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PHASE EFFECTS IN MONOPTIC AND DICHOPTIC TEMPORAL INTEGRATION: FLICKER AND MOTION DETECTION*

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Abstract—Observers detected two briefly pulsed sine-wave gratings presented sequentially to the same or different eyes. Gratings were separated by a range of interstimulus intervals and were related in phase by 0°, 90° or 180°. Temporal summation was found for 0° phase gratings viewed either monoptically or dichoptically. Gratings presented out of phase by 180° canceled at short intervals and summated at longer intervals under monoptic conditions but were detected independently when viewed dichoptically. With a 90° phase difference, gratings were detected independently regardless of whether they were presented to the same or different eyes. While 0° and 180° grating pairs were always detected as diffuse flicker, a strong motion percept was observed when 90° gratings were viewed monoptically but not when viewed dichoptically. In addition, observers were able to discriminate direction of apparent motion only under monoptic conditions. These results suggest that (1) the temporal response of the human visual system to briefly pulsed low frequency gratings is biphasic, (2) dichoptic temporal integration does not exist between excitatory and inhibitory components of the biphasic response, and (3) flicker is detected by mechanisms which receive only excitatory input while motion sensitive mechanisms require an interaction between excitation and inhibition from spatially adjacent loci.

INTRODUCTION

The complex scenes viewed in everyday life are not static but change as time passes. In order for these changes to be perceived, the human visual system must possess limited ability to integrate information over time. One method used to investigate the temporal properties of visual mechanisms is the two-pulse threshold, first employed by Granit and Davis (1931). They measured thresholds for detection of two briefly pulsed flashes of light as a function of the interval between them. When interflash interval was short, temporal summation was demonstrated by a lowered threshold for detection of the first pulse in the presence of the second, subthreshold flash. The facilitative effect of the second flash diminished with longer separation until a point was reached when the second flash had no effect on detection of the first. This presumably marked the limit of the temporal integration capability of the visual system. Subsequent studies (Ikeda, 1965; Rashbass, 1970) replicated and extended these results to include the more general case of temporal integration between pulses of like polarity (two increments or two decrements) and between pulses of opposite polarity (an increment and a decrement). These studies found that the visual system can integrate opposite polarity pulses as well as like polarity pulses. However, intergration of opposite polarity pulses followed a different time course, providing evidence for inhibitory as well as facilitory interactions. Light and dark spots contain broad-band Fourier spectra with identical components but with the phase of the components shifted by 180°. Watson and Nachmias (1977) performed an analogous two-pulse detection experiment with narrow-band stimuli, i.e. sine-wave gratings related in phase by 0° or 180°. They found results similar to those reported by Ikeda and Rashbass with test gratings of low spatial frequency while high spatial frequency gratings produced evidence only for facilitative interactions.

Other studies (Matin, 1962; Thorn and Boynton, 1974) have investigated whether temporal integration exists between like polarity pulses when each is presented to a different eye. Two distinct mechanisms could produce a superiority in binocular relative to monocular sensitivity. First, sensitivity would be expected to increase if a central neural mechanism summated inputs from the two eyes. Second, even when neural summation is absent and each eye acts independently, binocular sensitivity should be greater than monocular sensitivity due to probability summation (Pirenne, 1943). The relative importance of each of these factors in the superior sensitivity exhibited under binocular viewing is difficult to evaluate because different statistical models of probability

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summation make different assumptions about how the detection process operates (Blake and Fox, 1973; Thorn and Boynton, 1974). Rather than rely on statistical models for evaluating probability summation, Matin (1962) suggested an empirical method. Observers viewed two pulses separated by various intervals and presented to the same or different eyes. Matin reasoned that when flashes were far enough apart to be detected independently, sensitivity should be greater than for a single pulse due to the extra opportunity to detect the second flash. Temporal integration of flashes presented to the two eyes would be evidenced by an increase in sensitivity beyond this empirically determined probability summation baseline. Matin found that dichoptically presented light increments exhibited temporal integration similar to that found in monocular situations. No analogous measurements have been made with opposite phase test stimuli.

