Motion processing by chromatic and achromatic visual pathways

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We describe a family of stimuli consisting of colored bars of different orientations, which, when presented in rapid succession, may elicit unambiguous motion perception. These stimuli permitted the isolation of directional spatiotemporal information extracted from oriented luminance clues, from nonoriented chromatic-plus-luminance clues, or, when the stimuli were presented under equiluminant conditions, from pure chromatic clues. As a general rule, matching of orientation induces weaker motion-detection performances than does matching of color. When the orientation clues are in competition with the chromatic ones, motion perception based on the former is always overridden by motion perception based on the latter. We indirectly isolated an oriented chromatic mechanism that also contributes to motion perception. We finally showed that, under equiluminant conditions, matching of orientation across different colors is inefficient in eliciting motion perception, either because motion information is extracted poorly across different chromatic channels or because such channels show little orientational selectivity. Because motion strength determined by each of the manipulated attributes follows different functions with the displacement (or velocity) of the stimuli, we propose the existence of three underlying mechanisms, a luminance mechanism, a chromatic-plus-luminance mechanism, and a pure chromatic mechanism, each of which provides motion information.

INTRODUCTION

It has been reported repeatedly that, relative to luminancemodulated stimuli, equiluminous chromatic patterns provide weak motion output.¹⁻³ The main theoretical issue related to this chromatic-luminance motion imbalance concerns the processing of chromatic and luminance information by the motion-analyzing system(s). It has been proposed that chromatic and luminance channels share a common motion pathway with weaker input from the chromatic channels.^{4,5} The common-motion-pathway hypothesis was based on the demonstration of chromatic-motion cancellation by a luminance-modulated moving stimulus,^{3,4} of chromatic movement aftereffects that transfer to achromatic stimuli,⁶ etc. These same arguments were used to discard other possibilities, whereby chromatic and motion-processing channels might be distinct⁷ or whereby chromatic motion might be accounted for by residual noise in the luminance channel.^{4,5} However, taken together, the neuroanatomical and neurophysiological literatures strongly favor a partition between motion and color pathways as well as between color and form pathways, all of which do, however, interact and show luminance-related activity.8-10

The present study is concerned with providing additional evidence in favor of or against (1) the common-motion-pathway hypothesis and (2) the putative separation between color and form (i.e., orientation) in motion processing. To do so, we start with the quite reasonable assumptions that (a) motion information is processed in both the chromatic and achromatic units,¹¹ (b) chromatic as well as luminance motion pathways consist of both orientation-selective and orientation-nonselective cell populations¹¹⁻¹⁸ (albeit orientation selectivity appears to be underrepresented in the chromatic pathways¹⁹⁻²¹), and (c) whether within the chromatic or luminance pathways, the inputs to a Reichardttype motion unit²²⁻²⁴ are of the same type, namely, from units with similar characterizing selectivities.^{25–30} We refer to this last assumption as the *homogeneity hypothesis*. We then ask the question, is the observed chromatic-luminance motion imbalance due to a general imbalance or to a specific imbalance across the chromatic and luminance channels?

In the process of attempting to answer this question, we show that assumptions (a) and (b) are correct, namely, that motion processing does indeed take place in both chromatic and achromatic pathways and that the addition of orientational clues to a chromatically defined moving stimulus improves movement-detection performances. The homogeneity hypothesis has a particular status in the sense that what is physically inhomogeneous may be homogeneous for a given population of processing units. For example, a stimulus that is not spatiotemporally matched for orientation will nonetheless be homogeneous for nonoriented motion units. The same may apply for nonmatched colors if one assumes the existence of chromatic units responding to any chromatic contrast. For the sake of clarity, in the analysis developed below we assume that such units do not exist. However, we discuss this point in more detail when introducing experiments 4 and 5.

RATIONALE OF THE EXPERIMENTS

The psychophysical demonstration of the color-luminance motion imbalance has always been achieved through indirect techniques. These techniques involved a change in the experimental conditions designed to elicit color- and luminance-related motion, whether the task of the observer was to extract shape out of motion¹ or to estimate the strength (i.e., speed) of motion per se^{3,5} or of its aftereffects.⁴ In most of these experiments, characteristics of chromatic equiluminant motion were compared with and expressed in terms of characteristics of achromatic nonequiluminant motion.

This relative chromatic motion characterization is straightforward only to the extent that equiluminant and nonequiluminant stimuli can be represented within equivalent sensitivity spaces, which is not necessarily the case. For example, the matching of the chromatic contrast of an equiluminant stimulus to the luminance contrast of an achromatic stimulus in order to make them equally visible (i.e., set at a constant ratio relative to their respective thresholds) is problematic in several respects. In order for this procedure to be meaningful, one must ensure that matching across dimensions implies equal output in the respective channels; that this output is directly relevant to the feature under study (i.e., shape, direction, or speed sensitivity); and that, if the matching is used as a cancellation technique, the two stimuli under study (i.e., chromatic and achromatic) do not interact. These conditions are difficult, if not impossible, to satisfy simultaneously. Moreover, the question of how chromatic contrast should be measured is still debatable.³¹

Although finding a universal cross-dimensional metric remains a basic psychophysical problem that is not yet ready to be solved (see, e.g., Ref. 32), the problem of cross-dimensional comparisons related to stimulus differences across experimental conditions can be eliminated altogether by avoiding such intercondition differences. In an effort to achieve this objective, we created a new family of stimuli whose constituent elements are strictly identical across experimental conditions but that, depending on their spatiotemporal configuration, can elicit motion perception within color or luminance pathways or both. Such stimuli cannot be equiluminant, but, as explained below, they may isolate specific color and luminance motion-detection mechanisms whose outputs can be compared directly.

