

Two motion systems with common and separate pathways for color and luminance

(motion perception and processing/spatiotemporal mechanisms/equiluminance)

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ABSTRACT We present psychophysical experiments that reveal two motion systems, a specific and an unspecific one. The specific system prevails at medium to high temporal frequencies. It comprises at least two separate motion pathways that are selective for color and for luminance and that do not interact until after the motion signal is extracted separately in each. By contrast, the unspecific system prevails at low temporal frequencies and it combines color and luminance signals at an earlier stage, before motion extraction. The successful implementation of an efficient and accurate technique for assessing equiluminance corroborates further the main findings. These results offer a general framework for understanding the nature of interactions between color and luminance signals in motion perception and suggest that previously proposed dichotomies in motion processing may be encompassed by the specific/unspecific dichotomy proposed here.

Motion is displacement in space–time. The perception of apparent motion requires at least two spatiotemporal samples of the stimulus. How does the visual system match the elements of each sample to arrive at a veridical percept without making false target matchings in ambiguous situations? It has been shown that a covariance computation across space and time, proposed by Reichardt (1), provides an accurate metric for the extraction of direction (1–4). Covariance computation is equivalent to extracting the spatiotemporal energy of the stimulus by means of a convolution with a first-order spatiotemporally oriented receptive field (2, 3).

In this report we focus our interest on luminance and color. The role of color in motion has been debated over the past 2 decades. First reports suggested that motion perception drops to a minimum or even disappears when the stimulus is defined exclusively by a chromatic modulation (5–8). These results, together with some neurophysiological evidence (9), were taken as evidence that the motion system is color-blind. Nevertheless, more recent psychophysical (10–14) and physiological (15, 16) studies suggest that color contribution to motion is significant, and, under specific spatiotemporal conditions, even stronger than that of luminance (17, 18). The question then arises: How and at what processing level do the chromatic and luminance pathways interact to elicit the final motion percept?

Within the theoretical framework of a generalized Reichardt detector (1–3), Fig. 1 illustrates schematically two extreme cases: a common pathway (Fig. 1A) and a separate pathway (Fig. 1B) scheme. Consider a complex stimulus whose elements are defined in space x and time t , by both a luminance (L) and a chromatic (C) contrast, $L(x, t)$ and $C(x, t)$. In the common pathway, or unspecific, scheme (Fig. 1A), L and C are preprocessed by a common mechanism whose

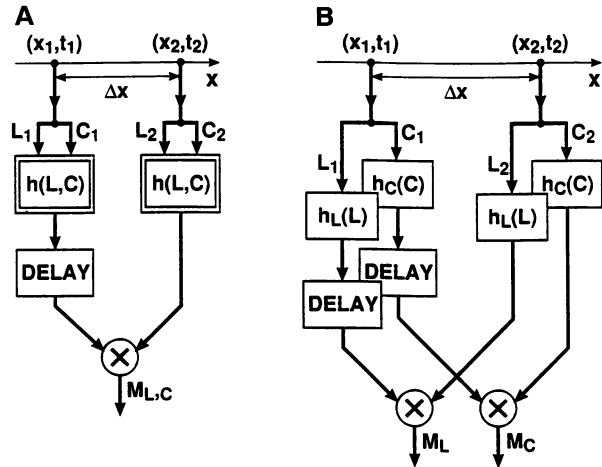


FIG. 1. Block diagrams showing two extreme possibilities of how L and C signals could be processed in the perception of motion. The schematics employ simplified bilocal Reichardt detectors (2) that signal motion to the right. The left pathway feeding each multiplier (\times) delays the signal by Δt . The right pathway is located Δx units to the right and is assumed to be activated by the same “target” that activated the left pathway, but Δt sec later; thus, the multiplier is optimally tuned to rightward motion with speed $\Delta x/\Delta t$. For each such detector, there is a symmetric opponent detector that signals motion to the left. The outputs of the right and left pathways are finally subtracted to form an opponent mechanism. (A) Unspecific, common pathway system; L and C are combined before motion extraction at the multiplication stage. (B) Specific system with separate pathways; motion is extracted separately for L and C and combined at later stages.

output $h(L, C)$ is fed into a multiplier, which yields the motion signal $M_{L,C}$ (19). In the separate pathways scheme (Fig. 1B), the L and C paths yield independent outputs $h_L(L)$ and $h_C(C)$. Each output is fed into distinct, or specific, multiplicative units producing independent motion signals M_L and M_C , which may combine at later stages. The experiments in this report were designed to test which of these two architectures is implemented in the human visual system.

