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AFOSR-80-0246

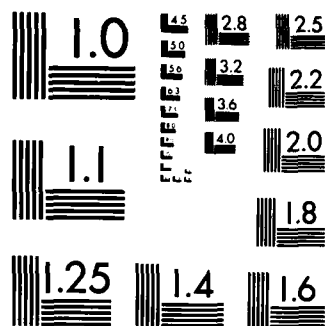
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REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM
1. REPORT NUMBER AFOSR TR- 80 633	2. GOVT ACCESSION NO.	3. RECIPIENT'S CATALOG NUMBER
4. TITLE (and Subtitle) ENHANCING VISUAL SENSITIVITY		5. TYPE OF REPORT & PERIOD COVERED Final 10/1/83-9/30/84
		6. PERFORMING ORG. REPORT NUMBER
7. AUTHOR(s) ROBERT SEKULER		8. CONTRACT OR GRANT NUMBER(s) AFOSR-80-0246
PERFORMING ORGANIZATION NAME AND ADDRESS NORTHWESTERN UNIVERSITY 2021 Sheridan Road Evanston, IL 60201		10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS 23121A5 61102 F
CONTROLLING OFFICE NAME AND ADDRESS Force Office of Scientific Research/NL ling AFB 20332		12. REPORT DATE May 24, 1985
MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office)		13. NUMBER OF PAGES 34
		15. SECURITY CLASS. (of this report) UNCLASSIFIED
		15a. DECLASSIFICATION/DOWNGRADING SCHEDULE
DISTRIBUTION STATEMENT (of this Report) Approved for public release; distribution unlimited.		
17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report) CONFIDENTIAL		
18. SUPPLEMENTARY NOTES		
19. KEY WORDS (Continue on reverse side if necessary and identify by block number) <i>Motion & Perception; Direction Discrimination</i>		
20. ABSTRACT (Continue on reverse side if necessary and identify by block number) This report summarizes the major studies carried out under AFOSR grant 80-0246 from October 1, 1983 through September 30, 1984. During this report period we did coordinated work on two aspects of motion perception. One work unit extended our earlier research on how training affects direction discrimination. These studies give new insights into the physiological locus and character of this particular form of perceptual learning. The second work unit		

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ABSTRACT

This report summarizes the major studies carried out under AFOSR grant 80-0246 from October 1, 1983 through September 30, 1984.

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RATIONALE FOR OVERALL APPROACH

The research effort described here comprises two complementary work units designed for progress toward a common goal -- understanding visual mechanisms that process motion information.

During this reporting period efforts on the first work-unit produced a series of experiments on improvement in direction discrimination as a function of practice. These experiments represent a significant extension and refinement of our preliminary work (Ball and Sekuler, 1982). In particular, the new studies confirmed that training's improvement in discrimination is restricted to the trained direction and that the improvement persists for at least several weeks. In an attempt to elucidate the anatomical locus of training's improvement the new experiments examine interocular and interhemispheric transfer of training. A large paper summarizing all our work on direction discrimination is virtually complete and will be submitted for publication in the next six weeks.

The second work-unit used motion metamers, analogous to metamers in color vision, in order to study such properties of direction-selective mechanisms as their number and bandwidth.

This sub-project extends work that we have been carrying out under AFOSR sponsorship. Some of these efforts have been reported by Williams and Sekuler (1984). A paper describing the new experiments on motion metamers has been submitted for publication.

The products of each work unit will be described in turn.

**WORK UNIT ONE:
ENHANCEMENT OF DIRECTION DISCRIMINATION**

A well-known aphorism proclaims "practice makes perfect." Though this claim may not always strictly true, practice certainly does improve many perceptual abilities, including the ability to discriminate one object from another. But many different sources can contribute to improved discriminative capacity. For example, discrimination may improve because an observer has succeeded in identifying particular details that distinguish one object from another. Alternatively, improvement in perception may reflect either heightened attention or greater efficiency in labelling one's perceptual experiences. Finally, some forms of improvement in perceptual performance seem to depend on a changed selectivity within the visual system itself. For us, this last sort of perceptual learning is the most interesting.

Three different results suggested that motion perception --more particularly, perception of direction of motion-- might be a promising arena within which to study perceptual learning. The first of these results showed that relatively brief exposure to a single direction of motion can produce adaptation that is very long-lived --twenty-four hours or more (Masland, 1969). Such enduring changes, as opposed to evanescent ones, would ease the empirical assessment of perceptual learning.

Second, repeated exposure diminishes the masking ability of particular directional components of broad-band directional, masking noise (Ball and Sekuler, 1979). This change in the effectiveness of the masking noise suggests two related hypotheses. On one hand, the change might be one consequence of enhanced selectivity in neurons that signal direction of motion; on the other hand, we could be seeing the change in some neural filter that is prior to the actual analysis of visual direction.

A third result related to motion perception caught our eye: the ability to discriminate between two directions of motion varies substantially among observers (Ball and Sekuler, 1980). Although only a few observers were studied, individual differences seemed to be at least roughly correlated with the amount of time individual observers had spent in the experiment. Hence, differential practice might lay behind some of the individual differences in ability to one discriminate direction of motion from another.

With these three sets of findings in mind, we decided to explore motion perception's plasticity further, in six related experiments that are reported here. Our focus was on the specificity and permanence of perceptual plasticity. A secondary focus was on the possible neural sites of such plasticity. Overall, our experimental strategy was to provide

discrimination-training for particular directions and then to examine the specificity of whatever improvement in direction-discrimination might result.

So that the reader will best understand the research done during the present report period, I shall summarize the earlier, background studies from which these new ones spring.

In all experiments, old and new in this work unit, stimuli were bright, spatially random dots traveling parallel paths across the face of a cathode ray tube at 10 degrees/second. At any one moment, approximately 400 dots were visible within an 8 degree, circular aperture. The dots, and their movement, were both highly visible; the luminance of the dots was about 50 times that required for them to be just seen against the constant veiling luminance of 2 cd/m². Opposite ends of the display were electronically linked so that dots disappearing at one side "wrapped around," to reappear at the opposite side. This electronic linkage made the dots appear to move as though they were fixed on an infinitely large sheet that was visible behind the circular aperture. To prevent observers from making any use of these structural clumps, a new array of random dots was generated every fifty trials.

Observers viewed the display binocularly, fixating a dark, stationary, central point.

Each trial consisted of two, 500-millisecond intervals. This pair of intervals was separated by a 200-millisecond period during which only the uniformly illuminated screen was visible. Two equiprobably types of trials, "same" and "different", were randomly intermixed. On "same" trials, motion took the same direction during both intervals. On "different" trials, motion in one interval was in a direction differing by three degrees from that of the other interval. On one half of all trials, chosen at random, the three degree difference was in a clockwise direction; half the time the three degree difference was in a counter-clockwise direction. After viewing both intervals' direction of movement the observer reported whether the two directions had been same or different. This report was communicated to the computer by means of a switch-throw.

Each block of fifty trials was characterized by some standard direction. This direction appeared in both intervals of "same" trials and in one interval of "different" trials. Discrimination was assessed around eight different directions: 0 degrees (rightward), 45, 90 (upward), 135, 180, 225, 270 and 315 degrees. Eight observers were tested: one was the first author; six were naive about the purpose of the experiment.