Isolation of Chromatic and Achromatic Motion-Detection Mechanisms

When a set of identical, equally spaced elements displayed on a black background (such that they differ from it both in color and in luminance) is shifted coherently from one frame to another by a displacement equal to half of the interelement spacing, its spatiotemporal Fourier spectrum presents equal energy components within opposite velocity bands²⁴ and is therefore drift balanced.³³ Because such stimuli do not elicit any dominant perception of drift, they cannot be used to isolate any specific motion mechanism.

The perceptual drift balance can, however, be resolved if the individual elements are matched from frame to frame according to one (or more) of their attributes (such as orientation, spatial frequency, or $color^{25-30}$). The stimulus, however, loses its drift-balance property only for mechanisms sensitive to the critical attribute. The manipulation of one (or more) critical attribute(s) permits the isolation of oriented and nonoriented chromatic and luminance motion-sensitive mechanisms even though the individual elements composing the stimulus are discriminable from the background in both color and luminance.

Theoretical Decomposition of Five Spatiotemporal Stimulus Types

Figure 1 illustrates schematically five stimulus configurations that are designed to induce motion perception dependent on the spatiotemporal matching of the color, the orientation, or both the color and the orientation of the individual elements. In each panel the abscissa represents space and Vol. 6, No. 4/April 1989/J. Opt. Soc. Am. A 591

STIMULUS

DECOMPOSITION



Fig. 1. (Left-hand column) Schematic representation of the five stimuli used in the present study. The horizontal dimension represents space, and the vertical dimension represents time. One row in each diagram represents one image frame. Different shadings of individual bars represent different but equiluminant colors. Three equiluminant colors, three orientations, and four rows per image frame were used in the actual stimuli. The gray background, as represented, was in fact either completely dark or set at the equiluminance point with respect to the individual bars. Dashed ellipses show the spatiotemporal matching of the color attributes (A), the orientation attributes (B), or both the color and the orientation attributes (C), (D), (E) determining the perceived direction of motion. For stimulus C the two attributes are matched in a conflicting way (see the text). (Right-hand column) Hypothetical analysis of the mechanisms presumably activated by each of the five stimuli. A b represents a balanced stimulation (i.e., in both directions), empty spaces indicate no activation, and arrows indicate the mechanisms that are stimulated in an unambiguous way. These last mechanisms presumably determine the perceived direction of motion (i.e., the ellipses in the left-hand column). This decomposition is valid only for individual elements that differ from the background in both color and luminance. For stimuli with an equiluminant background, all luminance channels have zero activity (see the text for more details).

the ordinate represents time such that each row in a panel represents one image frame. The darker and lighter elements refer to two different colors (say, red and green), which in the actual experiment were always equiluminant. The gray background was in fact either dark (nonequiluminant conditions) or set at the equiluminant point relative to the bar elements (equiluminant conditions).

The configuration of Fig. 1A is such that the individual elements are matched from frame to frame in color but not in orientation. The reverse is true for the configuration displayed in Fig. 1B. Figure 1C illustrates the combined case in which color matching induces motion to the left and orientation matching induces motion to the right. Finally, the stimuli illustrated in Figs. 1D and 1E are such that both color and orientation are matched to induce motion in the same direction.

Under the assumption that chromatic information and luminance information are processed through parallel pathways^{8,9,34,35} consisting of orientation-selective (O) and orientation-nonselective (nO) units and that these pathways are motion sensitive, the stimuli illustrated in Fig. 1 can be shown to activate the following types of units.

Stimulus A

In stimulus A the matched attribute is color but not orientation. This stimulus unambiguously stimulates the nO chromatic channels. Because the luminance clues are matched along opposite directions of drift, the stimulus induces driftbalanced activity in the nO luminance channels, which cannot therefore contribute to a stable motion perception. The O luminance channels are not stimulated at all. It follows that, if such a stimulus elicits stable motion perception,³⁶ then this perception should be attributed exclusively to the activation of the nO chromatic channels.

Stimulus B

In stimulus B the matched attribute is orientation but not color. According to the homogeneity hypothesis this stimulus should not stimulate any of the motion chromatic channels (see, however, experiment 5 and the Discussion section below), and it should induce drift-balanced activity in the nO luminance channels. Only the O luminance channels will be stimulated unambiguously.

Stimulus C

Stimulus C combines the spatiotemporal properties of stimuli A and B in a conflicting manner. It unambiguously activates the nO chromatic channels and the O luminance channels tuned to opposite directions of movement, induces drift-balanced activity in the nO luminance channels, and does not activate the O chromatic channels at all. It should be stressed at this point that the competition under scrutiny is not between color and orientation as it would be tempting to assume, given the spatiotemporal structure of the stimulus. In a general sense, orientation cannot be opposed to color or to luminance, since it is defined necessarily within one of these two dimensions. For this reason, the measurement of the dominant motion perception elicited by stimulus C will teach us something about the relative strength of the chromatic and luminance motion sensors in a situation of conflicting stimulation.

Stimuli D and E

Stimuli D and E combine the matching of color and orientation in a nonconflicting manner. In conjunction with stimuli B and A, respectively, they permit the indirect isolation of the O chromatic channels. This is explained in more detail in the discussion of experiments 6 and 7.

For stimuli A–C, the values of one attribute (color or orientation or both) are matched across the different values of the other attribute. For stimuli D and E, the values of either of the two attributes are matched within the given values of the other attribute. Whereas matching-within conditions were used extensively in previous apparent-motion studies,^{25–30} matching-across conditions are, to our knowledge, without precedent in the literature.

