



Image Segmentation Enhances Discrimination of Motion in Visual Noise

LISA J. CRONER,*† THOMAS D. ALBRIGHT*

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The primate visual system uses form cues—such as hue, contrast polarity, luminance, and texture—to segment complex retinal images into the constituent objects of the visual scene. We investigated whether segmentation of dynamic images on the basis of hue, luminance contrast polarity, or luminance contrast amplitude aids discrimination of motion direction. Human subjects viewed dynamic displays of randomly positioned dots, in which a variable proportion of the dots moved in the same direction at the same speed (“signal” dots) while the remaining dots were randomly displaced (“noise” dots). In agreement with previous reports, we observed a reliable relationship between the strength of the motion signal and subjects’ ability to discriminate motion direction, enabling the measurement of thresholds for direction discrimination. When signal dots had a different luminance contrast amplitude than noise dots, direction discrimination performance was directly related to the relative contrast of the signal dots, demonstrating the importance of matching the perceived contrast amplitude of signal and noise tokens when testing the effects of segmentation by other cues. When Michelson luminance contrast was matched, distinguishing signal from noise dots by hue or by luminance contrast polarity strongly improved direction discrimination, lowering thresholds by an average factor of five. These results reveal a strong influence of form cues on motion processing in the human visual system, and suggest that segmentation on the basis of form cues occurs prior to motion processing. © 1997 Elsevier Science Ltd.

Motion Image segmentation Random dots Psychophysics

INTRODUCTION

Consider the problem of visually tracking a scattered group of people moving in a common direction through a large crowd viewed from above. It is easy to imagine that the problem would be simplified if the target individuals wore a common article of clothing—red hats, perhaps—that distinguished them from the dynamic background. Described in the parlance of perceptual psychology, chromatic contrast forms the basis of pre-attentive “popout” under these circumstances (Treisman & Gelade, 1980; Bergen & Julesz, 1983). Motion processing appears to benefit from the unique visibility of the moving objects and the exclusion of irrelevant dynamic content. This simple example demonstrates a ubiquitous interaction between form cues (cues related to surface properties), hue in this case, and motion processing.

One of the key perceptual events in the above illustration is the grouping of objects that are similar in color to each other, yet different from other objects in the scene. This is an example of image segmentation: the

process of determining what pieces of a complex scene belong together. In general, we might expect that grouping and segmentation of relevant moving objects on the basis of cues that are unrelated to motion *per se* (e.g., color, texture), but that serve to distinguish the objects from others, would facilitate the visual system’s processing of their motion. The finding of such a generalized influence of form cues on motion processing would offer important clues to the neuronal mechanisms underlying form and motion processing. For example, such a finding would provide a significant counterexample to assertions that there are only few and weak interactions between cortical streams thought to underlie form and motion processing (for reviews related to this viewpoint, see Livingstone & Hubel, 1988; Merigan & Maunsell, 1993; Stoner & Albright, 1993). In addition, such a finding would suggest specific neuronal mechanisms by which form cues could influence motion processing. For example, if many cues were found to influence motion perception in the same manner, this would suggest that a generalized form-based segmentation mechanism gates the information about relevant image features reaching cortical motion detectors—a possibility we address in the Discussion.

To study how segmentation influences motion processing, we introduced simple but critical modifications to a

*Vision Center Laboratory, The Salk Institute, 10010 North Torrey Pines Road, La Jolla, CA 92037, U.S.A.

†To whom all correspondence should be addressed [Email croner@salk.edu].

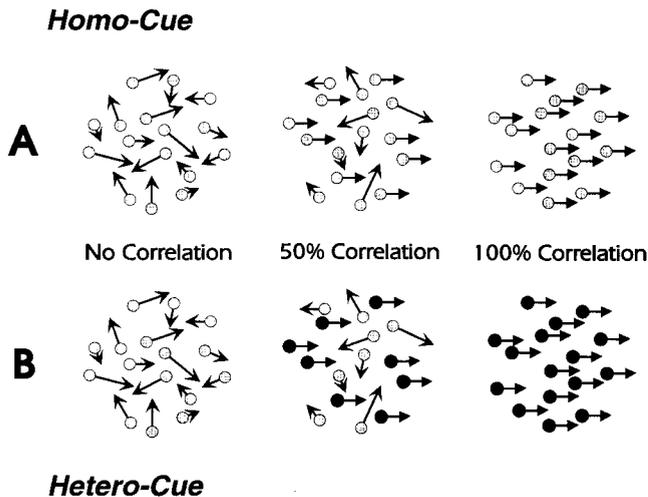


FIGURE 1. Schematic diagram of the motion stimuli used in this study. Each stimulus consisted of a sequence of frames of randomly positioned dots appearing on a CRT screen. Dots in each of the six circular apertures of the figure represent dots in six different stimuli. Arrows show the location of each dot in the next step of the motion sequence, and so represent velocity (direction and speed). (A) In the conventional configuration, which we used as our "homo-cue" condition, all of the dots have the same hue and luminance (shown as gray). The proportion of dots moving in the same direction at the same speed, expressed as "% correlation," describes the strength of the motion signal in the display. On the left, at 0% correlation, all of the dots are replotted at random positions, generating a purely stochastic motion display. In the middle, half of the dots (those with triangular arrowheads) are replotted at a fixed offset, rendering a motion signal of 50% correlation. On the right, all of the dots are replotted with the same offset, giving a motion signal of 100% correlation. (B) For the "hetero-cue" conditions of this study, the dots moving randomly are a different hue or luminance (shown as gray) from those moving in a correlated fashion (shown as black).

visual stimulus and psychophysical paradigm that have been used widely in recent studies of motion processing (Newsome & Paré, 1988; Downing & Movshon, 1989; Newsome *et al.*, 1989; Britten *et al.*, 1992, 1993). In its original guise, the stimulus [Fig. 1(A)] consisted of a dynamic array of dots, some variable fraction of which was displaced coherently in the same direction, while the remaining dots were randomly repositioned. The coherently moving dots thus constituted a motion signal of variable strength that was viewed in the presence of dynamic visual noise. Signal dots were distinguishable from noise dots solely on the basis of these dynamic properties and subjects were required to either detect or discriminate direction of signal motion. Results obtained previously using stimuli like those illustrated in Fig. 1(A) revealed a consistent psychometric relationship between signal strength and performance, with thresholds for human and non-human primate observers ranging from about 2–30% correlation depending on the speed of coherent motion and on the duration, area, and visual field position of the stimulus (Downing & Movshon, 1989; Britten *et al.*, 1992).

Our modified version of this stimulus [Fig. 1(B)] departs from the original only in the use of differences in one of several form cues to distinguish signal dots from noise dots. We predicted that segmentation of the signal

and noise dots on the basis of these cues would lead to a reduction in the signal strength required for threshold direction discrimination by human subjects. If this hypothesis were correct, any cue that allowed grouping and segmentation of the dots would facilitate direction discrimination. While many cues might induce such an effect, the most likely candidates are those that cause an item to popout when viewed in the presence of distracting items (Treisman & Gelade, 1980; Bergen & Julesz, 1983). Here we test our hypothesis when signal and noise dots are distinguished by hue (red vs green: Experiment 1), luminance contrast polarity (whether dots are defined by an increment or decrement of luminance relative to the background: Experiment 2), or luminance contrast amplitude (Experiment 3). We show that, in support of our hypothesis, discrimination improves when signal and noise dots are distinguished either by hue or by luminance contrast polarity. When signal and noise dots have different luminance contrast amplitudes with respect to the background, ability to discriminate signal direction is directly related to the relative contrast of the signal dots, demonstrating the importance of matching the perceived contrast amplitude of signal and noise dots (or other stimulus tokens) when testing the effect of segmentation by any other cue.

Some of these results were previously presented at the annual meeting of the Association for Research in Vision and Ophthalmology (Croner & Albright, 1994).

GENERAL METHODS

Subjects

Six subjects (three women, three men), ranging in age from 18 to 45 years, participated in the experiments. All subjects had normal color vision as assessed by the Farnsworth–Munsell 100 hue test, and normal or corrected-to-normal acuity. One subject was one of the authors (LC); the other subjects were naïve about the hypotheses being tested.

Visual stimuli

Apparatus. Visual stimuli were generated using a digital graphics display controller (Pepper SGT, Number Nine Computer Corporation: 640 × 480 pixels, analog RGB output, 8 bits/gun) installed in a personal computer. Stimuli were displayed on an analog RGB video monitor (14" Zenith ZCM 1490 for Experiment 1, 17" Nanao FlexScan T560i for Experiments 2 and 3, 60 Hz frame rate, non-interlaced).

