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Heterochromatic Fusion Nystagmus: Its Use in Estimating Chromatic Equiluminance in Humans and Monkeys

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The use of chromatic patterns that are equated for luminance has become increasingly popular in psychophysical and neurophysiological studies of visual processing. The currently available techniques for equating different colors for brightness rely upon human reports of perceptual events that are reduced at some luminance ratio. We report here the results of a study using a technique we have recently developed that produces a vivid and compelling motion percept only at isoluminance. That is, unlike previous methods, this technique relies upon a perceptual event (motion) that actually becomes more salient at isoluminance. We also observed that the optokinesis generated by the moving pattern mirrors the perceptual reports at all luminance ratios. If used in this manner, the technique can provide an estimate of chromatic isoluminance in a variety of species and can be used to corroborate a human subject's perceptual experience.

Isoluminance Flicker OKN Motion Color

INTRODUCTION

Psychophysical approaches to the study of the visual system often employ chromatic patterns that are equated for luminance. Historically, human judgements of chromatic equiluminance have been used to determine the relative sensitivity of the eye at different wavelengths and to obtain the spectral luminous efficiency functions (for review, see Pokorny & Smith, 1986). More recently, isoluminant patterns have been used to study the relative contributions of color and luminance pathways to the processing of different stimulus attributes. For example, the perception of motion (Ramachandran & Gregory, 1978; Cavanagh, Tyler & Favreau, 1984), stereopsis (Lu & Fender, 1972; deWeert, 1979) and certain aspects of form (Gregory, 1977; Livingstone & Hubel, 1987) have been reported to be impaired when there is no luminance modulation in the image. Indeed, psychophysical evidence for functional differences between the two principal geniculostriate pathways, i.e. the magnocellular and parvocellular streams (DeYoe & Van Essen, 1988; Livingstone & Hubel, 1987), has been based largely on visual performance with chromatic isoluminant patterns.

The use of isoluminant patterns has also gained importance in physiological studies of the primate visual system. Single-unit studies in the LGN (Kruger, 1979; Hicks, Lee & Vidyasagar, 1983), striate cortex (Gouras & Kruger, 1979; Lennie, Krauskopf & Sclar, 1990), and area MT (Saito, Tanaka, Isono, Yasuda & Mikami, 1989; Charles & Logothetis, 1989), among others, have used isoluminant chromatic patterns. Recent studies in awake, behaving primates which attempt to correlate behavioral responses with underlying neural mechanisms have also used isoluminance paradigms in order to examine the contribution of color to various visual processes (Schiller, Logothetis & Charles, 1990; Logothetis, Schiller, Charles & Hurlbert, 1990; Dobkins & Albright, 1990).

An accurate determination of isoluminance is therefore an essential part of any study which addresses the contribution of chromatic mechanisms to visual processing. Current approaches to the problem of equating different colors for luminance rely upon decisions of perceptual events that become less salient at some luminance ratio. One such approach is the Minimum Motion Technique (Anstis & Cavanagh, 1983; Cavanagh, MacLeod & Anstis, 1987) which yields perceived movement in one direction when the luminance ratio in a chromatic grating is less than 1.0, movement in the opposite direction when that ratio is greater than 1.0, and no movement at the isoluminant point. Optokinetic nystagmus (OKN), head, and body movements often coincide with perceived motion. These behavioral direction reversals can thus be used to estimate the isoluminant point, permitting use of this technique in non-verbal species (Anstis, Cavanagh, Maurer & Lewis, 1987; Teller & Lindsey, 1989; Anstis, Murasugi

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& Cavanagh, 1990; Logothetis & Charles, 1990). Whereas the Minimum Motion Technique relies on minimization of a perceptual (perceived motion) or reflexive (OKN) response, a technique has been recently developed by Chaudhuri (1990) that has the converse property, that is, a striking percept of motion and concomitant optokinetic response is produced only at chromatic isoluminance. Small deviations from the isoluminant point in either direction not only abolish the motion percept, they also abolish the eye movements entirely and in some cases produce an optokinetic response in the opposite direction (Chaudhuri & Albright, 1990). Because the procedure evokes a reflexive response, it can be used in all animals that display OKN, without the need for any special training or a verbal response. Furthermore, the OKN responses provide an independent assessment of chromatic isoluminance that can be used to confirm values obtained with paradigms which rely on decisions of perceptual events.

In this report, the technique, which we call Heterochromatic Fusion Nystagmus (HFN), will be described in detail. We will provide the results of a psychophysical and oculomotor assessment as well as a comparison with other techniques currently available for estimating isoluminance.

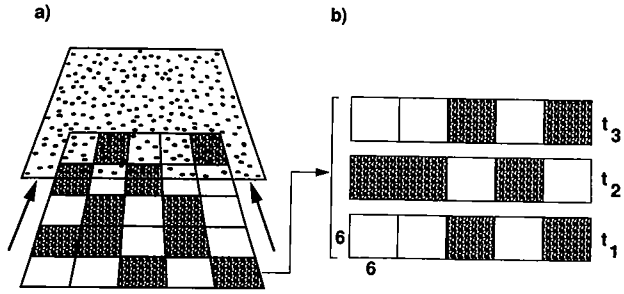


FIGURE 1. Schematic depiction of stimulus pattern used in Fusion Nystagmus photometry. (a) A two-color random-dot pattern is first created with an element size of 6 × 6 pixels. Superimposed upon this are randomly placed black dots which are 2 × 2 pixels with an average spatial density of 1/16. Both patterns are then displaced simultaneously in a particular direction (upward in this example). With each displacement, the underlying chromatic pattern undergoes a contrast reversal. (b) The color sequence for the bottom row in (a) is shown at three successive points in time as it is displaced. The two colors become interchanged with each displacement.

METHODS

Stimulus

The visual stimulus consisted of two components. The first was a chromatic-texture pattern which had 6 × 6 pixel elements, precisely juxtaposed, and randomly chosen to be one of two colors [Fig. 1(a)]. In these experiments, green/red and green/gray patterns were frequently used, although other combinations were created for the additivity and transitivity tests (see later). The luminance of the second color of each pair (Background) was maintained at a constant value while the first (Foreground) could be arbitrarily set by the experimenter. A standard photometer (United Detector Technology, Hawthorne, CA) was used to measure the luminance of each color.

The second component of the stimulus, which was superimposed upon the chromatic-texture pattern, was a luminance-noise pattern composed of 2 × 2 pixel black squares (Fig. 1a). These were generated randomly with a spatial density of 1/16 and the requirement that they not appear side by side. All black elements fully occluded that portion of the underlying chromatic-texture pattern.

The entire stimulus, both chromatic-texture and luminance-noise components, was then moved in a particular direction. Movement of the stimulus was achieved by displacing the stimulus at 30 Hz using displacement values chosen for particular experiments (usually 4–10 pixels/displacement). With each displacement, a contrast reversal occurred in the chromatic-texture pattern. For example, if a green/gray pattern was used, all gray components became green and all green ones became gray synchronously with each displacement [Fig. 1(b)]. At the next displacement, this process was again repeated so that the original chromatic pattern emerged, although displaced. The transformation occurred simultaneously with each displacement of the pattern for the duration of the experiment. The luminance-noise pattern moved in register with the chromatic pattern but was not affected by the contrast-reversal process.

A brief consideration of the stimulus described above will reveal that its essential components consist of a drifting luminance-textured pattern superimposed upon a drifting heterochromatic field. We hypothesized that the motion of the luminance patterns would become maximally salient when the contrast reversal in the chromatic pattern does not mask its movement. This should occur at the heterochromatic flicker fusion point. Thus, motion should be perceived only at the point where the two colors in the display are perceived to be equiluminant.

These stimuli were generated using a PC installed with a graphics co-processor (Number Nine Computer Corp., Cambridge, MA). The stimuli were displayed either on a Zenith flat-screen or a NEC Multisync color monitor. Each pixel subtended 2.6 min arc and 3.0 min arc for the two monitors respectively at a viewing distance of 57 cm.