Two additional experiments run with stimuli A and B under equiluminant conditions make possible the evaluation of the estimated motion chromatic output in the presence of luminance clues relative to a pure chromatic motion output. A full description of the equiluminant experiments is given in a separate paper.³⁷

Note that the principle used here to isolate orientednonoriented, chromatic-achromatic motion mechanisms can be used for the isolation of any other specific motion mechanism. Size (or spatial frequency) and depth attributes are of particular interest.^{38,39} Also note that our definition of a channel or mechanism is generic of any neurophysiological or psychophysical entity characterized by its selectivity for a particular attribute within a given sensory space.

METHOD

Stimuli

Stimuli were red, green, and blue bars oriented at 50°, 170°, and 290° and displayed on a Sony Trinitron color video monitor (PVM-1270Q) driven by an Adage RDS3000 raster display under the control of a VAX 11/750 computer. The CIE x and y coordinates of the monitor (as measured with a Minolta Color Analyzer II, TV/2130) were (0.65, 0.31) for red, (0.29, 0.59) for green, and (0.14, 0.05) for blue.⁴⁰ The three colors were adjusted for equiluminance (see below) near a mean of ~3.5 cd/m². The phosphor type was P22 (persistence is 62.5 μ sec).

The bars were 23 arcmin long and 5 arcmin wide. The distances between two adjacent bars measured at their midpoints subtended 0.50, 1.00, 1.44, and 2.00 deg, depending on the experimental condition. These distances corresponded to spatial displacements from frame to frame of 0.25, 0.50, 0.72, and 1.00 deg, respectively. For a stimulus duration of 33.33 msec/frame with no temporal interval between frames (i.e., 30 Hz), the four given displacements correspond to velocities of 7.6, 15.2, 21.8, and 30.4 deg/sec. In a few cases a displacement of 0.37 deg (11.2 deg/sec) was also used.

Four (instead of one, as schematically represented in Fig. 1) element rows were displayed in each frame. The average vertical spacing between rows was 0.50° . The vertical position of each individual element in a row was jittered randomly by ± 7 arcmin, and the horizontal offset of each row also was randomized within a range corresponding to 0.37 deg plus twice the horizontal distance between the individual elements. The randomization of the (x, y) coordinates of

the individual elements permitted the construction of a stimulus array with no obvious spatial structure. The randomization of one image frame entirely determined the spatial structure of the remaining frames. The stimulus array was surrounded by a dark background and subtended 6.5 deg horizontally and 2 deg vertically with a central fixation point intended to minimize eye movements. It was viewed in binocular vision with natural pupils at a distance of 120 cm.

The equiluminance settings were obtained with a modified flicker-photometry procedure. A magenta background [CIE (x, y) coordinates (0.25, 0.14)] was chosen in such a way as approximately to equalize its chromatic contrast with each of the three target colors. The stimulus array as used in the main experiment but with all bar elements of the same color (see stimulus D in Fig. 1) was then presented on the magenta background set at a luminance of 3.5 cd/m^2 . The colors of the individual elements and of the background were interswitched at a rate of 30 Hz. After each six-cycle presentation, the observer adjusted the luminances of the monochromatic lights so as to minimize his flicker perception. At least five settings were produced by each observer and for each color combination. In a second set of trials each target color was readjusted for equiluminance with respect to the two remaining target colors by using the same procedure. In this case the reference color was set at its equiluminant point with respect to the magenta background as determined previously. The equiluminant points for each color were independent of the specific color pair used for the bar elements and for the background (i.e., they obeyed the rule of equivalence among lights⁴¹).

The mean equiluminant points varied by no more than 10% among observers and had a standard deviation of at most 1.7%. The largest variabilities were observed for the adjustments of the blue target color irrespective of the background color.

Procedure

The two authors and a naïve observer served in all experiments. A two-alternative forced-choice procedure was used in all cases. The spatiotemporal matching of the individual elements 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. For the particular case in which leftward and rightward motion components were simultaneously present (Fig. 1C), the observer was instructed to choose what he thought to be the dominant direction of motion.

Performance was measured as a function of the number of displayed frames, i.e., two (67 msec), three (100 msec), four (133 msec), and five (167 msec) frames. Because even the longest stimulus presentation did not exceed the latency of a typical eye movement, oculomotor behavior cannot be invoked as an interfering factor in these experiments.

One session consisted of 200 trials, 50 per frame number. The number of frames was randomized across trials. Stimulus configuration and displacement size were randomized across sessions. Each experimental condition was repeated at least three times so that each percentage of correct responses was computed from at least 150 trials. With the exception of the ambiguous stimulus (i.e., Fig. 1C), all experimental conditions produced stable performances.

RESULTS

Experiments 1-3: Equiluminant Bars on a Dark Background

Figures 2 and 3 display percentages of correct responses for stimulus configurations A and B (see Fig. 1) for the three observers. The pattern of results is remarkably stable across observers. The standard error of the mean percentage pooled across the three or more repetitions was typically less than $\pm 4\%$.



Fig. 2. Percentages of correct detection of direction of motion as a function of the number of displayed frames for the three observers with stimulus displacement as a parameter: O, \Box, Δ , and ∇ represent results for displacements of 0.25, 0.50, 0.72, and 1 deg, respectively. Each datum point is computed from at least 150 trials. The chance level is at 50% (dashed horizontal line). A, color matching (sitmulus A). B, orientation matching (stimulus B). Asterisks and bold curves represent results averaged across stimulus displacements. The bold curves have been adjusted by eye.



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Fig. 3. The results of Fig. 2 redrawn as a function of stimulus displacement with the number of frames as a parameter. The symbols O, \Box, Δ , and ∇ represent results for two, three, four, and five frames, respectively. A, color matching; B, orientation matching. Asterisks and bold curves represent the results averaged across the number of frames. The bold curves have been adjusted by eye. Dashed lines indicate 50%-correct response levels.