Control of motion signal. We used a dynamic dot stimulus in which dot positions were manipulated so that a motion signal of variable strength was embedded in dynamic noise (Fig. 1) (e.g. Newsome & Paré, 1988; Britten *et al.*, 1992, 1993). The motion signal was generated by randomly selecting a percentage of the dots ("signal" dots) from each frame to be replotted at a location shifted 0.2 deg in a single direction after a delay of 50 msec [in Experiments 1 and 3 each dot was extinguished during the intervening frames, as in

previous studies (e.g. Britten *et al.*, 1992)], yielding apparent motion of 4 deg/sec. The remaining dots ("noise" dots) were replotted at random positions after the same temporal delay, yielding dynamic noise. There were seven signal strengths used in these experiments, ranging between 0.15 and 8% correlated motion.

Since signal dots were chosen at random in each stimulus frame, individual signal dots were not visible long enough to be tracked by attention or eye movements, or to enable subjects to use dot position cues to infer signal direction. For example, at the highest signal strength used in this study, the vast majority of signal dots appeared for only two frames within a motion sequence, with only 0.64% of the dots expected to appear for three frames.

Stimulus parameters and construction. Stimuli were created in computer memory as sequences of frames for animation. Dot positions varied across experimental sessions. One hundred 0.1 deg-diameter dots were drawn in each stimulus frame so as to appear in a 6.4 deg-diameter circular aperture at the center of the video monitor. If a dot overlapped a previously drawn dot, the second dot replaced the first, yielding an average density of 184 dots deg⁻² sec⁻¹. Signal dot starting positions were constrained so that motion would leave the dots inside the aperture. One sequence of 120 frames (2 sec) was created for each of the seven signal strengths. Rightward motion was displayed by running the animation forward, and leftward motion by running it backward. Each sequence was cyclical, and the starting frame was chosen randomly before each trial. Background was uniform and constant over the entire display during trials and during inter-trial intervals. The hues and luminances of the dots for different experimental conditions were controlled by changing the RGB values of particular dot populations. Luminances (measured with a United Detector Technology S370 Optometer while the monitor displayed dots of the same size and density as those used in the experiments) are described below for each experiment.

Experimental conditions. Two basic stimulus configurations were used: (1) in the *homo-cue* condition, signal dots were defined by the same form cues as noise dots [Fig. 1(A)]; (2) in the *hetero-cue* condition, signal dots were distinguishable from noise dots on the basis of hue (Experiment 1), luminance contrast polarity (Experiment 2), or luminance contrast amplitude (Experiment 3) [Fig. 1(B)]. For some experiments, subcategories of these two basic conditions defined additional conditions (see individual Methods).

Psychophysical procedure

Psychometric functions for direction discrimination were obtained using a two-alternative forced-choice paradigm. Subjects rested their heads against a chin and forehead rest, and were instructed to fixate a gray dot in the center of the display before and during stimulus presentation. Human subjects are capable of reliable fixation under these conditions (Murphy *et al.*, 1975).

Trials were initiated by a keyboard press by the subject once fixation was achieved. Stimulus duration was 2 sec, and the subject indicated perceived direction (left or right) with an appropriate keyboard press at the conclusion of each trial. Performance feedback was provided in the form of a short beep after each incorrect response.

The two critical independent variables manipulated in these experiments were: (1) the configuration of the stimuli (hetero-cue or homo-cue conditions); and (2) motion signal strength. Subjects viewed equal numbers of trials of each trial type (defined by a unique combination of the two critical independent variables) and equal numbers of trials of leftward and rightward motion each day, with trials of different types and directions randomly interleaved. Subjects were initially presented with practice trials until performance stabilized (approximately 2 weeks for most subjects).

Data analysis

For each subject, responses to leftward and rightward motion were pooled to give one data point for each signal strength of each experimental condition. The data were plotted as the proportion of correct responses against the strength of the motion signal (% correlation), for each condition separately. The Simplex curve-fitting algorithm (Nedler & Mead, 1965; Caceci & Cacheris, 1984) was used to fit these psychometric data with the function

$$p = 1 - 0.5e^{-(c/\alpha)\beta}$$

where p is the proportion of correct responses, c is the % correlation of the stimulus, α is the % correlation at which threshold performance (82% correct performance) is achieved, and β is the slope of the curve in the region midway between chance (50% correct) and perfect (100% correct) performance (Weibull, 1951; Quick, 1974). This function yielded satisfactory fits (χ^2 : $P < 0.05$) for all of the performance functions we measured.

For each subject, we performed a statistical test, based on that employed by Britten *et al.* (1992), to evaluate whether the thresholds fitted to the data from a given pair of experimental conditions (e.g., the hetero-cue and homo-cue conditions) were significantly different. For this test we performed maximum likelihood fits of the above function to the data from both conditions, comparing χ^2 from a fit that determined threshold and slope parameters independently for the two conditions with χ^2 from a fit that was constrained to generate the same threshold for the two conditions. If the difference in χ^2 exceeded the criterion value (χ^2 distribution, d.f. = 1, $P < 0.05$) we concluded that the two conditions had significantly different thresholds.

EXPERIMENT 1: HUE

A: Hue as the Sole Segmentation Cue

Experiment 1A tested directly whether segmentation on the basis of hue aids direction discrimination. Each

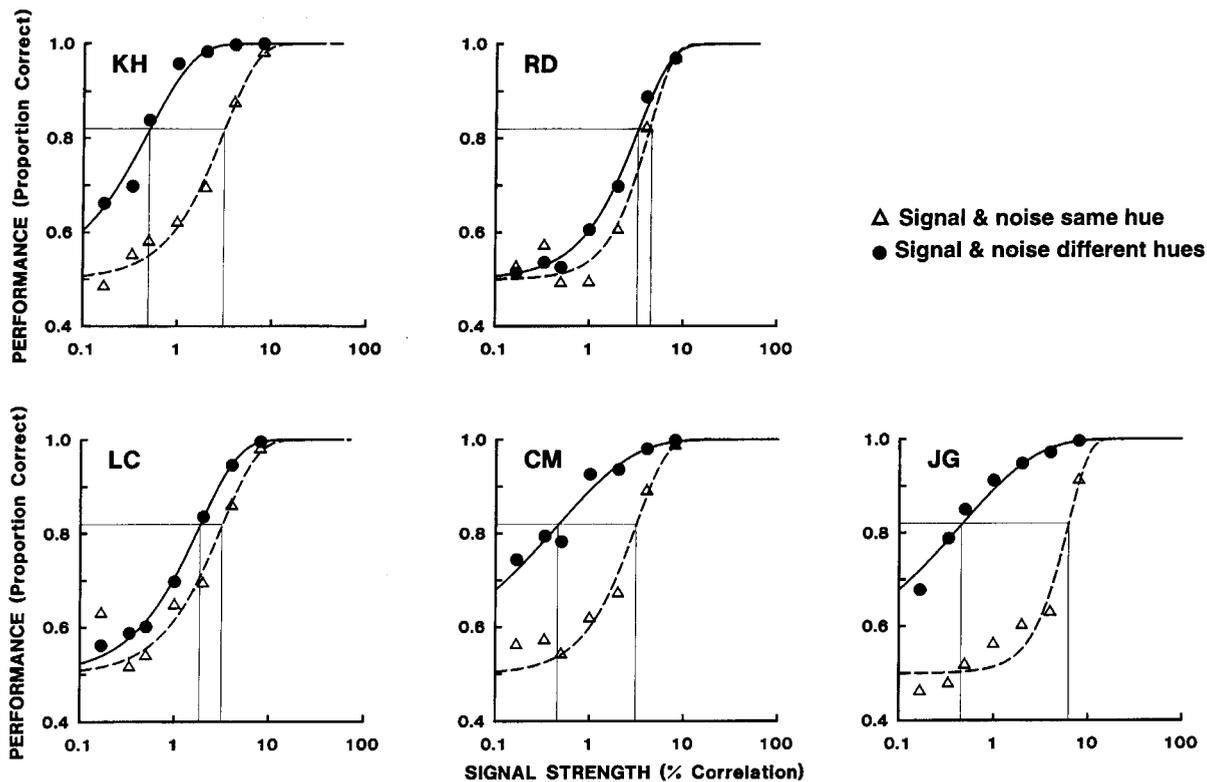


FIGURE 2. Psychometric functions measured for homochromatic (open triangles) and heterochromatic (filled circles) conditions in Experiment 1A. Also shown are curves of the form $p = 1 - 0.5e^{-(c/\alpha)^\beta}$ (see Methods) fit to the homochromatic (dashed lines), and heterochromatic (solid lines) data. In each plot, a thin horizontal line is drawn through threshold performance ($=0.82$). Where this line intersects each psychometric function, a thin vertical line is drawn to intersect the x -axis at the function's threshold signal strength. Number of trials per data point (N), fit thresholds (α_{homo} and α_{hetero}), and fit slopes (β_{homo} and β_{hetero}) for each subject are as follows: KH: $N = 480$, $\alpha_{\text{homo}} = 3.112$, $\beta_{\text{homo}} = 1.224$, $\alpha_{\text{hetero}} = 0.496$, $\beta_{\text{hetero}} = 0.909$. RD: $N = 500$, $\alpha_{\text{homo}} = 4.254$, $\beta_{\text{homo}} = 1.731$, $\alpha_{\text{hetero}} = 3.241$, $\beta_{\text{hetero}} = 1.227$. LC: $N = 500$, $\alpha_{\text{homo}} = 3.162$, $\beta_{\text{homo}} = 1.161$, $\alpha_{\text{hetero}} = 1.835$, $\beta_{\text{hetero}} = 1.042$. CM: $N = 500$, $\alpha_{\text{homo}} = 3.077$, $\beta_{\text{homo}} = 1.346$, $\alpha_{\text{hetero}} = 0.454$, $\beta_{\text{hetero}} = 0.538$. JG: $N = 500$, $\alpha_{\text{homo}} = 6.208$, $\beta_{\text{homo}} = 1.964$, $\alpha_{\text{hetero}} = 0.454$, $\beta_{\text{hetero}} = 0.541$. Each performance function consisted of responses pooled over the last N trials per data point obtained for each subject.

subject's threshold for discriminating direction obtained when the signal and noise dots were the same hue was compared with that obtained when the signal and noise dots were different hues.