$h_L(L)$ and $h_C(C)$ should be monotonic to satisfy the covariance metric and to account for the reverse- ϕ effect. Also, h should satisfy the following two conditions: $h(L_2, C) > h(L_1, C)$ if and only if $|L_2| > |L_1|$; $h(L, C_2) > h(L, C_1)$ if and only if $|C_2| > |C_1|$; absolute values are used because the unspecific system does not exhibit reverse- ϕ behavior. To simplify the analysis that follows, we will assume linearity for h_L and h_C , which is a valid assumption for 50–60% of the response range of h_L (20). In particular, we will use $h_L(L) = L$ and $h_C(C) = C$, because we will use equivalent contrast

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Abbreviation: EqLC, equivalent luminance contrast.
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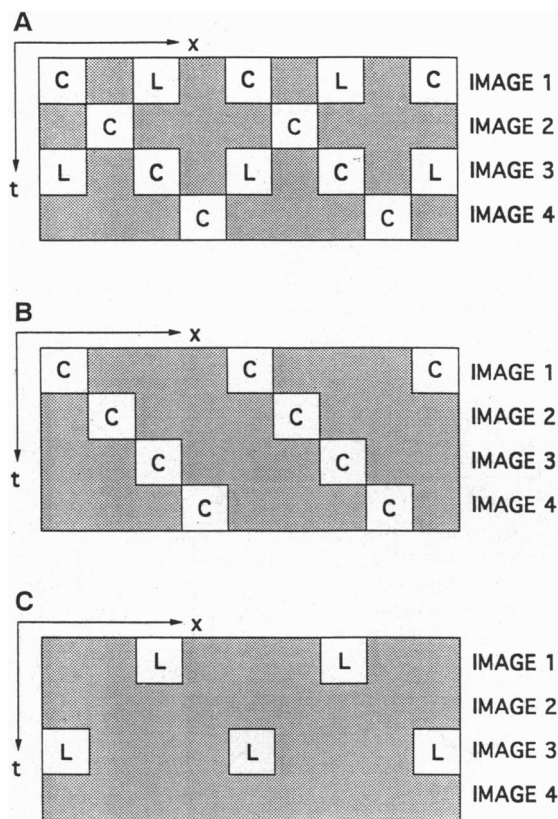


FIG. 2. (A) The space-time ($x-t$) diagram of the stimulus used in the first experiment. The four images are shown in temporal sequence. The yellow background is shown as uniform gray. (B and C) The $x-t$ diagram of A showing only those elements that are visible to ideal chromatic and achromatic pathways, respectively. The width of each element was 0.25 degree of visual angle at a viewing distance of 114 cm, producing a periodic spatial pattern of 1 cycle/degree.

units for L and C . By extension, we will use $h(L, C) = |L| + |C|$ for simplicity.

Fig. 2A displays a space (only the x dimension is shown)–time diagram of the stimulus used in the first experiment, a variant of stimuli used in recent studies (4, 21). Each row in the diagram represents one image frame with time running downward. The elements labeled L and C were displayed on a yellow background shown as a uniform gray. Elements labeled C were equiluminant to the background from which they differed in color only (i.e., they could be red or green). The equiluminance settings were obtained by an iterative heterochromatic flicker photometry technique (22). These elements were “invisible” to an ideal luminance mechanism. Elements labeled L were isochromatic to the background (i.e., yellow) and differed from it in luminance only (i.e., they could be brighter or darker than the background). Thus, they were invisible to an ideal chromatic mechanism. Fig. 2B and C shows the stimulus configuration as “seen” by the hypothetical chromatic and achromatic pathways, respectively. The stimulus is designed in such a way that the homogeneous, rightward motion path $C-C$ and the heterogeneous leftward motion path $C-L$ compete against each other.