The main portion of the experiment required seven sessions spread over ten to twelve days. In sessions One, Four, and Seven, we measured discrimination performance

for each of the eight directions. Within each session, the order of testing was separately randomized for the observer. At the beginning of the experiment, a unique training direction was assigned to each observer. In sessions Two, Three, Five and Six, each observer practiced making direction discriminations with the training direction that had been assigned to that observer. During each training session, an observer made 500 "same-different" judgments (ten blocks of 50 trials) with the direction assigned to that observer. For both training and test sessions observers were rewarded with two cents for each correct response; one cent was deducted for each incorrect response. Feedback was provided following each response.

Responses in a block of trials were reduced to a pair of proportions: the proportion of "different" trials correctly identified as such (hits), and the proportion of "same" trials misidentified as "different" (false alarms). These proportions were then converted by standard methods into d' , a measure of discrimination performance.

Comparing performance before and during training, we found that direction discrimination was much better for the principal directions than for the oblique directions. Considering only the training direction for each observer, performance improved significantly over the seven sessions. A gradual, steady improvement was seen for all observers, suggesting an underlying process different from the sudden improvement produced if observers learn to pick out the distinctive spatial features of a stimulus pair.

To pin down the specificity of training's effectiveness we used orthogonal contrasts to compare performance on the trained direction with performance on the three directions that were most different from that trained direction. The orthogonal contrasts showed that training had no significant effect on the three directions most different from the observer's training direction --including, of course, the direction opposite the training direction.

A second experiment, with eight new observers examined the effects of explicit knowledge of results after each trial. For cardinal training directions, knowledge of results had no effect; for oblique training directions, knowledge of results greatly facilitated improvement.

Green and Swets suggest that, in the absence of explicit feedback, psychophysical observers make trialwise perceptual adjustments, sharpening their internal representations of the expected stimuli (Green and Swets, 1966; p.395). The large oblique effect in direction discrimination may mean that when they must discriminate a three degree difference between two oblique directions observers may not have as clear an internal representation of the expected stimuli as do observers who must discriminate a similar difference between cardinal directions. Indeed, Leibowitz (1955) has

suggested this as the cause of the oblique effect found with static contours. Therefore, in our paradigm, feedback may be more important for observers training on oblique directions because feedback is essential in order to sharpen their representation of the stimuli they have to discriminate. Feedback is less important to observers training on cardinal directions because, at the outset, they already have a clearer, and more stable, representation of the stimuli.

Taken together, the preceding experiments demonstrate that training can produce specific and long-lasting improvement in the ability to discriminate between directions of motion. Because improvement was fairly-well restricted to the trained direction, it seems unlikely that the improvement was the product of some generalized, cognitive learning effect or familiarity with the task.

The experiments also suggest that feedback is a prerequisite for improvement under some, but not all, training conditions. However, the experiments leave a number of questions unanswered. Chief among these is the question of the actual magnitude of the improvement produced by training. Our results are expressed only in terms of the sensitivity measure, d' , and it is difficult to quantify them in other terms, such as the amount of change in the difference threshold for direction discrimination. Therefore we carried out a third experiment in order to allow us to express our results in an alternative, stimulus-based metric.

Our goal was to express the values of d' that we had obtained previously in terms of the direction differences required to achieve those d' values. This translation allowed us to specify the effects of training, in terms of the direction differences required to achieve particular levels of discrimination.

Four observers were tested; each was assigned one training direction and was tested on one of the cardinal directions (0, 90, 180, or 270 degrees) as well as one of the oblique directions (45, 135, 225 or 315 degrees). For his or her designated test directions, each observer was tested with varying degrees of separation between directions on "different" trials: 1, 2, 3, and 4 degrees. The order of testing at different separations was randomized for each session and observer. Each observer made a total of 100 "same-different" judgments (two 50-trial blocks) for each combination of direction and amount of separation.

Values of d' were averaged for the four observers for the cardinal and oblique directions. As the difference, Δ between directions increased, sensitivity increased linearly. This linear increase accounted for 97% of the variance in d' for the oblique directions, and 98% of the variance in d' for the cardinal directions. The equations for the best-fitting regression lines were

$$\underline{d'} = 1.25\Delta - 0.675, [1] \text{ and}$$

$$\underline{d'} = 0.695\Delta - 0.595, [2]$$

for cardinal and oblique directions, respectively.

We used these equations to express the size of the oblique effect in terms of stimulus differences, rather than in terms of response differences. Substituting any value of Δ in the regression equations above, shows that, to produce comparable discriminabilities, two directions around an oblique axis must be separated by 1.75 times more than two directions around a cardinal axis.

The same regression equations helped us quantify the amount of improvement produced by training in our earlier experiments. At the end of training with cardinal directions, mean performance was $\underline{d'} = 3.1$. The results from the present experiment shows that this level of performance could be achieved with a direction difference of about 3.1 degrees. Before training with cardinal directions, mean performance was $\underline{d'} = 1.62$; after training, a subject would achieve that level of performance with a direction difference of just 1.8 degrees. Since the improvement with training is very nearly linear, we can say that training with cardinal directions reduces the direction discrimination threshold by a factor of 3.1 to 1.8. An analogous derivation, for training with oblique directions, direction discrimination thresholds also are reduced by a factor of about 3.0 to 2.0. Assuming that the difference threshold corresponds to $\underline{d'} = 1.0$, we estimate that, in terms of difference thresholds, training improves performance by approximately 70% for either cardinal directions or oblique directions. Though the similarity may be merely coincidental, this magnitude of improvement with practice is not much different from that reported for improvement in vernier acuity (McKee and Westheimer, 1978).

Our earlier experiments demonstrated an improvement in direction discrimination that was highly specific to the training direction. For example, there was a significant difference between improvement on the training direction and improvement on a direction that was merely 45 degrees different from that training direction. Note though, that all of our measurements were made at a single speed, 10 degrees/second. While focusing on one dimension of movement, direction, we have ignored another key dimension, velocity. To rectify this situation, we measured direction discriminability with several different stimulus velocities.

Eight observers were tested; none had participated in any of the previous experiments. For all observers, discrimination was measured for both an oblique and a cardinal direction (each randomly determined). As before, on "different" trials, the two directions presented differed by three degrees.

Observers were tested with the same upward direction

at speeds of 2, 4, 8, and 16 degrees/sec. Test velocities were presented in blocks of 50 trials each, in different random orders for each observer. Feedback was provided following every trial and, as before, observers received 2 cents per correct response.

As speed increased, discriminability increased linearly for both the oblique directions ($r^2=.96$) and the cardinal directions ($r^2=.99$). The degree of linear regression was calculated for speeds of 2, 4, 6, 8 and 10 degrees/sec since performance had reached a ceiling somewhere between 8 and 10 degrees/sec. Note that the difference between oblique directions and cardinal directions remains large as speed is increased.

