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Effects of Background Color on Reaction Time to Stimuli Varying in Size and Contrast: Inferences About Human M Channels

BRUNO G. BREITMEYER,* JOSHUA I. BREIER*

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In two experiments we looked at the effects of the color of equiluminant backgrounds on simple reaction time (RT) to increment and decrement spot-stimuli varying in diameter. When comparing both red vs blue and red vs green backgrounds, we found that for the smallest diameter stimuli, RTs tended to be faster with red background; however, as the diameter of the stimuli increased, RTs were faster with the blue or green backgrounds. This trend held only for increment stimuli; no systematic or significant differences between RTs to decrement stimuli presented on red vs either blue or green backgrounds were found. We discuss these results in terms of the effects of diffuse lights of varying wavelength on magnocellular-channel activity.

Reaction time M channels Background-color effects Contrast effects

INTRODUCTION

In a series of metacontrast masking studies (Breitmeyer, May & Heller, 1991; Breitmeyer & Williams, 1990; Williams, Breitmeyer, Lovegrove & Gutierrez, 1991), we have found that the magnitude of metacontrast decreases when stimuli consisting of hue substitutions as well as luminance increments or decrements are presented on red as compared to either blue or green equiluminant backgrounds. Based on metacontrast masking theories which posit that the activity of sustained parvocellular (P) channels is inhibited by the activity of transient magnocellular (M) channels (Breitmeyer, 1992; Breitmeyer & Ganz, 1976), we interpreted these masking results to be the consequence of the suppressive effect that diffuse red lights are known to have on the activity of a substantial proportion of M neurons along the retino-geniculo-cortical tract (De Monasterio, 1978; De Monasterio & Schein, 1980; Livingstone & Hubel, 1984; Wiesel & Hubel, 1966). In the present series of experiments we compare simple reaction times (RTs) to luminance increment and decrement stimuli presented against either equiluminant red vs blue or red vs green backgrounds. Moreover, we vary the diameter of the stimuli in order vary the relative response of the P and M channels. Although Maunsell (1987) and Petersen, Miezin and Allman (1988) report that P neurons overall have longer response latencies than M neurons, parametric investigations of response latency as a function of stimulus diameter in P and M cells have not been reported. However, such an investigation has been made by Bolz, Rosner and Wässle (1982) of cat X and Y cells, which, with regard to size selectivity, can be viewed as analogs of P and M neurons (Breitmeyer, 1992). Bolz *et al.* (1982) found that for large area light spots Y cells responded faster than X cells; as spot size decreased the latency difference between the two types of cells initially also decreased until a size was reached at which the latencies were equal; with still further decreases in spot size responses of X cells become progressively faster than those of Y cells. If one makes the reasonable assumptions (1) that a similar relationship of spot size to response latency holds for P and M cells; and (2) that the faster of the two types of responses determines perceptual latency, then despite statistical response fluctuations within the two types of channels across trials, one would expect in the long run that the P channel dominates reaction time (RT) performance at smaller stimulus diameters and the M channels to increasingly dominate RT performance as stimulus diameter increases. Consequently, when comparing red to either blue or green backgrounds, our prediction is that, as stimulus diameter increases, RTs should be progressively slower on the red background due to the suppressive effect of diffuse red light on the M channels.

GENERAL METHOD

Stimuli and apparatus

All visual displays, generated by a Macintosh IIcx microcomputer driving a Spectrum/8 graphics card, were

*Department of Psychology, University of Houston, Houston, TX 77204-5341, U.S.A.

presented on a 19 in. Trinitron high-resolution color monitor (P-22 phosphors; CIE coordinates of the red, green, and blue phosphors, respectively, are $x = 0.625$, $y = 0.340$, $x = 0.280$ $y = 0.595$; and $x = 0.155$, $y = 0.070$, according to manufacturer's specifications). At a viewing distance of 57 cm the display dimensions were 29 × 22 deg. All target stimuli consisted of spots having diameters of 8, 16, 32, or 64 min arc and were presented at the center of the display screen. Subjects viewed the display screen binocularly with head positioned in a head and chin rest. All room lights were extinguished during the experiments.

Procedure

Simple RTs to the onsets of the target stimuli were measured in two separate experiments. In one experiment the stimuli were presented on either a red or equiluminant blue background; in the second experiment they were presented on either a red or equiluminant green background. Details of specifying equiluminace are given in the descriptions of the individual experiments. In both experiments the target stimuli consisted, in one condition, of 40% luminance increments relative to the backgrounds and, in another condition, of 40% luminance decrements relative to the backgrounds.

