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Sensitivity to colour- and to orientation-carried motion respectively improves and deteriorates under equiluminant background conditions

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Abstract—This study presents two distinct effects produced by manipulation of the background illumination on the directional sensitivity to colour- and orientation-carried motion. The two motion percepts were produced with two of a class of stimuli extensively used by the first and last authors in apparent-motion studies. The stimuli were designed to produce motion perception by virtue of spatiotemporal matching of (a) colour with orientation systematically mismatched (Colour *across* Orientation, CxO) and of (b) orientation with colour systematically mismatched (OxC). An increase in background illumination from dark to the equiluminance point (relative to the luminance of the discrete stimulus microelements) entails a significant increase and decrease of directional performances with CxO and OxC stimuli, respectively. It is proposed that these anti-symmetrical *background effects* have distinct neurophysiological origins. For CxO stimuli, improvement of directional performances at the equiluminant point is presumably due to the inactivation of the inhibitory effect of the luminance-motion pathway on the chromatic-motion pathway. The opposite effect obtained with OxC stimuli, previously referred to as the *veto effect* (Gorea and Papathomas, 1988 *Invest. Ophthal. Vis. Sci. Suppl.*, **29,** 265), is supposed to be entailed by the inactivation of the luminance-oriented mechanism, the only motion sensitive mechanism activated by this stimulus configuration.

INTRODUCTION

The current procedure used to isolate colour-carried motion is to eliminate all luminance-contrast information in the stimulus. Under such conditions, a few studies concluded that colour-carried motion was perceptually weaker than luminance-carried motion (Ramachandran and Gregory, 1978; Moreland, 1980; Cavanagh *et al.*, 1984; Troscianko, 1987), although very recent evidence points to the contrary (Stromeyer *et al.*, 1990; see also Cavanagh and Anstis (1991) for a review).

Elimination of all luminance-contrast information is not a necessary condition for isolating colour-carried motion. It is sufficient that such luminance-contrast (and, for that matter, any other type of) information be *drift-balanced* (Chubb and Sperling, 1988). With stimuli which are discrete in both space and time, colour contribution to perceived motion may then be isolated by unambiguously matching across space–time the colours characterizing the discrete stimulating elements.

In a series of recent papers, Gorea and Papathomas (1987a, 1988, 1989), Papathomas and Gorea (1988, 1989) and Papathomas *et al.* (1989, 1991) have demonstrated that, contrary to most of the previous reports (see references above) but in line with Stromeyer *et al.*'s (1990) work, colour is indeed a 'token' for motion perception.

Additionally, they showed that colour- and luminance-carried motions may add to improve directional performances and that, under conflicting situations, colour may override luminance-carried motion.

The experiments just described were performed with stimuli designed in such a way that the visual attributes (such as colour, orientation, luminance, and retinal disparity) characterizing a set of discrete elements could be manipulated independently to offer unambiguous perceptual cues for coherent motion. With such stimuli, Gorea and colleagues elicited unambiguous colour-carried motion under conditions where luminance cues were either: (a) directionally ambiguous; or (b) entirely absent (i.e. equiluminant background conditions).

In the first case (a), stimulus microelements were displayed on a dark background with their colour systematically matched across space and time. When the microelements were equiluminant across space and time, the luminance cues yielded a drift-balanced motion (Colour *within* Luminance—CwL). In contrast, the systematic mismatch of their luminance across space and time (Colour *across* Luminance—CxL), precluded any coherent spatiotemporal matching of the luminance cues.

In the second case (b), stimulus microelements were always equiluminant and were displayed on an equiluminant background, such that all luminance cues were eliminated. Microelements' colours were matched across space and time as above (CwL with equiluminant background) yielding the exclusive activation of the directional, chromatic sensitive mechanisms. The question then raises whether this stimulus configuration is equivalent, in terms of motion perception, to the CwL or CxL or both configurations with dark background. Its theoretical interest is related to the putative interactions between chromatic and achromatic (luminance) mechanisms in motion perception.

Two of us (Gorea and Papathomas, 1989) have shown that under a limited range of spatiotemporal conditions, directional performances for colour-carried motion are close to 100% for both dark and equiluminant background CwL stimuli. Gorea and Papathomas (1987b, 1988, 1989) have also shown that the Orientation attribute can carry motion *across* Colour (OxC) *only* if luminance information is available (i.e. dark background conditions). Under equiluminant background conditions, orientation *per se* cannot carry motion *across* colour, as if colour mismatching *vetos* orientation-carried motion.

The purpose of the present study is to provide a direct comparison between the above-mentioned effects and to propose a theoretical basis for their interpretation. Consequently, we assess their presence under a large (though not exhaustive) set of experimental conditions (different speeds, contrasts and mean luminances) not tested before. We show that colour-carried (CxO) motion perception measured with an equiluminant background, may be substantially stronger than when measured under "dark background" conditions (see also Green, 1989) and argue in favour of reciprocal inhibitory interactions between directional sensitive, chromatic and luminance pathways. In contrast, progressive elimination of the luminance cues plays a detrimental role for orientation-carried (OxC) motion perception and confirms the *veto effect* entailed by colour mismatching (Gorea and Papathomas, 1987b, 1988).

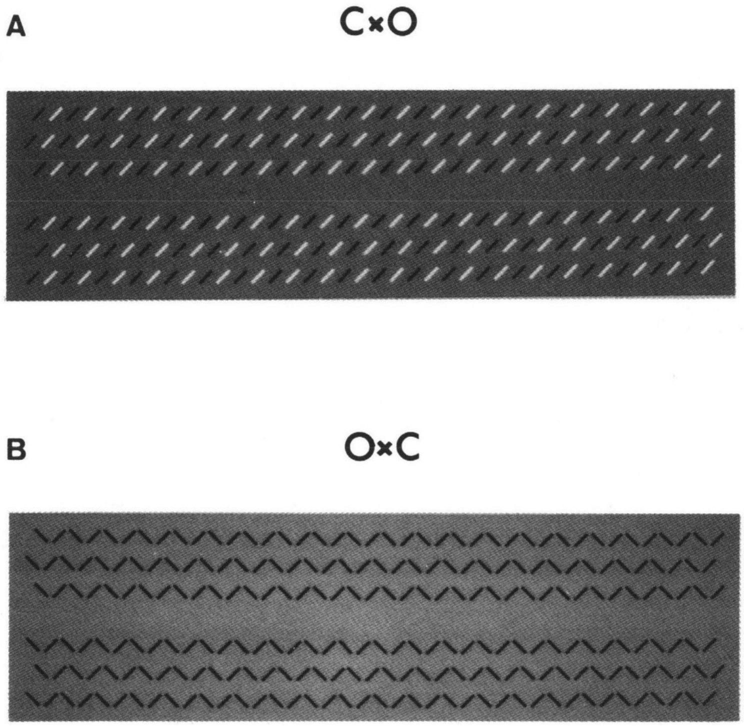

Figure 1. Representation of one stimulus frame for CxO (A) and OxC (B) stimulus configurations. All stimulus dimensions are proportional to those used in the actual experiments. Dark and white elements were in fact equiluminant red and green. The background, which is grey in this representation, was either dark or yellow. The fixation point has been omitted in this representation. See text for more details.