The purpose of the present experiment was to evaluate the effects of stimulus phase on the temporal integration characteristics of monoptic and dichoptic mechanisms in the human visual system. This was accomplished by determining sensitivity to pairs of sine-wave gratings with different spatial relations in a two-pulse paradigm. In all of the studies cited above, the authors reported that at threshold test stimuli produced the sensation of diffuse flicker. It may be assumed, therefore, that these experiments were investigating temporal integration in flicker sensitive mechanisms. We have extended these studies by measuring thresholds for monoptically and dichoptically presented test gratings of the opposite (180°) as well as same (0°) phase. When sensitivity was compared to an empirically-determined probability summation baseline, it was found that central flicker sensitive mechanisms can only integrate stimuli of the same phase. Temporal integration properties of motion sensitive mechanisms were also studied by employing test gratings related in phase by 90°. It was found that mechanisms which detected the apparent motion of these gratings exhibited integration only under monoptic conditions and motion percepts could not be obtained with dichoptic viewing. Results of these experiments are interpreted in terms of a model which suggests differences in the properties of mechanisms underlying flicker and motion perception.

EXPERIMENT I METHOD

Observers

Two observers, MG and JM, participated in the study. Only MG had knowledge of the purpose of the experiment. Both have normal acuity and good stereopsis.

Apparatus

Observers viewed two matched CRT screens, one with each eye, by means of a mirror haploscope. Details of the apparatus have been published elsewhere (Blake and Cormack, 1979). To aid in fusion, two steps were taken. First, both screens were masked down to a 5° circle (when viewed at 114 cm) with black surrounds which could be easily fused. Second, the center of each screen contained a small circle which was 15' dia with a width of 1.2', to further aid in fusion, accommodation, and fixation. Neither observer reported any difficulty in maintaining fusion. Stimuli were pairs of vertical sine-wave gratings generated by the standard television technique. Sine-wave gratings were used as test targets because stimuli such as spots contain a wide range of spatial frequency components. Since high and low frequencies are not processed with the same time course (Watson and Nachmias, 1977), different components could be used for detection under different temporal conditions. We further limited ourselves to a low spatial frequency, 0.75 c/deg, since the possibility of vergence errors make it difficult to realistically specify the phase relation of dichoptically presented gratings of high spatial frequency. On the basis of Watson and Nachmias (1977), it might be expected that use of higher spatial frequency gratings would have led to different results. Gratings were pulsed on without change in mean luminance of 7 cd m^{2} for one raster sweep (nominally 5 msec). The members of a pair of gratings were presented sequentially with a range on interstimulus intervals (ISI's) consisting of an integer number of sweeps. Since there was 1 msec between sweeps, the shortest possible ISI was 1 msec and all others were multiples of 6 msec (5 msec sweep plus 1 msec delay).

Procedure

Members of a pair of gratings were presented sequentially, either monoptically or dichoptically. The relative spatial phase between first and second gratings was 0°, 90° or 180°. Great care was taken to ensure that the alignment of phase between dichoptically presented gratings was as precise as possible. This was accomplished by presenting the test gratings steadily prior to each session and instructing the observer to shift the phase of one of the gratings until the fused target appeared in exactly the same plane as the surround. This presumably minimized the disparity between the dichoptically presented gratings and promoted stimulation of corresponding retinal points. The 90° and 180° conditions were then obtained by electronically shifting the phase of the second grating.

Grating pairs were presented every 3 sec following a 700 msec warning tone. The observer controlled contrast of the gratings (members of a pair were always of equal contrast) with a featureless knob. As a control condition, trials were also programmed in which only the first grating was presented. A threshold setting was recorded when an inhomogeneity could be detected on the screen in half the trials. Observers could view the stimuli as many times as desired to make the judgment. Data shown are the mean of four threshold determinations for MG at each condition, and two to six judgments for JM.