Prior to measuring RTs to the stimuli on a particular background, subjects adapted to that uniform background for 2 min. Whenever viewing the display screen subjects were instructed to fixate the center of the screen lying halfway between two narrow and short horizontal lines (1 × 0.09 deg) separated by 3 deg. After the adaptation period a series of four short tones alerted the subject to the beginning of an experimental block of trials. A block consisted of 42 trials. A trial consisted of the following sequence of events. A single warning tone came on. This was followed by a random foreperiod varying in 100-msec steps from 1000 to 1500 msec prior to a 133-msec presentation of the target stimulus. The onset of the target stimulus initiated a millisecond clock counter. Subjects were instructed to depress the space bar of a computer keyboard with their right index finger as soon as they saw the stimulus. Depression of the space bar terminated the clock counter. Each RT was stored on-line after each trial. After a block of trials was completed, the first two of the 42 trials were discarded and for each subject the mean of the remaining 40 trials was computed. Each block of trials required from 5 to 7 min to complete.

For both the red–blue and the red–green experiments, RTs to increment and decrement stimuli were measured in separate experimental sessions. Subjects participated in only one session per day. For each subject the order of increment and decrement stimuli was randomized across the two daily sessions. Each session consisted of eight blocks of trials. The eight blocks were divided into four pairs of blocks. Stimulus diameter was randomized across the four pairs, and background color was randomized within each pair of blocks. After each block of trials subjects were given a 4-min rest period. The duration of a session was approx. 1.25 hr.

EXPERIMENT 1: RED/BLUE BACKGROUNDS

In this experiment, we compared RTs to target stimuli flashed on otherwise uniform red and blue equiluminant backgrounds. Here, equiluminance was defined in terms of a gray scale setting for each of the blue and red backgrounds which yielded a luminance of 8.6 cd/m^2 as measured by a Tektronix J16 digital photometer. We initially attempted to use the technique of minimizing a 12.5 Hz heterochromatic flicker for each subject. However, with the red and blue colors, the settings were very unstable within and across subjects. Hence, this technique was abandoned for the simpler technique of matching photometer outputs. Relative to the 8.6 cd/m^2 background luminance, the 40% increment and decrement stimuli had luminances of 12.0 and 5.2 cd/m^2.

Besides one of the authors (BGB), four volunteer subjects, two males and two females, from the University of Houston undergraduate student population were used. All subjects had normal or corrected-to-normal vision. Subjects' ages ranged from 20 to 46 yr. The four volunteer subjects were naive with respect to the purpose of the experiment. Since they also were inexperienced psychophysical observers, they were given two practice blocks of trials. In one block a 40% increment stimulus against a white background of 8.6 cd/m^2 was used; in the other, a 40% decrement stimulus against the same white background. In both practice blocks the diameter of the target stimulus was 48 min arc.

Results: increment stimuli

Because there was significant inter-subject variability in RT performance (e.g. the overall RT differences between the fastest and the slowest subjects were on the order of 120 msec), in the present (and all subsequent) experiments we used a repeated-measure analysis of variance with univariate tests for within-subject effects. This analysis revealed that the main effect of background color was not significant [$F(1,4) = 0.84$, $P > 0.410$] whereas that of stimulus diameter was [$F(3,12) = 4.17$, $P < 0.031$]. Moreover, the interaction between background color and stimulus diameter also was significant [$F(3,12) = 3.58$, $P < 0.047$]. These trends are reflected in the results depicted in Fig. 1. For one, the results show that overall RTs tended to decrease as stimulus diameter increased. This result is expected since a number of prior studies have shown that RTs decrease as stimulus size increases or, alternatively, as spatial frequency decreases (Breitmeyer, 1975; Lupp, Hauske & Wolf, 1976; Vassilev & Mitov, 1976). The lack of a background-color main effect is most likely due to the significant interaction between background color and stimulus diameter. In Fig. 1 this is evident as a change in background-dependent RTs as a function of stimulus diameter. At the smallest diameter of 8 min arc, RTs were slower (by about 13 msec) on the blue as compared to red

backgrounds (this and subsequent RT differences at small stimulus diameters are discussed in the Discussion); at the 16 min arc, RTs were nearly equal on the two backgrounds; however, in contrast to the 8 min arc dia stimulus, at the 32 and 64 min arc dia, RTs were, as predicted, faster (by about 25 msec) on the blue as compared to red backgrounds.