GENERAL METHOD

Stimuli

The stimuli were displayed on a Sony Trinitron monitor (GDM-1601/1950) driven by an Adage PG-90/10 graphics card under the control of a Leanord-386 AT computer. The stimuli consisted of red (CIE coordinates: $x = 0.611$, $y = 0.353$) and green ($x = 0.285$, $y = 0.597$), ± 45 deg oriented bars 20 arcmin (25 pixels) long and 2.4 arcmin (3 pixels) wide. They were displayed in three rows above and three rows below the fixation point.

In a first set of experiments, the horizontal inter-element separation (i.e. within one row) subtended 0.35, 0.69, 1.38 or 2.76 deg, depending on the experimental condition. Only the highest density was used in the subsequent experiments. The vertical inter-element separation (i.e. between rows) was fixed at 0.5 deg. The vertical separation between the bottom row of the upper half and the top row of the bottom half was 1 deg. The whole stimulus array subtended 13 deg horizontally (i.e. 40, 20, 10 or 5 bars per row, depending on their density) and 3.4 deg vertically at 114 cm from the observer. Figure 1 (fixation point not shown) illustrates one stimulus frame (see below) for CxO and OxC stimulus configurations.

With one exception (Experiment 3), the red and green bars (as represented by the

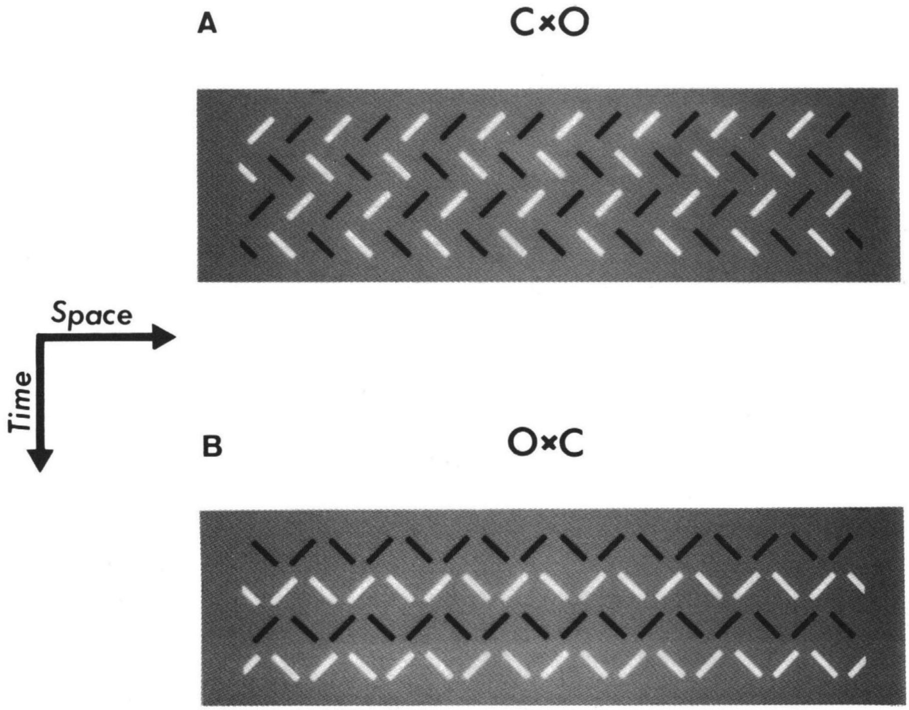

Figure 2. Schematic space-time representation of the stimuli with space and time represented along the horizontal and vertical axes, respectively. Each panel illustrates a four-frames presentation (one temporal period) with one element-row per stimulus frame. From one frame to the next, all microelements are displaced by half the inter-element distance such that spatial proximity cannot provide directional cues. Black and white stand for equiluminant red and green hues such that luminance *per se* cannot be a directional cue either, whether the background is dark or equiluminant. Panel A illustrates the Colour- (C) carried motion across Orientation (O; CxO) condition: Colour is systematically matched to the left, while Orientation is cyclicly changed between frames. Panel B illustrates the symmetrical condition where motion is Orientation-carried across Colour (OxC).

two shadings in Fig. 1) were equiluminant. Their luminance was set below, at, or above the luminance of the background which could be either dark or yellow (CIE coordinates: $x = 0.448, y = 0.475$). The luminance of the yellow background was set at 6.25, 12.5 or 25 cd/m^2, depending on the experimental condition.

Figure 2 illustrates schematically the spatiotemporal configurations of the stimuli. Space and time are represented along the horizontal and vertical dimensions, respectively. In each panel, one element-row (rather than six, as in the actual experiments; see Fig. 1) represents one *stimulus frame* (not to be confounded with the 60 Hz raster frames). From one stimulus frame to the next, all elements are displaced by half the inter-element distance such that spatial proximity cannot provide directional cues. One stimulus presentation always consisted of *four* stimulus frames. In the first set of experiments, stimulus frames were refreshed at 3.75, 7.5, 15, 30 or 60 Hz. Thus, the duration of one stimulus presentation was 1066, 533, 266, 133 or 67 ms, respectively. Only the last two stimulus refresh rates were used in the subsequent experiments.

Stimulus refresh rates should not be confounded with the temporal frequency of the drifting stimulus which is spatial-frequency dependent. Given that one temporal period of the drifting stimulus is completed after four successive stimulus frames (see Fig. 2), the drift temporal frequencies associated with the above refresh rates were 0.94, 1.88, 3.75, 7.5 and 15 Hz, respectively. These are the temporal frequencies referred to throughout the paper.

