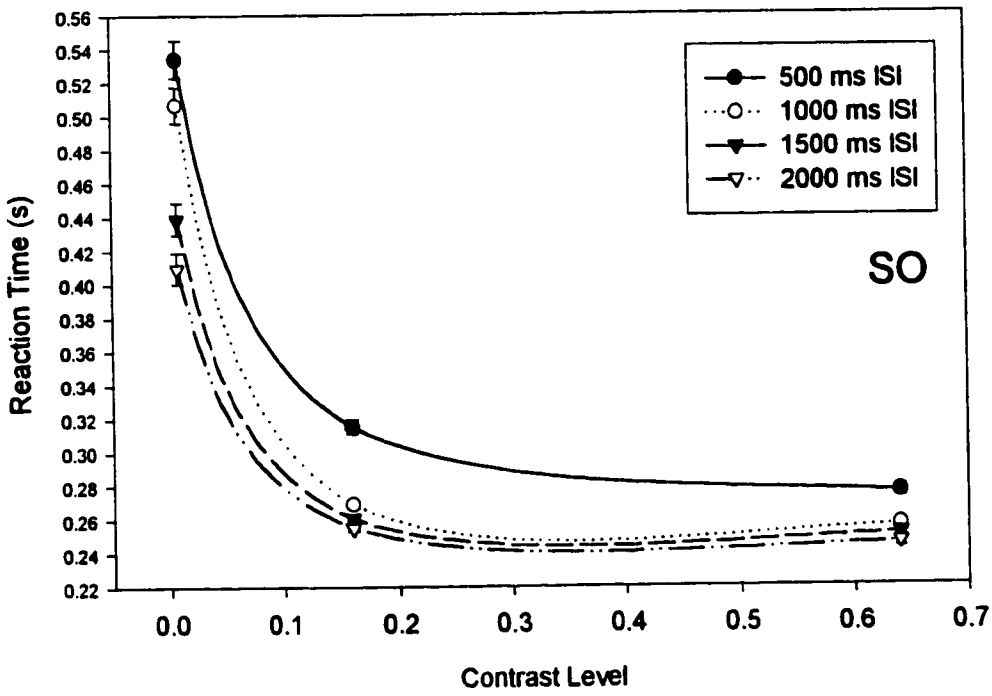

Figure 8. Data for one observer in Experiment 3, depicting RT as a function of contrast and ISI. Note the slower RTs for trials with a 500 ms ISI.

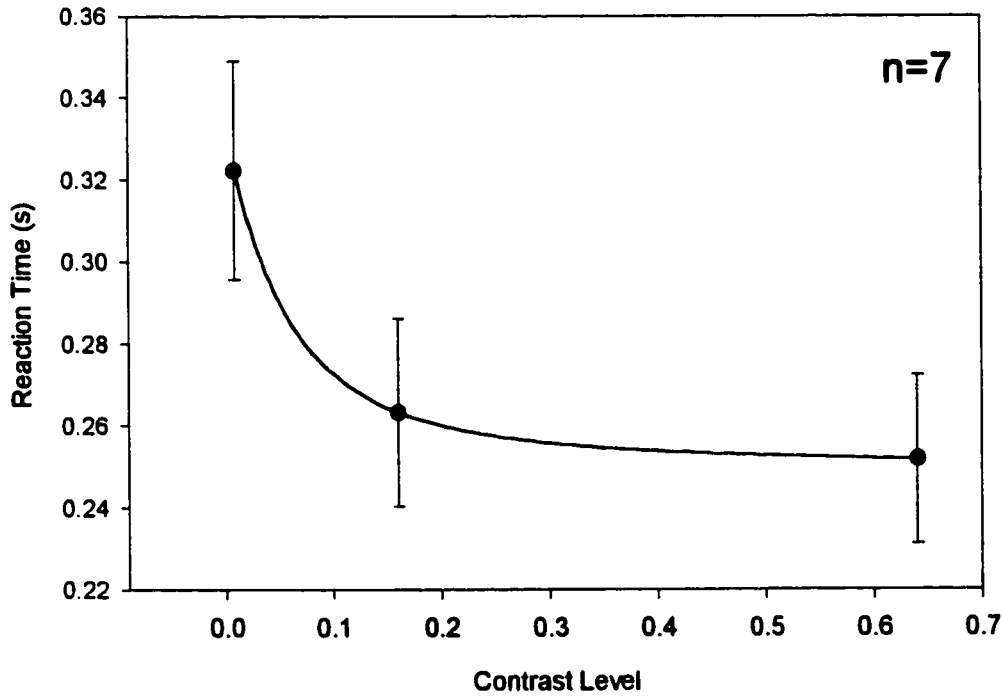

Figure 9. Group data from Experiment 4, depicting RT as a function of contrast.