Figure 2 shows performance as a function of the number of frames with stimulus displacement as a parameter. As a general rule, performance increases with the number of frames and decreases with displacement (or velocity). For short displacements (0.25 deg, open circles) performance is almost perfect (>90%) for both chromatic (nonoriented) motion (stimulus A, Fig. 2A) and luminance (oriented) motion (stimulus B, Fig. 2B). As displacement increases, luminance motion is impaired progressively more than chromatic motion is, so that by a displacement of 1 deg (30.4 deg/sec, inverted triangles) luminance motion is almost nonexistent (performance is close to the chance level) while chromatic motion is still quite strong (performance is 70%; see also Fig. 3). When the results are pooled across the four displacement conditions (asterisks and bold curves), it appears clearly that motion perception, which presumably is determined by the chromatic channels, is substantially stronger than motion perception, which presumably is determined by the luminance channels: performance obtained with stimulus A starts at ~73% for the two-frame presentation and reaches ~90% for the five-frame presentation, whereas for stimulus B performance starts at $\sim 64\%$ and reaches $\sim 75\%$ for the equivalent conditions ($\chi_1^2 = 320, p \ll 0.001$). Also note that, whereas performance for stimulus A keeps increasing for as many as five frames, performance for stimulus B appears to saturate for more than four frames. This suggests that chromatic (nonoriented) motion presents a longer integration stage than does luminance (oriented) motion.

Figure 3 presents the same data displayed as a function of stimulus displacement with the number of frames as a parameter. As one would expect from Fig. 2, chromatic-motion performances are systematically higher than luminance-motion performances for each number of frames condition and for each observer. When averaged across the number of frames (asterisks and bold curves), chromatic-motion performance (Fig. 3A) stays quite high for displacements of as much as 0.5 deg (15.2 deg/sec) and levels off beyond this limit at ~70%. Luminance-motion performance (Fig. 3B) is degraded dramatically for displacements larger than 0.25 deg (7.6 deg/sec) and approaches the chance level for displacements of 0.72 deg (21.8 deg/sec).

Taken altogether, the data indicate that motion perception elicited by stimuli A and B follows highly discriminable functions of both the number of frames (Fig. 2) and the displacement (or velocity; see Fig. 3) variables. This difference cannot be attributed to a ceiling effect at the shortest displacements and for the largest number of frames, since it is preserved for those conditions for which performances are significantly lower than 100%, i.e., for the 1-deg-displacement condition (inverted triangles in Fig. 2) and for the twoframe condition (circles in Fig. 3). It is therefore reasonable to assume that stimuli A and B activate distinct mechanisms for which chromatic and luminance labels seem quite appropriate.

Figure 4 displays percentages of color-related directionof-motion choices for stimuli in which color and orientation matchings induced antagonistic directions of motion (stimulus C). Performances were averaged across observers and are displayed as a function of the number of frames (with displacement as a parameter; see Fig. 4A) and as a function of displacement (with the number of frames as a parameter; see Fig. 4B). Asterisks and bold curves show means pooled either across the number of frames or across displacements. If the observers did not show any matching preference (i.e., for color or for orientation) all datum points would be lying on the 50% dashed line. Performances higher than 50% indicate a color-matching preference.

The large standard errors obtained for the shortest displacements are essentially due to the responses of observer AG, for whom the attribute matching determining his perceived direction of motion in this range varied substantially



Fig. 4. Percentages of cases in which color matching is preferred to orientation matching in the conflicting situation induced by stimulus C. The results have been averaged across observers and are displayed as a function of the number of frames with stimulus displacement as a parameter in A (O, \Box, Δ , and ∇ represent results for displacements of 0.25, 0.50, 0.72, and 1 deg, respectively) and as a function of stimulus displacement with the number of frames as a parameter in B (O, \Box, Δ , and ∇ represent results for two, three, four, and five frames, respectively). Vertical bars represent ±1 standard error. Asterisks and bold curves represent the results averaged across stimulus displacements in A and across number of frames in B.

from session to session. With this exception, chromatic motion was dominant for all observers and for all experimental conditions.

The chromatic-motion takeover phenomenon increases monotonically with the number of displayed frames but is an inverted-U-shaped function of stimulus displacement (or velocity) with a peak of ~87% for stimulus displacements of 0.5 deg. When estimated independently, chromatic-motion and luminance-motion strengths show the largest difference (~17%) for both 0.5- and 0.72-deg displacements. The sharp decrease of the chromatic-motion takeover for 0.72deg displacements in the combined condition suggests the existence of interactions between the chromatic and luminance motion mechanisms.^{42,43}

Taken together, the results obtained with stimulus configurations A, B, and C indicate that, contrary to the general idea conveyed by the psychophysical literature, the chromatic pathways not only are capable of processing motion information but appear to have stronger motion outputs than the luminance pathways. This statement should, however, be modulated by two observations, the second of which is developed in the Discussion section.

First, according to our stimulus decomposition (see the right-hand side of Fig. 1 and the Rationale of the Experiments section), the luminance motion isolated by stimulus B is due exclusively to the activation of the oriented luminance channels, whereas the chromatic motion elicited by stimulus A is related to the activation of the nonoriented chromatic channels. It may be that the oriented luminance units are

less numerous than the nonoriented chromatic ones, which might account for the weaker motion perception elicited by the activation of the former.

Second, and most important, the relative strengths of the two types of motion must depend somehow on the specific values chosen for each attribute. It is clear that if the red, green, and blue colors were replaced by any other triplet of less-discriminable colors, chromatic motion would have been correspondingly weaker. Similarly, luminance-oriented motion would have been even weaker if the three chosen orientations had been closer to one another. The color and orientation values that we have chosen are the most different ones within the respective sensory (and, for orientation, physical) spaces. For the time being, we shall limit our conclusion concerning the relative strength of the chromatic- and luminance-motion percepts to these extreme conditions.