Methods

Direction discrimination performance was tested for each of five subjects under two conditions. In the *homochromatic* condition, all dots were either red or green [Fig. 1(A)]. In the *heterochromatic* condition, either the signal dots were red and the noise dots were green, or vice versa [Fig. 1(B)].

The stimulus background was produced by setting all the Zenith monitor phosphors to their lowest setting, resulting in a gray background of luminance 0.5 cd/m^2 . Each dot had a luminance of 15 cd/m^2 , and was produced by modulation of either the red or the green phosphor. The C.I.E. chromaticity coordinates of these phosphors were: R (0.616, 0.336), G (0.316, 0.580). Cone contrast between the background and the dots was dominated by the luminance difference, so that any purely chromatic contrast had a negligible influence on local cone contrast. Our calculations (see Boynton, 1986) indicate that modulation between the red and green phosphors caused

34% M and 14% L cone modulation. Mean luminance over the stimulus aperture during trial presentation was approximately 1 cd/m^2 .

To ensure that the red and green dots were not distinguishable on the basis of luminance, we determined equiluminance for each subject using a form of heterochromatic flicker photometry in the following manner. Subjects viewed static displays of dots that were the same size, density, and extent as those in a single frame of the motion stimuli. With the luminance of the red dots fixed at 15 cd/m^2 , dot hue flickered from red to green at 30 Hz while subjects adjusted the intensity of the green dots in order to minimize perceived flicker. This procedure was performed at least three times, and the average green match to the 15 cd/m^2 red was used for subsequent experiments with that subject. Each subject was also tested using a more conventional heterochromatic flicker photometry procedure involving a solid square, 6.4 deg on a side, flickering from red to green at 30 Hz. This procedure invariably yielded a measure of equiluminance identical to that obtained using our modified procedure. Subjects found it much easier to judge the minimal flicker point when viewing the flickering square stimuli, and

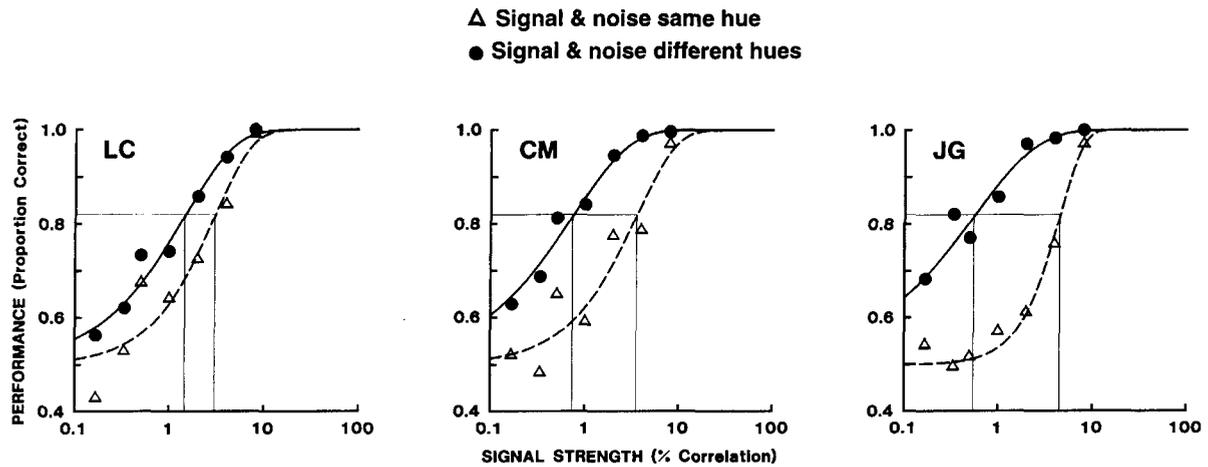


FIGURE 3. Psychometric functions measured for homochromatic (open triangles) and heterochromatic (filled circles) conditions with luminance noise in Experiment 1B. Also shown are curves fit to the homochromatic (dashed lines) and heterochromatic (solid lines) data. Thin solid lines illustrate thresholds, as in Fig. 2. Number of trials per data point (N), fit thresholds (α_{homo} and α_{hetero}), and fit slopes (β_{homo} and β_{hetero}) for each subject are as follows: LC: $N = 240$, $\alpha_{\text{homo}} = 3.021$, $\beta_{\text{homo}} = 1.090$, $\alpha_{\text{hetero}} = 1.449$, $\beta_{\text{hetero}} = 0.808$. CM: $N = 240$, $\alpha_{\text{homo}} = 3.526$, $\beta_{\text{homo}} = 1.015$, $\alpha_{\text{hetero}} = 0.734$, $\beta_{\text{hetero}} = 0.720$; JG: $N = 240$, $\alpha_{\text{homo}} = 4.529$, $\beta_{\text{homo}} = 1.738$, $\alpha_{\text{hetero}} = 0.550$, $\beta_{\text{hetero}} = 0.638$. Each performance function consisted of responses pooled over the last N trials per data point obtained for each subject.

hence we used this procedure periodically to confirm the stability of each subject's equiluminant point.

To prevent subjects from forming an expectation about the hue of signal dots, dot hue was randomly selected by the computer to be either red or green before each trial of the homochromatic condition; and dot hues were randomly selected by the computer to be either red signal and green noise or vice versa before each trial of the heterochromatic condition. Because pilot experiments indicated that performance was the same for red or green signal dots, responses to these complementary signal hues were pooled.

Results

Data from all subjects tested with the homochromatic condition of Experiment 1A are shown in Fig. 2 (open triangles). These data indicate that direction discrimination performance of each subject improved as motion signal strength was increased. Thresholds for the homochromatic condition ranged from 3.1 to 6.2% correlation, and were within the range of psychophysical thresholds reported by others using similar stimuli within a like paradigm (Britten *et al.*, 1992).

Data obtained from all subjects tested with the heterochromatic condition of Experiment 1A are also shown in Fig. 2 (filled circles). The most conspicuous effect of this manipulation was a leftward shift of the psychometric function, resulting in a reduction of threshold for direction discrimination. While the magnitudes of the thresholds and the threshold shifts varied between subjects, our statistical tests revealed a significant difference between the heterochromatic and homochromatic thresholds for each subject. The decrease in threshold varied from 1.3-fold (subject RD) to 13.7-fold (subject JG), being on average 6.0-fold.

B: Hue with Luminance Noise

In spite of our efforts to eliminate all but chromatic cues to distinguish signal and noise dots, dots of different hue might have induced slight luminance differences on the retina, stemming from small errors in our determination of equiluminance and/or from chromatic aberrations introduced by the cornea and lens of the eye. If the red and green dots were not equiluminant, the changes in thresholds observed in Experiment 1A might be due to differences in luminance, rather than hue, of the signal and noise dots. To investigate this possibility we tested three subjects in Experiment 1B, in which the stimuli and task were identical to those used in Experiment 1A with the exception that luminance noise was added to mask consistent luminance differences between the red and green dots. If the threshold reductions found in Experiment 1A were a consequence of the ability to discriminate dot populations on the basis of luminance, we should find no difference between thresholds for the homochromatic and heterochromatic conditions in Experiment 1B.