The left panel of Fig. 2 illustrates the CxO condition (colour is systematically matched to the left, while orientation is cyclically changed between stimulus frames; none of the two attributes is spatio-temporally matched to the right). The right panel illustrates the symmetrical condition where motion is orientation-carried across colour (OxC).

The graphics and animation software were developed by the second author (Lorenceau and Humbert, 1990).

Equiluminance settings

The equiluminance procedure (heterochromatic flicker photometry) has been described in detail elsewhere (Gorea and Papathomas, 1989). We stress here only the main modifications adopted in the present experiments.

The observer looked at a set of oriented microelements identical to those used in the main experiments and displayed at the highest density (i.e. 0.35 deg inter-element distance). The microelements were all red or all green and were displayed on a green or red background, respectively. In some control experiments, the background was yellow. At the beginning of one equiluminance setting, the luminance of one of the three hues was set close to either 25, 12.5, 6.25, 1.5 or 0.5 cd/m^2. Microelement and background hues were interswitched at rates of 15 and 30 Hz for the first three luminances above and at 7.5 Hz for the remaining two luminances. In the latter case, temporal modulations higher than 7.5 Hz were very close to, or above the critical flicker fusion point, while modulations below 7.5 Hz always produced flicker perception. The lowest two luminances were not used in the main experiments.

The observer's task was to adjust the luminance of one of the hues in order to minimize flicker perception. At least five adjustments per stimulating condition were obtained from each observer. For the first three luminances, adjustments obtained with 15 and 30 Hz temporal rates were practically identical and were thus averaged together. The measured green-to-red luminance ratios were well fitted by a power function. Any time luminances not directly tested in the equiluminance experiments were needed in the main experiments, the equiluminant points were interpolated on the power function fitted for each observer.

General procedure

The first three authors served as observers in all experiments. A two-alternative forced-choice procedure was used in all cases. The spatiotemporal matching of the colour or orientation cues was changed randomly from trial to trial to produce leftward or rightward motion and the observer decided on the perceived direction of motion. No feedback was provided. The variables randomized within one session and the number of sessions varied across experiments. Within one session, percentages correct were computed from 50 trials and each session was repeated at least three times (with one exception in Experiment 3) such that the experimental points displayed below were computed from at least 150 trials.

EXPERIMENT 1: THE SPATIOTEMPORAL DIRECTIONAL SENSITIVITY SURFACE

Procedure

Directional performances were measured for all microelement densities and for all temporal rates specified in the Method section. It became clear, however, that with equiluminant background stimuli, some spatiotemporal stimulus conditions were very close, or even below the classical detection threshold. Because it is meaningless to compare directional performances at unequal detectability levels, we display below only directional performances obtained for spatiotemporal conditions presumably entailing 100% detectability, according to observers' reports (as opposed to conditions where the observers experienced even the slightest difficulty in detecting the stimulus)[1].

Microelements were presented on either a dark or an equiluminant, yellow background at a mean luminance of 25 cd/m^2. In one session, temporal rate, background type and stimulus configuration (i.e. CxO or OxC) were fixed, while the spatial density of the stimulus was randomly varied. Temporal rate and background type were randomized across sessions. The order of presentation of the two stimulus configurations was varied across observers. All experimental conditions were repeated at least three times (i.e. at least 150 trials/condition).

Results

Figure 3 displays the spatiotemporal directional sensitivity surface of the three observers (average-data) given as percentages correct obtained with stimulus configurations CxO and OxC. Dark and equiluminant background conditions are shown in the upper and lower panels. The results display the following main characteristics:

(1) In addition to its characteristic dome-shape, the spatiotemporal directional sensitivity surface for CxO, dark-background stimuli presents striking similarities with Kelly's (1974, 1983) data obtained with red-green drifting gratings. However, a direct comparison between the two sets of data might be misleading both because of the different dependent variables used in the two experiments (Kelly measured chromatic thresholds) and because of the discrete nature of our stimuli (as opposed to the continuously drifting gratings used by Kelly).

(2) The spatiotemporal directional sensitivity surface for OxC, dark-background stimuli is more like a hillside with a hemicircular crest all along the highest density and lowest temporal modulation coordinates. The shift toward higher densities of the optimal sensitivity (relative to the CxO stimuli) may be related to the effective spatial scale of the orientation-sensitive motion detector. Indeed, matching microelements' orientation is a prerequisite for motion perception with OxC stimuli, while orientation discrimination is progressively lost at spatial scales larger than microelements' size.

(3) With CxO, highest density stimuli (element spacing 0.35 deg) modulated at the highest temporal rates (3.75–15 Hz), directional performances are close to chance level (50% correct) under dark-background conditions and almost perfect (90%) under equiluminant-background conditions. In the remainder, this effect will be referred to as the *background effect*. The background effect appears to be reversed for three spatiotemporal conditions, i.e. temporal rates of 1.88, 3.75 and 7.5 Hz and an element spacing of 0.69 deg (see below). The remaining data points are more-or-less equivalent for the two background conditions.