Working with both feline and human observers, Pasternak and Merigan (1984) found that, up to some limiting velocity, direction discrimination thresholds decreased linearly with the logarithm of stimulus velocity. Beyond that limiting velocity, directions discrimination was constant. Although our results have a similar form, we should note one significant difference. The performance of our observers reached asymptote at about 10 deg/sec, while the performance of Pasternak and Merigan's human observers reached asymptote from 1-3 deg/sec. We cannot account for this discrepancy between the asymptotic velocities in the two experiments, though procedural and stimulus variables may have played some role. To take but one variable, the diameter of our display, 8 degrees, was about one-third the diameter of Pasternak and Merigan's display. We call attention to display subtense because a large display stimulates not only central vision, but peripheral vision as well. And it is known that velocity sensitivity changes systematically with eccentricity (Tynan and Sekuler, 1982; Pasternak and Merigan, 1984). As a result, a large display probably evokes responses from retinal regions that are heterogeneous with respect to velocity sensitivity. Note that we have no proof that our own, criticism.

Our next pair of experiments represents two different approaches to defining the possible anatomical locus of the discrimination improvements found earlier. Using both both normal and stereoblind observers, the next experiment measured interocular transfer of direction discrimination after training.

Adults, whose visual axes were misaligned from birth until early childhood, show various deficits of binocular function. For example such people exhibit abnormally high stereo-depth thresholds, as well as abnormally little interocular transfer of monocularly-induced adaptation and aftereffects, including the motion aftereffect (Mitchell, Reardon and Muir, 1975). However, other researchers (Wade, 1976; Price and Keck, 1982) caution that not all strabismics show abnormal interocular transfer of the motion aftereffect.

Abnormalities in stereo-depth perception and in interocular

transfer have been attributed to the presence of abnormally few binocular cortical neurons. Assuming that strabismic subjects do indeed have fewer binocular cortical neurons than do normal subjects, it would be useful to compare how well monocular training of direction discrimination transfers between the two eyes in strabismic and normal subjects. If the training affected binocular neurons, either alone, or in combination with monocular neurons, strabismic subjects would show less transfer of training than would normal subjects when the test stimulus was presented to the non-trained eye. Such a result would delimit the locus of the training effect to regions of the visual system at or beyond area 17, where the binocular cells are first found.

Six stereoblind and eight normal, control observers were tested. Observers were screened using a Bausch and Lomb Orthorator and random-dot stereograms (Julesz, 1971). All of the control observers showed stereodepth perception that was within normal limits, no stereoblind observer saw any depth whatever on either the Orthorator or random-dot stereogram plates. In addition, we also determined for each observer which eye was dominant. In the training phase of the experiment, half the observers practiced with their dominant eye, and half used their nondominant eye.

Each observer practiced making "same-different" judgments, as described previously, for one of the cardinal directions. The other eye was covered with an opaque patch. Each observer was assigned one of the four cardinal directions as a training direction. On the first, fourth, and seventh sessions each observer was tested on their training direction, the direction opposite the training direction, and for two oblique directions --each 45 degrees from the training direction. On these days both eyes were tested. On days 2, 3, 5, and 6 each observer practiced on their training directions for a total of 500 trials per day.

Prior to training, for both normal and stereoblind observers, the two eyes were equal in direction discrimination ($t=.096$, $df=26$, $p>.50$). In particular, for stereoblind observers mean performance with the eye that would be trained was $d'=1.05$, while mean performance for the eye that would not be trained was $d'=1.20$. For normal observers, the to-be-trained eye averaged $d'=1.77$ before training, while the eye that would not be trained averaged $d'=1.76$. Overall, for both eyes, prior to training, normal observers showed somewhat better direction discrimination than did stereoblind observers, $d'=1.77$ vs. 1.13 , respectively ($t=1.83$, $df=12$, $p<.05$).

To examine the effects of training, we did an ANOVA on each observer's performance on the first and last days of the experiment. As expected from our previous experiments, performance was appreciably better on the last day of the

experiment as compared to the first day ($F=32.80$, $df=1,12$, $p<.001$). Also, the ANOVA showed that practice had a differential effect, improving performance with the trained eye significantly more than performance with the untrained eye ($F=8.49$, $df=1,12$, $p<.01$). However, this asymmetry of practice's effect, on trained versus untrained eyes, was comparable for both groups of observers ($F=0.06$, $df=1,12$, $p>.50$).

The ANOVA confirmed that after training eyes that had been trained gave slightly better direction discrimination than did eyes that were not trained. In particular, the average trained eye went from $d'=1.46$ to $d'=3.06$; the average untrained eye went from $d'=1.52$ to $d'=2.68$.

Although the ANOVA substantiated that the trained eye improved significantly more than did the untrained eye, it is clear that practice had a non-negligible effect on the untrained eye as well. We can consider the difference between the two estimates of improvement -- improvement in the trained eye and improvement in the untrained eye -- to provide an estimate of the interocular transfer of practice. Further, we can estimate the amount of such interocular transfer by taking the ratio between two quantities: in the numerator, the amount of improvement (change in d') for the untrained eye, and, in the denominator, the amount of improvement for the trained eye. This ratio suggests that about 72% of the monocular training is transferred to the other, untrained eye. Putting this result somewhat differently, the effect of training seems to have a monocular component as well as a binocular one, though the latter is considerably larger.

Finally, the amount of interocular transfer in this experiment is comparable to the interocular transfer reported by Price and Keck (1982), in their studies of the motion aftereffect with normal observers. In addition, Price and Keck reported that some, but not all, types of strabismics, showed about as much interocular transfer as did their normal observers.

The previous experiment showed that a significant portion of discrimination training transferred interocularly. This suggests that at least some of the training involves neurons that are influenced by both eyes. Anatomically, then, at least a portion of the training effect involves neurons that are in or beyond the primary visual cortex (V1), where binocular interactions are first seen in the primate visual system. The present experiment sought to localize the neural site of our effect, by determining whether training might be restricted to the trained hemisphere. To answer this question we took advantage of the fact that stimuli in the left and right visual hemifields project to different hemispheres of the cerebral cortex. In particular, stimuli to the left of fixation, project to the right hemisphere, and stimuli to the right of fixation project to the left

hemisphere.

This experiment had two other, subsidiary purposes. First, we wished to compare the cortical hemispheres' relative abilities to mediate discriminations of direction. Previous research on other spatial tasks --including orientation discrimination-- suggested a slight, but statistically significant right hemispheric superiority for various spatial tasks (Kimura, 1973). Second, evidence of hemispheric localization of training, would make it difficult to explain the training effect in terms of processes that are not hemispherically restricted, such as some generalized, cognitive change over time.

Fourteen new observers were tested. All had normal visual acuity and normal stereoacuity (as assessed by the Orthorater). Observers were tested monocularly, using only their right eyes.

Stimuli and apparatus remained the same. The observers were seated so that the display's center lay directly in front of the right eye. Thus, when the observer fixated a small, black cross located 15 degrees to the right of the display, the display was imaged on the nasal half of the right retina, from which information would first project to the right hemisphere. When the observer fixated a small, black cross 15 degrees to the left of the display, the moving stimulus was imaged on the temporal half of the right retina, from which information would be first project to the left hemisphere.

Each observer was assigned one training direction (either 90 degrees [upward], or 180 degrees [leftward], and was assigned one position of fixation point for use during training (either 15 degrees to the right or 15 degrees to the left of the center of the display). On day one of the experiment each observer were tested in four conditions, defined by the combination of 90 and 180 degree directions of movement together with fixation either 15 degrees to the left or 15 degrees to right of the display. Each of these four test conditions was presented in a block of 50 trials. Twelve blocks were run on days One, Four and Seven, with three repetitions of each condition randomly presented on each of those days.