If the units that preprocess the visual input combine the color and luminance signals before feeding them into a covariance motion detector (Fig. 1A), one would expect the $C-C$ path to dominate the $C-L$ path for small L contrasts of the L elements. As their L contrast increases (whether positively or negatively), the $C-L$ path should take over the $C-C$ path whenever $h(0, C) \times h(L, 0) > h(0, C) \times h(0, C)$. This prediction can be tested by asking the observer to judge the perceived direction of motion as a function of the L

contrast of the L elements. Overall, the expected performances should be similar to the solid curve of Fig. 3A, which shows the percentage of responses favoring the $C-C$ path.

If, on the other hand, the motion signals are first computed independently in the chromatic and achromatic pathways and combined at a later stage (Fig. 1B), then the $C-C$ path of Fig. 2A should dominate over the $C-L$ path, the latter stimulating none of the two independent mechanisms. Thus, on the assumption of motion processing by separate pathways, the stimulus configuration of Fig. 2A will activate exclusively the chromatic mechanism and the expected directional performances should mimic the dashed curve of Fig. 3A.

Finally, suppose that the common (or unspecific; U) and the separate pathways (or specific) motion processing modes coexist. Let S_U and S_C be the sensitivities of the unspecific and chromatic motion mechanisms, respectively. Then, the stimulus of Fig. 2A (which is such that it never activates a luminance motion mechanism) will yield the following overall response, R :

$$\begin{aligned} R &= S_C h_C(C) h_C(C) + S_U h(0, C) h(0, C) - S_U h(L, 0) h(0, C) \\ &= S_C C^2 + S_U |C|^2 - S_U |L| |C| \\ &= [S_C |C| + S_U (|C| - |L|)] |C|, \end{aligned} \quad [1]$$

where C and L stand for chromatic and luminance contrasts of the C and L elements and where the sign of each term is arbitrarily set to + or – for a rightward or a leftward physical displacement, respectively. The first term in Eq. 1 is the response of the chromatic system to the $C-C$ stimulus path; it is assumed that this system is (quasi)linear—i.e., a first-order system (23, 24). The second and third terms are the responses of the unspecific system to the $C-C$ and $L-C$ paths, respectively. The unspecific mechanism is sign insensitive (i.e., behaves as a full-wave rectifier) and is therefore equivalent in this respect to the second-order mechanism described in the literature (23, 24).

It is clear from Eq. 1 that leftward motion (i.e., $R < 0$) should never be perceived if the U mechanism does not exist—i.e., if $S_U = 0$. Thus, responses favoring the heterogeneous $C-L$ path must be taken as evidence for the existence of such a mechanism. Moreover, Eq. 1 may be used to test the coexistence of the U and chromatic mechanisms: if $S_C = 0$, Eq. 1 reduces to $R = S_U (|C| - |L|) |C|$ and the observer will be at the 50% directional performance level—i.e., $R = 0$ (see dashed horizontal line in Fig. 3A), when $|C| = |L|$.[§] Crossing the 50% performance level, given the slightest activation of the chromatic mechanism, would require that $|L| > |C|$ by an amount dependent on the S_C/S_U ratio, which is given, from Eq. 1 by

$$S_C/S_U = (|L| - |C|)/|C|. \quad [2]$$

The Commission Internationale de l’Eclairage (CIE) x and y coordinates of the yellow, red, and green used here were (0.448, 0.475), (0.611, 0.353), and (0.285, 0.597), respectively. To avoid potential artifacts due to chromatic aberration and/or to imprecise equiluminance settings, the luminance of all stimulus elements was varied across space and time by a random 5% luminance noise around their nominal value.

[§]Different techniques are applicable for assessing the equivalent luminance contrast (EqLC) of an arbitrary chromatic contrast. We used here the motion cancellation technique in which pure chromatic and pure luminance stimuli are pitted against each other. The EqLCs averaged across the two observers were as follows: for green/yellow stimuli, 8.98% at 2.5 Hz and 4.60% at 15 Hz; for red/yellow stimuli, 10.80% at 2.5 Hz and 5.33% at 15 Hz (see ref. 22 for more details).