In some monitors, it is unnecessary to add the luminance-noise component because of a small misalignment of the electron guns which causes a luminance artifact to be added at all chromatic borders (Troscianko & Low, 1985). This appears to be a rather common problem with dot-matrix color monitors and it is possible to make technical adjustments in some monitors to reduce the misalignment. The monitor used for our psychophysical experiments (Zenith) contained such artifactual edges, which provided the necessary luminance correlations to generate a motion signal at isoluminance. That is, as long as there was some luminance signal in the pattern that could generate a sufficient motion signal, whether this arose from electron gun misalignment artifact or in its absence, by addition of luminance-noise, perceived motion was appropriately affected by the luminance ratio in the background pattern (i.e. chromatic-texture). The monitor used for our oculomotor experiments (NEC) was more precisely adjusted for the convergence of the electron guns and therefore we found it necessary to add the luminance-noise component as described above.

Psychophysical assessment (humans)

The stimulus viewed by all subjects was a two-color textured pattern of a square configuration with sides subtending 10 deg arc. In the first experiment, a green/red stimulus was viewed by four subjects for 200 ms during which it was displaced either to the right or to the left within the square aperture. A contrast reversal accompanied each displacement, as described above. At the end of each trial, the subject had to indicate, by way of a key press, one of two directions of motion (i.e. right or left). No other choices were allowed. Each trial was randomly assigned a green luminance from a preset range. The luminance of the red components was fixed at 17.5 cd/m^2 for all trials. A total of 50 trials was presented for each green luminance level, with a 1 sec delay between each trial. There was a small gray fixation spot in the center of the display.

In order to establish that the HFN technique is applicable under a variety of conditions and that it obeys additivity and transitivity laws, we obtained isoluminance measures with different color combinations (green/red, blue/green and red/blue) and different luminance pedestal values for the fixed component (Background). In addition, we also employed patterns that contained variable mixtures of the red, green, and blue primaries as the fixed luminance component (Background). For these experiments, we used only two color-normal subjects, one of the authors (AC) and a naive observer (FN). The Method of Adjustment was used with a total of 5 trials being randomly presented at each of several pre-set Background luminance values. The subjects adjusted the luminance of the variable component until a smooth rightward drift of the pattern was perceived.

For comparative purposes, we further obtained isoluminant matches from the same two subjects using the Minimum Motion, Flicker Photometry, and Brightness Matching paradigms. The Minimum Motion stimulus was a 0.87 c/deg green/red square-wave grating (see Anstis & Cavanagh, 1983 for details). The Flicker Photometry test was performed with a 10 deg arc diameter circular field in which two spatially coextensive homogeneous patterns (red and green) were alternated at 15 Hz. The Brightness Matching paradigm used a 10 deg arc bipartite field of red and green segments. In all cases, the luminance of the red component was fixed while the green component luminance was varied by the observer until a criterion level, specific to the technique, was reached. For the three techniques named above, these were minimizing the drift of the grating, minimizing the flicker sensation, and estimating an equal brightness condition respectively. Stimulus conditions were randomized over a total of 10 trials for each of these paradigms.

Oculomotor assessment (humans and monkeys)

The stimulus containing both the chromatic-texture and luminance-noise patterns, as described at the beginning of this section, was presented on a 19″ NEC color monitor and viewed by two human subjects (FN and GS) and two female rhesus monkeys (Lefty and Lily). All subjects viewed the pattern through a tunnel (length—57 cm; diameter—16 cm) placed against the monitor screen. This obscured all environmental contours which could have interfered with the eye movements. The pattern viewed by all subjects was circular with a diameter of 16 deg arc. In some experiments, the stimulus lacked a fixation spot whereas in others, the fixation spot was flashed in the center of the pattern at a particular frequency (usually 2 c/sec). This was done in order to compare the eye movements obtained under restricted gaze conditions versus those evoked spontaneously by the stimulus.

Eye movements were monitored by the technique of magnetic search-coil oculography (Robinson, 1963) (CNC Engineering, Seattle, WA). In the human subjects, a search-coil implanted within a soft annular contact lens (Skalar, Holland) was placed in the right eye, which had been anaesthetized with Proparacaine HCl (0.5%) (see Collewijn, van der Mark & Jansen, 1975 for details). In the monkeys, a search-coil was surgically implanted under the conjunctiva (Richmond & Chu, 1980). During the experiment, each monkey sat in a specially constructed primate chair (Crist Instruments, Damascus, MD) with its head held rigidly by a restraining post attached to an acrylic skull cap. The eye movements were obtained in 4 sec epochs during which subjects viewed the moving stimuli with a preset luminance ratio. A total of 5 such trials were collected for each luminance ratio. The oculographic traces were analyzed off-line at the end of the experiment in order to examine eye drift velocity as a function of luminance ratio.

RESULTS

Psychophysical assessment (humans)

We begin our analysis of the HFN technique by examining the results from the psychophysical experiments on human observers. These experiments were conducted in order to establish quantitative relationships between perceived motion and pattern luminance and the dependence of this relationship upon several physical parameters of the stimulus. We were also interested in comparing the results obtained with the HFN technique with those from other well established ones, such as Minimum Motion, Flicker Photometry, and Brightness Matching.

In order to obtain the relationship between perceived motion and the luminance ratio of a green/red textured pattern, we collected the reports of four observers as they viewed 200 msec trials of the pattern moving either

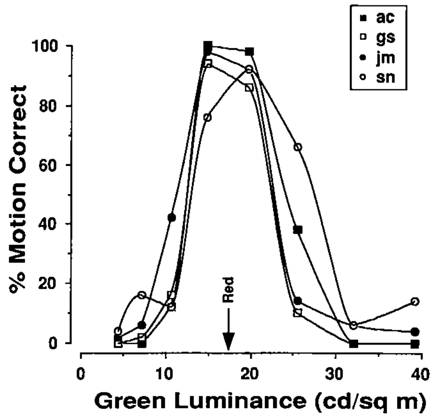


FIGURE 2. Psychophysical reports of four human subjects to a rightward or leftward drifting green/red HFN stimulus. A total of 50 trials was randomly presented at each luminance ratio from a preset range. All subjects reported veridical motion when the variable green luminance approximated the red, which was fixed at 17.5 cd/m². At large deviations above and below this value, the pattern appeared to drift in the direction opposite to its actual displacement, as indicated by the large percentage of incorrect responses. The full bandwidth at half-height is about 10 cd/m².

to the right or left at 4 pixels/displacement (5.2 deg/sec). The red component had a fixed luminance of 17.5 cd/m². As Fig. 2 shows, all four subjects were most likely to report motion correctly when the green component luminance approximated this value. Of equal interest is the performance at luminance ratios above and below the equilibrium point. Instead of providing mixed reports of perceived direction, all subjects consistently reported motion in the incorrect direction at large deviations from unity. At the largest deviations, all of the trials by some subjects were judged to be in the incorrect direction. These results are compatible with a previously demonstrated perceptual phenomenon termed "reverse-phi" and will be taken up further in the Discussion. The tuning curves shown in Fig. 2 each had a full bandwidth at half-height of about 10 cd/m² for all subjects except SN, for whom it was slightly larger. The luminance values indicated in Fig. 2 were obtained with a standard photometer and on the basis of these values, we took the luminance ratio that generated optimum veridical motion to be the isoluminant condition. Further confirmation was provided when we compared these results with those from other well established isoluminance paradigms (see below).

We obtained perceptual measures at a variety of spatio-temporal values using a green/red chromatic pattern in order to demonstrate that the HFN paradigm was robust under a variety of conditions. For this experiment, the same green/red pattern was used as in the previous psychophysical task, however, a Method of Adjustment paradigm was employed. The two subjects titrated the green luminance until optimal rightward drift was perceived. The results shown in Fig. 3 represent the data from 5 such measurements for both subjects at each spatial and temporal value. The temporal parameter was varied by presenting the patterns at several preset values of stimulus-onset-asynchrony (SOA) without any intervening blank fields. That is, each cycle of the stimulus could have a duration of 50, 100, 200 or 400 msec and then followed by the next cycle which was merely the same pattern but displaced rightward. Since a Method of Adjustment approach was used, the pattern continued to move until the subject indicated that an isoluminant condition was reached by the maximum motion criterion. The full spatio-temporal range that was studied encompassed a velocity range of 0.11–8.7 deg/sec. The results shown in Fig. 3 indicate that the same isoluminant point was obtained regardless of the displacement size and frequency of the stimulus. Furthermore, we found no discernible effect on the variability in the data with the different spatio-temporal values, as indicated by the standard deviation curves in Fig. 3.