RESULTS

Figure 1 shows thresholds for the detection of grating pairs with a 0° phase difference. Sensitivity is greatest at the shortest ISI in both monoptic and dichoptic conditions. For both observers monoptic sensitivity at ISI = 1 msec is about twice that for very long intervals, indicating complete temporal summation. For the two observers, monoptic presentation produced thresholds greater by factors of 1.5 and 1.39 than those obtained under dichoptic viewing. This measure of binocular summation agrees well with previous estimates (see Blake and Fox, 1973). As ISI is lengthened, sensitivity decreases and monoptic and dichoptic thresholds converge. However, at an ISI of 61 msec, monoptic thresholds show a slight dip. This effect is small but consistent with previous reports (Watson and Nachmias, 1977; Breitmeyer and Ganz, 1977). At the longest intervals, both monoptic and dichoptic sensitivities asymptote at a level slightly greater than that of single gratings. Presumably, the gratings were detected independently, but the increased likelihood of detection produced by probability summation (Matin, 1962) made the grating pair slightly more detectable than single gratings.

Figure 2 shows results for detection of 180° out-of-phase gratings. The pattern of results for monoptic and dichoptic presentation is radically different. Data from the monoptic condition resemble those of previous studies in which observers detected sequentially presented out-of-phase gratings (Watson and Nachmias, 1977) or light and dark spots (Ikeda, 1965; Rashbass, 1970). At short ISI's there is cancellation between 180° out-of-phase gratings so that sensitivity is far below that for single gratings. In fact, observers were unable to detect the test target at maximum available contrast (40%) at the shortest ISI. As the interval between gratings is lengthened, sensitivity improves until it reaches a level greater than that for single gratings or for the probability summation baseline. At the longest ISI's, sensitivity finally drops to a level slightly above that of single grating. Under dichoptic presentation, however, sensitivity remains constant at the probability summation level regardless of ISI, suggesting that there is no neural integration between inputs from the two eyes.

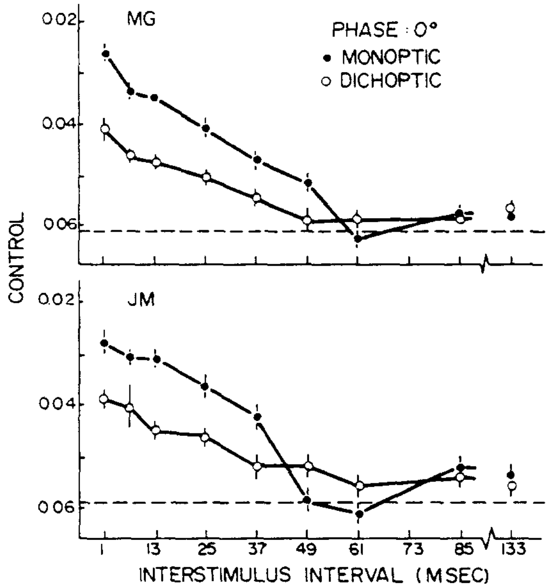

Fig. 1. Contrast thresholds for detection of 0° phase related gratings as a function of interstimulus interval. Closed circles represent data for monoptic conditions and open circles for dichoptic viewing. The horizontal dashed line indicates threshold level for detection of the first grating alone. Contrast was calculated as $(L_{max} - L_{min})/(L_{max} + L_{min})$. Vertical bars show ±1 SE. Where no bars are shown, the standard error is smaller than the data point. Observers: upper panel, MG; lower panel, JM.

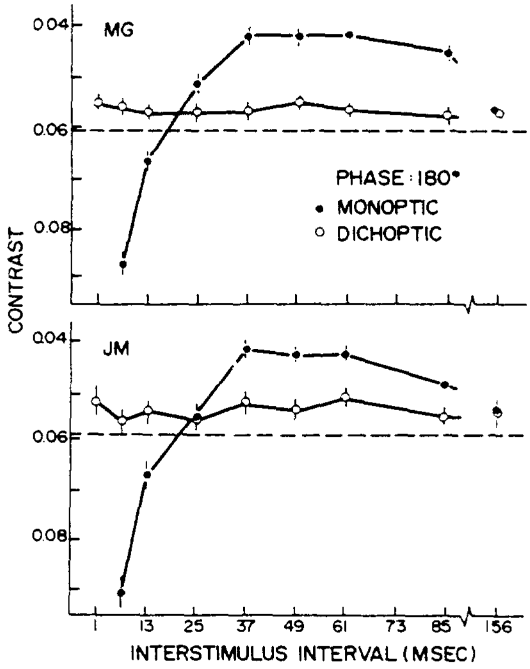

Fig. 2. Contrast thresholds for detection of 180° phase related gratings as a function of interstimulus interval. All other details are the same as described in Fig. 1.