Methods

Luminance noise was introduced by randomly assigning one-third of the dots to be 12.5 cd/m², a second third of the dots to be 15.0 cd/m², and the final third of the dots to be 17.5 cd/m². Values were reassigned with each temporal frame of the display. The decreases and increases resulted in dot luminances of $\pm 17\%$ relative to the dot luminance in Experiment 1A (while leaving the mean luminance over the stimulus aperture unchanged). The resulting maximum luminance difference among dots of one hue was at least as great as that expected between dots of different hues in Experiment 1A on the basis of chromatic aberrations (Flitcroft, 1989). These luminance variations were readily detected when viewing the stimuli, and effectively masked any unintended

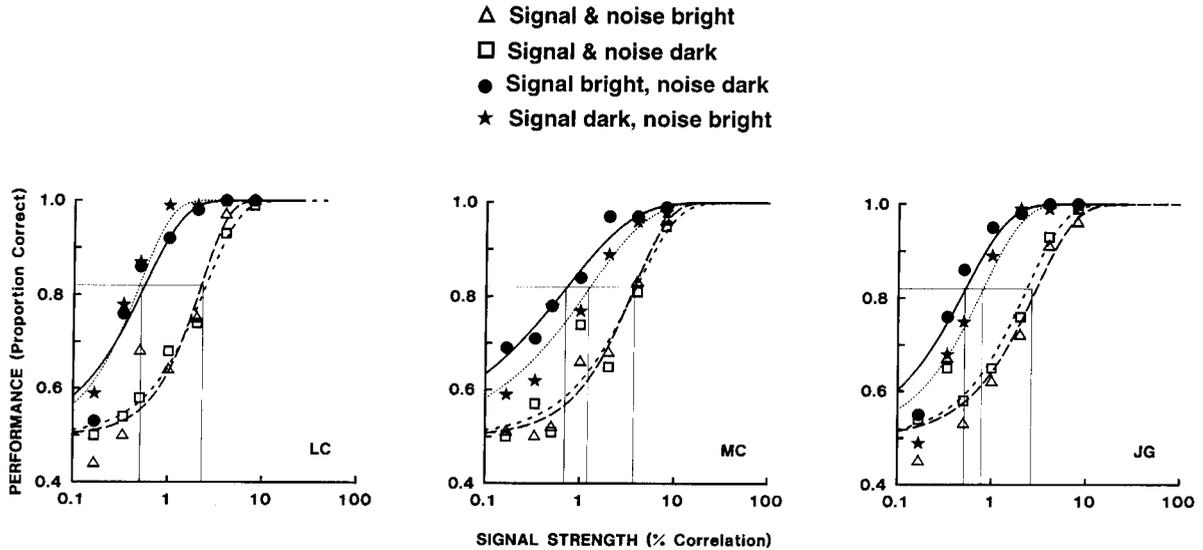


FIGURE 4. Psychometric functions measured for homopolar-bright (open triangles), homopolar-dark (open squares), heteropolar-Sbright (filled circles), and heteropolar-Sdark (filled stars) conditions in Experiment 2. Also shown are curves fit to the homopolar-bright (wide dashed lines), homopolar-dark (small dashed lines), heteropolar-Sbright (solid lines), and heteropolar-Sdark (dotted lines) data. Thin solid lines illustrate thresholds, as in Fig. 2. If two functions had statistically indistinguishable thresholds, a single vertical line is drawn to the average threshold signal strength for these two functions. Number of trials per data point (N), fit thresholds ($\alpha_{\text{homo-bright}}$, $\alpha_{\text{homo-dark}}$, $\alpha_{\text{hetero-Sbright}}$, and $\alpha_{\text{hetero-Sdark}}$), and fit slopes ($\beta_{\text{homo-bright}}$, $\beta_{\text{homo-dark}}$, $\beta_{\text{hetero-Sbright}}$, and $\beta_{\text{hetero-Sdark}}$) for each subject are as follows: LC: $N = 100$, $\alpha_{\text{homo-bright}} = 2.180$, $\beta_{\text{homo-bright}} = 1.478$, $\alpha_{\text{homo-dark}} = 2.442$, $\beta_{\text{homo-dark}} = 1.178$, $\alpha_{\text{hetero-Sbright}} = 0.545$, $\beta_{\text{hetero-Sbright}} = 1.002$, $\alpha_{\text{hetero-Sdark}} = 0.479$, $\beta_{\text{hetero-Sdark}} = 1.251$. MC: $N = 100$, $\alpha_{\text{homo-bright}} = 3.660$, $\beta_{\text{homo-bright}} = 1.162$, $\alpha_{\text{homo-dark}} = 3.804$, $\beta_{\text{homo-dark}} = 0.989$, $\alpha_{\text{hetero-Sbright}} = 0.692$, $\beta_{\text{hetero-Sbright}} = 0.604$, $\alpha_{\text{hetero-Sdark}} = 1.220$, $\beta_{\text{hetero-Sdark}} = 0.686$; JG: $N = 100$, $\alpha_{\text{homo-bright}} = 2.989$, $\beta_{\text{homo-bright}} = 1.033$, $\alpha_{\text{homo-dark}} = 2.292$, $\beta_{\text{homo-dark}} = 1.056$, $\alpha_{\text{hetero-Sbright}} = 0.507$, $\beta_{\text{hetero-Sbright}} = 0.988$, $\alpha_{\text{hetero-Sdark}} = 0.786$, $\beta_{\text{hetero-Sdark}} = 0.992$. Each performance function consisted of responses pooled over the last N trials per data point obtained for each subject.

luminance differences between dots of different hues. To ensure that these luminance ranges were perceptually equivalent for the red and green dots, we used the two methods of heterochromatic flicker photometry described above to determine, for each subject, the setting of the green gun necessary to match each of the three photometrically-defined luminances of the red gun.

Results

Data obtained in Experiment 1B are illustrated in Fig. 3. For the homochromatic condition (open triangles), subjects' ability to discriminate direction improved with increasing motion signal strength. Thresholds ranged from 3.0 to 4.5% correlation—within the range seen in Experiment 1A—indicating that the addition of luminance noise did not alter the capacity to discriminate global motion. The addition of a chromatic cue to distinguish signal dots facilitated direction discrimination, as shown by the leftward shifts of the psychometric functions obtained under the heterochromatic condition (filled circles). Statistical tests revealed significant differences between the thresholds for the two conditions for all three subjects. Moreover, the threshold reductions seen were similar in magnitude to those seen for the same subjects in Experiment 1A.

These results show that the facilitation of direction discrimination persists despite random conspicuous fluctuations of dot luminance. On the basis of these results, we feel confident that the threshold reductions

observed in Experiment 1A can only be attributed to the intended hue differences between signal and noise dots.

EXPERIMENT 2: LUMINANCE CONTRAST POLARITY

Experiment 2 tested whether segmentation on the basis of contrast polarity (increment vs decrement in luminance relative to the background) aids direction discrimination. Since dots of opposite contrast polarity pop-out relative to each other (Theeuwes & Kooi, 1994)—as do red and green dots—we expected to find that differentiating signal and noise dots by polarity would elicit an improvement in discrimination performance comparable to that seen with the chromatic segmentation cue in Experiment 1.

Methods

Direction discrimination performance was tested for each of three subjects under four conditions: (1) both signal and noise dots defined by positive contrast, and thus brighter than background [*homopolar-bright* condition; Fig. 1(A)]; (2) both signal and noise dots defined by negative contrast, and thus darker than background [*homopolar-dark* condition; Fig. 1(A)]; (3) signal dots defined by positive contrast and noise dots defined by negative contrast [*heteropolar-Sbright* condition; Fig. 1(B)]; and (4) signal dots defined by negative contrast and noise dots defined by positive contrast [*heteropolar-*

Sdark condition; Fig. 1(B)]. The two homopolar conditions are analogous to the homochromatic condition, and the two heteropolar conditions are analogous to the heterochromatic condition of Experiment 1, except that we analyzed the bright-signal and dark-signal data separately.

Only the green phosphor of the Nanao display monitor was modulated in this experiment; the red and blue phosphors were set to their lowest settings. For all four configurations, the background luminance was 10 cd/m^2 , the luminance of bright dots was 20 cd/m^2 , and the luminance of dark dots was 5 cd/m^2 . Thus, both bright and dark dots were of 33% Michelson contrast relative to the background. Despite the fact that the proportions of bright and dark dots varied with signal strength and stimulus condition, mean luminance over the stimulus aperture during trial presentation was dominated by the background and was approximately 10 cd/m^2 .

In order to compensate for the greater sensitivity of the OFF than the ON pathway to temporal flicker (Magnussen & Glad, 1975; White *et al.*, 1980), we removed the flicker associated with the absence of each dot during the interval between its original appearance and its displaced reappearance. This was achieved by increasing the duration of each stimulus frame from 17 to 50 msec and removing the two frames interspersed between the first and second appearances of each signal dot. These changes rendered our stimuli more similar to those in a related study (Edwards & Badcock, 1994; see below), which did not have dot inter-stimulus intervals and with which we wished to compare/contrast our results.

Results

Data obtained from the homopolar conditions are shown in Fig. 4 (empty triangles and squares). For each subject, thresholds for both the homopolar-bright and homopolar-dark conditions were statistically indistinguishable. These thresholds ranged from 2.2 to 3.8% correlation—within the expected range—indicating that neither elevation of the background luminance (relative to that used in Experiment 1), nor use of luminance decrements to define the dots, nor elimination of dot flicker altered the capacity to discriminate direction.