On the remaining days of the experiment --second, third, fifth, and sixth-- each observer received training on his or her particular condition of training. On these training days observers practiced the discrimination task for fifteen blocks of 50 trials each with their assigned direction of movement and assigned fixation point.

Our main concern was whether improvement in the trained direction would transfer between the trained- and the untrained-hemispheres. Specifically, we wanted to know whether performance on the training direction would differ with congruity of fixations during training and test. To answer this question,

we did an ANOVA on each observer's performance with his or her particular training direction.

As expected from our previous experiments, the overall effect of day of training was statistically significant ($F=12.93$, $df=2,26$, $p<.001$). Moreover, congruity of test- and training-fixation significantly affected discrimination ($F=72.12$, $df=1,13$, $p<.001$). Finally, the interaction between a) day of training and b) congruity of fixations was also significant ($F=29.19$, $df=2,26$, $p<.001$).

The significant interaction in the ANOVA indicates that training produces a greater effect when training and test fixations are congruent than when the two fixations are noncongruent. So, when training and test stimuli project to the same hemisphere (congruent fixations), discrimination improves significantly more than when those stimuli projects to different hemispheres (non-congruent fixations). We wondered, though, whether non-congruent fixations produced any practice effect at all. A t -test on data from each observer's training direction showed that discrimination with non-congruent fixation on the last day of training did not differ significantly from discrimination with non-congruent fixation on the first day of training ($t=0.41$, $df=12$, $p>.50$). So, when test and training fixations are non-congruent, and hence test and training stimulation goes to opposite hemispheres, direction discrimination does not improve. The benefits of training, then, appear to be restricted to the hemisphere that receives the training.

Turning to another issue, we were interested in comparing the two visual hemispheres' respective capacities for mediating direction discrimination. Recall that results by others suggested that the right hemisphere enjoyed a privileged status as a processor of spatial information. Our results, however, show that both directions of fixation, and hence both hemispheres, produce comparable direction discrimination. Overall, before practice, the mean d' achieved while fixating to the display's right was 0.77; mean d' achieved while fixating to the display's left was 0.79. This difference was not statistically significant ($t=-0.064$, $df=12$, $p>.50$). Thus, there is no evidence of an initial, right-hemisphere superiority in direction discrimination.

Finally, the average performance in this experiment was well below average performance in our previous comparable experiments. For example, before practice, the mean value of d' for the present experiment was only 0.75, compared to a value of 1.63 in Experiment 1. The reduced performance observed here is most likely the result of the eccentric fixation that our experimental design demanded of observers.

One other study has measured direction discrimination at different retinal eccentricities. Pasternak and Merigan (1984) tested one observer with a moving-dot display presented both in central viewing and with the display some 16 degrees

above fixation. Two of their findings are particularly relevant here:

first, the lowest direction threshold achieved with various velocities was the same for central and eccentric viewing; second, for many stimulus velocities, direction discrimination was considerably poorer with eccentric viewing than with central viewing. The present experiment used just one stimulus velocity, which would probably not produce asymptotically small difference thresholds. Consequently, Pasternak and Merigan's results support the suggestion that eccentricity of viewing accounts for the relatively low d' values obtained in the present experiment. To summarize the findings and implications of the six experiments on motion training:

1. The training effect is directionally-selective. It is restricted to the direction trained, and, to a lesser degree, to directions that are similar to the training direction. While directions that differ from the training direction by just 45 degrees do evince some improvement, with larger differences still no improvement is seen. In the limit, the direction opposite the training direction shows no improvement.

2. The training effect endures for quite some time. Following the termination of training, the improvement is maintained for at least 10 weeks with no discernible decrement.

3. Improvement for direction discrimination does not affect motion perception generally. In particular, direction-training has no effect on thresholds for motion detection.

4. Feedback following every trial makes a difference, but only for oblique directions where the initial performance is much worse to begin with.

5. Normal and stereoblind observers showed comparable improvements in direction discrimination. Also, both classes of observers show comparable, large amounts of interocular transfer of training.

6. The effect of training is restricted to the trained hemisphere. There were no differences found, however between the left and right hemispheres either for initial performance or for susceptibility to training.

Altogether, over various experiments, we trained several dozen different observers to discriminate directions of motion that differed by three degrees. Improvement was nearly universal among our observers.

Relation to other work on perceptual learning. Although the literature on perceptual learning is large, very few studies in that literature are close relatives of our own. Restricting the focus to vision studies, and further to studies that make use of signal detection procedures, we find the field narrowed to three studies: Mayer (1983), McKee and Westheimer (1978), and Fiorentini and Berardi. Of these,

only Fiorentini and Berardi's study, of grating waveform discrimination, examined enough different conditions of training and transfer to allow meaningful comparisons with our own findings.

Fiorentini and Berardi (1981) allowed observers to practice discrimination of briefly-flashed, binocularly-viewed complex gratings. Performance was defined in terms of percent correct responses in a two-alternative forced-choice procedure. Though improvement in discrimination appeared to be much more rapid than that found in our experiments, the more rapid approach to asymptotic performance could have resulted from the narrow range of performances of performance achievable in their experiments. Most observers, in most conditions, had an initial performance of about 75% correct; the highest attainable performance was 100% correct.

Rapidity of training aside, though, improvement in grating-waveform discrimination shows stimulus selectivity that can be compared to selectivity with direction-discrimination training. In particular, improvement in waveform-discrimination failed to transfer to gratings that differed from the trained spatial frequency by an octave; improvement also failed to transfer to gratings whose orientations differed from that of the training gratings by 90 degrees. Smaller differences, on either dimension, allowed observers to manifest some fraction of the improvement generated at the training orientation and spatial frequency.

Consider finally the question of interocular transfer. Although no details are given, Fiorentini and Berardi do remark that "Complete interocular transfer of the effects of training was found in four subjects tested." (p.1157) In contrast, although one experiment in our series showed considerable interocular transfer, a statistically significant component of discrimination practice failed to transfer between eyes.

The nature of perceptual improvement. Exactly what is the change that discrimination training produces? A refined description of the discrimination-training effect requires that we consider two general views of perceptual learning. One view holds that perceptual learning is largely a matter of increased differentiation -- after learning, stimuli are distinguishable that were not so before. Improvement in performance, then, results from an increased ability to recognize subtle differences between directions. For our paradigm, this view implies that practice increases the proportion of Different trials that our observers judge correctly.

But, of course, this is not the only possible view. After all, from one presentation to the next, a fixed stimulus generates sensory responses that vary somewhat. Take two examples. Andrews (1967) has shown that the perceived orientation of a briefly presented line fluctuates from one presentation

to the next. Similarly, the direction in which a briefly presented pattern appears to move varies somewhat between trials (Ball, Sekuler and Machamer, 1982).

In experiments on direction discrimination, such as the ones described here, random fluctuations in perceived direction could occasionally cause the identical directions presented on Same trials to appear different from one another. As a result, an observer would have to learn not to respond "different" every time the two presentations in a trial did not appear perfectly identical. He or she would need to learn by how much sensory events must differ in order for their difference to be diagnostic of the fact that two different stimuli had been presented. More specifically, this view predicts that performance improves because of a reduction in frequency with which an observer mistakenly judge Same trials as "different."