Experiments 4 and 5: Equiluminant Bars on an Equiluminant Background

If taken literally, the conclusion above and the stimulus decomposition described in the Rationale of the Experiments section are subject to an important restriction. It relates to what one means by the term chromatic channels. In a strict sense, a chromatic unit should be selective to wavelength (or to color as perceived by the human observer⁴⁴) and insensitive to any luminance modulation. However, a large majority of chromatic cells also respond to luminance contrast.^{11,45,46} If this neurophysiological fact has (as

it should) a psychophysical counterpart, then motion-detection performances measured with stimulus A (see Figs. 2A and 3A) need not be equivalent to those that would be obtained with the same stimulus but under equiluminant conditions (i.e., with a background of the same luminance as the bar elements). The equiluminant bars presented on a dark background would jointly stimulate chromatic units that are also responsive to luminance and pure chromatic units, whereas the equiluminant stimulus would mainly activate pure chromatic units.

Figure 5 displays motion-detection percentages obtained with stimulus A under equiluminant conditions as a function of stimulus displacement (or velocity) for the three observers. The results are averaged across the number of displayed frames. Asterisks and dashed lines are redrawn for comparison from Fig. 3A (stimulus A with a dark background).

For displacements of 0.25 deg (or smaller), motion-detection performances under equiluminant conditions (i.e., equiluminant background) are as high (close to 100%) as under the nonequiluminant conditions (i.e., dark background) for the three observers. We take this as direct proof of highly efficient motion processing within the pure chromatic pathway. However, for displacements larger than 0.25 deg (observers AG and TVP) or larger than 0.72 deg (observer DD), motion-detection performance obtained under equiluminant conditions drops practically to the chance level. This dramatic difference between the nonequiluminant and equiluminant conditions cannot be attributed to a ceiling effect at the shortest displacements (for which performances are close to 100%), since it is preserved even when only the twoframe equiluminant and nonequiluminant conditions (for which performances are decreased globally) are compared. For the same reason, it is unlikely that it may result from a horizontal shift of one function with respect to the other and related to a difference in the effective contrast of the equiluminant and nonequiluminant stimuli. It follows that the reported difference is indicative of the existence either of two types of chromatic pathway (i.e., a pure chromatic pathway and a chromatic-plus-luminance one) or of a facilitatory effect on the luminance output induced by a chromatic input.^{42,43} The second alternative, however, is not supported by electrophysiological data.^{46,47}

The theoretical analysis developed in the Rationale of the Experiments section is based on the principle that motion perception elicited by our stimulus configurations is dependent on the spatiotemporal matching of color and luminance or of luminance alone, regardless of whether the orientation of the individual elements to be matched is kept constant from frame to frame. In the former case, motion would be processed both by O and nO units, whereas in the latter case only the nO units would be active. Under these assumptions, motion perception should not be elicited by an equiluminant stimulus whose individual elements are not matched for color. In other words, our motion analysis implies that chromatic motion cannot be extracted across chromatic channels regardless of whether the spatial attributes of the individual elements (e.g., orientation) are kept constant. We referred to this assumption as to the homogeneity hypothesis (see the Introduction). The homogeneity hypothesis leads to the prediction that, if presented under equiluminant conditions, stimulus B should not elicit any motion perception because, in the absence of any luminance clues, orientation could not be matched across distinct chromatic channels. This should be true, however, only to the extent that motion perception cannot be processed by multiplecolor cells that are known to respond to any chromatic contrast.45,46

Figure 6 displays the motion-detection performances obtained by the three observers with stimulus B under equiluminant conditions. The results have been averaged across the number of frames and are displayed as a function of



Fig. 5. Motion-detection performances obtained with stimulus A (color matching) under equiluminant conditions as a function of stimulus displacement. The results are averaged across the number of frames for each observer. Asterisks and dashed lines are redrawn from Fig. 3A. Vertical bars represent ± 1 standard error, computed over the three (or more) sessions of 200 trials each.

Fig. 6. Motion-detection performances obtained with stimulus B (orientation matching) under equiluminant conditions as a function of stimulus displacement. The results are averaged across the number of frames for each observer. Asterisks and dashed lines are redrawn from Fig. 3B. Vertical bars represent standard errors computed as in Fig. 5.

stimulus displacement (velocity). For comparison, performances obtained with the same stimulus under nonequiluminant conditions are redrawn from Fig. 3B (asterisks and dashed lines).

For the shortest displacement, the responses of observers AG and DD are ~68% correct, and those of observer TVP are 81% correct. For the same displacement but under non-equiluminant conditions all observers gave close to 100%-correct responses. At a displacement of 0.5°, motion perception under equiluminant conditions is at the chance level for all observers, whereas it stays at an average of 74% under nonequiluminant conditions. Overall, the drop in motion-detection performances for stimulus configuration B presented under equiluminant conditions is significantly sharper than for stimulus A ($\chi_1^2 = 2695$, $p \ll 0.001$).

Performances above the chance level may be due to spurious luminance clues that could not be eliminated completely with our (or any other) equiluminance-setting procedure.^{5,48-51} If so, our hypothesis is verified globally: motion information cannot be extracted across chromatic channels. The possibility remains that motion perception under these conditions is at least partly due to the activation of multiplecolor units. However, in order for these units to respond in an unambiguous way, they must be O. It follows then either that such multiple-color units have weak, if any, motion output or that they lack orientational selectivity. In a related series of experiments^{37,38} we showed that orientation selectivity is present in pure chromatic channels. Another possibility is that multiple-color units are sensitive only to short stimulus displacements, which have not been studied here.