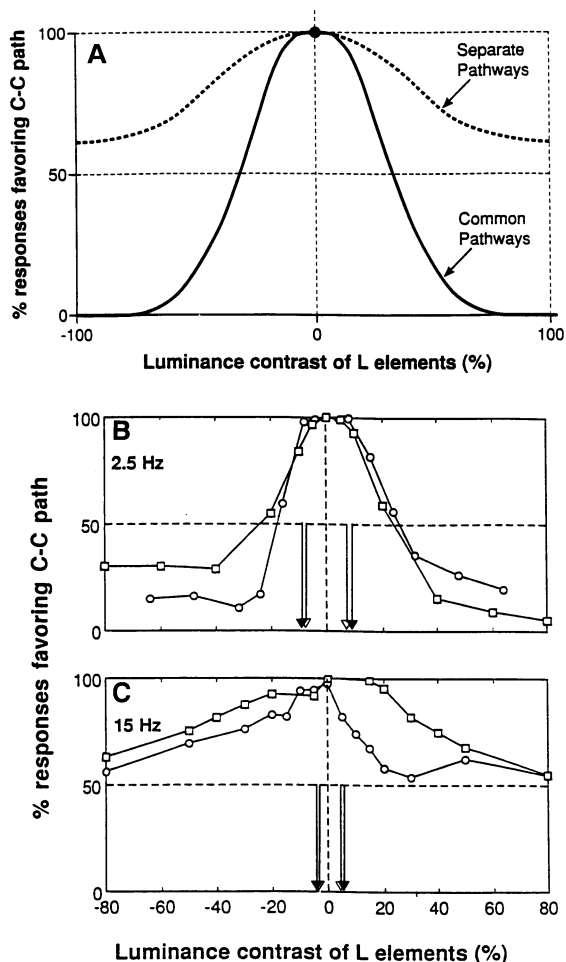


FIG. 3. (A) Qualitative predictions of the two models of Fig. 1 for the stimuli of Fig. 2A: solid and dashed curves are for the unspecific and specific models, respectively. (B and C) Results with the stimuli of Fig. 2A at 2.5 and 15 Hz. Percentages of the responses favoring the C-C path are displayed as a function of the luminance contrast of the L elements. Each experimental point was obtained from at least 150 trials. Circles and squares are for observers AG and CA. A luminance noise of $\pm 5\%$ was used for all conditions but one (i.e., observer CA at 15 Hz). Data are shown only for green elements, but very similar results were obtained with red elements. Open and solid vertical arrowheads point to the equivalent luminance contrasts (EqLCs) of AG and CA, respectively.

Results for noiseless conditions were similar. The stimuli were presented on a Sony Trinitron (GDM 1601/1950) video raster with a 60-Hz temporal resolution (16.7-ms frame duration) driven by an Adage PG-90/10 graphic card. They were vertical red, green, or yellow rectangular bars displayed on a 20 cd/m² yellow background with a periodicity of 1 cycle/degree. Since the sequence of Fig. 2A has a temporal period of four images, the maximum drift rate was 15 Hz—i.e., the case in which each still image coincides with one video frame with no interstimulus interval (ISI). Drift rates of 2.5 Hz were obtained by assigning three video frames each to both the stimulus and ISI images. The ISI image consisted of the uniform yellow background. The overall inspection field subtended 17×13.5 degrees; the grating stimuli subtended 6.5×6.5 degrees.

Percentages of directional responses favoring the C-C path for two observers (circles and squares) and for 2.5- and 15-Hz drift rates are shown in Fig. 3 B and C. Only data obtained with green C elements (see Fig. 2A) are shown. (Performances obtained with red C elements were very similar.) Vertical arrows show for each observer the EqLCs of the green/

yellow chromatic contrast estimated at the two temporal frequencies (see footnote §). At low (2.5 Hz) temporal frequencies, the data bear a remarkable similarity with the predicted performances shown by the solid curve of Fig. 3A—i.e., supporting the common pathway model of Fig. 1A. The crossover of the 50% horizontal line occurs for luminance contrasts of about twice the estimated EqLC (arrows). Given Eq. 2, this finding implies that the unspecific and chromatic motion mechanisms are about equally sensitive at this temporal frequency. These data provide no indication as to the sensitivity of a specific luminance mechanism, because the stimulus does not activate such a mechanism.