Although the HFN technique shares certain features with the Heterochromatic Flicker Photometry technique, we were nevertheless interested in obtaining

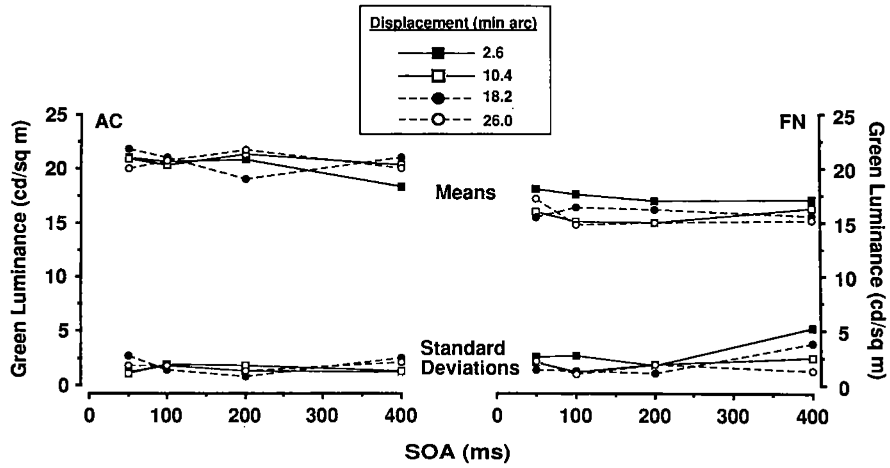


FIGURE 3. The results of two subjects with the green/red HFN stimulus presented at a number of spatial and temporal values. A Method of Adjustment paradigm was used with 5 trials at each displacement and SOA value. The luminance of the red component was fixed at a particular value. The subjects titrated the luminance of the green component until optimal rightward drift was perceived. The means and standard deviations were found to be similar for both subjects in all spatio-temporal values tested.

luminance linearity, additivity, and transitivity measures. The Flicker Photometry technique is known to pass additivity tests (Richards & Luria, 1964; Eisner & MacLeod, 1981). The aim of this set of experiments was to confirm the utility of the HFN technique at several luminance levels and with different color mixtures. Two-color chromatic-texture patterns composed of green/red, blue/green, and red/blue components were used for the first part of this experiment. The second color of each of the above pairs (Background) was set at one of several pre-determined luminance values. At each of these, subjects (AC and FN) obtained an isoluminance match by adjusting the luminance of the Foreground component (first color of each pair) until optimal rightward motion was perceived. As the results of Fig. 4(a) show, the isoluminance matches followed a linear trend with the luminance pedestal of the Background component indicating that regardless of the actual luminance values used, a correct isoluminance match could be obtained. The upper two curves in both of these figures were offset by 10 and 20 cd/m^2 respectively along the y-axis in order to facilitate comparison. The inset table provides the characteristics of the linear fit to the data and is presented in the same order as the functions indicated in the legend. The finding that correlation coefficients approached 1.0 in all cases and that the y-intercepts were close to 0 are good indicators of linearity in these psychophysical measures.

In a similar manner, we obtained isoluminance measures in patterns in which the Background component was a mixture of two colors and studied the effect of varying the relative proportions of these in the mixture [Fig. 4(b)]. Because the original luminances were varied in units corresponding to monitor RGB gun voltages, which are highly non-linear, the luminance pedestals of the two-color mixtures vary from one sample to another. As can be seen in Fig. 4(b), in most cases the luminance values obtained with the HFN technique for the variable component approximated those of the two-color mixtures. For example, as the relative contribution of green in a green/blue mixture (Background) was reduced, we found that the variable red component (Foreground) had a similar luminance when adjusted for maximum motion by the two subjects. Similar results were obtained when green was titrated against a variable red/blue mixture. These results confirm that the HFN technique is robust over a wide range of luminance values and color mixtures.

In order to promote a technique as a bonafide way of determining isoluminance, one must demonstrate that the method is also transitive. That is, if two colors are matched for luminance then a third color should independently provide an identical isoluminant match with the same two colors when measured separately. Our attempt to demonstrate transitivity with the HFN technique is shown in Fig. 4(c). For both subjects, we began with four red settings and obtained an isoluminant green match with each (filled squares) using the Method of Adjustment with 10 trials per luminance setting. The green values from the previous matches then became the independent variable for an isoluminant blue match (open squares). These blue values in turn were used to obtain an isoluminant red match (solid circles). Now, if transitivity holds, we should obtain the original red values we began with. This was indeed found to be the case, within experimental error, and shown in the inset bar graphs that accompany both figures. Since the measure in this case was a comparative one, we retained the actual RGB lookup-table values in these figures. As the insets show, red RGB starting values of 75, 100, 125, and 150 produced a similar set of values upon completion of the transitivity test. The actual luminance range in this test was 6–22 cd/m^2.

We wish to argue that the luminance ratio at which veridical motion is perceived using our technique represents the isoluminant condition. We base this on theoretical grounds (the technique shares certain features with the classical approach known as Heterochromatic Flicker Photometry) and on similarities in the photometric values (obtained with a standard photometer—see Methods). To further substantiate our claim, we compared the HFN results with those from three other standard techniques. In all cases, a green/red field was used and, as before, the two subjects titrated the green luminance until a satisfactory criterion level was reached. As shown in Fig. 5(a), the Brightness Matching paradigm provided results which had a significant amount of variability and, for one subject (FN), were quite different from those obtained from other methods. There are two sources for this difference. The increased difficulty of Heterochromatic Brightness Matching due to subjective judgements of perceptual similarity is well recognized (Wagner & Boynton, 1972). Secondly, this paradigm measures a different dimension (brightness) than other methods which require two components to be equated for luminance in order to achieve a desired goal (e.g. flicker minimization). A better approach is to use the Minimum Border Method, which is known to be both additive and transitive (Wagner & Boynton, 1972). Our use of this technique was complicated by monitor artifacts (see Methods) which introduced a luminance border at the intersection of the two chromatic patches. However, we obtained similar values for the equiluminant condition with the Fusion Nystagmus approach as with Minimum Motion and Flicker Photometry. That is, the green luminance value that approximated an isoluminant match with the red component was found to be nearly the same with all three techniques, as well as with that provided by the photometer [arrows in Fig. 5(a)].

In Fig. 5(b), we compare the Fusion Nystagmus and Minimum Motion techniques. In this experiment, the HFN stimulus (green/red) moved rightward and was presented at various luminance ratios in a random manner from a pre-set range. The Minimum Motion stimulus was a 0.87 c/deg green/red specially constructed square-wave grating whose motion was ambiguous and influenced by the luminance ratio (see Anstis & Cavanagh, 1983 for details). With this technique, the criterion is the minimization of perceived motion, which in a two-alternative forced-choice paradigm can be approximated by a 50% motion judgement of a particular direction. As Fig. 5(b) shows, this criterion is reached at a luminance value that represents the converse percept with the Fusion Nystagmus method, that is, maximization of perceived rightward motion. This point will be taken up in greater detail in the next section.

In Fig. 5(c), we compare the luminance tuning curves obtained with fusion nystagmus and flicker photometry. As this figure illustrates, both functions peak at the same point for both subjects. The tuning bandwidth is actually smaller with the HFN technique for subject AC and nearly identical to the flicker photometry value with subject FN. As reported previously, the correct identification of the direction of motion rapidly declines at small deviations from the isoluminant point with the HFN stimulus. Each of the data points in this figure represents the percentage of responses from 40 trials. Both stimuli subtended 10 deg arc and was presented for a duration of 500 msec following which the subject had to indicate either the direction of motion or whether or not flicker was perceived.

In summary, we have found that the HFN technique generates a compelling and unequivocal motion percept when the colored components of the stimulus are at isoluminance. The technique was robust to spatiotemporal manipulations within the range that we attempted. Furthermore, the HFN technique obeyed additivity and transitivity laws, provided reliable results at several luminance levels, and yielded results that were consistent with other standard methods. We next discuss the results of an oculomotor approach to the HFN assay of isoluminance.

Oculomotor assessment (humans and monkeys)

As with other techniques, the psychophysical approach to HFN photometry requires a behavioral response that accurately reflects a perceptual event. Behavioral paradigms are generally difficult to employ in non-humans because of the extensive discrimination training required. In the case of HFN photometry, a more direct approach is available, that is, to observe the optokinetic eye movements that are generated by the stimulus. In pilot studies with humans and non-human primates, we found that the moving luminance-noise pattern was very effective in driving the eyes in the same direction as perceived motion at isoluminance and that, in general, the optokinetic responses mirrored perceived motion at non-isoluminant conditions as well (Chaudhuri & Albright, 1990). In this section, we expand on our earlier results.

