MONOCULAR AND BINOCULAR DETECTION OF MOVING SINUSOIDAL GRATINGS*

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Abstract—We compared observers' contrast sensitivities for monocularly presented drifting gratings with their sensitivities to various pair-combinations of these gratings. If the two gratings are presented one to each eye, are of low spatial frequency, and move in same direction, contrast sensitivity is nearly twice the monocular value; if the gratings move in opposite directions, there is little or no sensitivity difference between the monocular and dichoptic conditions. As spatial frequency increases, the difference between the same- and opposite-direction conditions becomes less marked, and both pair-combinations are about 1.4 times as detectable as their monocular components. A monocular combination of gratings drifting in opposite directions (a counterphase modulated grating) gives results much like the dichoptic opposite-direction combination at all spatial frequencies. If spatial frequency is fixed at a moderate value, and drift rate is varied, then the difference between same and opposite conditions increases with drift rate; the natural conclusion that stimulus *velocity* determines this difference is not, however, completely borne out by experiments in which spatial and temporal frequency are varied to hold velocity constant. Thus under conditions where velocity and direction information are known to be available at detection threshold, our results show that binocular combination depends on the direction of movement: directional information must thus be extracted at or prior to the confluence of binocular signals.

INTRODUCTION

Much recent research in motion perception has focused on the concept of direction selectivity. Hubel and Wiesel (1962) made the fundamental physiological observation that many visual cortical neurons exhibit directional preferences: these cells respond best to a single direction of movement of a bar or grating, while movement in other directions elicits either a smaller response or no response.

Direction selectivity has been studied in a variety of psychophysical situations, including selective adaptation (Sekuler and Ganz, 1963), motion aftereffects (Barlow and Brindley, 1963) and subthreshold summation (Levinson and Sekuler, 1975a). Moreover, psychophysical studies point to an additional property of the motion system: detection of opposite directions of motion proceeds *independently*, in that the physical sum of two patterns that move in opposite directions is little or no more detectable than one of its single moving constituents (Levinson and Sekuler, 1975a; Watson, Thompson, Murphy and Nachmias, 1980). This and other evidence (see Sekuler, 1978, for a review) indicates that, at least for moving patterns near threshold, detection is mediated by an array of directionally tuned mechanisms, each sensitive to a limited range of directions. Independent detection of two simultaneously presented moving gratings might thus be expected when the directions of motion of the gratings differ widely enough so that two different populations of direction mechanism are stimulated by each grating. When, on the other hand, the two gratings are moving in directions sufficiently close to one another to stimulate common mechanisms, detectability of the pair should be enhanced relative to that of its moving constituents because of combination of the inputs in a common pathway.

This type of reasoning has of course been applied to other psychophysical situations. Usually, summation of sensitivity to two inputs is interpreted as evidence that the inputs are treated by the same mechanism or channel, whereas independence (lack of such summation) indicates that separate mechanisms or channels can be identified. For example, the enhanced detectability (usually termed "binocular summation") that results from stimulation of two eyes rather than one is usually interpreted as evidence of the convergence of monocular inputs into a common binocular mechanism mediating detection (Blake and Fox, 1973). However, when patterns are positioned on very disparate retinal loci (Eriksen and Greenspon, 1968), or differ widely in orientation (Westendorf and Fox, 1975; Blake and Levinson, 1977), spatial frequency (Blake and Levinson, 1977), or temporal frequency (Blake and Rush, 1980) in the two eyes, there is no enhancement of detectability beyond that expected by probability summation: the detection of patterns that

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differ markedly between the eyes occurs independently. It also appears that it is possible to obtain information about the sensitivity of binocular mechanisms to various stimuli by examining the effects of varying interocular stimulus differences on binocular summation.

We have compared the detectability of several combinations of drifting gratings presented to a single eye and to both eyes, in an attempt to examine the manner in which information about direction of movement is combined between the eyes. Our results suggest that detection of most stimuli is mediated by mechanisms that are both binocular and direction selective, and that information about direction of movement is available at or prior to binocular combination.