Performances obtained with the 15-Hz modulation never cross the 50% level. Overall, the data are in qualitative agreement with the predictions of the separate pathways hypothesis (Fig. 1B and dashed curve in Fig. 3A). Specifically, they indicate the absence of an unspecific/common pathway mechanism at this temporal rate (see Eq. 1 and related discussion). Thus, directional discrimination is entirely monitored by the chromatic mechanism.[¶]

An additional test of the existence of two distinct motion systems is offered by a second experiment, with the stimulus of Fig. 4A. This very same test has been developed into a very efficient and accurate technique for assessing the equiluminance of two colors. The L elements in Fig. 4A are isochromatic with the yellow background and are all set at either +5% or -5% L contrasts. The C + L' elements are defined by their chromatic contrast (they are either green or red) and by a variable L contrast, L'. The observer is asked to report the direction of motion as a function of L'.

Given the results of the first experiment, the key idea behind this technique is as follows: The slightest nonzero luminance signal L' in the C + L' elements will activate the specific achromatic/luminance system, which sees the stimulus of Fig. 4C. This system is assumed to be of the first-order type (23, 24) and will see motion to the right (along the physical displacement in Fig. 4A and C) if the luminance contrasts L' and L are of the same polarity and to the left (opposite the physical displacement) if L' and L are of opposite polarities [reverse- ϕ motion (25, 26)]. The chromatic system, which sees the stimulus of Fig. 4B, will always provide ambiguous directional information and can thus be ignored. When L' = 0—i.e., at equiluminance—motion will be ambiguous if the unspecific system is inoperative (i.e., at medium to high temporal frequencies), or it will be perceived along the direction of the physical displacement if the unspecific system, which combines chromatic and luminance information, is activated (i.e., at low temporal frequencies). If the unspecific system dominates over the luminance system—i.e., when S_U is much larger than S_L (presumably at low temporal frequencies)—the perceived direction will always coincide with the physical displacement: direction reversal should not be observed independently of L'. Hence, the stimulus in Fig. 4A could be used to assess equiluminance of the C + L' elements with respect to the background, provided that the temporal frequency is sufficiently high. Following the notations in Eqs. 1 and 2, the overall response, R, to the stimulus of Fig. 4A can be written as

$$\begin{aligned} \dot{R} &= S_L h_L(L') h_L(L) + S_U h(L', C) h(L, 0) \\ &S_L L' L + S_U (|L'| + |C|) |L|, \end{aligned} \quad [3]$$

[¶]One may argue that at these temporal rates the chromatic mechanisms lose their opponency and therefore behave as if they were luminance mechanisms responding to a luminance modulation. Such an artifactual luminance modulation should be specified by the EqLC (see footnote §). While this possibility remains to be tested psychophysically, previous findings strongly suggest that the chromatic mechanisms respond to motion at these modulation rates (see refs. 17 and 18).