We used a green/gray chromatic-texture pattern with added luminance-noise, consisting of the black dots, as described earlier (see Methods). The oculographic traces of Fig. 6(a) show the OKN obtained from two humans and two monkeys. The pattern was moved upward and the luminance ratio was varied. The gray luminance in all cases was set at 9.0 cd/m^2. A blinking (2 Hz square-wave temporal modulation), centrally placed fixation spot was used and all eye movements occurred during the period when the spot was not present. This approach allowed gaze to be restricted to one part of the visual stimulus and reduced the frequency of large saccadic eye movements by the monkeys. As can be seen in Fig. 6(a), when the luminance of the variable green component was similar to the gray (indicated in the box along the x-axis), all subjects exhibited a striking optokinetic response in the veridical direction.

There are three noteworthy features of these eye movements. First, there is a symmetric decline in the OKN slow-phase velocity at deviations from isoluminance. At deviations greater than 1.0 cd/m^2 from the isoluminant point, the OKN velocity was found to be significantly attenuated in all of our subjects [Fig. 6(a)]. This is best illustrated by the tuning curve of Fig. 6(b) which shows the OKN velocity and gain as a function of the luminance of the variable component (green). From the oculographic traces of Fig. 6(a), OKN velocity was obtained by differentiating the slow-phase components with respect to time and neglecting the saccadic portions. OKN gain was then calculated as the ratio of eye velocity to pattern

FIGURE 4. (*Facing page*) The results of isoluminance measures at different luminance pedestals and color measures. (a) The results of three different color combinations, with the luminance of the second color in each pair (Background) being held constant at a particular value while the observer adjusted the Foreground luminance in order to obtain an isoluminant match. Five trials were presented at each Background pedestal value. In all cases, a linear trend is found as the luminance pedestal (Background) is increased. The data points for blue/green and red/blue have been offset along the y-axis by 10 cd/m^2 and 20 cd/m^2 respectively in order to facilitate comparison. Error bars represent standard deviation. The inset table provides the characteristics of the linear fit to the data and are presented in the same sequence as the functions indicated in the legend above. These results suggest that the HFN technique can be performed within a wide range of luminance values and color combinations. (b) The experiment is similar to that in (a) except the Background (fixed component) was a mixture of two colors, green/blue and red/blue. In each of these mixtures, the relative contributions of the two colors was varied, as shown by the second bar in each pair in the figure. An isoluminant match was then made with a primary color (red or green) by the Method of Adjustment (5 trials/mixture). The luminances of the matching color are represented by the first bar of each pair. In nearly all cases, an isoluminant match was correctly made with each two-color mixture by the two subjects regardless of its spectral composition. Error bars represent standard deviation. These results indicate that the HFN technique can be applied to a variety of color mixtures. (c) Demonstration of transitivity with the HFN technique. The first task involved adjusting the green RGB values to match four pre-set red values (75, 100, 125, and 150) in order to obtain maximum motion (solid squares). These green values in turn were used to obtain an isoluminant blue match (open squares). The blue values were then used to obtain an isoluminant red match (solid circles). The inset bar graphs show that the final set of red RGB values (y-axis) approximated the starting values (x-axis). Error bars represent standard deviation from 10 trials.

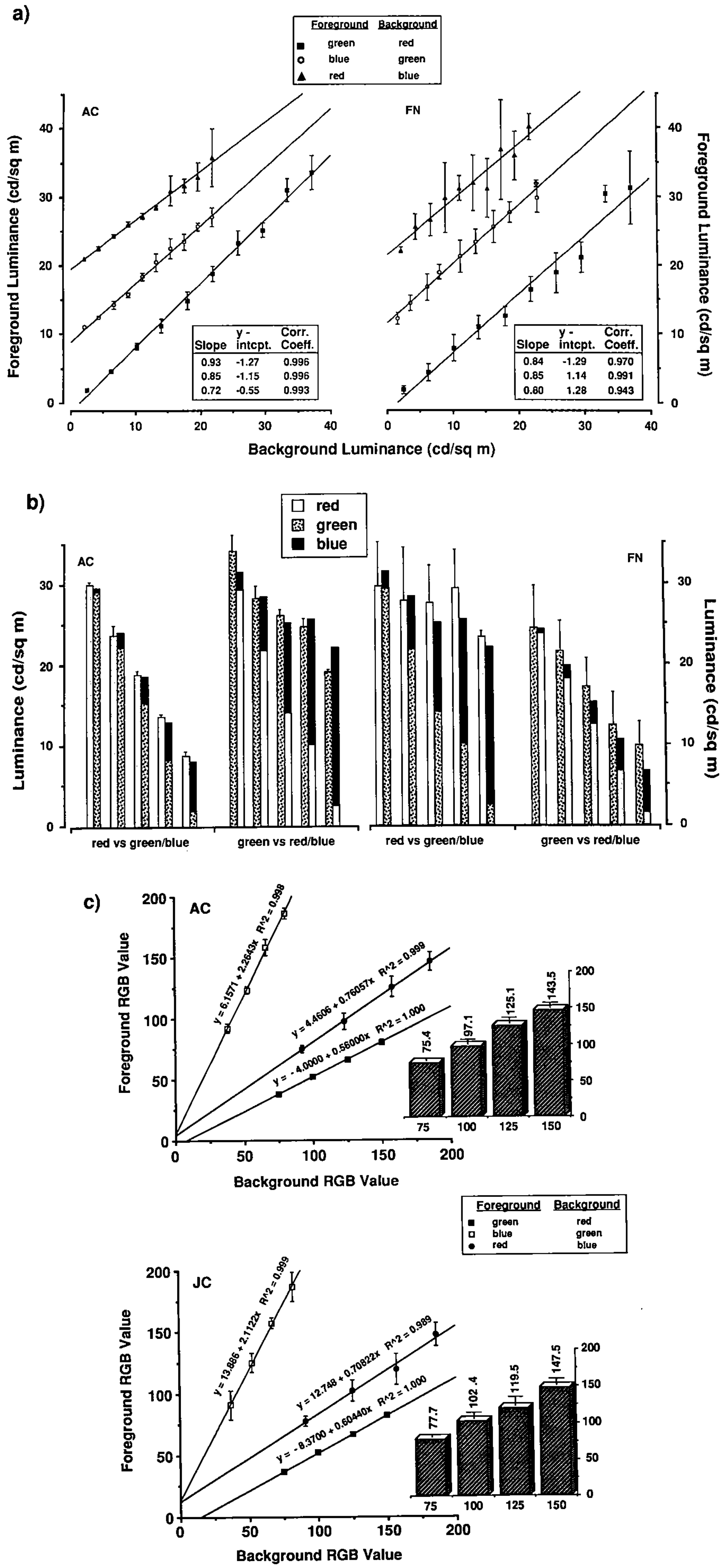

a)
Foreground Background
green red
blue green
red blue
AC
FN
Foreground Luminance (cd/sq m)
Background Luminance (cd/sq m)
Slope y-intcpt. Corr. Coeff.
0.93 -1.27 0.996
0.85 -1.15 0.996
0.72 -0.55 0.993
Slope y-intcpt. Corr. Coeff.
0.84 -1.29 0.970
0.85 1.14 0.991
0.80 1.28 0.943
b)
red
green
blue
AC
FN
Luminance (cd/sq m)
red vs green/blue
green vs red/blue
red vs green/blue
green vs red/blue
c)
AC
Foreground RGB Value
Background RGB Value
y = 6.1571 + 2.2643x R^2 = 0.998
y = 4.4606 + 0.76057x R^2 = 0.999
y = - 4.0000 + 0.56000x R^2 = 1.000
75.4
97.1
125.1
143.5
Foreground Background
green red
blue green
red blue
JC
y = 13.886 + 2.1122x R^2 = 0.999
y = 12.748 + 0.70822x R^2 = 0.989
y = - 8.3700 + 0.60440x R^2 = 1.000
77.7
102.4
119.5
147.5

FIGURE 4

velocity (6 deg/sec). As can be seen in Fig. 6(b), we observed an OKN gain at 0.25–0.50 at isoluminance. Second, at larger deviations from the isoluminant ratio, we observed negative OKN, i.e. movement in the direction opposite to pattern motion. This effect, which was more pronounced in the human subjects, mirrored the psychophysical observation reported in the preceding sections (i.e. "reverse phi motion"). Third, the human subjects reported that they were unable to suppress the eye drift by willful effort, indicating that the eye movements were generated by a reflexive mechanism, i.e. OKN. On some trials of isoluminance, we observed large amplitude, large gain eye drifts which may have been caused by tracking particular luminance features, i.e. black dots, and thereby invoking a smooth pursuit mechanism. This is one likely factor in the larger variability in slow-phase velocity we found at isoluminance [see inset to Fig. 6(b)]. The enlarged OKN gain at isoluminance shown by one monkey (Lily) also may be the product of a greater amount of feature tracking displayed by this animal.