As the preceding paragraphs suggest, improved direction discrimination could have arisen either from increases in the proportion of Different trials that observers correctly classify, or from decreases in the proportion of Same trials that observers incorrectly classify, or both. Elsewhere, we tested these alternatives using data from training of direction discrimination in observers of different ages (Ball and Sekuler, in press). The data, which will not be presented in detail here, were collected from nine older (mean age=68 years) and eight younger observers (mean age=21 years). Employing stimuli and methods like those used here, we trained observers with two and four degree separations between directions of motion (as compared to three degrees in most of the present experiments).

We compared the relative changes in two conditional probabilities that, together, determine d' --these probabilities are $\text{Pr}(\text{"different"}/\text{Different})$ and the $\text{Pr}(\text{"different"}/\text{Same})$. Figure 9 shows how each of these conditional probabilities changes with training. The lefthand panel shows the results with one training separation (2 degrees), while the righthand panel shows the results with the other training separation (four degrees). Data are for each observer's training direction. To linearize the data, probabilities have been expressed as standard, normal scores (z -transformed).

Note that upper and lower curves in each panel are virtually mirror images of one another. This horizontal symmetry shows that both views of perceptual learning (summarized above) have some rightful claim on truth: observers improve equally in two different ways, with $\text{Pr}(\text{"different"}/\text{Different})$ increasing at just about the same rate that $\text{Pr}(\text{"different"}/\text{Same})$ decreases. The influence of age on direction discrimination, which is also suggested by the figure, has been discussed fully elsewhere (Ball and Sekuler, in press).

Possible neural loci of training. One goal of our study was the characterization of the neural substrate for adult

perceptual plasticity. In this regard, three results are of particular importance:

1. The effect of practice is directionally-selective, but does affect, in some measure, performance with directions that are as much as 60 degrees away from the training direction (see, Experiments 1, 2, and 5).

2. Although the effect of training shows considerable interocular transfer, a non-negligible component of that effect fails to transfer between trained and untrained eyes.

3. When the training stimulus projects to one cerebral hemisphere, the effect of training is not accessible to the other, untrained hemisphere.

Taken together, these results support the following interpretations:

1. Training alters the properties of neurons whose responses are directionally selective, but relatively broadly-tuned for direction.

2. The major effect of training is upon units that receive inputs from both eyes. Hence, training must influence neural units that lie at or beyond the point of binocular combination in the visual system.

3. Training involves a neural locus that has a representation of just one visual hemifield. Such a neural locus would be prior to significant callosal inputs from the contralateral hemisphere.

With these constraints in mind, we can speculate about the neural locus, or loci, of the training effects reported in this paper. Both the first and second implications given above --direction selectivity and binocular sensitivity-- implicate some area of the visual cortex, since earlier stages of the primate visual system show neither direction selectivity nor binocular sensitivity. As the excellent review by van Essen and Maunsell (1983) showed, the primate visual cortex covers quite a bit of territory, including at least a dozen different projection sites beyond Area V1, the initial cortical projection site. In fact, van Essen and Maunsell suggest that virtually the entire posterior half of the primate cortex may be involved in processing visual information.

But it is possible to specify the possible neural locus of the training effect with any greater precision? Although considerable uncertainty remains, one interesting candidate is the middle temporal visual area (MT). Lying in the posterior bank of the superior temporal sulcus, area MT receives a projection from V1, the striate cortex, and contains

a preponderance of neurons that respond selectively to direction of visual motion in the contralateral field (Maunsell and Van Essen, 1983). Moreover, all neurons that have been studied in area MT respond only to stimuli presented to the contralateral visual field.

Electrophysiological recordings from a great many MT neurons led Maunsell and Van Essen to comment that "the width of the average tuning curve for MT is consistent with the spread of effects seen in studies of adaptation of human direction sensitivity... and masking by directional noise..." (1983a; p.1145). In other words, many MT neurons exhibit directional selectivity that is similar to that revealed in humans by psychophysical techniques in humans, and are consistent with the directionally-selectivity shown by the present experiments on discrimination training. In addition, the strong binocularity of most MT neurons (Maunsell and Van Essen, 1983b) is consistent with the ease with which the effects of discrimination training transfers between eyes.

Though these parallels are suggestive, there remains a large gap between psychophysics and physiology of motion perception. Recently, however, behavioral experiments with macaque monkeys closed an important part of that gap.

Using ibotenic acid to create small chemical lesions in MT, Newsome and his colleagues demonstrated a disruption in the initiation and control of eye movements made in response to moving targets (Newsome, Wurtz, Dursteller and Mikami, 1985). No disruption was found, however, with stationary targets. In addition, the deficits appeared to result from disruption of visual motion processing rather than from disruption of eye movements. These observations strengthen the idea that MT plays a major role in motion perception. We hope that our own psychophysical results will encourage others to undertake behavioral and physiological studies of MT, and other areas, in an effort to identify the locus of the training effects described here. But whatever the ultimate locus of our effect, we believe that direction-discrimination training provides an excellent arena within which to test competing theories of perceptual learning.

**WORK UNIT TWO:
VISUAL MOTION IN STATISTICALLY DEFINED DISPLAYS**

Stimuli that are perceptually indistinguishable even though physically different are called metamers. The existence of metamers has been thoroughly exploited in the psychophysical exploration of color vision. But, in principle, metamers can be used to investigate any sensory dimension for which information is processed by bandlimited neural filters (Richards, 1979). Two facts make this approach particularly well suited to the study of the perception of visual motion. First, information about visual motion appears to be processed by bandlimited mechanisms selectively sensitive to different directions of motion (Sekuler, Pantle and Levinson, 1978). Second, it's already been shown that motion metamers can be produced if one adds together appropriate patterns that move in different directions. In such stimuli the components, which lose their individual identities, generate a percept of global coherent unidirectional motion (Adelson and Movshon, 1982; Levinson, Coyne and Gross, 1980; Williams and Sekuler, 1984).

In color vision, spectrally broad-band light, such as sunlight, can be perceptually matched by the sum of only a few suitably chosen spectrally narrow-band lights. Demonstrations of metamerism lent crucial support to the hypothesis that color information is processed initially by means of a few independent mechanisms selectively sensitive to light in somewhat different, but overlapping spectral regions. With color metamerism in mind, we set out to examine analogous metameric relations between patterns composed of a broad-band of directions of motion and patterns containing only a discrete number of directions. The aim of our experiments was to determine how few directions would have to be added together in order to be perceptually indistinguishable from a broad-band pattern of a particular bandwidth.

To anticipate, the results suggest that motion perception is analogous to color vision: a surprisingly small number of discrete directions yield a metameric match to the percept of motion generated by a broad-band of directions. Moreover, our results are consistent with the idea that motion perception depends on only twelve, evenly spaced, direction-selective mechanisms each with half-amplitude, half-bandwidth of 30 degrees.

Our displays were dynamic random-dot cinematograms in which each dot took an independent, two dimensional random walk of constant step size. Though all dots travelled the same distance from frame to frame, the directions in which each dot moved was independent of the directions in which the other dots moved. Moreover, the direction

in which one dot moved between successive frames was independent of the directions in which it had moved previously. Allowing dots' movements to vary in this way produced a stimulus in which many different local motion vectors were spatially and temporally intermingled.