A linear summation of two gratings out of phase by 90° produces a third grating of the same spatial frequency but shifted in phase and with an amplitude 1.4 times that of the individual gratings. Therefore, this grating should be 40% more detectable than a single pulse (assuming that phase of the grating with respect to the display edges is not critical). Figure 3 shows data for detection of sequentially presented gratings separated in phase by 90°. The prediction of linear summation fails even at the shortest ISI. Both monoptic and dichoptic sensitivity remain constant at a level suggesting only probability summation and no neural integration. At middle intervals, monoptic sensitivities exhibit a slight rise. However, a second experiment employing a two-alternative forced-choice paradigm showed that monoptic and dichoptic gratings were about equally detectable (see below). In order to determine whether the departure of the data from the simple linear summation prediction might be due to the phase shift resulting from the addition of the two tests gratings, observations were made with gratings shifted by various degrees with respect to the display edges. Results confirmed that position of the grating within the circular surround had little effect on sensitivity. These data indicate that, even under monoptic presentation, gratings separated by 90° were detected independently.

Both observers reported that they could not discriminate whether 0° or 180° phase related gratings were employed. At threshold, only a structureless flicker was detected. As reported by Watson and Nachmias (1977), perception of vertical striations required higher contrast. Rashbass (1970) noted that his observers detected flicker at threshold and could not discriminate between increments and decrements. We also found that when 0° and 180° grating pairs were employed it was not possible to determine whether one or both eyes were being stimulated which indicates a failure of utrocular discrimination (Blake and Cormack, 1979). Although 90° out-of-phase grating pairs were about equally detectable whether presented monoptically or dichoptically, observers could easily discriminate which condition was being tested. It was noted that monoptic presentation produced a vivid motion perception. However, when gratings were presented dichoptically, only flicker was seen. A second experiment systematically investigated this difference in monoptic and dichoptic percepts by requiring observers to rate strength of apparent motion and to discriminate its direction.

EXPERIMENT II—METHOD

Apparatus and stimuli were the same as those employed in the first experiment, except that stimuli were set to a contrast 0.3 log unit above threshold. Two gratings were presented 90° out of phase 1 sec after the observer pressed a switch. The task was to rate strength of apparent motion produced by the sequentially pulsed gratings. This was accomplished by means of a 5 point rating scale with a rating of 1 indicating no seen motion and 5 signifying most vivid motion. Grating pairs were presented in quasirandom order with respect to ISI, direction of the 90° phase shift, and whether monoptic or dichoptic presentation was used. In addition to trials with pairs of gratings, single gratings were presented on occasion. Data shown are the mean of eight ratings for each condition.

In separate sessions, observers were simply asked to state direction of phase shift. When observers reported translations in the direction of the 90° phase shift, the response was considered correct. Data are based on a minimum of 50 trials at each ISI for monoptic and dichoptic presentation.

Of the two observers serving as subjects, one (JM) had participated in the first experiment. Neither had knowledge of the purpose of the experiment.

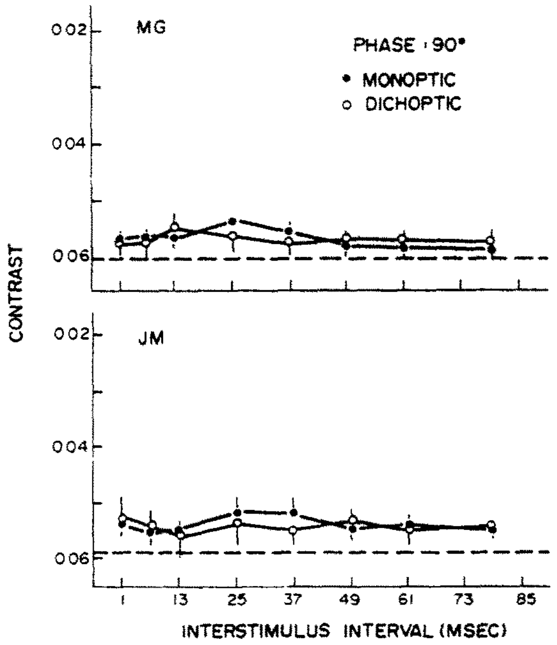

Fig. 3. Contrast thresholds for detection of 90° phase related gratings as a function of interstimulus interval. All other details as described in Fig. 1.