METHODS

Stimuli

All the stimuli used in these experiments were moving sinusoidal gratings, or combinations of moving sinusoidal gratings. A sinusoidal grating is a pattern of light and dark bars whose luminance profile in a direction orthogonal to the bars is a sine wave. The orientation of the gratings in these experiments was either vertical or horizontal; and they always moved in a direction orthogonal to their orientation. The spatial frequency of a grating is the number of spatial cycles that subtend one degree of visual angle. The drift rate is given as a temporal frequency, which is the number of cycles that traverse an arbitrary point on the screen in 1 sec; the angular velocity of grating movement is thus given (in degrees of visual angle per second) by the ratio of the temporal and spatial frequencies. The contrast of a grating is the difference between the maximum and minimum luminances in the grating divided by twice the mean luminance, and contrast sensitivity is the reciprocal of the contrast level at detection threshold.

We examined the detectability of moving sinusoidal gratings presented either singly to one eye or the other, or in combination. The gratings were generated by a PDP 11 computer on the faces of two Tektronix 608 display oscilloscopes with matched P31 phosphors, using a television technique; the frame rate of the display was 64 Hz. The two screens formed the two image fields in a conventional Wheatstone stereoscope; they subtended 10 deg by 12 deg at the viewing distance of 57 cm, and always had a space- and time-average luminance of 25 cd/m². Observers viewed the display against a dim background without artificial pupils through their normal refractive correction; a small fixation circle and a pair of Nonius lines assisted proper binocular alignment.

The stimuli in each of the experiments discussed below fell in 5 classes, schematically shown in Fig. 1. All the stimuli in a given class were identical in spatial frequency, temporal frequency and orientation. Stimuli could be delivered to one or both eyes; when
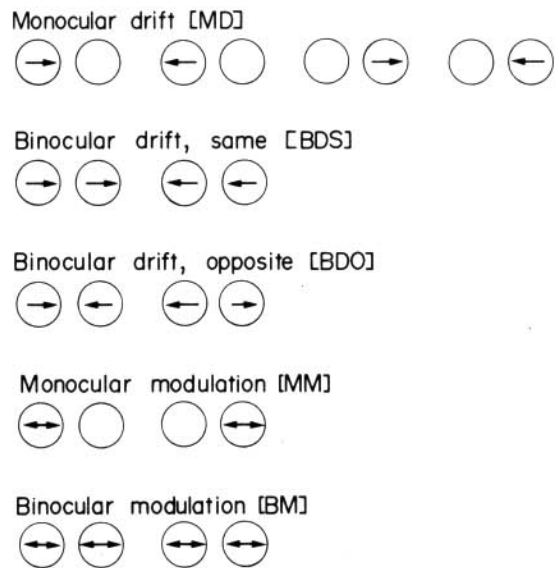

Fig. 1. Schematic diagram of the 5 classes of stimuli used in the study.

stimulation was monocular, the other eye viewed a blank screen of the usual space-average luminance.

The monocular drift class (MD) consisted of sinusoidal gratings moving in either direction in either eye. The other eye viewed a blank field of the same space-average luminance as that of the patterned field. These four conditions provided the baseline measure of detectability with which the detectabilities of the other stimuli were compared. All the other stimulus classes contained stimuli that were various combinations of the stimuli in this class.

The *binocular drift same* and *binocular drift opposite* classes (BDS and BDO) consisted of pairs of gratings presented dichoptically; these moved either in the same direction in the two eyes or in opposite directions. These stimuli resulted from the combination of one left-eye and one right-eye stimulus from the MD class.

The *monocular modulating* class (MM) consisted of monocularly presented gratings whose contrast was sinusoidally modulated in time ("counterphase" gratings). These contrast-reversing gratings result from the addition of two identical gratings that move in opposite directions, and thus represent the combination of either both left-eye or both right-eye stimuli from the MD class.