For any stimulus, the set of directions in which all dots moved was chosen from the same probability distribution, which could be either a uniform distribution or a multinomial distribution. A uniform distribution of dot directions produced a cinematogram containing a broad-band spectrum of directions; the spectrum's bandwidth was defined by the range of the uniform distribution. As indicated below, such broad-band patterns can generate a percept of global coherent unidirectional flow along the mean of the distribution (Williams and Sekuler, 1984). A multinomial distribution of dot directions produced a cinematogram containing only a discrete set of directions. When the multinomial distribution was composed of a sufficient number of directions, a global percept resulted that proved to be indistinguishable from that produced by a broad-band pattern.

If motion information is processed by direction-selective, bandlimited mechanisms, the minimum number of directions that suffice to match a stimulus containing a broad-band of directions helps to define the number of different direction-selective mechanisms in the visual system (Richards, 1979). For any bandwidth, however, an exhaustive search would be required to guarantee that the minimum number of matching directions had actually been found. Such a search would have to examine an infinite set of stimuli in which not only the number of discrete component directions varied, but the particular identity of component directions was varied as well. To say the least, this type of search would be enormously time consuming. In our experiments, therefore, we restricted the set of discrete stimuli to only those stimuli constituted according to the following algorithm. For any broad-band stimulus with bandwidth, B degrees, a discrete stimulus containing N directions was constructed such that the directions were aligned symmetrically about the center direction of the broad-band pattern, with the separation between any two adjacent component directions given by

$$\text{Separation} = B/N. [1]$$

With this algorithm the directions in each discrete stimulus span the bandwidth, B , of the broad-band stimulus. Further note that as the number of directions in the discrete stimulus increases the discrete stimulus more closely approximates the broad-band stimulus.

For broad-band stimuli of various bandwidths we determined the minimum number of directions, N_m , constituted according to the algorithm, that would match each broad-band stimulus. Note that any empirical value of N_m is not necessarily the absolute obtainable minimum since we are not considering

all possible combinations of number and identity of directions for the discrete stimuli. Thus, by itself, a single empirical value of N_m cannot be an reliable guide to the number of underlying^m psychophysical mechanisms. However we can ask what form the underlying structure of bandlimited mechanisms would have to take in order to best account for such a result. Structural features include the number of differently tuned mechanisms, their shape, bandwidth and number. Once a preliminary model had been derived to account for a restricted set of matching data we would test that same model's ability to account for additional data. By requiring it to account for results at several different bandwidths simultaneously, any model is given a very stringent test.

The choice of bandwidths to be studied was based on results reported by Williams and Sekuler (1984). Their experiments measured the probability of seeing coherent global unidirectional flow in the direction of the mean of the uniform distribution as a function of the range, or bandwidth, of the distribution. When the bandwidth was smaller than 180 degrees, observers saw directional flow along the mean 100 percent of the time; when the bandwidth was larger than approximately 270 degrees, observers did not see coherent unidirectional flow. For the present study we decided to work with bandwidths between these two extremes. Within this range the probability of seeing coherent, unidirectional flow changes most rapidly with bandwidth --small changes in bandwidth producing strikingly different percepts of global coherent motion. By appropriate selection, then, it should be possible to choose a set of bandwidths, such that each will generate a coherent global motion percept that is distinguishable from the percept produced by the others. Altogether, six different bandwidths were used in this study. First we tested with bandwidths of 210, 226, 240, 256 and 270 degrees; the study was completed by testing at 180 degrees. In all cases, the center direction of the broad-band stimulus was upward.

The displays were generated by a PDP 11/34 computer that passed values through a digital-to-analog converter for display on a Hewlett Packard 1321A X-Y display with a P31 phosphor. A "wrap around" scheme caused dots to disappear when displaced beyond the boundary of the display and then reappear at the opposite sides of the display. A cardboard mask restricted the visible pattern to a circular region 16° diameter. Observers fixated the center of the screen; viewing was monocular, with the other eye occluded by a translucent eye patch. No fixation point was used since it might provide a reference for judging the direction of nearby local motion vectors and we did not want the observers to base their response on only a restricted region of the display.

Each dot measured 0.1° in diameter. The spatial density

of dots was 1.6 dots/deg^2 . From one display frame to the next each dot was displaced by 0.9° . Frame duration, the time required to present all the dots once, was 9.0 msec; the interval between frames was 95.0 msec. Total stimulus duration was 1.0 second, during which 11 frames were presented. For a more detailed discussion of the stimulus' spatial and temporal properties, see Williams and Sekuler (1984).

The display itself provided the only luminance in the room and observers adapted to the light level of a blank screen for five minutes before starting an experimental session. At the beginning of each session the threshold luminance for seeing stationary dots was established using a von Bekeesy tracking procedure (Tynan and Sekuler, 1977). Thereafter, each dot in the patterns was maintained at twice threshold luminance.

A two-alternative forced-choice procedure was used to determine when a pattern with a discrete set of directions perceptually matched a pattern containing a broad-band of directions. The trial structure consisted of two stimulus representations, each 1.0 second in duration and separated by a 4.0 second interstimulus interval. On half the trials, randomly chosen, the broad-band stimulus was presented first, followed by the discrete stimulus; on the other trials, this order was reversed. After both intervals, the observer tried to identify the interval that had contained the discrete stimulus. A computer generated sound informed the observer when the response had been correct. A session consisted of 40 trials.

For each bandwidth of broad-band stimulus we begin by testing with a discrete stimulus containing a small number of components, typically five. After collecting data in at least nine sessions, we continued testing at that same bandwidth, but with a discrete stimulus to which one more component direction had been added. Again, nine sessions were run. Thereafter, we continued to increase the number of directions in the discrete stimulus, and run a new set of nine sessions, until a statistical criterion (see below) confirmed that the observer was not able to discriminate discrete from broadband stimulus. Once that criterion was reached, two more sets of nine sessions were run with that same bandwidth: in these final sets, the discrete stimulus contained first one and then two more components than previously.

On the assumption that our two-alternative forced-choice procedure reflects binomial random variability, we calculated the percent correct performance below which one can be 95% confident that the observer could not discriminate between broad-band and discrete stimuli. This confidence level, at 55% correct over nine sessions, provided a convenient benchmark for deciding when an observer was or was not able to make the discrimination. Three observers have been tested.

With bandwidths of 210, 226 and 240 degrees, as the number of directions in the discrete stimulus increases, the observer's ability to distinguish between broadband and discrete stimuli decreases. For each bandwidth we identified the minimum number of directions, N_m , that produces confusion with the broad-band stimulus (N_m was defined by the first data point that fell below the 95% confidence limits). For each of the bandwidths, 210, 226 and 240 degrees, N_m was eight. For a bandwidth of 256 degrees, however, $N_m=10$. Apparently, although the increase in bandwidth from 210 to 240 had no effect on N_m , an increase in bandwidth of 16 degrees from 240 to 256 increases N_m substantially. Moreover, a further increase in the bandwidth, this time by 14 degrees (from 256 to 270 degrees), caused N_m to decrease, back to nine. So for the five bandwidths tested, N_m was a non-monotonic function of stimulus bandwidth.