Data from the heteropolar conditions are also shown in Fig. 4 (filled circles and stars). There was a leftward shift of the psychometric functions for all subjects, resulting in statistically significant decreases in thresholds for heteropolar relative to homopolar conditions. Subject LC's performance for the heteropolar conditions was independent of signal dot polarity. Differentiating signal and noise dots by contrast polarity elicited a 4.6-fold improvement in direction discrimination by this subject. For the other subjects the different heteropolar conditions elicited slightly different performance: there was an average 3.2-fold decrease in threshold for the *Sdark* condition, and a 5.3-fold decrease for the *Sbright* condition. Averaging across all conditions and subjects, we found a 4.3-fold decrease in threshold when signal and noise dots were distinguished by contrast polarity.

Edwards & Badcock (1994) independently adopted an approach similar to ours in order to investigate whether dots of opposite contrast polarity contribute to a common motion pathway. These investigators found that negative contrast noise dots were as effective as positive ones at masking motion signal carried by positive contrast dots. This result seems to contradict our finding that segmentation of negative noise from positive signal dots decreases the masking of the motion signal. In evaluating this discrepancy, it is important to note that the Edwards and Badcock experiment differed from ours in three important respects. Firstly, the Edwards and Badcock stimulus did not incorporate a unique association between distinguishing-cue and signal/noise assignment (i.e., some noise dots were the same polarity and some were the opposite polarity as signal dots). The distinguishing-cue and signal/noise assignment were always uniquely associated in our experiments. Secondly, Edwards and Badcock used a stimulus duration of 400 msec, as opposed to our 2000 msec. Thirdly, Edwards and Badcock equated the Weber contrasts (defined as $\Delta L/L_b$, where ΔL is the difference between the dot and the background luminances, and L_b is the background luminance) of their dots, while we equated the Michelson contrasts [defined as $\Delta L/(L_{\max} + L_{\min})$, where L_{\max} and L_{\min} are the dot and background luminances, with L_{\max} being the brighter and L_{\min} the dimmer of the two values]. Because $L_{\max} + L_{\min}$ is smaller for decrements than increments, a smaller ΔL for dark dots is required in order to equate Michelson contrast to that of bright dots.

The first two procedural differences do not account for the different results: we have repeated the manipulations of our Experiment 2 using 400 msec presentation times and using noise dot populations with mixed polarities. Neither change altered the basic result. The key difference between the two studies appears to be the relative contrasts of the positive and negative dots. Equating Weber contrasts, as Edwards and Badcock did, results in the negative polarity dots having a greater Michelson contrast than the positive dots. Because perceived contrast covaries with Michelson contrast (Burkhardt *et al.*, 1984; Whittle, 1986), negative dots are perceived as having greater contrast than positive dots of equivalent Weber contrast. The greater perceptual salience thus associated with the negative dots in the Edwards and Badcock study enabled them to partially mask the positive contrast dots, which carried the motion signal. The outcome of this masking was the reduction of any benefit that might have been afforded by polarity-based segmentation of the dots.

The negative and positive contrast dots in our study, though of opposite polarity with respect to the background, were of the same Michelson contrast and thus had approximately the same perceived contrast. Our finding of approximately equivalent enhancement of direction discrimination for both heteropolar conditions with dots of equal perceived contrasts reveals the potential importance of perceptual salience in influencing

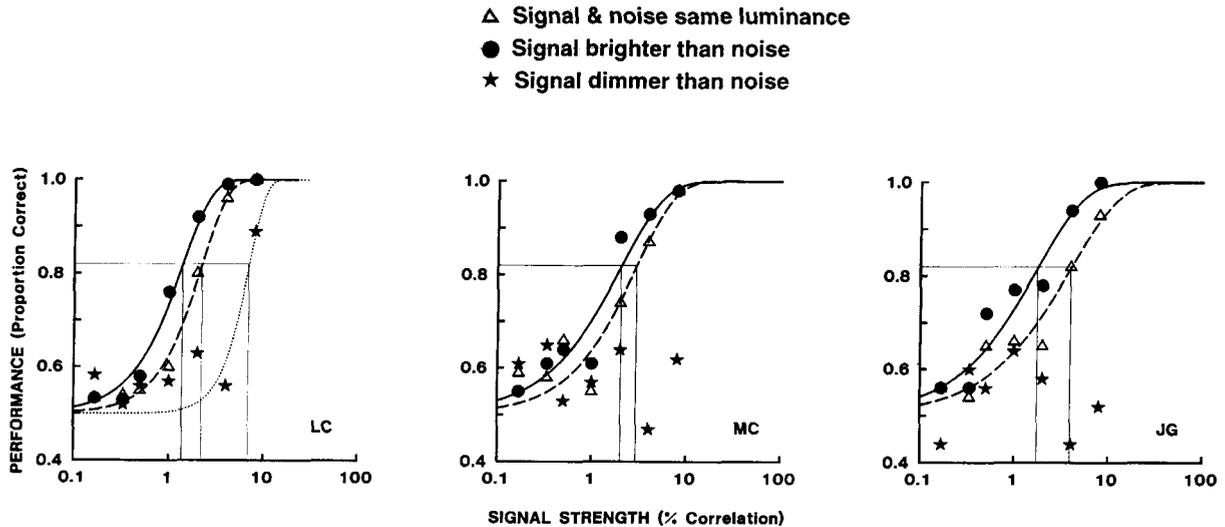


FIGURE 5. Psychometric functions measured for homoluminant (open triangles), heteroluminant-Sbright (filled circles), and heteroluminant-Sdim (filled stars) conditions in Experiment 3. Also shown are curves fit to the homoluminant (dashed lines), heteroluminant-Sbright (solid lines), and heteroluminant-Sdim (dotted lines) data. Thin solid lines illustrate thresholds, as in Fig. 2. For subjects MC and JG, performance never reached threshold for the heteroluminant-Sdim condition. Number of trials per data point (N), fit thresholds (α_{homo} , $\alpha_{\text{hetero-Sbright}}$, and $\alpha_{\text{hetero-Sdim}}$), and fit slopes (β_{homo} , $\beta_{\text{hetero-Sbright}}$, and $\beta_{\text{hetero-Sdim}}$) for each subject are as follows: LC: $N = 100$, $\alpha_{\text{homo}} = 2.201$, $\beta_{\text{homo}} = 1.582$, $\alpha_{\text{hetero-Sbright}} = 1.377$, $\beta_{\text{hetero-Sbright}} = 1.391$, $\alpha_{\text{hetero-Sdim}} = 6.902$, $\beta_{\text{hetero-Sdim}} = 2.511$. MC: $N = 100$, $\alpha_{\text{homo}} = 2.939$, $\beta_{\text{homo}} = 1.048$, $\alpha_{\text{hetero-Sbright}} = 2.027$, $\beta_{\text{hetero-Sbright}} = 0.924$; JG: $N = 100$, $\alpha_{\text{homo}} = 3.953$, $\beta_{\text{homo}} = 0.826$, $\alpha_{\text{hetero-Sbright}} = 1.755$, $\beta_{\text{hetero-Sbright}} = 0.861$. Each performance function consisted of responses pooled over the last N trials per data point obtained for each subject.

the integration of signal and noise motion tokens—a connection we explore in Experiment 3. Additionally, our results show that when perceptual contrast is equated, distinguishing signal and noise dots by contrast polarity enhances direction discrimination, in support of our original hypothesis.

EXPERIMENT 3: LUMINANCE CONTRAST AMPLITUDE

The results of Experiment 2 highlight the importance of the relative perceptual contrast amplitude, or salience, of signal and noise dots to their contribution to motion processing. In order to demonstrate this effect explicitly we performed Experiment 3, in which signal and noise dots were both defined by positive contrast with respect to the background but were distinguished by luminance amplitude.

Differentiating signal and noise dots by luminance amplitude has two consequences, which we anticipated would have either convergent or opposing influences on direction discrimination. First, if the generality of our hypothesis is correct, distinguishing signal and noise populations by any popout cue—including sufficient luminance differences (Nagy & Sanchez, 1992)—should weigh in favor of direction discrimination performance. Second, if both signal and noise dots are brighter (or darker) than background, the luminance differences between the dots correspond to differences in contrast amplitude. This may translate to a difference in perceptual salience, which, as we have seen from Experiment 2, will in turn affect direction discrimination performance. Thus, when signal dots are sufficiently

brighter than noise dots, these two factors should work together to facilitate direction discrimination: signal and noise dots should be grouped separately, and signal dots' greater contrast relative to the background should render them more salient. On the other hand, when signal dots are sufficiently dimmer than noise dots, the two factors should work in opposition: while signal and noise dots should be grouped separately, signal dots should be *less* salient than noise dots. If relative salience of the dots has a strong effect on performance, direction discrimination for this condition may be less facilitated than for the bright signal condition—or perhaps even degraded relative to the homo-cue condition.