The *binocular modulating* class (BM) consisted of binocularly presented counterphase gratings. These stimuli result from the combination of all four members of the MD class.

There were four stimuli in the MD class, and two stimuli in each other class, for a total set of 12 stimuli. We did not find any systematic differences in sensitivity for the different stimuli within any of the classes, and so in the subsequent presentation data within classes are always pooled and presented as mean sensitivities for the stimuli within a class.

Definition of contrast. Following Watson *et al.* (1980), we defined the contrast of all our stimuli as the contrast of the drifting gratings that composed them. Thus the combination of two gratings that move in opposite directions (a counterphase grating) is considered to have the same contrast as either of its moving components, despite the fact that the peak *physical* contrast of the counterphase grating is twice that of the components. This arbitrary definition simplifies comparison among the various stimulus classes, and the detection performance associated with each. It does not in any way affect interpretation of the results.

Psychophysical methods

We determined contrast sensitivity in these experiments using one of three procedures: the method of adjustment, the method of constant stimuli, or a transformed staircase method. In all cases, the computer controlled the stimulus presentations and collected the observers' responses.

In adjustment threshold experiments, the various stimuli were presented in a random order, and the observer adjusted stimulus contrast with a potentiometer read by the computer's analog-to-digital converter. Up to 48 different stimuli were tested in single sessions. The initial stimulus contrast was determined by the computer to be within 6 dB (a factor of 2) of the observer's previous threshold setting for that stimulus; on each trial this contrast value was associated with the position of the potentiometer's knob at the beginning of the trial, ensuring that there was no reliable relationship between hand or knob position and stimulus contrast. Normally the results of 8 separate measurements for each stimulus were averaged; the standard error of the mean of these measurements rarely exceeded 0.075 log units (1.5 dB).

In experiments using the staircase method or the method of constant stimuli, data were collected using a balanced temporal two-interval forced-choice (2IFC) procedure. A stimulus was present in one of two time intervals marked by tones; the intervals were normally 750 msec in duration, and were separated by 200 msec. After the observer selected the interval in which he believed the stimulus had been presented, a tone provided feedback about the correctness of the judgment.

In staircase experiments, we used the method described by Levitt (1970) to converge to a particular point on the psychometric function; the point normally chosen corresponds to a detection probability of 0.79. The step sizes in the staircases were initially 0.3 log units (6 dB), and reduced progressively to 3 and then 1 dB. Twelve staircases were normally interleaved, one for each stimulus condition in the experiment (see Fig. 1), and each staircase was run for 75–100 trials; all data points after the fifth reversal were averaged to give the sensitivity estimate.

Subjects. The three authors served as subjects for most of the experiments reported below. All had normal or corrected-to-normal visual acuity, and valid stereopsis. The substance of the findings was confirmed on four other observers naive to the aims of the experiment. All observers noted that it was difficult to discriminate among the stimuli at the contrast levels employed in these experiments; it was particularly difficult to identify the eye of origin of monocular stimuli, or tell monocular from binocular stimuli (Blake and Cormack, 1980).

RESULTS

Binocular direction selectivity and spatial frequency

Initially, we determined contrast sensitivity for the set of stimuli shown in Fig. 1 using the staircase method. We made measurements at low and high spatial frequencies, for gratings that drifted at a moderate rate. Fig. 2 shows contrast sensitivity for 0.6 c/deg gratings drifting at 4 Hz, for two observers. In accord with previous studies, we found the monocular combination of gratings drifting in opposite directions (monocular modulating gratings) to be only slightly
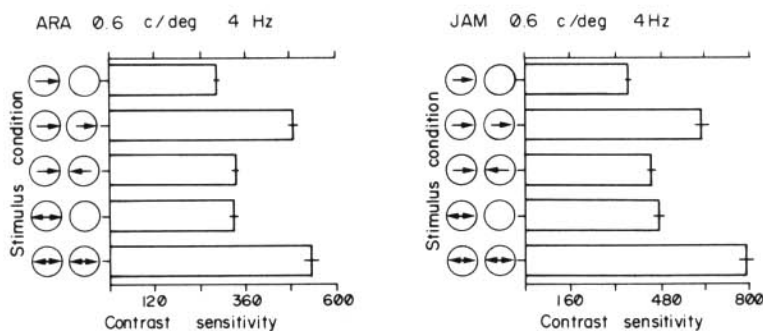