The results just described imply that the separation between directions in a discrete stimulus that just produces a perceptual match is, like N_m , a non-monotonic function of stimulus bandwidth. According to the rule for constructing discrete stimuli, the separation between adjacent directions is a function of both the bandwidth of the broad-band stimulus and the number of directions in the discrete stimulus (see Equation [1]). No single separation between discrete directions produced confusion for all bandwidths. With bandwidths of 240 and 270 degrees, a separation of 30 degrees was required. For each of three bandwidths, 210, 226 and 240 degrees, N_m is constant at eight, but the separation between discrete directions increases from 26.5 to 30 degrees, with increasing bandwidth.

Structure of the Model. As stated before, our objective was to develop a formal model for motion perception that could account for the perceptual matches, and non-matches, between broad-band stimuli and stimuli containing discrete directions. The model assumes that there are only a small number of bandlimited mechanisms, each selectively sensitive to a particular range of directions. The sensitivity profile of each mechanism is assumed to be Gaussian and all mechanisms are assumed to have the same bandwidth. The choice of a Gaussian profile is supported by studies of subthreshold summation between moving stimuli (Wilson, in press).

For the i^{th} mechanism centered at direction of motion θ_i , the sensitivity to direction of motion θ is given by

$$S_i(\theta) = \exp\{-[\theta - \theta_i]^2 / h^2 \ln 2\}. \quad [2]$$

where h is the half-amplitude half-bandwidth of the mechanism. The mechanisms are assumed to be evenly spaced as far as their center directions are concerned, with center-to-center separation between adjacent mechanisms equal to the half-amplitude half-bandwidth. Note that for this scheme, once the number of mechanisms, M , is chosen, the bandwidth is fixed and hence the center-to-center separation.

The response of the i^{th} mechanism to a stimulus containing a distribution of directions of motion, $D(\theta)$, is given by

$$R_i(D) = S_i(\theta) \text{pr}\{D(\theta)\}, \quad [3]$$

where $S_i(\theta)$ is the sensitivity of the i^{th} mechanism to direction θ , and $\text{pr}\{D(\theta)\}$ is the proportion of dots in distribution $D(\theta)$ that move in direction θ . To predict the discriminability of two distributions, one, $D_1(\theta)$, with a discrete number of components, and the other, $D_2(\theta)$, with a broadband of components, we first determine the difference in each individual mechanism's response to the two patterns:

$$\Delta R_i = R_i\{D_1(\theta)\} - R_i\{D_2(\theta)\}. \quad [4]$$

We then pool the individual mechanisms' differences in response, using a Q^{th} norm rule:

$$\Delta R = \left(\sum_{i=1}^M |\Delta R_i|^Q \right)^{1/Q}. \quad [5]$$

where M is the number of mechanisms. This pooling formula allows for possible effects of probability summation (Quick, 1974). ΔR represents the overall, effective difference between the responses the two stimuli evoke within the visual system. Q determines the way response differences, ΔR_i , within individual mechanisms will be combined. With $Q=1.0$, all values of ΔR_i are given equal weight. Hence the system behaves as though it were taking a simple sum of all values of ΔR_i . With $Q>1$, larger values of ΔR_i are weighted more than smaller values. At the extreme, $Q=\text{infinity}$, the visual system behaves as a peak detector and only the largest value of ΔR_i is taken into account, with all others being ignored.

In order to relate predicted values of ΔR to the empirical results obtained in our 2-alternative forced-choice experiments, we used the psychometric function:

$$\psi(\Delta R) = 1 - 2^{-(1+k/\Delta R)^3}. \quad [6]$$

This function gives a computationally convenient approximation to the cumulative normal distribution (Wilson, 1980). In this formulation, the parameter k is related monotonically to the bandwidth of the normal distribution, and, hence to the bandwidth of noise within the visual system.

As the preceding suggests, our model has three free parameters: M (the number of mechanisms), Q (the exponent of the equation for pooling responses), and k (the bandwidth of noise in the visual system). We chose values for these parameters that would provide the best fit to the discrimination data, using the fewest number of mechanisms, M .

Although the model as described thus far does define the separation between mechanisms as well as the mechanisms' bandwidth, one necessary element has not been considered: what values should be assigned to the mechanisms' center directions. To see what this omission means consider a model with M directionally-selective mechanisms represented on a polar coordinate system. Any rigid rotation of the mechanisms about the center of that coordinate system would leave M , the number of mechanisms unchanged, as well be the bandwidths and separations. A rotation within polar coordinates represents a constant phase shift for all mechanisms. To complete the model's specification, then, one must define the absolute phase of at least one mechanism (only one need be defined

since the phases of mechanisms relative to one another were already specified). A useful way to specify phase is to define the arrangement of the model's mechanisms relative to the center direction, upward, of the broad-band stimuli.

For simplicity we concentrated on just one phase of the mechanisms relative to the center of the broad-band stimulus. In this arrangement of phase, one mechanism's center direction was assumed to be located at the center of the broad-band stimulus. Most of our calculations were done with this arrangement, though, as will be shown later, we did selectively examine two other phase arrangements.

The model gave a predicted psychometric function --relating the probability of discriminating broad-band from discrete stimuli as a function of the number of components in the discrete stimulus. For each broad-band stimulus, of bandwidth B , and each discrete stimulus with N directions, the model predicted the probability of confusion, $PC(B,N)$. Calculations were made with various values of Q and M for each bandwidth of broad-band stimulus.

Testing the Model's Predictions.

In order to identify the best fitting set of parameters we took advantage of the fact that one of our parameters, k , is merely a vertical scaling factor. With k initially fixed at some arbitrary value, we used the model to compute predictions of discriminability for integer values of Q ranging from one to ten and with $M=3$ to 15. Since changes in k shift all of the psychometric, or discriminability, curves up or down en masse leaving invariant their individual shapes or the relation among curves, we sought a set of parameters that would match these invariant features.

To extract the empirical invariants that a model would have to account for, various ordinal relations, or inequalities, in the data were used to express those invariants. The inequalities in a set of predicted values of $PC(B,N)$ were tested against the corresponding inequalities in a set of empirical values of $PC(B,N)$. To understand what is meant by "inequalities," consider the pair of bandwidths 240 and 256 degrees. The empirical values of $PC(240,N_1)$, for all $N_1 < 8$, were greater than the empirical values of either $PC(240,N_2)$, for $N_2 > 8$ or those of $PC(256,N_3)$, for $N_3 \geq 10$. Similarly, empirical values of $PC(256,N_4)$, for $N_4 < 10$, were greater than either the empirical values of $PC(240,N_2)$, for $N_2 > 8$, or than empirical values of $PC(256,N_3)$, for $N_3 \geq 10$. The complete set of empirical data consists of a great many other inequalities as well. We sought a single set of parameters that might account for all these inequalities.

Virtually every parameter set we explored made several erroneous predictions, but results with some parameter sets failed to satisfy just one or two of the inequalities. In

contrast to these failures, large and small, every prediction generated by only one parameter set, with $Q=2$ and M , the number of mechanisms, equal to 12, was successful. We were pleased that $Q=2$ was successful, since in color discrimination the same value of Q has also been used (Graham, 1965; Bouman and Walraven, 1972). Note that twelve mechanisms implies a half-amplitude half-bandwidth of 30 degrees and a center-to-center separation of the same value. Once this parameter set passed the test of predicting all the empirical inequalities we determined the value of the scale factor, k , that would bring all the predicted and empirical curves into best agreement. This value of k is 0.1024.