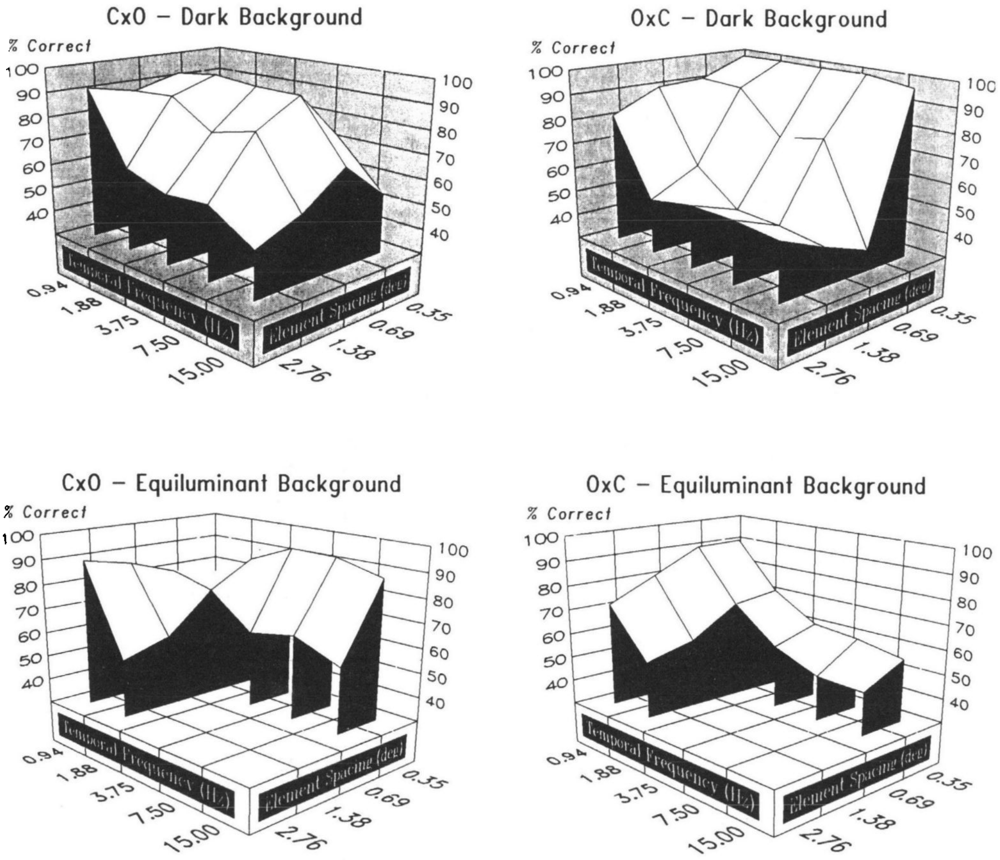

Figure 3. The spatiotemporal directional sensitivity surface (average percentages correct for the three observers) obtained with stimulus configurations CxO and OxC. Dark and equiluminant background conditions are shown in the top and bottom panels. Percentage correct (leftward/rightward) are shown on the ordinate while temporal modulation rate and microelement horizontal density are shown on the horizontal and 45 deg axes.

(4) With OxC stimuli under equiluminant-background conditions, performances are close to chance level for all spatiotemporal conditions with the exception of the lowest temporal rate (i.e. 0.94 Hz). This overall drop in directional performance under equiluminant background conditions is a confirmation of the *veto effect* (Gorea and Papathomas, 1987b, 1988): *in the absence of luminance cues, unmatched colour vetos orientation-carried motion.* The veto effect may also be regarded as a background effect.

It should be noted that the 100% detectability condition as a prerequisite for directional discriminability measurements (see Procedure section) does not imply that all elements of the stimulus array are simultaneously detected. Perception of apparent motion may be significantly disrupted by such a 'sparse detectability'. Attenuation or even reversal of the background effect with CxO stimuli for the spatiotemporal conditions given above (i.e. 0.69 deg spacing at 1.88, 3.75 and 7.5 Hz) may be explained in terms of such a 'sparse detection' effect. Indeed, all three observers

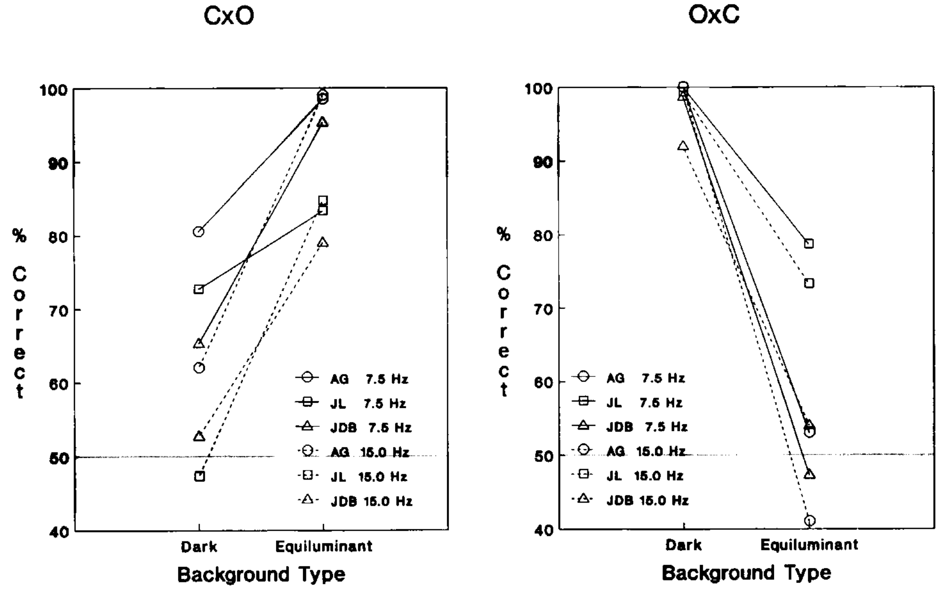

Figure 4. The *background effect* at high densities (0.35 deg interelement spacing) for CxO and OxC stimuli (left and right panels, respectively). Individual data.

reported under these spatiotemporal conditions and for equiluminant background stimuli, a relative difficulty in detecting the whole stimulus array.

As a general rule, high performances obtained for the lowest modulation rates with both CxO and OxC stimuli may be partly due to involuntary (i.e. despite the fixation point) pursuit eye-movements. Indeed, tracking the relevant attribute from frame to frame would provide full directional information. For modulation rates of 0.94 and 1.88 Hz, the durations of one stimulus presentation (i.e. four frames) are long enough (1066 and 533 ms, respectively) for a tracking behaviour to be initiated.

Given the above restrictions on the validity of the spatiotemporal directional sensitivity surfaces of Fig. 3, we limited our subsequent experiments to the highest density (0.35 deg inter-element spacing) and to the highest temporal rates (7.5 and 15 Hz) stimulating conditions (see Note 1). Figure 4 displays the individual results obtained under these restricted conditions with both CxO and OxC stimuli.

Reversal of the background-effect as a function of stimulus configuration is clear cut for the three observers: when background luminance increases from dark to the equiluminance point, directional performances increase from almost chance level to almost 100% for CxO stimuli and decrease from almost 100% to almost chance level for OxC stimuli.

EXPERIMENT 2: THE BACKGROUND EFFECT AS A FUNCTION OF MEAN-LUMINANCE AND OF LUMINANCE-CONTRAST

The background effect may be related to a change of either the mean luminance of the stimuli or the luminance contrast of the individual elements. To test which is the case, we re-measured directional performances at three adaptation (background-luminance) levels (i.e. 6.25, 12.5 and 25 cd/m^2) and for a variety of luminance contrasts.