Fig. 2. Contrast sensitivity plotted on a linear abcissa, to the 5 classes of stimuli in Fig. 1, for two observers. The 5 stimulus groups are identified schematically by the circle and arrow symbols, in which a circle represents an eye and an arrow a direction of movement. Here, as elsewhere in the paper, data from the several stimuli in each group are pooled. The data were collected using the staircase procedure. The spatial frequency was 0.6 c/deg, and the gratings were horizontally oriented. The error bars show ±1 SEM.
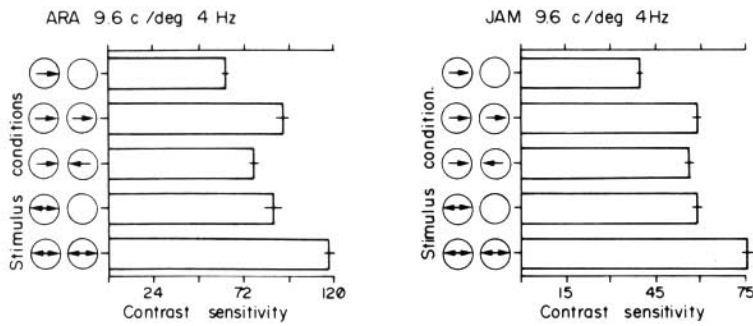
Fig. 3. As Fig. 2, but for a spatial frequency of 9.6 c/deg.

more detectable than monocular drifting gratings presented singly. Similarly, the combination of gratings moving in opposite directions in the two eyes was only slightly more detectable than a single monocular drifting grating. Watson *et al.* (1980) analyzed the enhancement in detectability expected from probability summation between independent detection channels. Given plausible assumptions about the slope of the psychometric function and a high-threshold model of probability summation (see below), they predicted a sensitivity improvement of 1.5–2 dB from probability summation; this value is similar to the ones observed here, so it seems that gratings moving in opposite directions are detected independently. On the other hand, a combination of gratings that drift in the same direction in the two eyes was considerably more detectable than the corresponding monocular gratings. Binocular modulating gratings also showed this binocular summation, being slightly more detectable than binocular gratings moving in the same direction, and considerably more detectable than any of

the other types of grating. These results indicate that at low spatial frequencies binocular summation exceeding probability summation occurs only when the gratings move in the same direction in the two eyes.

Figure 3 shows results for the same observers for 9.6 c/deg gratings. Under these conditions, binocularly presented gratings that moved in opposite directions in the two eyes were markedly more detectable than monocular drifting gratings; the enhancement seen probably exceeds that attributable to probability summation. Similarly, monocular modulating gratings were better detected than their monocular drifting constituents—also by an amount in excess of that expected by probability summation. Conversely, the improvement in sensitivity for binocular gratings drifting in the same direction in both eyes was definitely less than that observed at low spatial frequency (Fig. 2). Thus all three pairwise combinations of monocular drifting gratings were more nearly equally detectable at high spatial frequency than at low; the
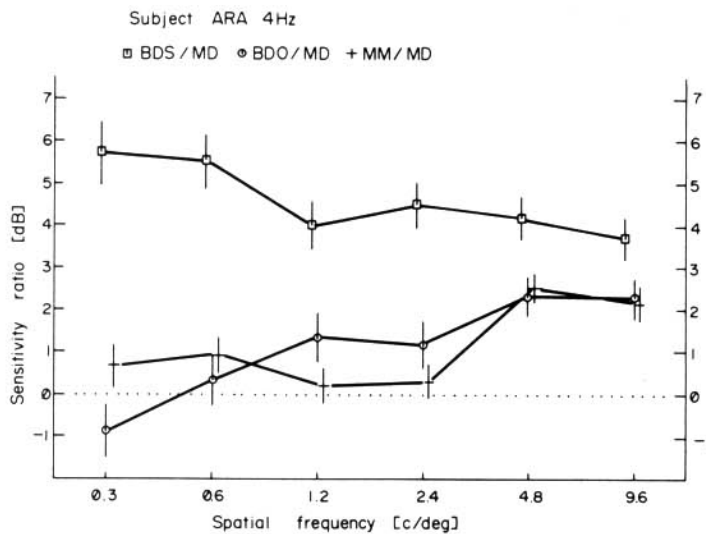