Methods

Direction discrimination performance was tested for each of three subjects under three conditions: (1) signal and noise dots the same luminance [*homoluminant* condition; Fig. 1(A)]; (2) signal dots brighter than noise dots [*heteroluminant-Sbright* condition; Fig. 1(B)]; and (3) signal dots dimmer than noise dots [*heteroluminant-Sdim* condition; Fig. 1(B)].

The background was produced by setting all the Nanao monitor phosphors to their lowest setting, resulting in a gray background of 0.5 cd/m^2 . Dots were produced by modulation of the green phosphor. In the homoluminant condition, all dots were 10 cd/m^2 . In the heteroluminant-Sbright condition, the signal dots were 17.5 cd/m^2 and the noise dots were 10 cd/m^2 . In the heteroluminant-Sdim condition, the signal dots were 2.5 cd/m^2 and the noise dots were 10 cd/m^2 . The luminance of the dimmest dots in this experiment was approximately 20 times that required for detection of an increment on a 0.5 cd/m^2

background (see Walraven *et al.*, 1990). The difference between the dot luminances in the heteroluminant-Sbright condition was approximately five times the discrimination threshold, and in the heteroluminant-Sdim condition was approximately 23 times the discrimination threshold (Whittle, 1986). Despite the fact that the proportions of bright and dim dots varied with signal strength and stimulus condition, mean luminance over the stimulus aperture during trial presentation did not vary appreciably, and was approximately 1 cd/m^2 .

Results

Results obtained in Experiment 3 are shown in Fig. 5. Thresholds for the homoluminant condition (empty triangles) varied from 2.2 to 4.0% correlation, within the expected range for homo-cue configurations. When signal dots were brighter than noise dots performance of all subjects improved, as is evident from the leftward shifts of the psychometric functions obtained for the heteroluminant-Sbright condition (filled circles). Our statistical tests revealed significant differences between the homoluminant and heteroluminant-Sbright conditions for all three subjects. The average threshold reduction was 1.7-fold. However, relative to the homoluminant conditions, subjects were poorer at discriminating direction when signal dots were dimmer than noise dots (heteroluminant-Sdim condition; filled stars). In fact, only the most experienced subject (LC) was able to reliably discriminate signal direction at the highest signal strength in this condition; the other subjects were unable to do so for any of the signal strengths used.

The effects observed in Experiment 3 are different from those seen in the previous experiments in two respects. Firstly, the average threshold decrease obtained in the heteroluminant-Sbright condition (1.7-fold) was smaller than that in Experiment 1 (6.0-fold) or 2 (4.3-fold). This is surprising; if a generalized grouping process influences motion processing and if the luminance differences used were sufficient to elicit segmentation of the two dot populations, we should find approximately equal facilitation for the hetero-cue stimuli in all the experiments. Secondly, when the signal dots had a lower luminance contrast amplitude than the noise dots, performance was degraded relative to that for the homoluminant condition—an effect that was never seen in Experiments 1 and 2.

The most parsimonious explanation of these differences from our previous results is that performance in Experiment 3 was less influenced by grouping processes than it was by the relative perceptual salience of the signal and noise dots. While we do not have direct evidence concerning whether our heteroluminant signal and noise dots were grouped separately by the visual system, hints come from studies of how luminance differences affect visual search. Nagy and Sanchez (1992) found that popout occurred regardless of whether targets were brighter or dimmer than distractors, provided the luminance difference was sufficiently large. Interestingly, the luminance difference in our heteroluminant-

Sdim condition exceeded that which elicited popout in the Nagy and Sanchez search task, but that was not the case for our heteroluminant-Sbright condition. While stimulus and task differences preclude confident predictions from the Nagy and Sanchez result, the facilitation found for the heteroluminant-Sbright condition may not have been due to segmentation of the two dot populations, but rather to the increased perceptual salience of the signal relative to the noise dots. Similarly, the degraded performance for the heteroluminant-Sdim condition may have resulted from the decreased perceptual salience of the signal relative to the noise dots.

This interpretation can be easily understood by considering that many early visual neurons would be differentially modulated by the luminance contrast amplitudes used in Experiment 3 (e.g. Kaplan & Shapley, 1986; Sclar *et al.*, 1990). A directional mechanism integrating neuronal responses to the dots in, for example, the heteroluminant-Sdim condition would have received stronger input about each noise dot than about each signal dot, and the stronger noise input would be a more effective mask of the weaker signal input than if signal and noise had the same contrast amplitude.

DISCUSSION

We have investigated how image segmentation contributes to motion processing, using a stimulus in which populations of dots with different motion properties are distinguished by each of several form cues. The results of Experiments 1 and 2 show that direction discrimination is enhanced when coherently moving dots are distinguished either by hue or by luminance contrast polarity from randomly moving dots, with thresholds decreasing by, on average, a factor of five. The results of Experiment 2 also highlight the importance of matching the relative perceived contrast amplitude, or salience, of the signal and noise dots in hetero-cue stimuli, a point that is further emphasized by the results of Experiment 3.

Our findings in Experiment 1 add to a growing list of demonstrated interactions between color and motion processing—a list that includes the perception of movement of forms against equiluminant backgrounds (e.g., Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Palmer *et al.*, 1993), the use of hue as a motion correspondence cue (e.g., Saito *et al.*, 1989; Dobkins & Albright, 1993, 1994; Gegenfurtner *et al.*, 1994), the use of hue to resolve motion ambiguities (e.g., Green, 1989; Paphomas *et al.*, 1991), the use of hue to segregate drifting plaid components (e.g. Krauskopf & Farell, 1990; Kooi *et al.*, 1992), and the appearance of motion aftereffects contingent upon hue and vice versa (e.g. Stromeyer & Mansfield, 1970; Favreau *et al.*, 1972; Mullen & Baker, 1985). The phenomenon we have uncovered is unique (see also thesis work by Møller, 1992) in utilizing the process of image segmentation, which can be mediated by many form cues.

In the remainder of the Discussion we address these results in the context of two possible mechanisms that might mediate the observed contribution of form

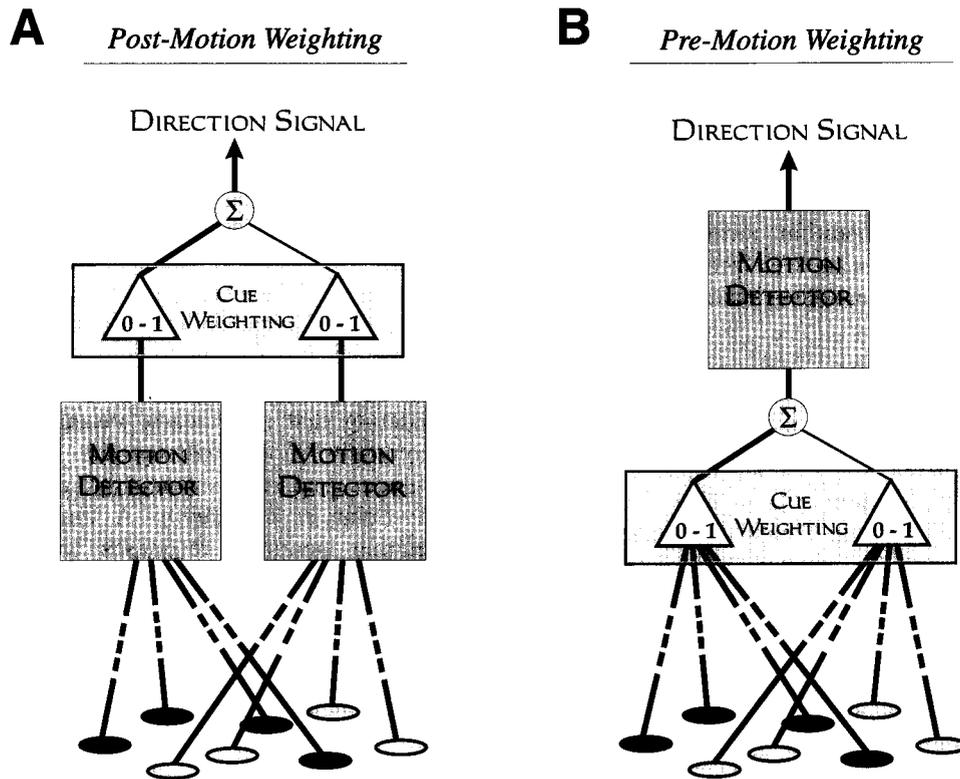


FIGURE 6. Diagrams of two alternative mechanisms that can account for the observed influence of form cues on motion processing. The flow of information is from the bottom, where a retinal image of randomly positioned dots is depicted, to the top. (A) The hypothesized post-motion weighting mechanism. Two cue-specific motion detectors each receive input signaling the positions of tokens defined by a particular cue. The cue-specific motion signals output from these detectors are weighted (on the basis of attention and task demands) and summed to determine the final direction signal. (B) The hypothesized pre-motion weighting mechanism. The distinguishing feature of this mechanism is that cue-specific weighting occurs before motion extraction. Information about positions of tokens defined by two different cues is segregated into cue-specific groups on the basis of form segmentation processes. Signals about each segregated group are weighted (on the basis of attention and task demands) and then summed before serving as input to a motion detector. Although the motion detector is not itself selective for any particular cue, it provides a direction signal that is influenced by the relative weights applied to the two cues. In this figure "0-1" represents the range of weights that can be applied to a cue; the weight applied to signals about black dots in the retinal image is greater than that applied to gray dots, as is represented by the thicker lines for the weighted signals about black dots.

segmentation cues such as hue and contrast polarity to motion processing. We also consider the relevance of our findings to recent neurophysiological studies of cortical motion detectors.