Procedure

Luminance-contrast was defined as dL/L, where dL is the average luminance of the red and green elements subtracted from the luminance L of the yellow background. Negative and positive contrasts refer to conditions where the luminance of the microelements was below and above the setting for equiluminance with the yellow background. In all cases, red and green elements remained equiluminant.

In one session, temporal rate, background luminance and stimulus configuration (i.e. CxO and OxC) were fixed, while luminance contrast was varied randomly. Temporal rate and background luminance were randomized across sessions. The order of presentation of the two stimulus configurations was varied across observers. All experimental conditions were repeated at least three times (i.e. at least 150 trials/condition).

Results

Figure 5 displays mean directional performances as a function of luminance contrast with background luminance as a parameter. CxO and OxC conditions are shown in the left and right panels, respectively. Performances obtained with 7.5 and 15 Hz temporal rates are shown in the upper and bottom panels. The results display the following main characteristics:

(1) Under both CxO and OxC conditions, performance decreases by at most 20% when L decreases by a factor of 4.

(2) For CxO conditions, performance is negatively correlated with absolute contrast. A contrast change from 0 to $|0.5|$ entails a performance drop of as much as 50% for negative contrasts and of less than 20% for positive contrasts.

(3) For OxC conditions, performance jumps from chance (*veto effect*) to 100% for an increase of about $|0.2|$ contrast units, independently of L.

The results indicate that the background effect is related to both mean-luminance and luminance-contrast with a stronger dependency on the latter. However, the symmetry of the results obtained with CxO and OxC stimuli is related exclusively to the luminance-contrast parameter which is positively correlated with OxC performances and negatively correlated with CxO performances.

The veto effect (for OxC stimuli) has been explained previously in terms of a lack of 'trans'-chromatic motion detectors, i.e. detectors capable of integrating red and green spatiotemporal information at equiluminance (Gorea and Papathomas, 1987b, 1988; for more details, see the Discussion). In order to substantiate this interpretation we should be in a position to show that the veto effect is not a trivial consequence of a lack of orientation discriminability under equiluminant conditions.

This possibility was tested by measuring directional performances with OwC stimuli (see Introduction) under equiluminant background conditions. By construction, motion perception with OwC stimuli is based on orientation matching which should be impossible, had orientation discriminability been close to chance (under equiluminant background conditions). Mean directional performances obtained with OwC stimuli for the three background luminances are presented as solid symbols in

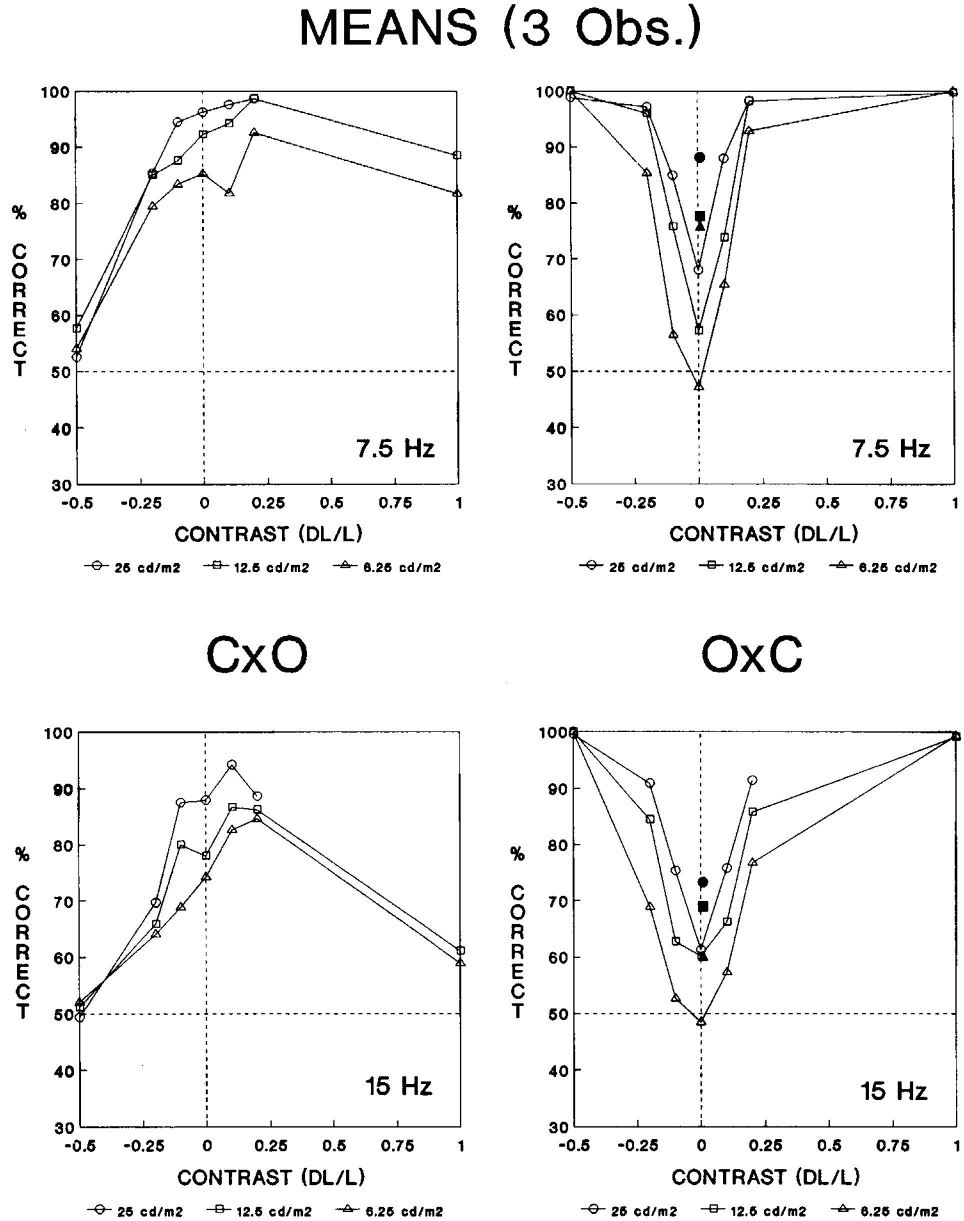

Figure 5. Directional performance (mean data) for CxO (left panels) and OxC (right panels) stimuli as a function of luminance contrast with background luminance as a parameter (open symbols; circles, 25 cd/m^2; squares, 12.5 cd/m^2; triangles, 6.25 cd/m^2). Top and bottom panels show data for 7.5 and 15 Hz modulation, respectively. Contrast is given as $\mathrm{d}L/L$, where $\mathrm{d}L$ is the average luminance of the red and green microelements subtracted from the luminance L of the yellow background. Solid symbols in the right panels show mean performances with OwC, equiluminant background stimuli for the three mean luminances. Typical interobserver standard deviations are less than 10%.