Fig. 4. Ratios of sensitivity (in dB) at different spatial frequencies of binocular combinations of gratings drifting in the same direction in the two eyes to monocular drifting gratings (BDS/MD), binocular combinations of gratings drifting in opposite directions in the two eyes to monocular drifting gratings (BDO/MD), and monocular combinations of gratings drifting in opposite directions in a single eye (monocular modulating gratings) to monocular drifting gratings (MM/MD). The gratings were horizontal. The error bars show ±1 SEM sensitivity ratio.

direction of movement of the components was relatively less important. We also noticed that at 9.6 c/deg it was difficult to distinguish stationary from moving gratings near threshold, or to identify the direction of movement. This suggests that mechanisms responsible for the detection of high spatial frequencies do not convey information about movement (Tolhurst, 1973; Watson et al., 1980).

Using the method of adjustment, we examined these changes in binocular and bidirectional summation over a range of spatial frequencies. Figure 4 shows some results of these experiments. This figure plots sensitivity ratios (in dB) between the monocular drifting gratings and each of their three pairwise combinations: binocular gratings drifting in the same direction (BDS/MD), binocular gratings drifting in opposite directions (BDO/MD) and monocular modulating gratings (MM/MD).

Binocular summation of gratings that move in the same direction was greatest at the low spatial frequencies, and decreased gradually with spatial frequency. Conversely, there was a gradual increase in the sensitivity ratios with spatial frequency for gratings that move in opposite directions in the two eyes. Finally, the sensitivity ratio of a monocular combination of gratings drifting in opposite directions to the single monocular drifting grating closely followed the binocular combination ratios, indicating that sensitivity is about the same whether one presents gratings of opposite direction of drift monocularly or dichoptically.

Binocular direction selectivity and temporal frequency

The changes with spatial frequency in binocular summation of moving stimuli described above suggest the possibility that mechanisms having different properties might mediate grating detection at low and high spatial frequencies, with those at high frequencies being less sensitive to direction than those at low frequencies. Since the visual system might contain spatially and temporally distinct mechanisms operating differentially under these two conditions, we examined the effect of varying the temporal frequency of movement on binocular summation for gratings of moderate spatial frequency. Typical results are shown in Fig. 5 for one observer, for a spatial frequency of 2.4 c/deg. There was a dramatic increase in the sensitivity ratios for both monocular and binocular combinations of gratings drifting in opposite directions at low temporal frequencies. Taken with the results described above, this suggests that at high spatial and low temporal frequencies information about stimuli moving in opposite directions, presented either monocularly or dichoptically, is combined prior to detection. At low spatial and high temporal frequencies, on the other hand, directional movement information is strictly segregated prior to detection.