RESULTS

Ratings of the strength of apparent motion are shown Fig. 4. It should be remembered that rating procedures produce only ordinal scale data. This means that a rating of 4 does not necessarily signify a percept twice as strong as one indicated by a rating of 2. Although this method can reveal the general relationship between ISI and strength of apparent motion, the precise form of the obtained curves should not be taken too literally.

In monoptic conditions, apparent motion is seen readily at short ISI's with strongest percept at intervals of 13–25 msec. At separations of 60 msec and longer, however, flickering stripes rather than motion were seen. Under dichoptic presentation, virtually no apparent motion was reported; the very low frequency of such reports was similar to those for single grating presentations. Apparent motion seen under these circumstances may have been due to eye movements during the trial. The apparent motion percept produced by the monoptically presented gratings was that of a single grating which appeared to pulse on and then "bleed" or "smear" in the direction of the 90° phase shift. This perception was quite different from one of a grating simply appearing to change

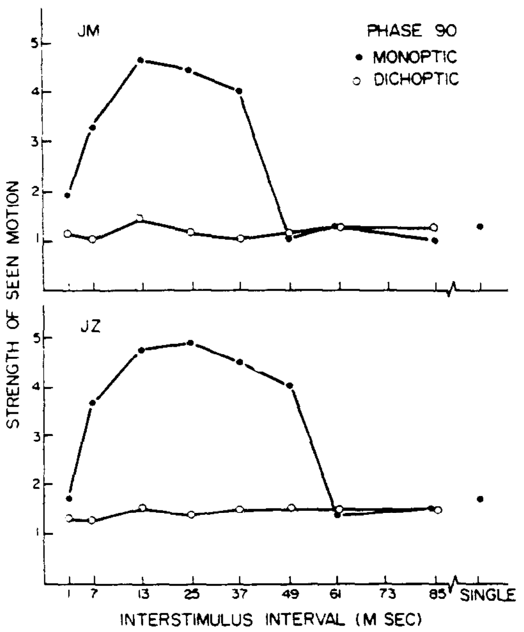

Fig. 4. Strength of apparent motion with 90° phase related gratings as a function of interstimulus interval. A ranking of 5 indicates strongest motion percept while 1 indicates no seen motion. Closed and open circles represent data for monoptic and dichoptic conditions, respectively. Observers: upper panel, JM; lower panel, JZ.

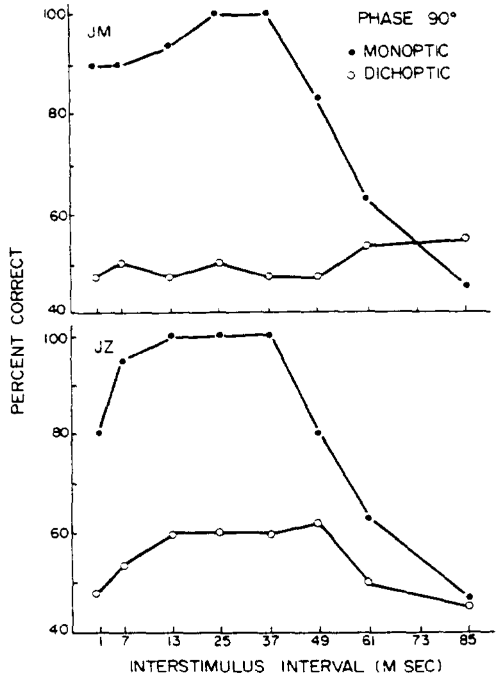

Fig. 5. Percent correct in detection of 90° phase shift as a function of interstimulus interval. Closed and open circles represent monoptic and dichoptic conditions, respectively. Observers: upper panel, JM; lower panel, JZ

position. The bleeding sensation was not seen under dichoptic conditions, where only flickering bars were observed.