Fig. 5, right panels. The fact that they are significantly higher than OxC performances obtained under equivalent background conditions ($\chi^2_1 = 192.9$, $P \ll 0.001$, for the 7.5 Hz condition and $\chi^2_1 = 39.1$, $P < 0.001$, for the 15 Hz conditions) provides strong evidence that the veto effect cannot be explained in terms of poor orientation discriminability. Recently, Cavanagh *et al.* (1990) confirmed that orientation may be easily discriminated under equiluminant conditions.

Before elaborating on the background effect obtained with CxO stimuli, we present a control experiment whose purpose was to establish the extent to which this effect might be contaminated by unavoidable luminance cues.

EXPERIMENT 3: LUMINANCE CUES AND THE BACKGROUND EFFECT

If the equiluminance setting between red and green elements is not perfect, then unambiguous luminance matching will provide directional cues. Luminance cues under equiluminant conditions may be unavoidable for at least four reasons: (1) intrinsic variability of the equiluminant setting; (2) chromatic aberration (not taken care of in this study); (3) impossibility of equating luminance across retinal areas larger than 2 deg (e.g. Cavanagh *et al.*, 1987); (4) intrinsic variability of the equiluminant point across a large population of chromatic units (Cavanagh and Anstis, 1991).

If luminance cues are present in our stimuli, then their relative efficiency (Weber ratio) in activating directional neurons should be higher under equiluminant–than under dark–background conditions. This is related to the retinal process accounting for illumination increment thresholds under steady (in our case, equiluminant background) and transient (dark–background) adaptation conditions with briefly flashed stimuli (e.g., Geisler, 1983; Hayhoe *et al.*, 1987). The higher efficiency of the hypothetical luminance cues under the equiluminant-background condition may thus account for the higher performances obtained under this condition with CxO stimuli. This possibility was checked and rejected in the following manner.

Procedure

CxO performances were re-measured as before but under three luminance-noise conditions. Additional equiluminance settings were obtained for a mean luminance close to 25 cd/m^2. Luminance values for green and red microelements leading to minimum flicker perception were measured in ascending and descending series. The observer was asked to stop increasing (or decreasing) the adjusted luminance as soon as he estimated that flicker perception was substantially reduced.

Ascending and descending settings encompassed, for Red, a luminance range (of minimum flicker) of approximately ±2.5 cd/m^2 about a mean of 23 cd/m^2 (22%), and for Green of ±4.4 cd/m^2 about a mean of 28 cd/m^2 (31%). In all cases, the midpoint of these 'minimum flicker ranges' was very close to (within less than 10% of) the equiluminant point initially assessed (see Method). Note that these large 'minimum flicker ranges' are by no means correlated with the standard deviation of the equiluminance settings *per se* which was less than 2%.

Given the new equiluminance settings, we defined three luminance-noise conditions as follows: (1) the 0-*noise* condition was a replica of Experiment 1; (2) in the 1-*noise-unit* condition, the luminance of each red and green microelement was randomized across space and time within the 'minimum flicker range' of each observer as defined above; (3) in the 2-*noise-units* condition, the luminance of the red and green microelements was randomized across space and time within a range twice the 'minimum flicker range' of each observer (i.e. an average of ±5 and ±8.8 cd/m^2 for red and green, respectively).

Directional performances were obtained with CxO stimuli, only. Each microelement's luminance was randomized across space (within one stimulus frame) and time (from one frame to the next) within a fixed luminance noise range (0, 1, or 2). Background luminance (dark or 25 cd/m^2), temporal frequency (7.5 or 15 Hz) and noise range were randomized across sessions. All experimental conditions were repeated at least twice (i.e. at least 100 trials/condition). The data were collected about six months after the beginning of Experiment 1.

Results

Figure 6 displays directional performances of the three observers and their mean data, as a function of luminance noise under dark (continuous lines) and equiluminant (dashed lines) background conditions. Circles and squares represent the 7.5 and 15 Hz conditions, respectively. The results display the following characteristics:

(i) When compared with Experiment 1, performances measured under the 0-*noise* condition show an overall improvement. Prolonged practice is a very likely explanation of this effect.

(ii) Directional performances with dark background are independent of noise level (within the specified range), whether they are close to chance (at 15 Hz) or to 100% (at 7.5 Hz).

(iii) For the equiluminant background conditions, performances drop in the 2-*noise-units* condition for two of the three observers. Performances never drop below 70% and they are above 75% in most cases.

Since it is quite unlikely that our equiluminance settings are 2 (or even 1) noise-units off the 'true' equiluminance point, we conclude that the higher efficiency of the hypothetical luminance cues under equiluminant background conditions cannot account for the increase in directional performance with CxO stimuli under equiluminant (as compared to dark) background conditions. Also note that potential chromatic aberration artefacts are eliminated since, due to luminance randomization, edge polarity information cannot be strictly correlated with a given colour. For this reason and also because orientation is changed from frame to frame, potential edge information cannot provide motion cues for CxO stimuli. While edge related information could be relevant for OxC conditions, the veto effect clearly shows that it is not.

GENERAL DISCUSSION

The three experiments presented in this study established the following three facts related to the directional sensitivity with colour- and with orientation-carried motion as a function of the background illumination (background effect).