These data are consistent with the idea that detection of patterns of high spatial frequency and low temporal frequency is mediated by one set of mechanisms in the visual system—"sustained" channels—while patterns of low spatial frequency and high temporal frequency are detected by another set—"transient" channels (Kulikowski and Tolhurst, 1973). The spatial and temporal properties of the direction selectivity of binocular summation would be consistent with the idea that "sustained" channels sum between the eyes irrespective of the direction of stimulus movement, while "transient" channels sum only inputs that move in the same direction. It is, however, the case that the stimuli for which strongly direction selective binocular interaction obtains all move rapidly, while those eliciting weaker directional effects move more slowly. If the limiting factor in direction

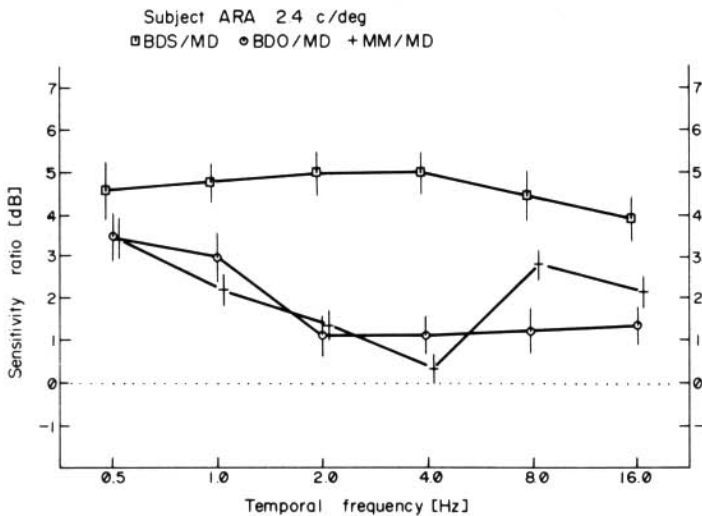Subject ARA 2.4 c/deg
□ BDS/MD   ○ BDO/MD   + MM/MD

Fig. 5. Sensitivity ratios as in Fig. 4, but as a function of the temporal frequency of drift. The gratings were horizontal.

selective interactions were stimulus *velocity*, this might provide an alternative explanation.

Binocular direction selectivity at constant stimulus velocity

We investigated the possibility that the apparent diminution of summation (both binocular and direction selective) for same directions of motion at high spatial frequencies and the apparent presence of summation for opposite directions of motion at high spatial and low temporal frequencies, might be purely an effect of stimulus velocity. The stimulus set was similar to that in the preceding experiments, save that in each session the spatial and temporal frequency covaried to maintain a constant stimulus velocity.

Data are shown in Fig. 6 for a velocity of 0.8 deg/ sec. It may be seen that summation between opposite directions of motion combined binocularly or monocularly increased as spatial frequency increased; this effect was similar in form to, but smaller in magnitude than the effects seen in Fig. 4 when temporal frequency was held constant. Tests made at other fixed velocities between 0.2 and 3.2 deg/sec showed that summation between opposite directions of movement was most marked at lower velocities, but increased systematically with spatial frequency at any constant velocity. This suggests that no explanation based simply on stimulus velocity can account for all of our results. For example, if instability of fixation perturbed retinal velocity by an amount that masked stimulus movement below some critical velocity, then the data from a constant-velocity experiment like that of Fig. 6 should be independent of spatial and temporal frequency. Since they are not, some other form of spatio-temporal variation in the properties of the detection mechanisms involved in this task is indicated.

Independent processing of opposite directions of movement

Our results suggest that for stimuli of low or moderate spatial frequency moving more rapidly than about 0.5 deg/sec, combination of information in either monocular or binocular detection channels is direction selective. Indeed, for the binocular combination of gratings of low spatial frequency that move in the same direction, binocular combination is nearly additive: an improvement in sensitivity close to 6 dB is observed. What is less clear is the nature of the combination of patterns moving in opposite directions, either binocularly or monocularly. The initial observations of Levinson and Sekuler (1975a) on this point suggested that sensitivity for the monocular combination of drifting gratings was in fact identical to that of the drifting components, but subsequent careful work by Watson *et al.* (1980) revealed a small but significant improvement in the detectability of two gratings compared to one. This they attributed to probability summation between mechanisms sensitive to opposite directions of movement. The computation of the expected sensitivity improvement due to probability summation is, unfortunately, model-bound, relying as it does both on a two-state model of probability summation (Eriksen, 1966; Green and Swets, 1966), and on an estimate of the slope of the psychometric function (Watson *et al.*, 1980).