Up to this point, the results of our experiments provide strong evidence that both chromatic (stimulus A) and orientational (stimulus B) clues are strong motion carriers, that (at least under our stimulus conditions) the chromatic clues show a marked advantage over the orientational clues, and that, when presented in a conflicting situation (stimulus C), motion perception carried by the former takes over motion perception carried by the latter. On the basis of our stimulus decomposition (see the Rationale of the Experiments section), which is contingent on the assumption (supported by experiment 5 (see Fig. 6) that motion information cannot be extracted, or is extracted only weakly from, different chromatic inputs in the absence of luminance clues (the homogeneity assumption), we can be positive in asserting that we have isolated a chromatic nonoriented motion pathway and a luminance-oriented motion pathway. Moreover, given the different performance-versus-displacement functions obtained under the dark- and equiluminant-background conditions (see Figs. 5 and 6), we also speculated on a distinction between a pure chromatic and a chromatic-plusluminance nonoriented motion pathway. We are now interested in determining the contribution of an oriented chromatic pathway to motion perception.

Experiments 6 and 7: Additional Equiluminant-Bars-Dark-Background Stimuli

As is discussed in the Introduction, orientation selectivity appears to be underrepresented in the color pathway, although this matter is still under debate.¹⁰ It has been shown in psychophysical experiments that the detection of an orientation-color conjunction requires some additional processing time that would not be needed if these two attributes were processed by a unique pathway (see Refs. 52 and 53, but also cf. Ref. 54).

Comparing the motion-detection performances obtained with stimuli A and B with those obtained with stimuli E and D, respectively (see Fig. 1) allows us to estimate the contribution of the O chromatic channels to motion perception. A null contribution could be interpreted as evidence for either the nonexistence of such channels or their insensitivity to motion. On the other hand, any significant contribution will be taken as evidence that such units do exist and that they provide motion information.

Fig. 7. Motion-detection performances obtained with (A) stimulus E and (B) stimulus D for the three observers as a function of stimulus displacement and averaged across the number of frames. In both stimuli, color and orientaion are matched in a nonconflicting manner (see Fig. 1). Asterisks and dashed lines are redrawn from Figs. 3A and 3B. Vertical bars represent standard errors computed as for Fig. 5.

Stimulus D (see Fig. 10) is a one-color stimulus (consisting of red, green, or blue individual elements) with orientation matched spatiotemporally. It is supposed to activate the O chromatic and luminance channels and to induce drift-balanced activity within the remaining ones. Because stimulus B isolates only the O luminance channel, a comparison of the performances obtained with these two stimuli should permit the estimation of the contribution of the O chromatic pathways to motion perception.

Stimulus E (see Fig. 1) is a one-orientation stimulus (individual elements oriented at 50, 120, or 290 deg) with color matched spatiotemporally. It is supposed to activate all the chromatic pathways, and therefore it differs from stimulus A in that it activates the O chromatic channels. The comparison of performances obtained with stimuli A and E is thus equivalent to that made of performances obtained with stimuli B and D to the extent that each of the described pathways behaves as an independent channel.

Figure 7A displays the motion-detection performances obtained with stimulus E for the three observers and as a function of stimulus displacement (velocity). Performances are averaged across the number of frames. Performances are also averaged across the red, green, and blue conditions, for which the pattern of results was quite similar. The results obtained with stimulus D (pooled across the number A. Gorea and T. V. Papathomas

of frames and the orientations) are displayed in a similar way in Fig. 7B. For comparison, the results obtained with stimuli A and B (redrawn from Figs. 3A and 3B, respectively) also are shown (asterisks and dashed lines).

Taken together, motion-detection performances obtained with stimuli E and D are better than those obtained with stimulus A ($\chi_1^2 = 128.6$, $p \ll 0.001$) and with stimulus B (χ_1^2 = 55.2, p < 0.001), respectively. This is clear evidence that, on one hand, O chromatic channels do exist and that, on the other hand, they contribute substantially to motion perception. This conclusion is supported by additional experiments in which the use of stimulus D with an equiluminant background allowed us to isolate directly the contribution of the oriented chromatic channels to motion perception.^{37,38} That these channels are insensitive to large displacements (or high velocities or both) is suggested by the fact that the difference in performances obtained for the two sets of experimental conditions tends to decrease (its reversal being necessarily due to experimental error) with an increase in displacement (for observers DD and TVP only). These results do not, however, permit us to infer whether the putative O chromatic channels behave differently when stimulated jointly with the nO chromatic channels (stimulus E) and with the O luminance channels (stimulus D).

DISCUSSION

In this study we have created a family of stimuli capable of isolating directional spatiotemporal information extracted from oriented luminance clues, from nonoriented chromaticplus-luminance clues, or from pure chromatic clues. The general finding of our study is that motion perception can be elicited by any of these clues and that, under our experimental conditions and contrary to expectations, motion perception elicited by nonoriented chromatic clues is stronger than (and, in a situation of competing clues, overrides) motion perception elicited by oriented luminance clues. We have isolated an oriented chromatic channel indirectly and shown that it also contributes to motion perception. We have also shown that, under equiluminant conditions, motion information is extracted only poorly, if at all, across different colors. This results might imply (1) that multiple-color units do not process motion information, (2) that they have weak orientational selectivity, or (3) that they respond only to small displacements.