In order to examine the influence of different pattern velocities upon the oculomotor assay of isoluminance, we first obtained the isoluminant ratio in an upward drifting green/gray pattern and then presented it at different displacement values while keeping the alternation rate constant at 30 Hz. Figure 7(a) shows the vertical eye movement profiles at isoluminance at different velocities in one human and monkey. At the higher velocities, there was a clear reduction in the frequency and amplitude of the OKN movements in both species, although the monkey appeared to perform somewhat better [Fig. 7(b)].

In order to obtain an isoluminant match between two disparate colors (e.g. green and red), one approach is to first find an isoluminant match with a neutral color. This reduces the annoying misalignment artifacts in those monitors in which this problem is severe (Troscianko & Low, 1985). Figure 8 shows the results of eye movements in one monkey to a red/gray and green/gray chromatic-texture/luminance-noise pattern. The stimulus drifted upward at 15 deg/sec. The peak eye movements with both patterns occurs in the same vicinity and corresponds to an isoluminant match with the fixed gray luminance.

An additional feature of the above experiment was the absence of a fixation spot in the stimulus. This produced spontaneous OKN interspersed with saccades (see eye movement traces in the insets). Furthermore, from an examination of the oculographic traces and performance during the experiments, it appeared that significantly higher gain eye movements were produced if fixation was not constrained to a particular region. That is, the OKN gain was somewhat higher than in the intermittent eye movements produced with a blinking fixation spot. The disadvantage of this approach is that in the absence of gaze restriction, the oculographic traces become rather noisy. Nevertheless, a "passive-looking" paradigm is convenient in that fixation training is not required and therefore can be applied to a larger number of species. It seems reasonable to use this approach first since a high gain OKN signal is produced at isoluminance.

It was shown earlier that a psychophysical approach using the Minimum Motion and Fusion Nystagmus techniques approximated the same isoluminant point. We have also found a similar correspondence with optokinetic eye movements [Fig. 9(a)]. The chromatic grating from the Minimum Motion test had similar spatial excursions and temporal characteristics to the HFN stimulus. However, the eye movements we obtained with the Minimum Motion technique were considerably weaker [Fig. 9(b)]. That is, at non-isoluminant conditions we found the Minimum Motion stimulus to evoke significantly weaker OKN than the HFN stimulus at isoluminance. Nevertheless, an isoluminant match occurred at the same luminance with the respective criteria for the two techniques.

In summary, we have found that the same stimulus that produced a compelling motion percept at isoluminance also evoked a concomitant optokinetic response in both humans and monkeys. The amplitude and gain of the resulting eye movements varied with the physical parameters of the stimulus and whether or not gaze restriction was employed. A comparison of the Minimum Motion and Fusion Nystagmus techniques showed the latter to generate a better optokinetic response.

FIGURE 5. (*Facing page*) Comparison of the HFN technique with other paradigms. (a) A green/red isoluminance measure with four paradigms. The red luminance was fixed at the value indicated by the arrows along the *y*-axes. The green luminances that produced an isoluminant match were found to be similar using the techniques of Fusion Nystagmus, Flicker Photometry, and Minimum Motion. The Method of Adjustment was used with 10 trials for each technique. The Brightness Matching data were somewhat different from those obtained with the other methods and were more variable. Error bars represet standard deviations from 10 trials. (b) The directions of perceived motion at different luminance ratios using the Fusion Nystagmus and Minimum Motion techniques. A green/red pattern was used in both cases with 50 trials at each luminance ratio. The trials were presented randomly from a preset range of luminance ratios. With the HFN stimulus, optimal motion in the rightward direction was seen only at isoluminance and opposite motion at non-isoluminant ratios. As a result, a tuning curve with a central peak was obtained. With the Minimum Motion stimulus, luminance ratios (green/red) which are less than 1.0 produced rightward motion whereas ratios greater than 1.0 produced leftward motion. The isoluminant point is defined by equal instances of left and right motion percepts (50%), which corresponds to the peak in the Fusion Nystagmus curve. (c) Comparison of tuning bandwidths for fusion nystagmus and flicker photometry. Subjects were randomly presented 10 deg fields of either stimulus for 500 msec and required to indicate the direction of motion or the presence of flicker. A total of 40 trials was presented at each luminance ratio. The results show that the same isoluminant ratio is obtained with both techniques and that both have similar tuning curves.

DISCUSSION

Comparison with previous techniques

The classical techniques for determining isoluminance require perceptual judgements on the minimization of a particular sensory parameter. For example, in Heterochromatic Brightness Matching, a reference light of fixed wavelength and luminance is presented adjacent to a comparison field of a different wavelength and the observer is required to adjust the luminance of the lâtter