While the rating experiment confirmed that motion was seen only under monoptic viewing, it did not answer the question of whether (1) observers were unable to detect a phase shift under dichoptic conditions or (2) the phase shift could be seen but no motion sensation resulted. We therefore performed a second experiment in which observers were required to discriminate direction of the phase shift, using any clues available. Data for this experiment are shown in Fig. 5. Both observers in monoptic conditions showed a good ability to discriminate at short intervals, perfect performance at intermediate intervals and chance performance at longer intervals. Under dichoptic presentation, observer JM was totally unable to discriminate direction of the phase shift. Observer JZ, however, showed performance slightly but reliably above chance at intermediate ISI's. This observer reported that dichoptic judgments were based on a different criterion than that used in monoptic trials. Whereas the smearing sensation was used for monoptic presentation, dichoptic judgments were based on a vague impression of positional translation of the bars rather than on a motion percept.

In the experiments reported above, phase shift discrimination was tested with gratings of fixed contrast slightly above threshold. In an additional experiment, JM was tested for direction discrimination as a func-

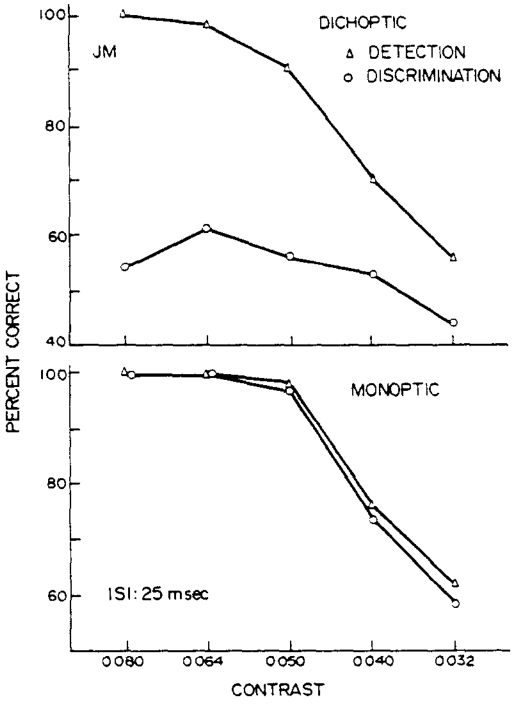

Fig. 6. Percent correct in detection and discrimination as a function of test grating contrast. Triangles represent simple detection of which of two intervals contained the test gratings. Circles represent detection of direction of the 90° phase shift. Upper panel shows results for dichoptic conditions and the lower panel, monoptic conditions. Observer: JM.

tion of grating contrast. A series of two alternative forced-choice trials were run with gratings separated by 25 msec. On each trial the observer reported whether the gratings appeared in the first or second interval as well as direction of phase shift. Results for this experiment are shown in Fig. 6. In both monoptic and dichoptic conditions, ability to perform detection and discrimination declined with lower test contrast. Detection sensitivity was similar in monoptic and dichoptic presentation. Under monoptic conditions, ability to discriminate direction was about as good as the ability to simply detect presence of the gratings, suggesting that the motion sensitive mechanism was operating at detection threshold for the test gratings. In dichoptic conditions, detection was always better than discrimination, which was near chance performance.

We also made several control observations to ensure that the failure to induce apparent motion under dichoptic conditions was not due to a vergence error. In order to mimic the effects of such an error, observers viewed sequentially pulsed gratings related in phase by 80° and 100°. In addition, tests were made with a lower spatial frequency grating (0.375 c/deg) in order to further minimize the effects of vergence errors. None of these changes altered the pattern of results reported above. Grating duration was also varied up to 50 msec. Although longer duration gratings had much higher apparent contrast, apparent motion was still not seen under dichoptic conditions nor could direction of the phase shift be readily determined.