Results: decrement stimuli

In comparison to the results obtained with the increment stimuli, for the decrement stimuli a repeated-measures analysis of variance also yielded a significant effect of stimulus diameter [$F(3,12) = 17.26$, $P < 0.0001$] and a nonsignificant effect of back-ground color [$F(1,4) = 0.18$, $P > 0.690$]; however, the interaction between background color and stimulus diameter was not significant [$F(3,12) = 1.71$, $P > 0.217$]. These results are reflected in trends evident from inspection of Fig. 2. On both backgrounds there is an expected overall decrease in RTs as stimulus diameter increases. However, there is little systematic difference between RTs obtained with the red as compared to blue backgrounds. Although the red background yielded faster RTs (again by about 13 msec) than the blue background at the smallest diameter of 8 min arc, at the larger stimulus diameters of 32 and 64 min arc the two backgrounds yielded nearly equal RTs. What was predicted at the larger diameters, however, was that the blue background would yield faster RTs than the red one. We defer further treatment of these apparently discrepant findings until the Discussion.

EXPERIMENT 2: RED/GREEN BACKGROUNDS

In this experiment, we compared RTs to stimuli flashed on otherwise uniform red or green equiluminant backgrounds. Equiluminance was determined for each subject using the technique of minimal heterochromatic flicker. Two centrally presented fields, 3 deg in diameter, one red the other green, were alternated in square-wave fashion at a rate of 12.5 Hz. The green field's luminance was fixed at a value of 12.0 cd/m^2; the red field's luminance started at a value either clearly above or else below that of the green field so that subjective flicker was clearly present. The red-field luminance was varied by the subject in three series of descending and three series of ascending steps of single gray-scale values until flicker appeared minimal. The average of the six red-field luminance values at which a subject experienced no or minimum flicker was taken as his/her red field's matching luminance. Relative to the 12.0 cd/m^2 luminance of the green background and the matched luminance of the red background, the target stimuli, as in Expt 1, consisted of luminance increments or decrements of 40%. Three of the subjects (including BGB) participating in Expt 1 also participated in the present experiment. These subjects were not given any practice blocks of trials. Two