Two alternative mechanisms

The simplest mechanisms that can account for the observed influence of segmentation cues on direction discrimination are of two types, diagrammed in Fig. 6. Both types utilize differential weighting of signals arising from different image sources, but differ in terms of when this weighting occurs relative to the stage of motion processing. The particular implementation of motion detectors is not critical; any detector that computes a spatiotemporal cross-correlation across different regions of the retinal image will suffice (e.g. Reichardt, 1961; van Santen & Sperling, 1984; Adelson & Bergen, 1985).

Figure 6(A) illustrates the hypothesized "post-motion weighting" mechanism as two motion detectors, each receiving input about the positions of one of two kinds of image features present in the retinal image depicted at the

bottom of the figure. These features are defined by two different values along some stimulus dimension unrelated to motion (such as red and green hues), symbolized as gray and black dots, respectively. This architecture enables the independent encoding of motions of features defined by different cues. A final stage then integrates the outputs of the separate motion detectors, weighted by attention and/or task demands, to achieve a representation of global stimulus motion. Referring back to our original example of tracking people moving through a crowd, a pathway selective for motion of forms reflecting long-wavelength light would respond to motion of the red hats but would be unaffected by attire of other hues, and signals from this pathway would weigh more heavily in processing the motion of the target individuals.

Figure 6(B) illustrates the hypothesized "pre-motion weighting" mechanism. According to this scheme, a generalized image segmentation stage weights inputs to a motion detector that is not selective for particular form cues. Unlike the post-motion weighting mechanism, signals about each segmented group of tokens are

represented separately and are weighted by attention and/or task demands prior to motion detection. The weighted signals are summed and conveyed to the motion detector, which renders a representation of global stimulus motion. Referring again to our example, grouping of the target individuals on the basis of their red hats would allow them to be segregated from the rest of the crowd. The weighting process would selectively enhance signals about this group, and the enhanced signal would weigh more heavily in motion processing.

To appreciate the difference between these two mechanisms, consider the computation of the signal delivered by each. The outputs of the two mechanisms can be expressed as

$$D_{\text{post}} = \gamma_A \cdot M(S_A, N_A) + \gamma_B \cdot M(S_B, N_B)$$

$$D_{\text{pre}} = M(\gamma_A S_A, \gamma_A N_A, \gamma_B S_B, \gamma_B N_B),$$

where D is the output (related to performance on the direction discrimination task used in our experiments), D_{post} and D_{pre} indicate the two alternative mechanisms, M is the motion computation (influenced by the direction of coherent motion, the directional selectivity of the detector, and the motion energy algorithm), S and N are proportions of signal and noise dot pairs, respectively, and γ is a weighting factor. The subscripts A and B indicate parameters associated with two segmentable values of a form cue. In the case where the motion computation, M , perfectly reflects the signal strength, these equations become:

$$D_{\text{post}} = \gamma_A \cdot \left(\frac{S_A}{S_A + N_A} \right) + \gamma_B \cdot \left(\frac{S_B}{S_B + N_B} \right)$$

$$D_{\text{pre}} = \frac{\gamma_A \cdot S_A + \gamma_B \cdot S_B}{\gamma_A(S_A + N_A) + \gamma_B(S_B + N_B)}.$$

While S_A , N_A , S_B , and N_B are quantities associated with the retinal stimulus, γ_A and γ_B take on different values depending on attentional states and/or task demands.

By appropriate adjustment of the weighting factors, γ_A and γ_B , both mechanisms can account for the results of our experiments. However, the two mechanisms make different predictions for other stimulus conditions, which can be readily tested (Croner and Albright, in preparation). Below, we consider other grounds for judging the credibility of the two hypothesized mechanisms.

Arguments against the post-motion weighting hypothesis

At least two arguments limit the credibility of the post-motion weighting mechanism. The first is the combinatorial problem associated with the presumed generality of the effects we have observed. Specifically, improved direction discrimination occurs when signal and noise are distinguished by a variety of cues besides those we have tested here—including other hue pairs, as well as different textures and binocular disparities (Croner and Albright, unpublished observations). Extending the logic of the post-motion weighting mechanism leads to the conjecture that there are independent motion channels for each of these cues. Even allowing for coarse coding along

each cue dimension, the combinatorial problem of crossing cues with motion detectors is formidable in neuronal terms.

The second—and perhaps the stronger—argument against the post-motion weighting mechanism is that it is inconsistent with known neuronal response properties. To date, there is little evidence for single neurons with the requisite conjunction of selectivities for direction of motion and non-motion cues. This type of joint selectivity is particularly inconsistent with known response properties of neurons in the middle temporal visual area (area MT), which is likely to contribute to the perception of these stimuli (Newsome *et al.*, 1989; Britten *et al.*, 1992). Rather than showing selectivity for non-motion cues, directionally selective MT neurons have the same preferred direction regardless of the cues that define the moving tokens, a property termed “form-cue invariance” (Albright, 1992; Stoner & Albright, 1993). These neurons therefore do not have the characteristics required of motion detectors in the post-motion weighting mechanism.

Consideration of the pre-motion weighting hypothesis

The essential characteristic of the hypothesized pre-motion weighting mechanism is that segmentation on the basis of form cues influences motion processing without requiring that the motion detectors themselves be selective for particular form cues. In addition to being a more economical solution to the problem of dynamically pairing each of many form cues with motion directional output, this mechanism is consistent with the observed form-cue invariance of directionally selective neurons in cortical area MT.

In contrast with the post-motion weighting mechanism, the pre-motion weighting scheme predicts that inputs to motion detectors should be influenced by attention. Hence, responses of motion detectors themselves should vary as attention is directed to specific moving features. This is consistent with recent reports of attentional modulation of activity in area MT and other parietal areas (e.g., Buračas & Albright, 1995; Treue & Maunsell, 1995). The inclusion of attentional modulation of inputs to motion detectors suggests that this mechanism could also mediate third-order “attention-based” motion processing, which has been hypothesized to enable tracking of features despite the absence of first- or second-order motion cues in the retinal image (e.g., Cavanagh, 1992; Lu & Sperling, 1995). In the application of the pre-motion weighting mechanism to our study, however, attention acts to enhance signals about a subset of the first-order motion cues present in the stimulus.

Implications for physiological studies of cortical motion detectors

Stimuli like our homo-cue stimuli have been used in a revealing series of studies of cortical motion processing (Newsome *et al.*, 1989; Britten *et al.*, 1992; Celebrini & Newsome, 1994). These studies showed that monkeys discriminating direction in homo-cue stimuli had perfor-

mance thresholds like those obtained for human subjects. When recording from cortical areas MT and MST (medial superior temporal cortex) while monkeys performed the task, Newsome and colleagues found that directional discrimination by individual neurons covaried with behavioral performance. Simultaneously obtained neuronal and behavioral thresholds were nearly identical in many cases. These results suggest that the responses of such neurons may form the basis for the perceptual decision. If that is true, manipulations that alter perceptual performance on the task (such as segmenting signal from noise) should be associated with measurable changes in direction discrimination by the underlying population of neurons. Failure to find such changes would suggest that altering the stimulus conditions has caused performance to rely upon information provided by a different neuronal population or code. Studies to explore these possibilities are in progress in our laboratory (see Croner & Albright, 1995, 1996).

Conclusions

Similarity of visual features along a single cue dimension can indicate that they are parts of the same or related objects, even if the features are disparately placed in a complex scene. This grouping can assist in determining other qualities that are common to the grouped features. We therefore expect that differentiation of a stimulus along one cue dimension will influence differentiation along other cue dimensions. In the experiments described here, we studied such cue interactions by investigating how segmentation of signal from noise by form cues in a stochastic motion display influences discrimination of motion signals. Our approach can be expanded to address interactions between cues besides the ones we have studied here, and promises to be useful in investigating the neuronal mechanisms that mediate the integration of information provided by different cues.