The sensitivity improvements we observed for combinations moving in opposite directions were between 1 and 2 dB for gratings of moderate spatial and temporal frequency, and these values are plausibly accounted for a by a probability summation model of the sort employed by Watson *et al.* We verified this in experiments in which direct comparisons of detection probabilities were made using the method of constant stimuli

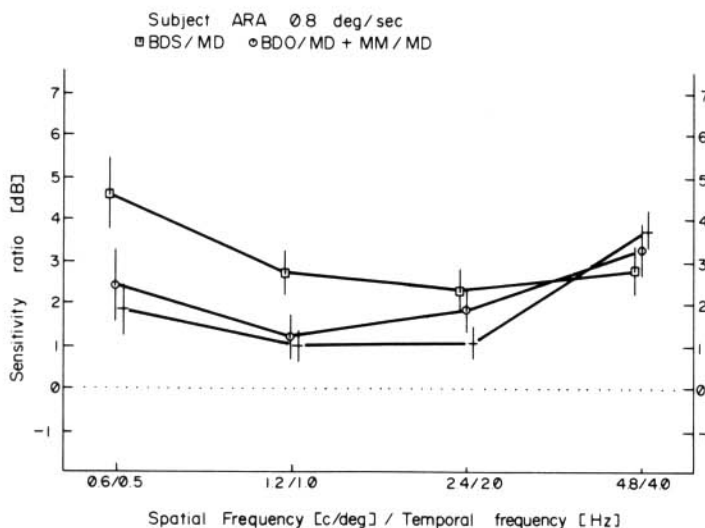Subject ARA 0·8 deg/sec
□ BDS / MD   ○ BDO / MD + MM / MD

Fig. 6. Sensitivity ratios as in Fig. 4, as a function of spatial and temporal frequency, which were covaried to maintain a constant angular velocity of 0.8 deg/sec.
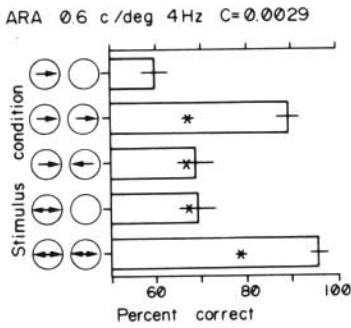
ARA 0.6 c/deg 4Hz C=0.0029

Fig. 7. Detection probabilities for the 5 classes of stimuli in Fig. 1, presented in a format similar to that of Figs 2 and 3. The asterisks denote expectations for the four classes of combination stimuli based on the observed probabilities for single moving stimuli computed using the two-state model of probability summation.

Initially, a staircase experiment was run for monocular drifting gratings, using Levitt's rule for converging on the 0.71 point on the psychometric function. The method of constant stimuli was then used to determine detection probabilities for all five groups of stimuli at the contrast value taken from the staircase. The results of such an experiment are shown in Fig. 7.

The detection probabilities observed for either the binocular or monocular combination of gratings drifting in opposite directions were indistinguishable from predictions made from the probabilities observed for single gratings using the high-threshold model (indicated by asterisks); detectability for the other combinations clearly exceeded that attributable to probability summation of this sort. We therefore may not reasonably reject a model in which different directions of movement are detected by multiple mechanisms that are independent and whose outputs are logically combined before a response decision is made.