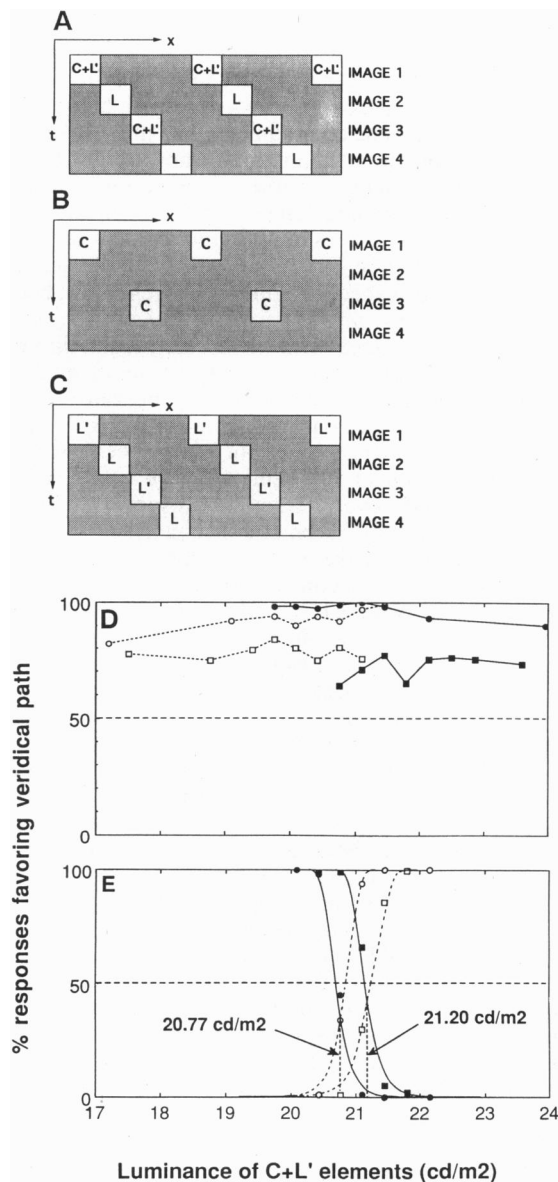


FIG. 4. (A) The x - t diagram of the stimuli of the second experiment. The yellow background is shown as uniform gray. $C + L'$ denotes elements defined by both C and L' contrasts; L' is variable. L denotes yellow elements defined only by luminance contrast. (B and C) The x - t diagrams for the sequence of A showing only those elements that are visible to the ideal chromatic and achromatic pathways, respectively. (D and E) Percentages of responses favoring the vertical motion path of the stimulus illustrated in A as a function of L' , for temporal frequencies of 2.5 and 15 Hz, respectively. Circles and squares are for observers AG and CA. Open and solid symbols are for cases in which elements L have positive and negative 5% luminance contrasts with respect to the background. Each experimental point was obtained from at least 150 trials. The intersection of the fitted psychometric functions defines the equiluminant point (dashed vertical lines). Data are shown for green elements. Data for red elements were very similar.

with S_L the sensitivity of the specific luminance system. It is clear from Eq. 3 that R will change its sign—i.e., motion direction will reverse—when L' and L are of opposite signs and when $S_L > S_U(|L'| + |C|)/|L'|$. It is also clear that for $L' = 0$ only the unspecific system will be active (provided that it is stimulated in the appropriate temporal frequency range—i.e., $S_U > 0$).

The data of Fig. 4 support the above analysis. For low (2.5 Hz) modulation rates, performances never drop below 50%—

that is, direction reversal is never observed—whatever L' (Fig. 4D). At medium (15 Hz) rates, however, direction reversal is quite abrupt (Fig. 4E). At this temporal frequency, the L' (averaged over the symmetrical $-L$ and $+L$ conditions) yielding 50% performances (as estimated from the two psychometric functions fitted to the data) is identical, within the eight-bit precision of our equipment (i.e., 0.4%), to the equiluminance value obtained by the heterochromatic flicker photometry procedure. This coincidence confirms the unique activation of the specific achromatic system at this temporal frequency. Taken together, the results shown in Fig. 4D and E confirm the existence of an unspecific system responsive at low temporal frequencies and discriminate it from a second specific system, the luminance one, activated at higher temporal frequencies. The results confirm that the stimulus shown in Fig. 4A can be used as a powerful technique for the assessment of equiluminance.

In conclusion, the present experiments strongly suggest the existence of two motion systems with common and separate pathways for color and luminance. The first experiment demonstrated the existence of the unspecific system and of a specific chromatic system. The former was shown to be active at low temporal frequencies and totally absent at 15 Hz. The latter was shown to be active at 15 Hz and about as active as the unspecific system at 2.5 Hz. The second experiment confirmed the existence of the unspecific system at low temporal frequencies and isolated it from a specific luminance system responsive at higher temporal rates. It remains a matter of discussion whether the unspecific system characterized by the present experiments may be subserved by the magnocellular pathway known to respond equally well to chromatic and luminance transients (27). While the present results do not allow the specification of the relative temporal frequency preferences of the chromatic and achromatic systems, it is well established (28, 29) that the former is substantially more sluggish than the latter.

Although the present characterization of the specific and unspecific motion systems is limited to color-luminance interactions, it may well encompass previous dichotomies put forth in the literature [short/long range (30), slow/fast (31, 32), first/second order (23, 24)]. A more exhaustive temporal characterization of these mechanisms supports this claim (33). As an example, the temporal characteristics and the front-end nonlinearity [using absolute values for the arguments of $h(L, C)$ —i.e., full-wave rectification] of the unspecific system are entirely compatible with those of the second-order motion system described in the literature. In that respect, full-wave rectification in the luminance domain may be regarded as a particular case of unspecificity to the polarity of the luminance signal. As for the temporal characteristics of the chromatic and achromatic specific systems, it can only be said from these and additional data (33) that these systems operate optimally at higher temporal rates than the unspecific system. This is compatible with previous specifications of the first-order chromatic and luminance systems.

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