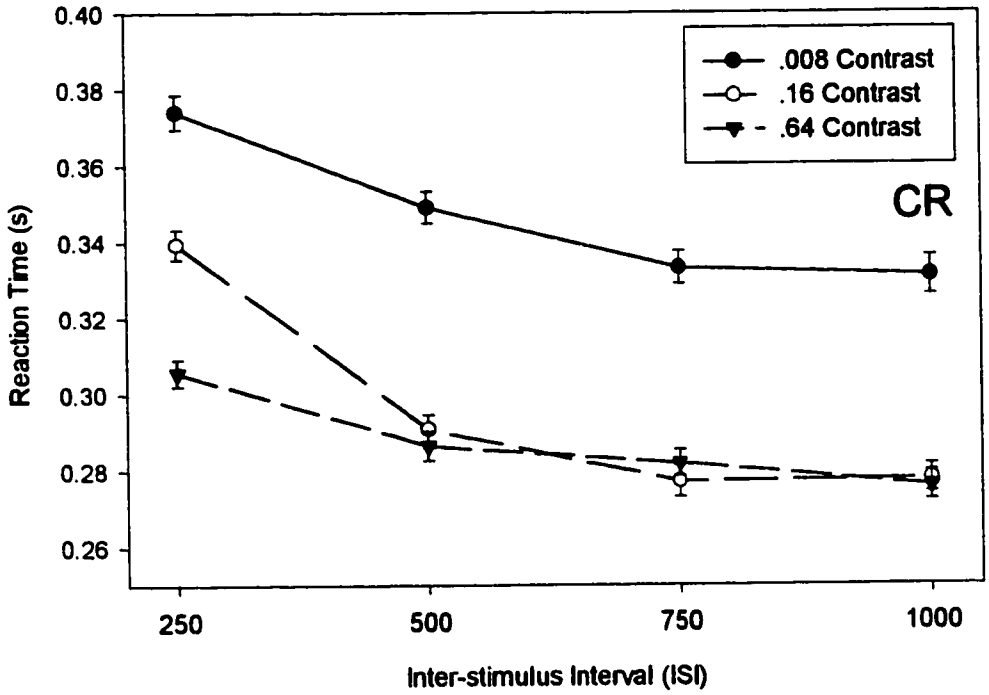

Figure 10. Data for one observer from Experiment 4, depicting RT as a function of ISI and contrast. Note the slower RTs following trials with a 250 ms ISI. This pattern of results was characteristic of all observers.