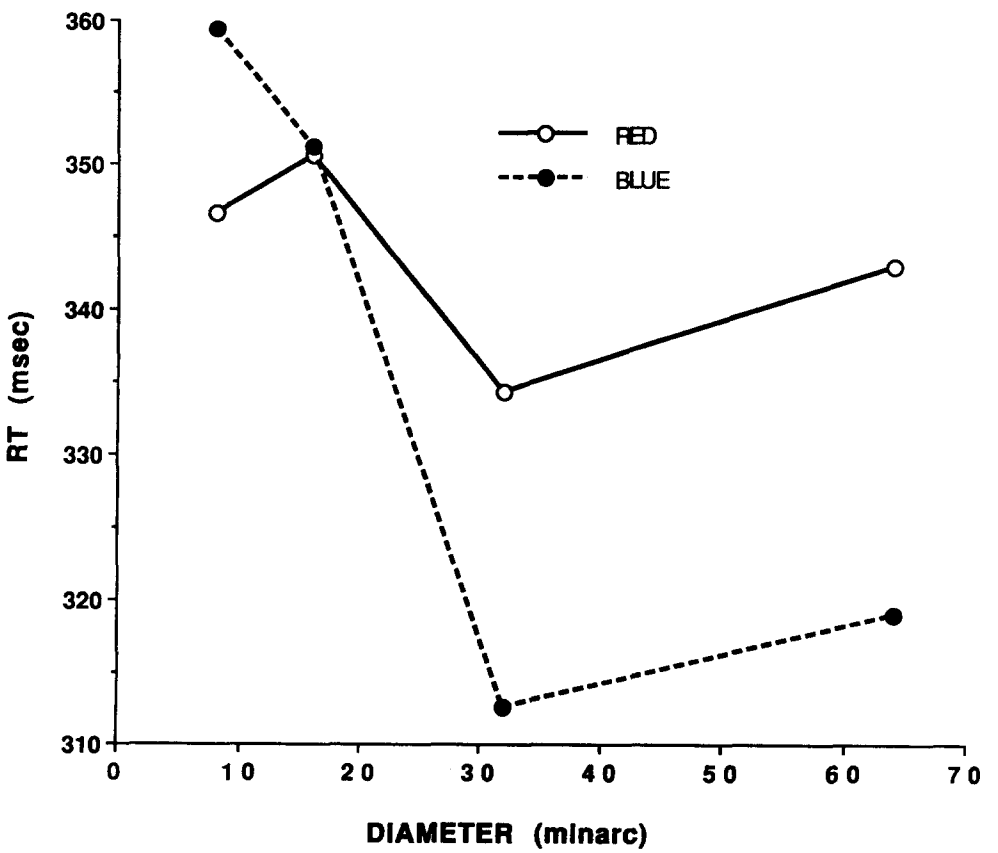

FIGURE 1. Reaction time (RT) to onsets of luminance increment stimuli flashed on red or blue backgrounds as a function of stimulus diameter.

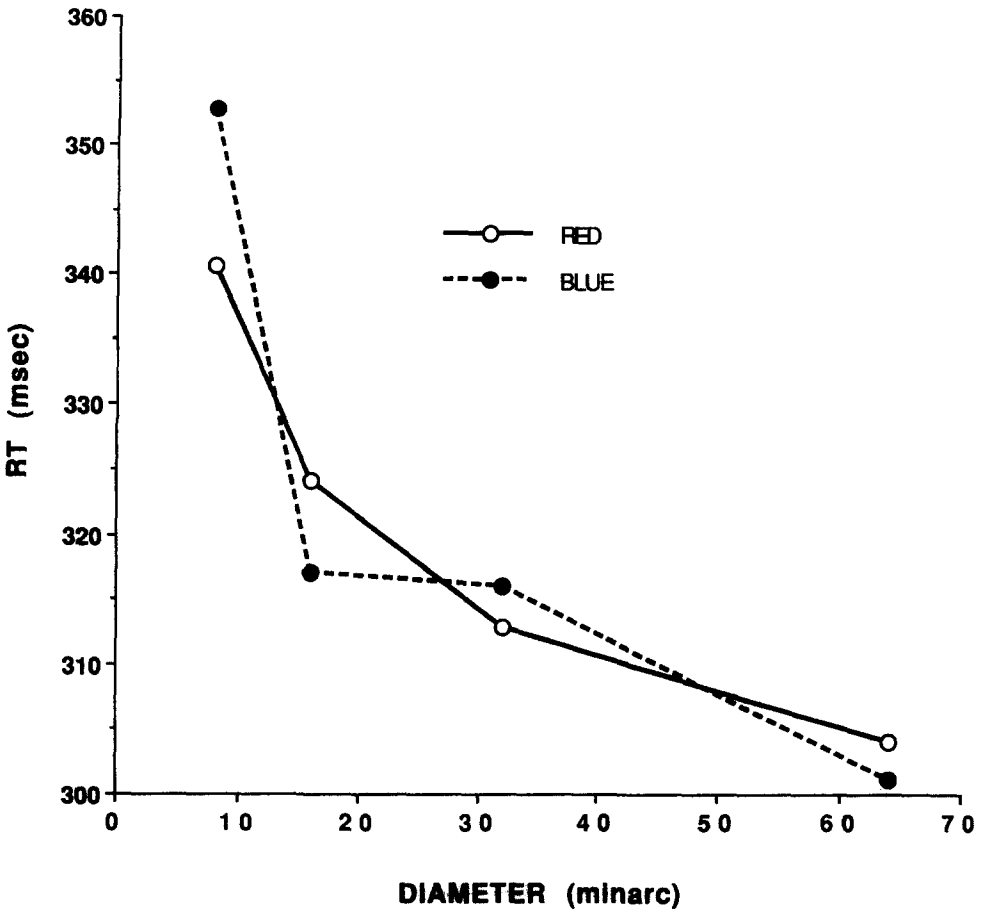

FIGURE 2. Reaction time (RT) to onsets of luminance decrement stimuli flashed on red or blue backgrounds as a function of stimulus diameter.

additional subjects with normal or corrected-to-normal vision were recruited from the undergraduate student population at the University of Houston. These subjects were given practice blocks as described in Expt 1 before participating in the experimental sessions. In other respects, the procedure in Expt 2 was the same as that used in Expt 1.