The present experiment differs in two ways from previous studies which found dichoptically induced apparent motion. First, we employed low frequency sine-wave gratings. Second, in most previous studies, stimuli were presented to different retinal points in the two eyes while our observers viewed stimuli that overlapped in space. To test whether it was ever possible to obtain a perception of apparent motion with dichoptically presented sine-wave gratings, the display was altered so that one grating was presented to the left half of the CRT screen viewed by one eye and a second grating was subsequently presented to the right half of the screen viewed by the same or contralateral eye. In this case, the gratings did not stimulate corresponding retinal areas. Observers reported vivid motion percepts of about equal strength under monoptic and dichoptic conditions. The percept was that of a single grating which appeared to jump across the screen and no smearing was seen.

DISCUSSION

Flicker detection

The monoptic pattern of results obtained with 0° phase grating pairs can be summarized as follows: (1) summation at short interstimulus intervals, (2) cancellation at intermediate intervals, and (3) independence at long intervals. This pattern is consistent with results obtained in previous studies (Ikeda, 1965; Rashbass, 1970; Watson and Nachmias, 1977) Breitmeyer and Ganz (1977) found results similar to ours at short and intermediate ISI's. At long intervals, however, they found sensitivity to grating pairs was slightly less than for single gratings. The reason for this disparity in data is not clear. Results for 180° out-of-phase gratings are summarized as (1) cancellation at short intervals, (2) summation at intermediate intervals, and (3) independence at long intervals. These results have been previously explained (Ikeda, 1965; Rashbass, 1970; Watson and Nachmias, 1977) by assuming that the temporal response to each stimulus is biphasic with a fast component of one sign followed by a slower component of the opposite sign. For example, Ikeda (1965) suggested that stimuli of opposite phase produce biphasic temporal responses of opposite phase. A light spot produces a positive response followed by a slower negative response while a decrement first produces a negative response followed by a positive component. At short ISI's in-phase stimuli would produce temporal responses which summate but out-of-phase stimuli produce temporal responses which cancel. At longer ISI's, however, the opposite would be true. This explanation is consistent only with the data we obtained under monoptic viewing. Dichoptically presented in-phase gratings summated at short interstimulus intervals but failed to cancel at intermediate separations. Further, 180° gratings failed to exhibit cancellation at any interval. This result suggests a neural mechanism which integrates like sign components of the biphasic temporal response from the two eyes. On the other hand, the independent detection of out-of-phase gratings suggests the absence of an analogous mechanism for the integration of response components of different sign. This explanation is supported by a previous study (Johnson and Enoch, 1976) in which "transient-like" functions were measured with test stimuli consisting of a center and surround presented to the same or different eyes. Antagonistic inhibitory influence of the surround on the center was found only when both were viewed with the same eye. This failure to find integration between excitatory and inhibitory temporal response components is consistent with our failure to find cancellation between 180° out-of-phase gratings or dichoptic motion perception.

Failure to find interaction between steadily presented stimuli with 180° phase differences has previously been reported. Westendorf and Fox (1974) and Bacon (1976) both concluded that out-of-phase stimuli are detected independently by each eye. However, Blake and Levinson (1977) found similar subthreshold summation between dichoptically presented gratings, whether in or out of phase. Their result may have been due to the use of higher spatial frequency gratings. With the use of narrow stripes, small vergence errors could bring stimuli back in phase. A large number of studies have investigated whether binocular interaction occurs between spots of light flickering in or out of temporal phase (Sherrington, 1904). Cavonius (1979) measured the temporal modulation transfer function for spots flickering in phase, in counterphase or with one eye receiving a steady field matched in mean luminance to the flickering test spot presented to the other eye. When lights were flickering temporally in phase, they were spatially in phase (both light or dark) and when temporally out of phase, they were also spatially out-of-phase (one light and one dark). It was found that at high flicker rates sensitivity to in-phase spots was higher than to out-of-phase spots. However, out-of-phase sensitivity was about the same as sensitivity measured when one eye received a steady field. This result is consistent with ours in demonstrating that the greater sensitivity to in-phase stimuli was due to summation between these stimuli rather than to cancellation between out-of-phase stimuli.

Other data, however, suggest the existence of a mechanism capable of integrating opposite phase stimuli from the two eyes. At low flicker rates, Cavonius found a true cancellation between his dichoptically-presented out-of-phase spots. Cohn and Lasley (1976) reported that small foveally viewed increments and decrements cancelled when presented dichoptically. In both of these experiments, binocular cancellation was found under conditions favoring detection by a sustained rather than a transient mechanism.