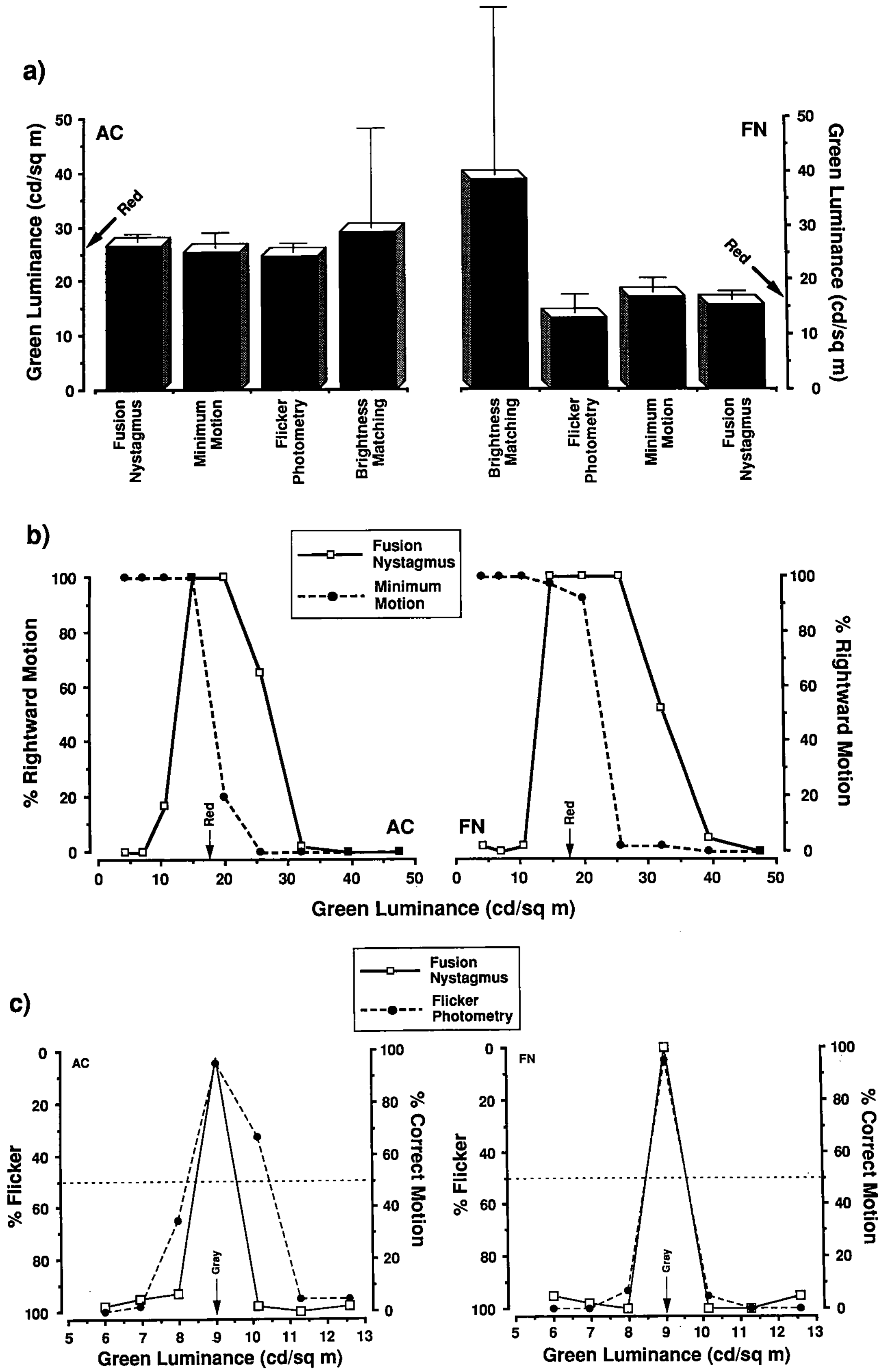


FIGURE 5

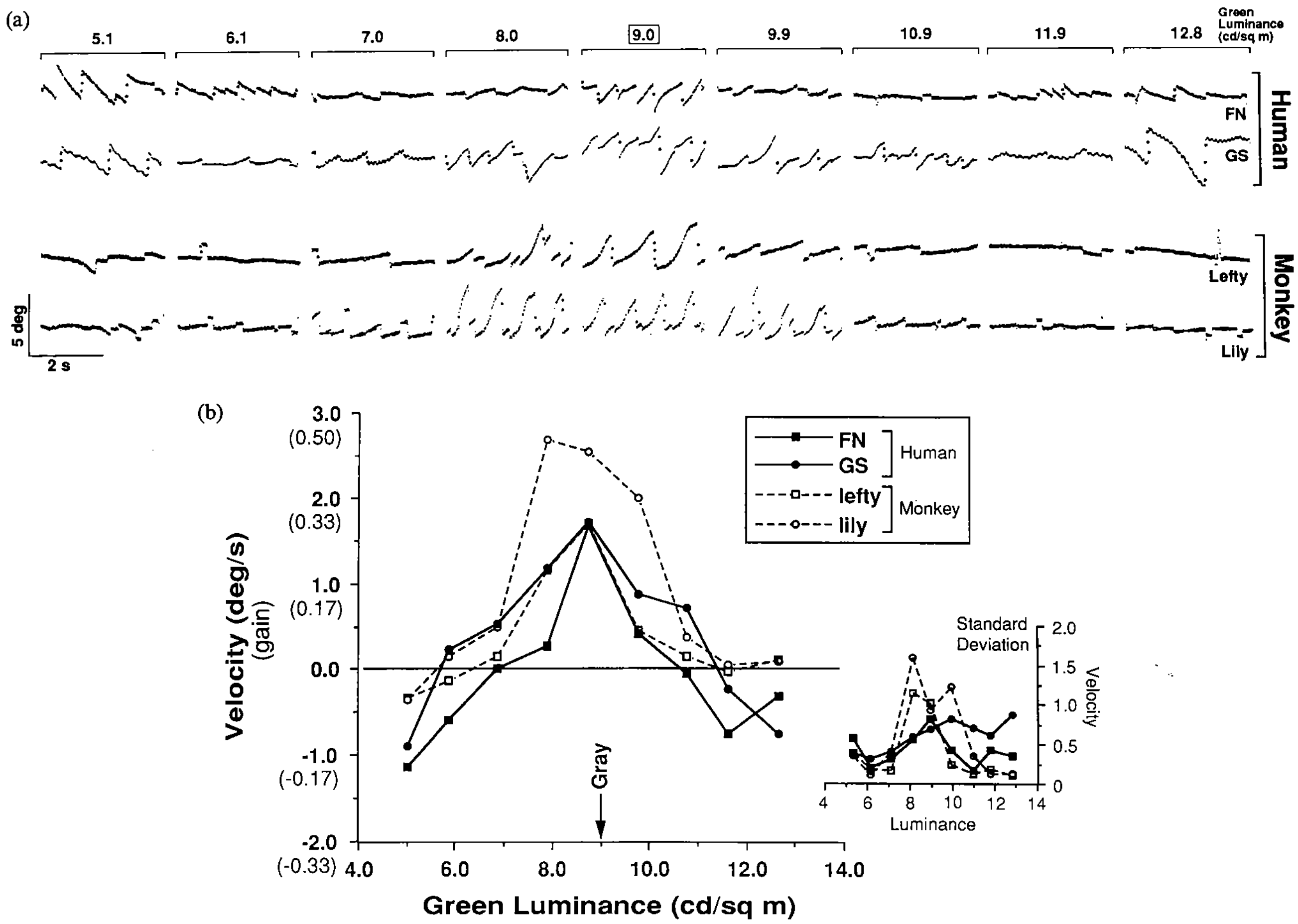


FIGURE 6. Optokinesis produced by the Fusion Nystagmus stimulus. (a) A green/gray chromatic-texture pattern with added luminance-noise was displaced upward at 6 deg/sec. The luminance of the gray components was maintained at 9.0 cd/m^2 while the green luminance was varied from 5.1 to 12.8 cd/m^2. Each panel in this figure presents the vertical eye movement trace for a 4 sec epoch during which the luminance ratio of the chromatic pattern was kept at a constant value. For all subjects, a striking upward OKN was seen when the green luminance matched the fixed gray luminance (boxed). There was a symmetric decline in the OKN at non-isoluminant ratios and at larger deviations, reverse OKN was found in the human subjects, and to a smaller extent in the monkeys. (b) The mean results from 5 slow-phase segments (velocity and gain) in the data shown in (a). OKN velocity was obtained by differentiating the slow-phase components in the oculographic traces with respect to time and neglecting the saccadic portions. OKN gain was then calculated as the ratio of eye velocity to pattern velocity (6 deg/sec). As noted already, the peak in the OKN occurs at the isoluminant ratio. The full bandwidth at half-height is about 1–2 cd/m^2. The inset shows the standard deviations (5 trials) for each luminance ratio tested.

in order to minimize a brightness difference between the two (Walters & Wright, 1943; Ikeda & Shimozono, 1981). Similarly, in Heterochromatic Flicker Photometry (HFP), two coextensive fields of different wavelengths are alternated at frequencies greater than 10 Hz and the observer is required to adjust the luminance of one of the components until the sensation of flicker is minimized and the field takes on the appearance of an intermediate color (Ives, 1912). Finally, in the Minimally Distinct Border technique, subjects adjust the luminance of one field in order to reduce the contrast of a precisely juxtaposed border with a reference field at a different wavelength (Boynton & Kaiser, 1968). In contrast, the Heterochromatic Fusion Nystagmus (HFN) technique produces a striking motion percept only at an isoluminant ratio and a degraded motion percept at all other ratios. This distinguishes it from other techniques because the isoluminant point is positively defined.

An additional feature of the HFN technique that distinguishes it from most earlier techniques is that it can evoke a reflexive (optokinetic) response. Paradigms which rely only on reports of perceptual events are susceptible to variability and imprecision and resist an objective evaluation since criterion responses are based solely on a subjective decision making process. Their use in non-humans is further complicated because the perceptual measure is often abstract, e.g. brightness matching and flicker reduction, and therefore requires extensive training. There are, however, reports in which flicker discrimination paradigms have been used successfully in non-human primates to estimate isoluminance (Schiller *et al.*, 1990; Logothetis *et al.*, 1990; DeValois, Morgan, Polson, Mead & Hull, 1974). Although the HFN technique can be used psychophysically (e.g. Method of Adjustment, Method of Constant Stimuli), its utility and power lies in the optokinesis it evokes at isoluminance. This makes it not only a powerful tool for use with humans but one of the few techniques that can be employed in non-humans that display OKN. Prior attempts at using OKN for assessing the contributions