Clearly, however, there are some circumstances in which this model may be rejected. For one thing, at high spatial frequencies and low velocities, the enhancement observed exceeded that predicted; conversely, results at low spatial frequency frequently appeared to show a reduction in sensitivity, especially for the binocular combination of oppositely moving gratings. In addition, it can be seen from Figs 4, 5 and 6 that the sensitivity ratios for the binocular combinations were often smaller than those for monocular combinations—the same model cannot predict both sets of data, and it may be that there is a weak interocular inhibitory process that cancels all or part of the "natural" improvement due to probability summation. Some evidence for a process of this sort may be seen in the results of Levinson and Sekuler (1975a).

Whatever the cause, there were gradual but reliable changes in these sensitivity ratios with spatial and temporal frequency. It thus appears that strict independence can hold for oppositely moving gratings only over a limited spatio-temporal range. To estab-

lish the bounds of this spatio-temporal region would require a firm commitment to a particular model of probability summation, and a great deal more data than we have presented here. Such an exercise is beyond the scope of this report.

DISCUSSION

Binocularity and direction selectivity

One interesting conclusion from this study is that binocular combination in human vision is selective for direction of movement. Levinson and Sekuler (1975a) demonstrated direction selectivity for monocularly presented gratings, but their data do not address the issue of binocular combination. For low and moderate spatial frequencies, information about direction of movement must be extracted at or prior to binocular combination, since binocular interactions between otherwise identical stimuli depend on their direction of movement. Thus binocular mechanisms that subserve detection might receive their inputs from monocular mechanisms having similar directional tuning in the two eyes. It is, of course, conceivable that binocular combination occurs at the same level of the visual system at which directional movement information is extracted; this would make it difficult to isolate putative monocular, direction selective mechanisms. Nonetheless, it is logically necessary that information about direction selectivity be available to whatever mechanisms combine input from the two eyes.

This conclusion is slightly at variance with physiological data on the directional tuning of binocular cortical neurons in cats and monkeys. While many cortical cells are strongly binocular, and most are direction selective, these properties are not closely associated (Hubel and Wiesel, 1962, 1968). There certainly exist substantial numbers of cortical neurons sensitive to movement of an optimally oriented stimulus in either direction, and which show this sensitivity for stimuli delivered to either eye. It is possible that all such neurons are sensitive to relatively high spatial frequencies, where our data show that information about opposite directions of movement is not segregated before binocular combination. This is not, however, in agreement with physiological observations from this laboratory (J. A. Movshon, unpublished observations). We must therefore suppose that if binocular, bidirectional neurons sensitive to low spatial frequencies exist in the human visual cortex, they are not important in the detection of stimuli of the sort we used in these experiments. Similarly, binocular mechanisms sensitive to opposite directions in the two eyes, for which both psychophysical and physiological evidence exists (Pettigrew, 1973; Regan and Beverly, 1973; Zeki, 1974), must be insufficiently sensitive or numerous to contribute importantly to the detection of moving gratings. This is also suggested by the fact that none of the observers in this experiment ever

reported a compelling impression of movement in depth for stimuli whose contrast was near threshold.

Two sets of channels in binocular movement combination?

In recent years, considerable attention has been devoted to the idea that distinct mechanisms are involved in pattern and movement detection (for a review, see Legge, 1978). Several lines of both neurophysiological and psychophysical evidence suggest that these two mechanisms are differentially sensitive to high and low spatial frequencies, and to low and high temporal frequencies. This general model seems to be consistent with our data if we suppose that binocular combination in "movement" channels is direction selective, while in "pattern" channels it is not. This idea is further supported by our observation that no simple effect of stimulus velocity can account for our results.

On the other hand, it must be noted that the changes in binocular combination we observed when spatial or temporal frequency were varied were always gradual and apparently continuous across virtually the whole frequency range. The two-mechanism model would probably predict rather more abrupt shifts in behavior (e.g. Kulikowski and Tolhurst, 1973) than these. So in the absence of further evidence compelling us to adopt this idea, it seems simpler to suppose that our results reflect some gradual change in the properties of the relevant detection mechanisms as stimuli vary in spatial and temporal character.

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