Motion perception

While flicker sensitive mechanisms showed strongest integration (cancellation or summation) with the shortest separation between pulses, optimal apparent motion was seen at ISI's ranging from 13–37 msec. Previous studies (Van Nes, Koenderink, Nas and Bouman, 1967; Richards, 1971) have also reported that flicker is seen at higher temporal frequencies than is motion.

Earlier studies of apparent motion under dichoptic presentation (Shipley *et al.*, 1945; Ammons and Weitz, 1951) have reported that motion percepts are readily obtainable. In these studies, stimuli were flashed to non-corresponding regions on the two retinae. Several more recent studies have found that when stimuli share corresponding areas in the two eyes, dichoptic motion percepts may be altered or even absent. Braddick (1974) found that motion could be seen in sequentially presented random dot stereograms only when both stimuli were presented to the same eye. Pantle and Picciano (1976) employed a display which produced two distinct motion percepts. While both could be obtained monoptically, one could never be seen with dichoptic viewing. These and other results have led several authors (Braddick, 1974; Anstis, 1978) to postulate the existence of two different motion sensitive mechanisms in human vision. A "long range" system detects motion of stimuli displaced across large retinal distances and operates whether stimuli are presented to one or separate eyes. Since this system can detect motion even when stimuli are presented to the monocular crescent of each eye (Smith, 1948), no local neural interaction seems required for its operation. A second, "short-range," system detects sequentially presented (or continuously moving) stimuli separated by no more than 10′–15′ and operates only when stimuli are viewed monoptically. Unlike the long range system, this motion sensitive mechanism requires local neural interaction. Presumably the short range system signaled the motion produced by sequential presentation of the 90° out-of-phase gratings. However, a 90° phase shift of 0.75 c/deg gratings amounts to a 20′ translation in space. Further, we found similar results with 0.375 c/deg gratings with a 90° phase shift represents a 40′ movement. Considering the size of these movements, it is somewhat misleading to call this a "short range" system. The "short range" system may actually operate over a fixed phase range rather than a fixed retinal distance (cf. Bell and Lappin, 1973). When gratings were alternately presented to left and right halves of the display, the motion percept was presumably mediated by the long range system.

Neural mechanisms for flicker and motion perception

Results of the first experiment suggested that the response of the visual system to briefly presented low frequency sine-wave gratings is biphasic. Further, binocular temporal integration occurs between components of like sign while opposite sign responses fail to cancel. The second experiment demonstrated the operation of a motion detection mechanism (the "short range" system) which operates only on monoptic inputs. The absence of dichoptic effects in this system may be due to the failure of opposite sign components of the temporal response to cancel at a central locus. King-Smith and Kulikowski (1975) have proposed that while detection of flicker requires only an excitatory mechanism, motion detection requires interaction between spatially adjacent mechanisms producing excitation and inhibition, i.e. responses of opposite sign. Since we found no integration of excitation from one eye and inhibition from the other, no motion was seen with dichoptic viewing.

The view that motion detection is sometimes mediated by a mechanism which receives both excitatory and inhibitory input is consistent with physiological data. For example, Barlow and Levick (1965) tested two alternative physiological models of motion detection. One was based on a mechanism which summates excitatory responses generated by stimuli appearing sequentially at different locations in the "preferred" direction. A second model postulated that delayed inhibition cancels excitation produced by stimuli moving in the "null" direction. This model requires temporal integration between response components of different sign. The single unit recording data reported by Barlow and Levick strongly supported the inhibitory model.

In summary, it appears that the human visual system contains a motion sensitive mechanism which operates by temporally integrating excitatory and inhibitory inputs from different retinal locations. Since no neural mechanism exists to integrate excitation and inhibition from the two eyes, motion is not seen under dichoptic presentation. Gratings presented to non-corresponding retinal points produce a different motion percept which is mediated by a second motion sensitive mechanism receiving input from the two eyes. Although the existence of a separate motion detector for large displacements has long been appreciated (Exner, 1875), its physiological basis remains largely unknown.

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