(1) Experiment 1 demonstrated that when the background illumination approaches the equiluminant point, directional performances increase for CxO stimuli and decrease (*veto effect*) for OxC stimuli. Of all spatiotemporal stimulation conditions used in Experiment 1, those entailing exceptions to this rule (see also Fig. 5 in Gorea and Papathomas, 1989) may be accounted for by stimulus detectability or by eye-movement-related artefacts. Until experiments void of these potential artefacts are

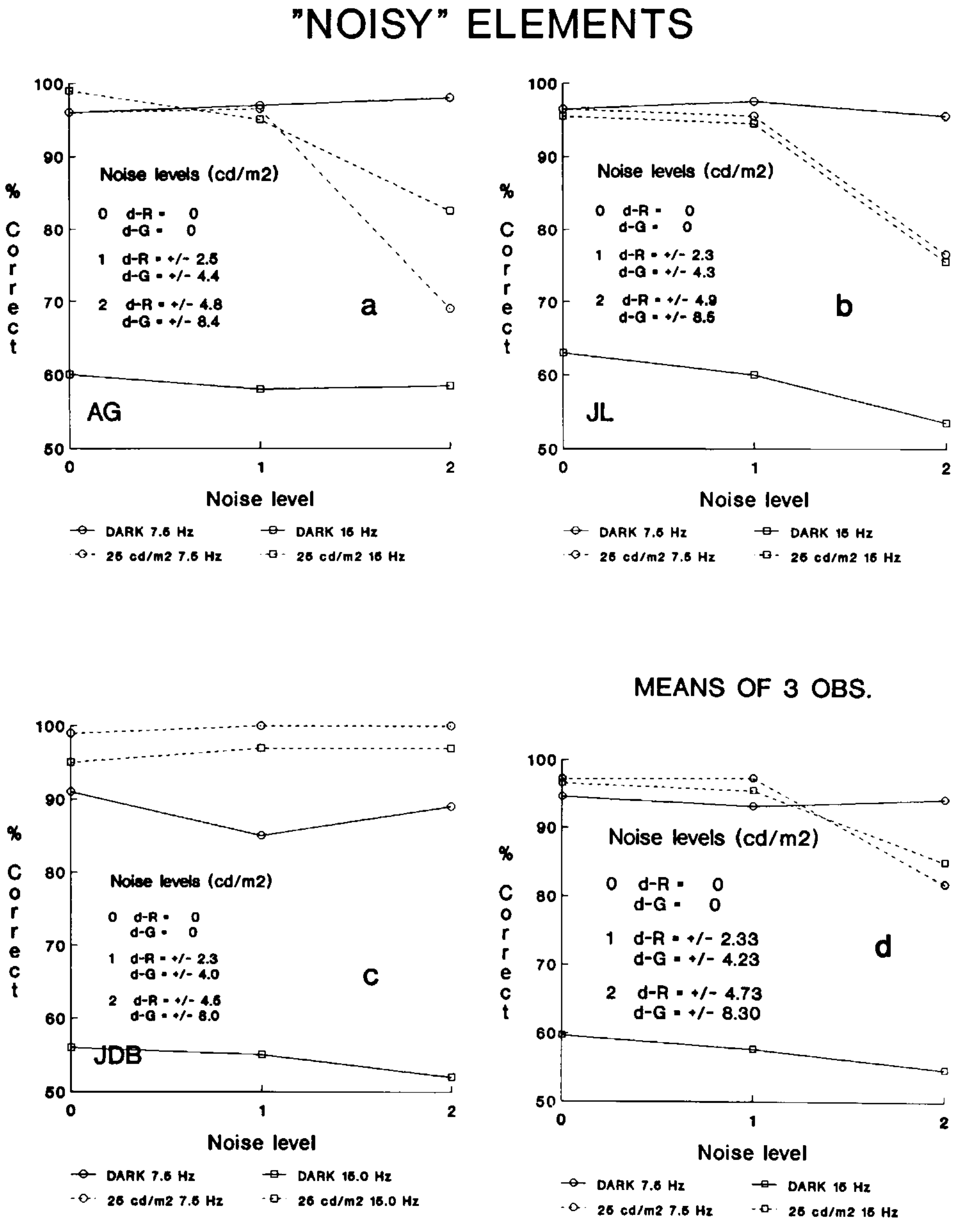

Figure 6. Directional performances for CxO stimuli as a function of the number of luminance *noise units* as defined in the text and as specified in the insert for each observer and for the mean data (bottom-right panel). Data obtained with dark and with equiluminant backgrounds are shown as continuous and dashed lines respectively. Circles and squares are data points obtained with 7.5 and 15 Hz temporal modulations, respectively.

performed, our conclusions must be confined to the specific spatiotemporal conditions where the *background effect* was observed.

(2) Experiment 2 established that the symmetry between the CxO and OxC *background effects* depends exclusively on luminance contrast. In contrast, directional performances are directly proportional to the adaptation-level for both CxO and OxC stimuli. This adaptation-level effect is probably related to an overall drop in stimulus detectability and, for CxO stimuli in particular, to a drop in the activation of the chromatic units (at lower luminances). An additional experiment performed with OwC stimuli demonstrated that the *veto effect* cannot be accounted for in terms of a loss of orientation discriminability.

(3) Finally, in Experiment 3 we showed that the *background effect* with CxO stimuli is not likely to be accounted for in terms of uncontrolled luminance cues.

Gorea and Papathomas (1987b, 1988, 1989) proposed the following interpretation of the *background* (*veto*) *effect* obtained with OxC stimuli. When proximity cues are eliminated, as in the present experiments, apparent motion perception requires the *unambiguous* spatiotemporal matching of at least one stimulus attribute. Unambiguous attribute matching is a necessary but not sufficient condition, however. In order for the matching to be effectively processed by the visual system, i.e. to activate unambiguously a motion detector, most of the remaining stimulus attributes must also be matched. This additional matching may be ambiguous. Ambiguous matching is obtained under all *within* conditions (where one attribute is kept constant across space and time; see Introduction). Its consequence is that the stimulus contains energy along opposite directions of motion.

Ambiguous matching (*within* conditions) should be distinguished from mismatching (*across* conditions) where directional energy within the unmatched dimensions is null. Attributes (such as colour, spatial frequency, retinal disparity, polarity) whose spatiotemporal configuration is random or systematically mismatched and which prevent motion perception normally elicited by matching of some other attribute, were referred to as *veto attributes* (Gorea and Papathomas, 1987b, 1988). Gorea and Papathomas showed that orientation cannot play such a veto role and hypothesized that stimuli whose orientation is mismatched across space-time may still activate nonoriented motion units. The general idea accounting for the *veto effect* is that the inputs to a motion detector share the same selectivities within an n-dimensional sensory space.