For three bandwidths, 210, 226 and 240 degrees, the model was consistent with the data: N_m for each broad-band pattern is eight. Consider, now the m largest bandwidths, 256 and 270 degrees. As pointed out earlier, as bandwidth increases from 256 to 270 degrees, N_m decreases from ten to nine. The model's predictions were m consonant with this result.

Since the model was so successful in accounting for results post hoc, we used the same set of parameters to examine the model's predictions for other bandwidths, ones for which we had not collected psychophysical data. Predictions for one bandwidth struck us as distinctly anomalous and, therefore, interesting. For a broad-band stimulus of bandwidth 180 degrees, the model with $M=12$ and $Q=2$ predicts that while six components would match the broad-band stimulus (that is, $N_m=6$), with an increase in the number of discrete components, m to seven, the match achieved with six components would no longer hold. In other words, unlike the other cases we had worked with, for a stimulus of 180 degrees bandwidth the predicted psychometric function should be non-monotonic. To give the model a further strong test we collected discrimination data with a broad-band stimulus of 180 degree bandwidth.

Again, when we compared the predictions to empirical results, the two were in agreement: the minimum number of directions required for a perceptual match was six. More important, although a stimulus containing six directions cannot be discriminated from the broad-band stimulus, a stimulus containing seven can be discriminated. Those non-monotonic, empirical psychophysical curves are just as the model predicted they would be.

In our discrete stimuli, given sufficient component directions, the identities of the individual components seem to be lost to perception. Faulty registration of correspondences (Braddick and Adlard, 1978) offers one possible explanation: perhaps the visual system simply loses track of the components. However, results with the 180 degree bandwidth stimulus show that this cannot be a full account. Although a discrete stimulus containing

six components, did match the 180 degree broad-band stimulus, adding one more component destroyed the match. This implies that a perceptual match with six directions is not simply a consequence of failed correspondence processes. The matches do not result just from having so many discrete directions that the observer's visual system can not keep track of them individually.

There is, however, an alternative explanation: one might also suspect that confusion occurs because the separation between directions in the discrete stimulus becomes sufficiently small that individual directions can no longer be distinguished. According to Equation [1], for a fixed bandwidth, the separation between adjacent direction of the discrete stimulus decreases with increasing number of directions. Again, the results with bandwidth of 180 degrees falsifies the hypothesis: the finding that six directions produce a match but that seven directions do not eliminates the possibility that confusion is caused by too small a separation between directions in the discrete stimulus.

Motion perception, then, seems to resemble color vision: in each, a small number of narrow-band components sum to yield metameric matches to broadband stimuli. More particularly, in motion perception, several directions can be summed to match the percept of motion generated by a broad-band of directions of motion. However, since color and motion stimuli differ in important ways one must be cautious in interpreting what this analogy may mean for direction-selective mechanisms of motion perception. For color, all of the stimulus' spectral components can be superposed at the same spatial location and at the same time. This is not true for our moving stimuli. First, each stimulus is only a random sample of a predefined distribution of directions of motion. Second, the sample is randomly distributed both in space and time over the visual field. In other words, the particular local motion vectors present at any moment may differ from one spatial location to the next, and the vectors present at any single spatial location may vary from moment to moment.

Richards (1979) has used the term "quasi-metamer" to describe pairs of stimuli that are perceptually indistinguishable but at the same time are samples drawn from two different stimulus populations. Conclusions based on quasi-metameric matches reflect population properties; that is, the results represent a sum of the properties of all mechanisms stimulated by the quasi-metameric display. The visual field covered by the display in our experiments is a disk shaped region 16° in diameter and the properties of direction-selective mechanisms may not be homogeneous over this large spatial extent. In fact there is some evidence that certain aspects of motion perception do vary with retinal eccentricity. For example, estimates by Richards

(1971) suggest that the size of motion detection mechanisms increase with regional eccentricity. Also, detection of coherent movement for a random dot pattern varies with retinal location (van de Grind, van Doorn and Koenderink, 1983). One of the studies proposed herein will examine possible regional variation in direction-selective mechanisms.

At present, though, no experimental results tell us how retinal location might affect direction-selectivity. Neglecting complications that would be introduced by spatial inhomogeneities, our results can be accounted for by assuming only twelve such mechanisms at each retinal location.

As indicated before, the best fitting model was one containing twelve mechanisms, each with 30 degree half-bandwidth at half-amplitude. If one substitutes $M=11$ or $M=12$ into the model, in place of $M=12$, changing the number of mechanisms by only one, the model can no longer account for the results. With eleven mechanisms, the model is consistent with the data for the four smallest bandwidths used, but incorrectly predicts $N_m=8$ for the 256 degrees bandwidth and $N_m=12$ for a bandwidth of 270 degrees. Thirteen mechanisms give predictions that are generally consistent with the data, but fail with bandwidths of 180 and 270 degrees. A model with thirteen mechanisms predicts $N_m=8$ for both these cases.

Variations in Phase. Thus far, our model has assumed one phase relation for the psychophysical mechanisms: for all values of M that we examined we always allowed the center direction one mechanism to be upward, the center direction of the broadband stimulus. Quite naturally, we wondered how the predictions of the model might be altered if other phase relations were introduced. To answer this question we examined two arrangements. In one, the mechanisms were aligned such that the center of the broad-band stimulus was midway between two adjacent mechanisms. Like the case we studied in more detail (one mechanism centered at upward), this arrangement also postulates mechanisms that are symmetrically aligned with respect to the center of the broad-band stimulus. The other case we examined involves an asymmetric alignment of mechanisms relative to the center of the broad-band stimulus. For this last arrangement the mechanisms were situated so that the center of the broad-band stimulus is $1/4$ of a mechanisms's bandwidth away from the nearest mechanism. Calculated values of N_m were in poor agreement with the empirical data.

For efficiency of covering all directions of motion, our model has assumed that the half-amplitude half-bandwidth of the mechanisms is equal to the center-to-center separation of the mechanisms. With twelve mechanisms, this assumption yields half-amplitude half-bandwidths and center-to-center separations of 30 degrees. If this assumption is relaxed, we find that the data can also be accounted for with 24 mechanisms, providing that the half-amplitude half-bandwidth

is maintained at 30 degrees. The center-to-center separation in this case is 15 degrees. A model incorporating 24 mechanisms, but with half-amplitude half-bandwidths of only 15 degrees provides a poor fit to our psychophysical results.

Watson and Ahumada (1984) recently proposed a model for motion perception consisting of ten direction-selective mechanisms, each with a Gaussian direction sensitivity profile with a half-amplitude full-bandwidth of 38 degrees. We wondered whether their model might be able to account for our metameric matching data. Our calculations show that Watson and Ahumada's model predicts that with a broadband stimulus of 180 degrees discrimination will decline monotonically as the number of discrete components increases, with $N_m=5$. In contrast, our empirical results showed a non-monotonic relation between discrimination and number of components, as well as $N_m=6$. For bandwidths of 210 and 226 Watson and Ahumada's model seems to predict $N_m=6$, while for bandwidths of 240, 256 and 270 the model incorrectly predicts $N_m=8$. In fairness it should be noted that Watson and Ahumada's formulation was derived from results obtained at detection threshold and therefore may not be entirely applicable to suprathreshold stimuli such as those used in our experiments.

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