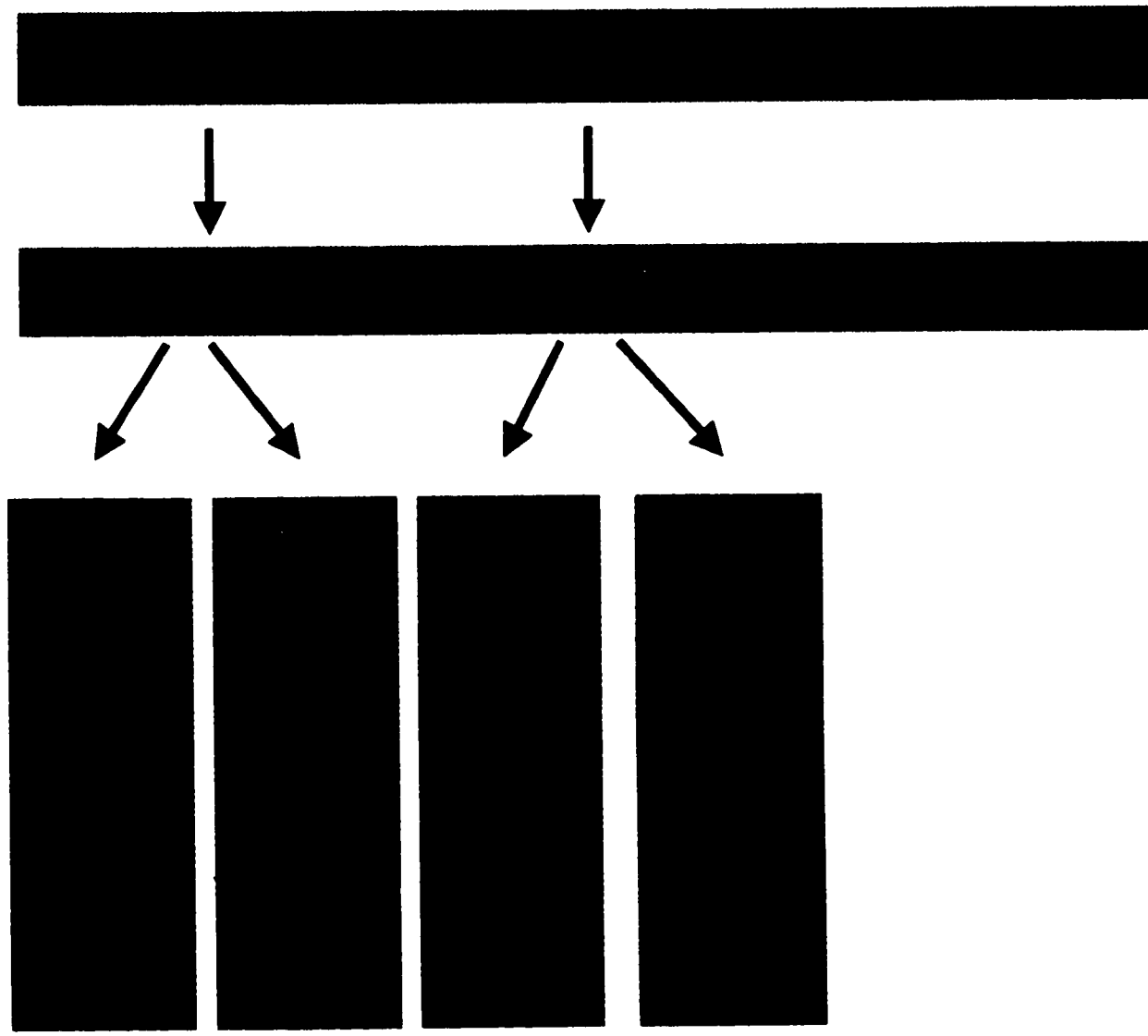

Figure 11. Diagram modified from De Valois and De Valois (1993). The arrows indicate which signals are pooled together and the "=" indicates the resulting perception.

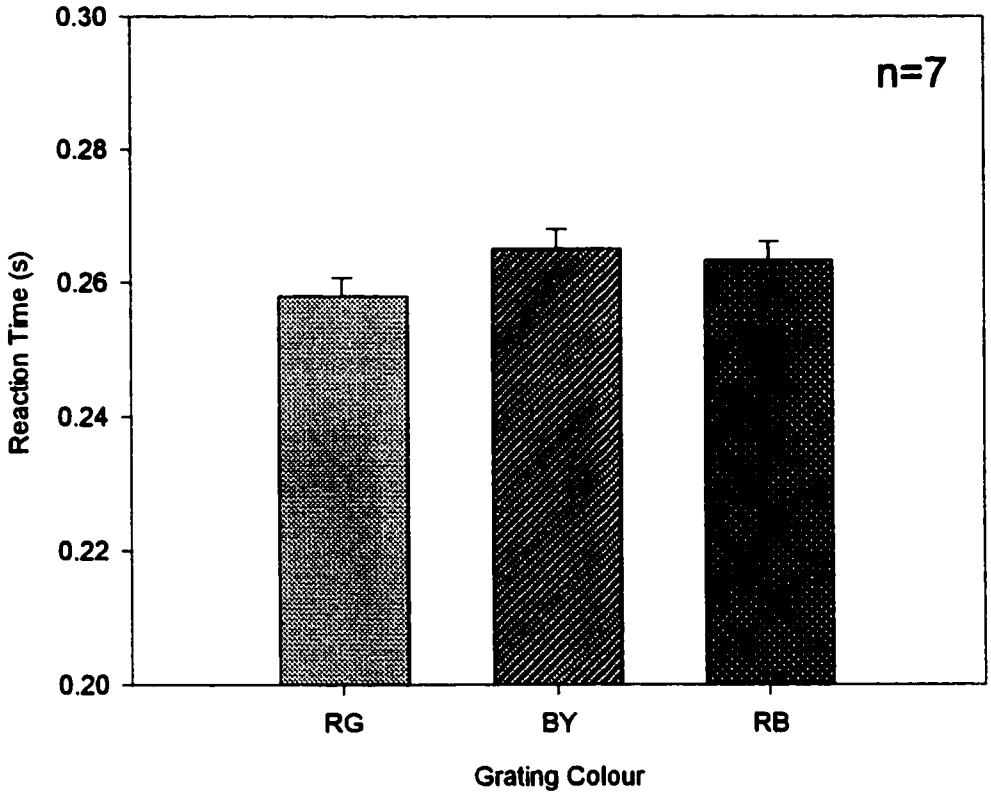

Figure 12. Group data from Experiment 5, depicting RT as a function of grating colour.