Finally, an interesting aspect of our data concerns the difference between performances obtained for color matching with a dark background and with an equiluminant background (see Fig. 5). We argue in the Results section that a ceiling effect at short displacements is unlikely to account for this difference and that the two performance-versusdisplacement functions cannot therefore be just horizontally displaced versions of each other. Alternatively, we suggested that the two experimental conditions might have isolated a chromatic-plus-luminance pathway and a pure chromatic pathway or that the joint stimulation of the luminance and chromatic pathways might produce facilitatory effects on the chromatic pathway. In view of the literature, 11,42,43,46,51 both interpretations are plausible. However, because the two functions are not just shifted versions of each other, the facilitation argument implies the existence of strong interactions between the type of motion carrier and the displace-

ment (or velocity) of the stimuli. Since this kind of interaction is rather unusual, in the remainder of this paper we maintain the distinction between chromatic and chromaticplus-luminance pathways and show that it agrees with previous data.

One possible problem with our experiments might arise from the retinal inhomogeneity of the blue cones that produces inhomogeneous sensitivity to blue light "not only inside versus outside the 2° macular area but within the macula as well."⁴⁸ Because of this inhomogeneity (our inspection field covered a 6.5 deg \times 2 deg retinal area), the contribution of the blue bars to motion perception could not have been matched, over the whole inspection field, to that of the red and the green bars.

In response to these remarks we offer the following empirical observations.

When measured independently for only red, only green, and only blue bars (experiment 6, stimulus D), motion-detection performances did not show any systematic dependence on color. This permitted us to average performances across colors and supported the idea that the red, green, and blue stimuli provided approximately equal inputs to the putative chromatic-plus-luminance channels.

As mentioned in the Method section, the equiluminous settings produced very small variations among observers (at most a 10% difference; precisely 10% for the blue bars), which we take as evidence supporting the efficiency of our method. Even if, despite this consistency, perfect equiluminance could not be achieved, the attenuation of the luminance clues was strong enough to produce a significant interaction between the effect of equiluminant and nonequiluminant conditions, on one hand, and the effect of the nature of the attribute (color or orientation) to be matched spatiotemporally (see Figs. 5 and 6), on the other hand. Because of this strong interaction effect, we did not consider that chromatic aberration and accommodation effects^{4,48,50} were sufficiently critical to be taken into account. We thus conclude that the choice of our three colors in interaction with the size of our inspection field did not produce disruptive effects strong enough to prevent us from generalizing our results to a representative population of putative pure chromatic, chromatic-plus-luminance, and luminance motionprocessing pathways.

A second problem relates to the metric underlying our comparison between motion strengths as determined by chromatic and orientation clues. Because large within-dimension differences, in general, and color differences, in particular, cannot be measured in terms of a times-threshold-based metric (see Refs. 32 and 40), the interdimensional metric problem remains to be solved. Our only contribution in this respect was to offer a general class of stimuli permitting interdimensional comparisons that are not subject to stimulus differences across experimental conditions. While our results do not permit a generalization of our conclusion concerning the relative strength in motion perception of chromatic and orientational clues to other color and orientation triplets with smaller intervalue differences, we can, however, extend it to pairs with larger intervalue differences. In a series of control experiments run with stimuli A, B. and C and consisting of ± 45 -deg red and green bars, we confirmed that color clues elicit stronger motion than do orientational ones. Because in this series of experiments the orientation but not the color difference between bars was increased relative to the triplet experiments (90 deg instead of 60 deg), we could have expected stronger orientationbased motion detection (which presumably was reinforced) than color-based motion detecting. This was not the case.

The weaker motion detection induced by orientational matching may be related to the fact that motion is processed optimally at spatial scales larger than those fitted for the processing of the orientation of the individual elements.⁵⁵ This might account for the steeper performance drop for orientation matching with an increase in displacement (i.e., when the spatial density of stimuli is decreased). It remains, however, that oriented and nonoriented motion-detection mechanisms might have different spatiotemporal properties.

We shall now briefly discuss our results along three lines of interest: (1) their relevance with respect to motion perception in general; (2) their agreement with the psychophysical literature addressing similar questions, and (3) their possible neurophysiological correlates.

(1) It is not as yet clear how the present results may be related to the dichotomy introduced by Braddick⁵⁶ between short-range and long-range motion mechanisms. Because the smallest displacement used in this study was 0.25°, our stimuli should have activated mainly, according to this distinction, the long-range mechanism. On the other hand and according to the same distinction, the zero interframe interval that we have used should have favored the activation of the short-range mechanism.⁵⁷ In fact, these spatial and temporal limiting conditions for the activation of the two mechanisms have been shown to depend on many factors such as the size of the overall display and of the individual elements, their density, and the number of displayed frames.⁵⁸⁻⁶¹ In principle, all these factors may be accounted for in terms of the window-of-visibility concept⁶² and thus may be related to an energy-based motion analysis.²⁴ If so, the short-range-long-range distinction would be related to the spatiotemporal filtering properties of the relevant motion-analyzing systems. For that matter our findings (and any others) obtained with sampled motion should be generalizable to continuous motion.

There is substantial evidence that the spatiotemporal sensitivity envelope for chromatic stimuli is more low pass and presents a lower high-frequency cutoff^{28,63-65} than that obtained with achromatic gratings. Since in the present study temporal frequency was kept constant while displacement (and therefore velocity) was varied, the higher sensitivity to motion of the putative (nonoriented) chromatic-plus-luminance channel relative to the (oriented) luminance channel may be directly explainable in terms of their respective spatial-frequency filtering characteristics. However, our results obtained with equiluminant backgrounds indicate, along the same line of argument, that the putative pure chromatic channel is quite insensitive to low spatial frequencies. It follows that a more coherent interpretation of our results obtained with pure chromatic and with chromaticplus-luminance stimuli is that, in contrast to the chromaticplus-luminance channel, the pure chromatic channel is insensitive to high velocities (see also Ref. 66 and below).