REFERENCES

- Adelson, E. H. & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A*, 2, 284–299.
- Albright, T. D. (1992). Form-cue invariant motion processing in primate visual cortex. *Science*, 255, 1141–1143.
- Bergen, J. R. & Julesz, B. (1983). Parallel versus serial processing in rapid pattern discrimination. *Nature*, 303, 696–698.
- Boynton, R. M. (1986). A system of photometry and colorimetry based on cone excitations. *Color Research and Application*, 11, 244–252.
- Britten, K. H., Shadlen, M. N., Newsome, W. T. & Movshon, J. A. (1992). The analysis of visual motion: a comparison of neuronal and psychophysical performance. *The Journal of Neuroscience*, 12, 4745–4765.
- Britten, K. H., Shadlen, M. N., Newsome, W. T. & Movshon, J. A. (1993). Responses of neurons in macaque MT to stochastic motion signals. *Visual Neuroscience*, 10, 1157–1169.
- Buračas, G. T. & Albright, T. D. (1995). Neural correlates of target detection during visual search in area MT. *Society for Neuroscience Abstracts*, 21, 1759.
- Burkhardt, D. A., Gottesman, J., Kersten, D. & Legge, G. E. (1984). Symmetry and constancy in the perception of negative and positive luminance contrast. *Journal of the Optical Society of America A*, 1, 309–316.
- Caceci, M. S. & Cacheris, W. P. (1984). Fitting curves to data. *Byte*, 9, 340–362.
- Cavanagh, P. (1992). Attention-based motion perception. *Science*, 257, 1563–1565.
- Cavanagh, P. & Anstis, S. M. (1991). The contribution of color to motion in normal and color-deficient observers. *Vision Research*, 31, 2109–2148.
- Celebrini, S. & Newsome, W. T. (1994). Neuronal and psychophysical sensitivity to motion signals in extrastriate area MST of the macaque monkey. *The Journal of Neuroscience*, 14, 4109–4124.
- Croner, L. J. & Albright, T. D. (1994). Segmentation by color improves performance on a motion discrimination task. *Investigative Ophthalmology and Visual Science (Supplement)*, 35, 1643.
- Croner, L. J. & Albright, T. D. (1995). Segmentation by color does not enhance motion discrimination by MT neurons. *Society for Neuroscience Abstracts*, 21, 281.
- Croner, L. J. & Albright, T. D. (1996). MT responses do not match perceptual reports during viewing of color-segmented motion displays. *Society for Neuroscience Abstracts*, 22, 717.
- Dobkins, K. R. & Albright, T. D. (1993). What happens if it changes color when it moves?: psychophysical experiments on the nature of chromatic input to motion detectors. *Vision Research*, 33, 1019–1036.
- Dobkins, K. R. & Albright, T. D. (1994). What happens if it changes color when it moves?: the nature of chromatic input to macaque visual area MT. *The Journal of Neuroscience*, 14, 4854–4870.
- Downing, C. J. & Movshon, J. A. (1989). Spatial and temporal summation in the detection of motion in stochastic random dot displays. *Investigative Ophthalmology and Visual Science (Supplement)*, 30, 72.
- Edwards, M. & Badcock, D. R. (1994). Global motion perception: interaction of the ON and OFF pathways. *Vision Research*, 34, 2849–2858.
- Favreau, O. E., Emerson, V. F. & Corballis, M. C. (1972). Motion perception: a color-contingent aftereffect. *Science*, 176, 78–79.
- Flitcroft, D. I. (1989). The interactions between chromatic aberration, defocus and stimulus chromaticity: implications for visual physiology and colorimetry. *Vision Research*, 29, 349–360.
- Gegenfurtner, K. R., Kiper, D. C., Beusmans, J. M. H., Carandini, M., Zaidi, Q. & Movshon, J. A. (1994). Chromatic properties of neurons in macaque MT. *Visual Neuroscience*, 11, 455–466.
- Green, M. (1989). Color correspondence in apparent motion. *Perception and Psychophysics*, 45, 15–20.
- Kaplan, E. & Shapley, R. M. (1986). The primate retina contains two types of ganglion cells, with high and low contrast sensitivity. *Proceedings of the National Academy of Sciences USA*, 83, 2755–2757.
- Kooi, F. L., De Valois, K. K., Switkes, E. & Grosz, D. H. (1992). Higher-order factors influencing the perception of sliding and coherence of a plaid. *Perception*, 21, 583–598.
- Krauskopf, J. & Farell, B. (1990). Influence of colour on the perception of coherent motion. *Nature*, 348, 328–331.
- Lindsey, D. T. & Teller, D. Y. (1990). Motion at isoluminance: discrimination/detection ratios for moving isoluminant gratings. *Vision Research*, 30, 1751–1761.
- Livingstone, M. & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*, 240, 740–749.
- Lu, Z.-L. & Sperling, G. (1995). Attention-generated apparent motion. *Nature*, 377, 237–239.
- Magnussen, S. & Glad, A. (1975). Brightness and darkness enhancement during flicker: perceptual correlates of neuronal B- and D-systems in human vision. *Experimental Brain Research*, 22, 399–413.
- Merigan, W. H. & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, 16, 369–402.
- Møller, P. (1992). Influence of color on motion segmentation. Ph.D. thesis, University of Rochester, Rochester, New York.
- Mullen, K. T. & Baker, C. L. Jr. (1985). A motion aftereffect from an isoluminant stimulus. *Vision Research*, 25, 685–688.

- Murphy, B. J., Kowler, E. & Steinman, R. M. (1975). Slow oculomotor control in the presence of moving backgrounds. *Vision Research*, *15*, 1263–1268.
- Nagy, A. L. & Sanchez, R. R. (1992). Chromaticity and luminance as coding dimensions in visual search. *Human Factors*, *34*, 601–614.
- Nedler, J. A. & Mead, R. (1965). A simplex method for function minimization. *Computer Journal*, *7*, 308–313.
- Newsome, W. T., Britten, K. H. & Movshon, J. A. (1989). Neuronal correlates of a perceptual decision. *Nature*, *341*, 52–54.
- Newsome, W. T. & Paré, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *Journal of Neuroscience*, *8*, 2201–2211.
- Palmer, J., Mobley, L. A. & Teller, D. Y. (1993). Motion at isoluminance: discrimination/detection ratios and the summation of luminance and chromatic signals. *Journal of the Optical Society of America A*, *10*, 1353–1362.
- Papathomas, T. V., Gorea, A. & Julesz, B. (1991). Two carriers for motion perception: color and luminance. *Vision Research*, *31*, 1883–1891.
- Quick, R. F. (1974). A vector-magnitude model of contrast detection. *Kybernetik*, *16*, 65–67.
- Reichardt, W. (1961). Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In Rosenblith, W. A. (Ed.), *Sensory communication* (pp. 303–317). Cambridge: MIT Press.
- Saito, H., Tanaka, K., Isono, H., Yasuda, M. & Mikami, A. (1989). Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent color stimuli. *Experimental Brain Research*, *75*, 1–14.
- Sclar, G., Maunsell, J. H. R. & Lennie, P. (1990). Coding of image contrast in central visual pathways of the macaque monkey. *Vision Research*, *30*, 1–10.
- Stoner, G. R. & Albright, T. D. (1993). Image segmentation cues in motion processing: implications for modularity in vision. *Journal of Cognitive Neuroscience*, *5*, 129–149.
- Stromeyer, C. F. III, Mansfield, R. J. W. (1970). Colored aftereffects produced with moving edges. *Perception and Psychophysics*, *7*, 108–114.
- Theeuwes, J. & Kooi, F. L. (1994). Parallel search for a conjunction of contrast polarity and shape. *Vision Research*, *34*, 3013–3016.
- Treisman, A. M. & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, *12*, 97–136.
- Treue, S. & Maunsell, J. H. R. (1995). Attentional modulation of direction-selective responses in the superior temporal sulcus of the macaque monkey. *Society for Neuroscience Abstracts*, *21*, 1759.
- van Santen, J. P. H. & Sperling, G. (1984). Temporal covariance model of human motion perception. *Journal of the Optical Society of America A*, *1*, 451–473.
- Walraven, J., Enroth-Cugell, C., Hood, D. C., MacLeod, D. I. A. & Schnapf, J. L. (1990). The control of visual sensitivity: receptor and postreceptor processes. In Spillman, L. & Werner, J. S. (Eds), *Visual perception: the neurophysiological foundations* (pp. 53–101). San Diego: Academic Press.
- Weibull, W. (1951). A statistical distribution function of wide applicability. *Journal of Applied Mechanics*, *18*, 293–297.
- White, T. W., Irvin, G. E. & Williams, M. C. (1980). Asymmetry in the brightness and darkness of the Broca–Sulzer effects. *Vision Research*, *20*, 723–726.
- Whittle, P. (1986). Increments and decrements: luminance discrimination. *Vision Research*, *26*, 1677–1691.

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