With OxC stimuli, the relevant sensory space is 2-dimensional. Moving stimuli defined within this space may activate one (or more) of the following hypothetical sensors: Colour-Oriented (C-O), Colour-non-Oriented (C-nO), Luminance- (or achromatic)-Oriented (L-O) or Luminance-non-Oriented (L-nO). With dark background stimuli, orientation matching will activate unambiguously the L-O sensor. (Colour mismatch will prevent the activation of the chromatic motion sensors.) For equiluminant background stimuli, all luminance cues are eliminated and the L-O (and L-nO) sensor will not respond. It follows that the visual system should be blind to motion of OxC stimuli presented on an equiluminant background, which it is. Gorea and Papathomas (1991) showed that this interpretation may be integrated within a texture discrimination theory, as well. The present study assessed the presence of the *veto effect* under an extended range of spatiotemporal and mean luminance conditions and established the luminance-contrast range within which it is confined.

We propose that, for CxO stimuli, the *background effect* is of an entirely different nature. When the equiluminant microelements of the CxO stimulus are discriminable from the background on the basis of both their hue and their luminance (dark-background condition), luminance cues are drift-balanced (Chubb and Sperling, 1989; according to our terminology, a more complete notation of the CxO stimulus should be CxOwL.) Thus, luminance-carried motion is ambiguous, i.e. L-nO sensors selective to opposite directions of movement are simultaneously active.

In line with previous results (Gorea and Papathomas, 1989), we assume that chromatic-carried and luminance-carried motions are processed by parallel Reichardt-type detectors which converge on an unique motion pathway (Cavanagh and Favreau, 1985; Papathomas *et al.*, 1989, 1991). We then propose that the luminance channel inhibits the chromatic channel responding to the opposite direction of motion. This inhibition must take place before the algebraic summation stage (shared by the two pathways) where the "interfering" drift-balanced luminance signals cancel out. Moreover, inhibition between same-sign luminance and chromatic channels is unlikely since adding chromatic and luminance motion information enhances directional performance (Papathomas *et al.*, 1991). The proposed interaction model is illustrated in Fig. 7.

One may argue that an increase in the simultaneous activation of the two (opposite-sign) directional sensitive luminance subunits is equivalent to an increase in the noise level of the motion detector. It is indeed plausible that fluctuations away from the null output at the level of the summation unit of Fig. 7 increase proportionally with the activation level of the two luminance subunits. The *background effect* could thus be related to the noise level in the motion pathway.

The results obtained in Experiment 3 with the CxO configuration argue, however, against this possibility. In this experiment, random variations in the luminance of the microelements produce noisy directional signals that can be compared to those presumably elicited by an overall increase in the luminance of the microelements. Our results showed that random luminance variations of as much as $\pm 2.5\,\mathrm{cd/m^2}$ (for red) and $\pm 4.4\,\mathrm{cd/m^2}$ (for green) entail no significant drop in directional performances. The possibility that an increase in the activation level of the directionally opponent luminance pathways yields an equivalent noise at the summation stage is quite unlikely.

In Fig. 7, the chromatic and luminance motion pathways display reciprocal inhibitory connections, while the present results support the presence of inhibitory connections from the latter to the former only. The existence of symmetrical inhibitory connections between the two pathways is supported, however, by preliminary experiments where the *chromatic* (rather than luminance) *contrast* between stimulus microelements and background was systematically varied (LwC stimulus configurations; Gorea *et al.*, 1991).

The present model obviously requires further, more comprehensive evaluation. In particular, its generality is critically dependent upon assessment of the *background effect* under spatiotemporal conditions which could not be studied here. Additionally, the model may be criticized on grounds that the parallel processing of chromatic and luminance motion information is not supported by the literature. Although this point has been durably under debate, recent evidence clearly substantiates the 'parallel'

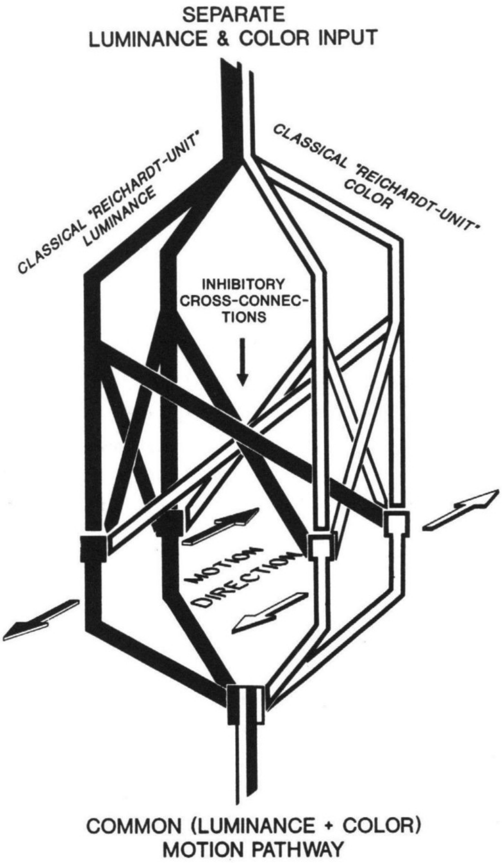

Figure 7. A hypothetical chromatic and luminance Reichardt-type processing unit accounting for the background-effect with CxO stimuli. Luminance channels (black branches) inhibit opposite-sign chromatic (white branches) channels. The symmetrical inhibition of the luminance channels by opposite-sign chromatic channels is strongly suggested by experiments in progress in the authors' laboratory.

option (Cavanagh and Anstis, 1991; see also the Discussion in Gorea and Papathomas, 1989).

It should be finally noted that the reciprocal inhibition proposed here takes place between luminance and chromatic motion-sensitive *channels* rather than between generic attributes. Since attributes such as shape or stereopsis are necessarily defined in terms of either luminance or chromatic contrast, speaking of shape-colour or shape-luminance interactions would be incongruous both logically and neurophysiologically. Instead, one should refer to interactions between Luminance-Oriented and Luminance-nonOriented and between Color-Oriented and Color-nonOriented mechanisms, respectively. This formulation is liable to confer some generality to the proposed model, although interactions of this kind are difficult, if not impossible, to assess experimentally.

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NOTE

1. These are also the stimulus conditions most frequently used in previous papers. They yield relatively smooth motion perception, entail classical motion aftereffects (as reported by the observers), and can be readily used to assess perceived speed (Gorea and Castet, 1991).