(2) If restricted to equiluminant stimuli, the present results are not, as they might seem, in contradiction with the results of Ramachandran and Gregory¹ and Livingstone and Hubel⁶⁷ or those of Cavanagh and co-workers^{3,4} The first group of authors reported vanishing motion perception at the equiluminant point with an experimental setup in which the extraction of global shape from random-dot cinematograms either was a prerequisite for motion perception¹ or represented the dependent variable itself.⁶⁷ It has since been argued⁵⁰ that equiluminance may introduce positional errors into the image, thereby degrading shape perception based on the computation of spatiotemporal correlations. The difficulty of extracting shape information under such experimental conditions would then explain the correlative loss of directional information.

The most plausible explanation, however, of the different conclusions reached by previous authors who used apparentmotion paradigms is that chromatic-motion perception vanishes for displacements larger than ~ 0.5 deg. Ramachandran and Gregory¹ and Livingstone and Hubel⁷ reported the absence of chromatic motion for displacements larger than this limit.

Cavanagh and co-workers^{3,4} never actually advanced the theory that the chromatic pathway is motion blind. Their results simply show that the perceived velocity of an equiluminant grating is smaller than the perceived velocity of an equivalent luminance-modulated grating. Our observers did not seem to experience a drop in the perceived velocity under the present equiluminant conditions. However, the sharper decrease in the percent-correct directional reports for the equiluminant stimuli (relative to those for the nonequiluminant ones; see Figs. 3 and 5) is correlated positively with the Cavanagh-Favreau⁴ perceived-velocity estimates as a function of the objective velocity of their adapting stimuli (see Figs. 3 and 4 of Ref. 4) and similar to more-recent results obtained with equiluminant random-dot cinematograms.⁶⁶ All in all, results of recent studies do agree that pure chromatic information is fed into a motion-detection mechanism.49,50,66,68,69

A question for debate is whether the chromatic and luminance pathways share the same motion-detection mechanism. Cavanagh and co-workers favor the first alternative, whereas we suggest that motion processing is specific to each of the (pure chromatic, chromatic-plus-luminance, and luminance) isolated pathways. The cancellation of chromatic motion by a luminance-defined stimulus drifting in the opposite direction and the transfer of motion aftereffects induced by luminance-modulated stimuli to wavelength-modulated stimuli (or the reverse⁴) both would take place within the chromatic-plus-luminance channel, which is sensitive to chromatic and luminance clues.

According to our interpretation, the chromatic-plus-luminance channel is not equivalent to a common motion-detection pathway, which, as defined, requires that chromatic information and luminance information be processed within converging pathways, at least one of which (in fact, the chromatic one) should show poor motion processing. The observation that the addition of color to a low-luminancecontrast stimulus reduces the motion aftereffect (in terms of the required velocity needed to cancel it) contingent on a stationary chromatic stimulus⁴ can easily be accounted for in terms of inhibitory interactions among these channels^{42,43} and/or be related to the response of some pure chomatic cells that reduce their activity in the presence of a luminance gradient. 46,47

In fact, evidence against the existence of a common motion-detection pathway comes from our experiment with equiluminant stimuli in which orientation, but not color, was matched spatiotemporally (see Fig. 6). Since such a common motion-detection pathway is not supposed to discriminate between luminance and chromatic inputs, it should not discriminate among different chromatic inputs either. It follows that a common motion-detection pathway should be able to match spatial attributes across color channels. Our results show, however, that this is not the case: motion perception is weak for the spatiotemporal matching of the orientations of differently colored bars. Whereas the remaining motion perception obtained under these conditions might be attributed at least partly to the multiple-color units described by De Valois and De Valois,45 these multiple-color units cannot be a reasonable candidate for a common motion-detection pathway since, according to our results, they must either have a weak motion output or be shape (orientation) insensitive.

(3) There is ample evidence in the neurophysiological literature that, starting with its earlier processing stages, the visual cortex contains at least three types of neuron that are discriminable with respect to their response to wavelength: (a) cells that respond to luminance modulation but are insensitive to chromatic modulation; (b) spectrally opponent cells responding to more-or-less narrow spectral bands, most (but not all) of which also respond to white light; and (c) pure chromatic cells (which may or may not show dual spectrally opponent characteristic) that respond preferentially to color contrast but show a weak response or no response to luminance modulation. All these three types of cell population were described in area 17 of the monkey visual cortex by Hubel and Wiesel¹² and have been studied extensively since. The literature is, however, unclear about their relative numbers in different visual areas.

According to Thorell et al.,46 for example, 53% of the striate cells respond equally well to color and to luminance. 21% prefer achromatic stimuli, and 26% prefer pure chromatic stimuli. These three types of neural population are obvious candidates for the underlying mechanisms of the luminance, chromatic-plus-luminance, and pure chromatic channels postulated in this study to the extent that they do show motion (i.e., direction) sensitivity. The task of establishing cell distributions on the basis of their responses to two physical dimensions, such as color and motion, is more difficult. This difficulty is, of course, increased when a third dimension (e.g., shape or orientation) is taken into account. In fact, most of the authors did not test for all these selectivities at one time, or, if they did, they either used different response and/or classification criteria or recorded from different visual areas. Practically all possible combinations of color, motion, and orientation sensitivities are present in the monkey striate cortex.^{11,70-73} The fact that these attributes appear to be more and more dissociated at higher visualprocessing stages^{8,9} does not preclude the possibility that perceptual experience relies in part on the activity of the lower processing levels.

We conclude that, despite the increasing neurophysiologi-

cal evidence for a separation of visual functions at the higher stages of visual processing, our results indicate that color, motion, and shape (orientation) are processed simultaneously at some lower stages.

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