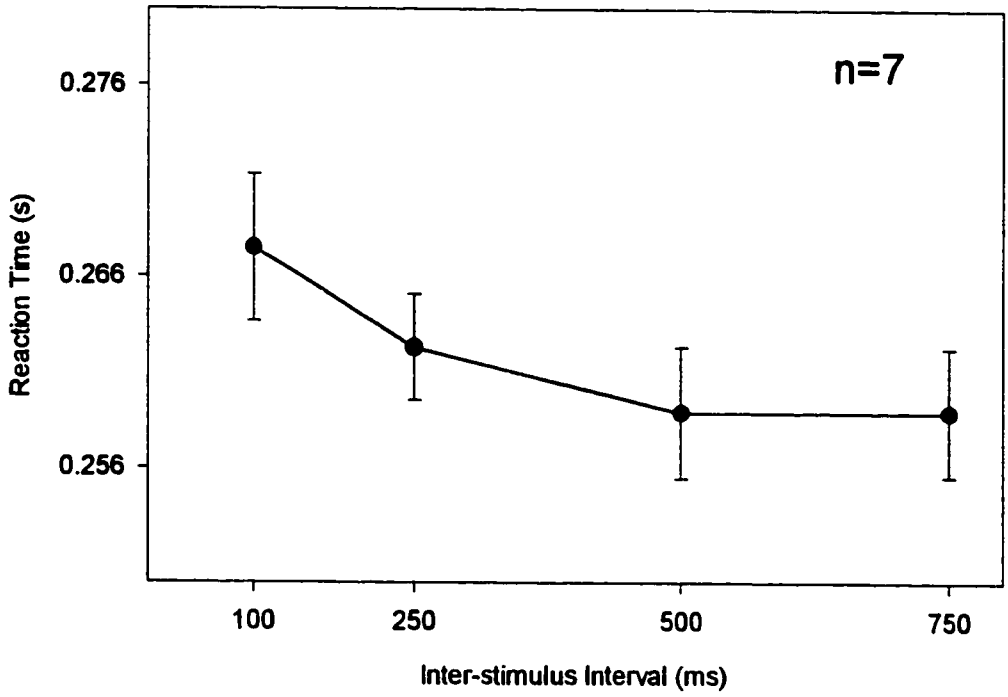

Figure 13. Group data from Experiment 5, depicting RT as a function of ISI.

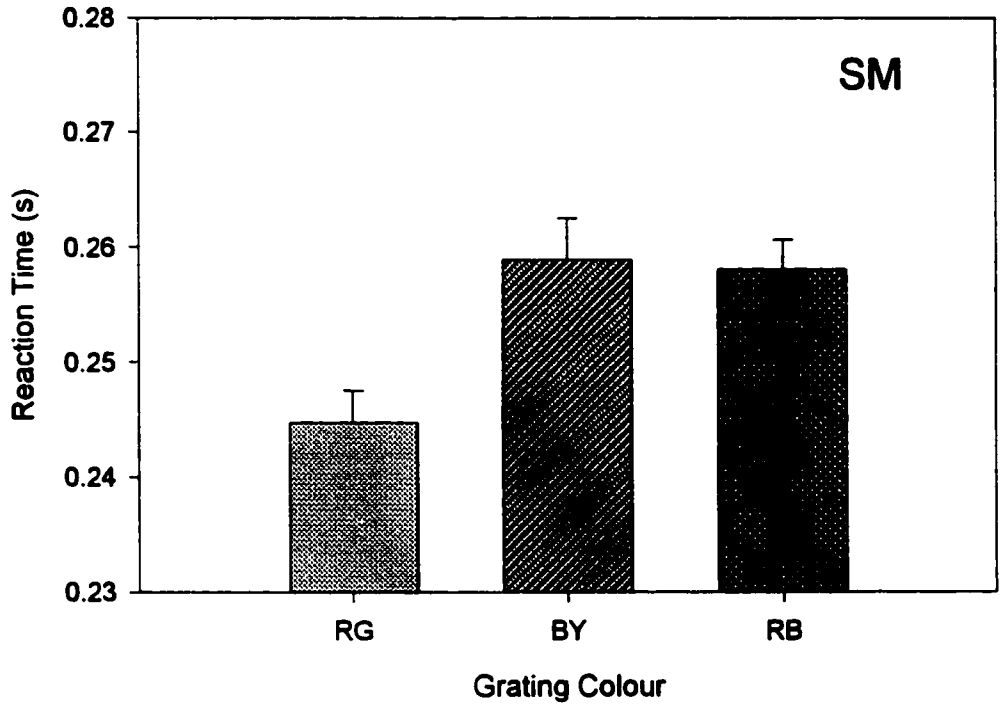

Figure 14. Data for one observer from Experiment 4, depicting RT as a function of grating colour. Note the faster RTs in trials with RG gratings. This pattern of results was characteristic of all observers.