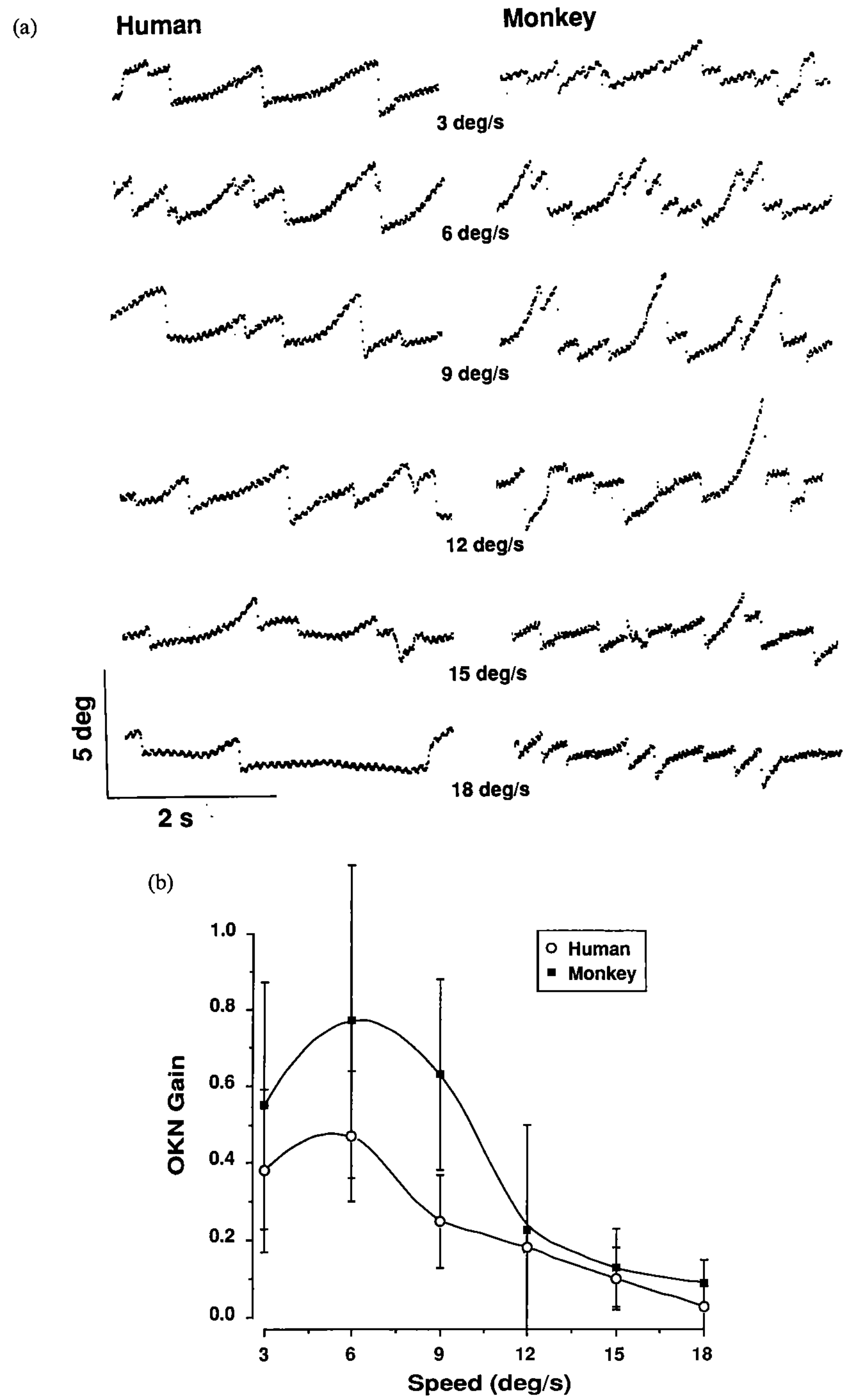


FIGURE 7. The influence of pattern velocity on OKN. (a) Vertical eye movement traces are shown for an upward drifting isoluminant green/gray HFN stimulus. Beyond 18 deg/sec, we failed to observe OKN in humans and only a weak response in monkeys. (b) The results of (a) are plotted in terms of OKN gain at the velocities tested. At all velocities, mean OKN gain (5 trials) was found to be larger in the monkey. Error bars represent standard deviations.

of color to motion and diagnosing color vision deficiencies have relied on moving gratings, usually by way of the Minimum Motion Technique (Logothetis & Charles, 1990; Maurer, Lewis, Cavanagh & Anstis, 1989; Teller & Lindsey, 1988; Anstis, Cavanagh, Maurer, Lewis, MacLeod & Mather, 1986; Cavanagh, Anstis & Mather, 1984). Although there is no *a priori* reason to believe that oculomotor and perceptual measures should necessarily yield similar results, there is recent evident that visual signals required for pursuit eye movements (Hawken, Sabatini, Port, Crystal, Lisberger & Movshon, 1991) and optokinetic nystagmus (Chaudhuri, 1991) are very similar to the signals that are used for visual judgements of motion.

The HFN technique is comparable to the Minimum Motion Technique in that both evoke reflexive eye movements. Logothetis and Charles (1990) obtained high-gain OKN with the Minimum Motion stimulus. We have found that with similar spatial excursions and temporal frequencies, the HFN stimulus produces a stronger signal (i.e. higher gain OKN). This must be interpreted cautiously, however, because modification of

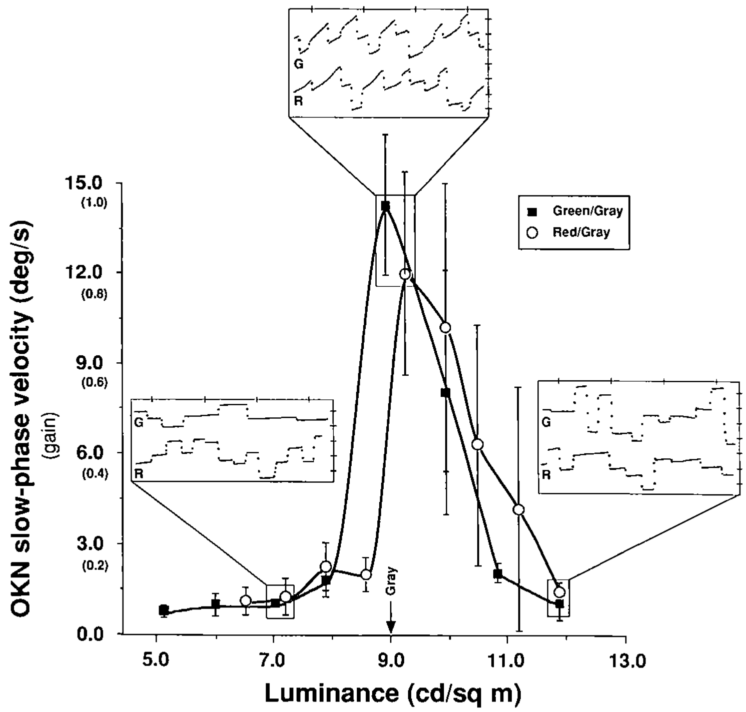


FIGURE 8. Comparison of OKN velocity and gain in a monkey (Lily) for an upward drifting green/gray and red/gray pattern. The data points are the mean of 5 slow-phase segments and error bars represent standard deviations. The luminance of the gray component in both patterns was fixed at 9.0 cd/m^2. As the results show, peak OKN in both patterns occurred at isoluminance. For this experiment, spontaneous OKN was recorded, that is, there was no gaze restriction by way of a blinking fixation spot, as used in the previous experiments. As the vertical eye movement traces in the insets show, there are numerous saccades as the monkey shifted fixation over the stimulus. The "G" and "R" labeled traces represent the eye movements to the green/gray and red/gray patterns respectively.

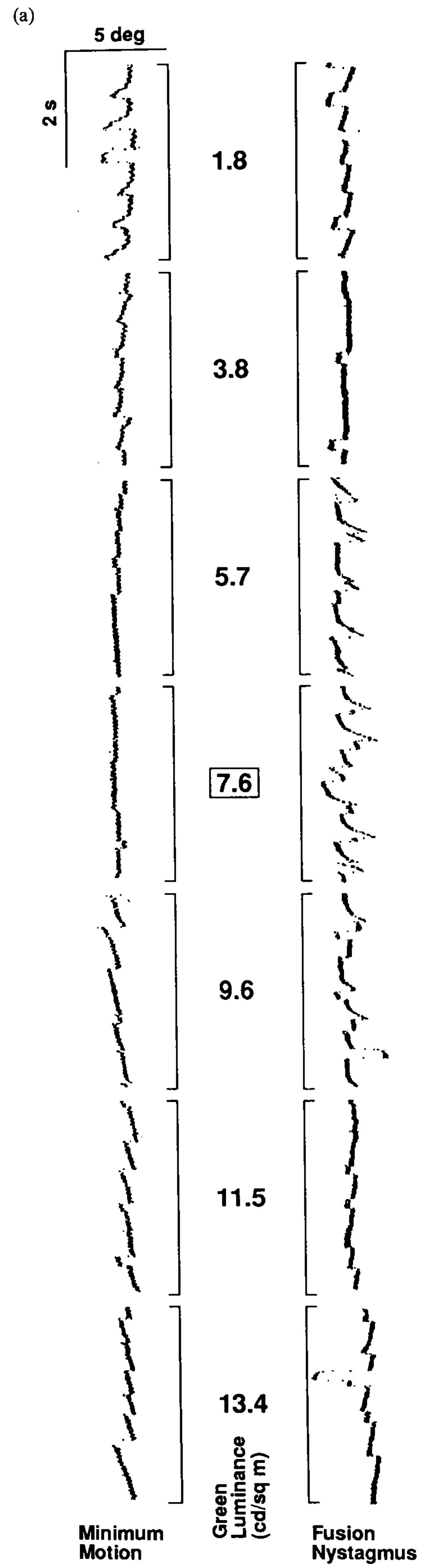
the Minimum Motion stimulus, which we did not rigorously attempt, may yield better eye movements. It is possible that the drifting gratings in the Minimum Motion stimulus are, in general, less capable of driving the eyes and generating an OKN response since such stimuli typically contain fewer contours and less luminance contrast than the chromatic-texture/luminance-noise pattern used here. An added advantage of the HFN technique is that since the stimulus is composed of random-dot patterns, drift rate is not constrained by any considerations of frame-to-frame correlations, as is the case with drifting gratings, thereby allowing free use of any pattern velocity capable of producing an OKN response. Therefore, the HFN technique is an improved version of the Minimum Motion approach in both utility and sensitivity.

Psychophysical assessment

In this report, we have documented both the psychophysical and oculomotor approaches to HFN photometry. Our psychophysical studies showed that the optimal motion percept occurred at a particular ratio of luminance of the two colors in the chromatic-texture pattern. From the photometric values obtained with a standard photometer, and later verified by standard psychophysical techniques for photometry, we ascertained that this ratio represented the isoluminant condition. We further showed that the same ratio prevailed at different luminance pedestals and color mixtures thereby demonstrating that the technique obeys additivity and transitivity laws. Although there is some evidence that spatio-temporal parameters influence the isoluminant point (Anstis & Cavanagh, 1983), because of the nature of our stimulus we were unable to systematically manipulate these variables except to modify the frame rate and spatial excursions of the chromatic tokens. These manipulations did not produce significant changes in the isoluminant point.

We obtained psychophysical reports, later verified by the oculomotor results, of perceived motion in the opposite direction at large deviations from isoluminance. This was a very compelling percept since for a number of subjects in the psychophysical experiments, all trials at a particular luminance ratio were judged to have opposite motion. This paradoxical percept is identical to that reported in the past ("reverse-phi") with luminance-contrast patterns that undergo contrast reversals as they are displaced (Sato, 1989; Anstis & Rogers, 1975; Anstis, 1970).

The HFN stimulus can therefore be parsed into two components—veridical motion of the black dots opposed by reverse-phi of the dichromatic-textured pattern. At non-isoluminant ratios, the drifting contrast-reversing dichromatic pattern produces an overpowering reverse-phi signal which masks the true motion of the black dots (luminance-texture pattern). As the luminance contrast in the dichromatic pattern is reduced, i.e. when approaching equiluminance, the reverse-phi signal is diminished and with it unmasks the true motion



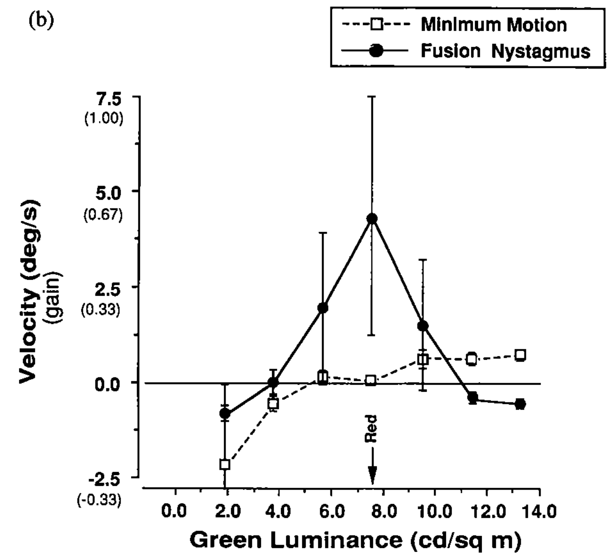


FIGURE 9. Comparison of OKN evoked by the Fusion Nystagmus and Minimum Motion techniques in one monkey (Lily). (a) A green/red HFN stimulus drifted to the right and evoked a similar eye movement at isoluminance, i.e. when green luminance approximated a fixed red luminance of 7.6 cd/m^2 (boxed). At the same ratio, the Minimum Motion stimulus produced no eye movements, as expected. At deviations from this ratio, the Minimum Motion stimulus produced either leftward or rightward eye drift. The HFN stimulus began to show negative OKN (leftward) at larger deviations from isoluminance. (b) Mean OKN velocity and gain (5 trials) is shown for the different luminance ratios in the two stimuli. A null OKN condition with the Minimum Motion stimulus occurs at an OKN peak obtained with the HFN stimulus. Error bars represent standard deviations.

of the black dots. A motionless flickering chromatic pattern can also create the necessary stimulus for masking at non-isoluminant conditions. However, we found that opposing veridical motion with reverse-phi generated a sharper tuning curve and therefore enhanced the sensitivity of our technique. Similarly, it is possible to substitute the contrast-reversing dichromatic field with a non-reversing one moving in the opposite direction. The same reasoning would apply in this case since the motion signal in the chromatic pattern would be minimized at isoluminance and therefore unmask the true motion of the black dots. However, we found that the luminance artifacts that accompany the chromatic edges in most color monitors produced a strong motion signal in itself at isoluminance and therefore interfered with the motion of the black dots. The use of a contrast-reversing background ensures that such signals at isoluminance would be in the same direction as the black dots.

Oculomotor assessment

It is known that a moving pattern often evokes an eye movement in the same direction as perceived motion and therefore, as expected, we found OKN to parallel the perceptual results using the HFN stimulus. Moreover, the optokinetic movements mirrored perceived motion at all luminance ratios. That is, at isoluminance we recorded OKN in the veridical direction and at certain non-isoluminant ratios, we recorded OKN in the opposite direction. The gain of these eye movements was dependent upon the physical parameters of the stimulus (e.g. velocity) and the fixational requirements. A large gain was observed when there was no gaze restriction, that is, the subjects passively viewed the stimulus. However, this approach produces considerable spatial dispersion in the eye movement records of the monkey since the animal routinely changes fixation. These random eye movements are considerably reduced if a blinking (2 Hz) fixation point is superimposed upon the HFN stimulus. The eye movements occur during the off-phase. This approach, however, reduces the gain of the OKN somewhat. The choice of whether or not to maintain gaze restriction is largely determined by the extent to which an animal can be trained to maintain fixation. If this is not possible, then a spontaneous-OKN paradigm can be used.

We noticed subtle differences in the OKN records between species and individual subjects. The OKN gain for any given stimulus condition appeared to be quite variable. Furthermore, reverse-phi motion was found to be more effective in our human subjects than in the monkeys in producing optokinesis. We suggest that these differences may be due in part to attentional effects. We noticed that a stimulus which yielded optimal perceived motion was ineffective in driving the eyes in some trials, yet on subsequent trials, generated large amplitude eye movements. This was particularly evident in the monkeys and rarely seen in our human subjects, who were instructed to maintain fixation yet attend to the moving background.

A second feature of these eye movements is the likely contribution of smooth pursuit. At the isoluminant condition, the luminance-noise pattern is seen to move in the correct direction. Any one of the features in this pattern (i.e. black dots) can be "locked-on" by the fovea and thereby invoke a smooth pursuit response. There may be some variability to the contribution of this mechanism, which is generally regarded to produce high gain output at the velocities employed (Lisberger, Evinger, Johanson & Fuchs, 1981). As a result, the variability in the eye movements at isoluminance may be the consequence of variable contributions from the smooth pursuit and the reflexive component of the OKN mechanism.

In conclusion, the Heterochromatic Fusion Nystagmus technique offers a simple, sensitive, and reliable approach to estimating chromatic isoluminance. The technique may be used in a psychophysical paradigm or by way of direct recording of optokinesis. The HFN stimulus produces a striking percept of motion and concomitant optokinetic response only at isoluminance. Small deviations from the isoluminant point eliminate the motion percept and abolish the eye movements entirely. Because the procedure evokes a reflexive response, it can be used in all animals that display OKN without the need for any special training.

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