Results: increment stimuli

The mean RTs obtained by the five subjects were subjected to a repeated-measure analysis of variance which revealed the following results. Although the effect of background color was not significant [$F(1,4) = 2.05$, $P > 0.225$], the effect of target stimulus diameter was significant [$F(3,12) = 12.01$, $P < 0.0007$] as was the interaction between background color and stimulus diameter [$F(3,12) = 4.88$, $P < 0.02$]. These findings parallel similar results obtained with the increment stimuli in Expt 1 and can be explained similarly by inspection of Fig. 3. It is evident from Fig. 3 that overall RTs decrease with stimulus diameter. Moreover, the significant interaction between background color and stimulus diameter (1) contributes in part to the lack of a main effect of background color; and (2) is consistent with experimental predictions. At the smallest stimulus diameter of 8 min arc, the red-background RT was about 10 msec faster than the green-background RT. However, at the stimulus diameters of 16, 32, and 64 min arc, the red-background RTs were, respectively, about 7, 25, and 15 msec slower than the green-background RTs.

Results: decrement stimuli

The repeated-measure analysis of variance on subjects' mean RTs revealed the following results for the decrement stimuli. Neither background color [$F(1,4) = 0.27$, $P > 0.632$], nor stimulus diameter [$F(3,12) = 1.65$, $P > 0.231$], nor their interaction [$F(3,12) = 0.06$, $P > 0.981$] had a significant effect on RT. However, inspection of Fig. 4 reveals that most of the obtained trends in the results are in the expected direction. In particular, there is a trend for an overall decrease in RT as stimulus diameter increases. Moreover, at the larger stimulus diameters of 32 and 64 min arc, the red-background RTs are, as expected, somewhat higher than the green-background RTs. However, contrary to the results found in the other experiments, this trend also holds at the smallest diameter of 8 min arc.

DISCUSSION

On the basis of prior metacontrast masking studies (Breitmeyer *et al.*, 1991; Breitmeyer & Williams, 1990; Williams *et al.*, 1991) and supporting neurophysiological findings (De Monasterio, 1978; De Monasterio & Schein, 1980; Livingstone & Hubel, 1984; Wiesel &

Hubel, 1966), we had predicted that, relative to a red background, equiluminant blue and green ones would yield faster RTs to onset of larger stimuli favoring the M-channels. Our predictions applied indifferently to increment and decrement stimuli and were motivated by the fact that a red background decreased the magnitude of metacontrast masking, and thus of underlying M-channel activity (Breitmeyer, 1992), when stimuli consisted of either increments, decrements, or isoluminant hue substitutions relative to the background luminance.

However, our expectations were only partially confirmed. The expected results, slower RTs on red backgrounds with larger stimuli favoring M channels, were obtained consistently with increment stimuli but not with decrement stimuli. These apparently discrepant results may be due to several factors. For one, metacontrast masking may provide a more sensitive measure of the effects of background color on M-channels activity and thus be indifferent to the contrast polarity of the target and mask stimuli relative to the background. However, although the metacontrast studies reported by Breitmeyer and Williams (1990) and Williams *et al.* (1991) obtained evidence for the suppressive effects of red backgrounds on M-channels activity regardless of stimulus contrast polarity, it could be the case that if one were to explicitly design a metacontrast experiment to compare the effects of a red background on stimuli of opposite contrast polarity, one may find that the suppressive effects of a red background on M channels, though present at both polarities, are actually stronger when increment stimuli are used. Such an experiment remains to be done.

In line with this prediction, we suspect that as an alternative to the apparently discrepant results, there is a genuine interaction between the effects of contrast polarity of the stimuli and the effects of diffuse red backgrounds on M-channel activity. Our reasoning is based on a second, more careful reading of the physiological findings reported by Wiesel and Hubel (1966), De Monasterio (1978), and De Monasterio and Schein (1980). Wiesel and Hubel (1966) reported that the suppressive effects of diffuse red light were particularly evident in their type IV M neurons of the monkey LGN and, moreover, that these type IV neurons were of the on-center variety. These findings were also reported in De Monasterio's (1978) study of ganglion cells and were attributed to the dominant red-cone input to the receptive-field surrounds of retinal on-center type IV M cells. Moreover, De Monasterio and Schein (1980) also report red-cone dominant input to the receptive-field surround of foveal type III M ganglion cells, of which a majority (68%) is on-center (De Monasterio, 1978). Assuming that the red-suppressed cortical M cells (Livingstone & Hubel, 1984) are also predominantly of the on-center type, it seems highly likely that the effects of red vs blue

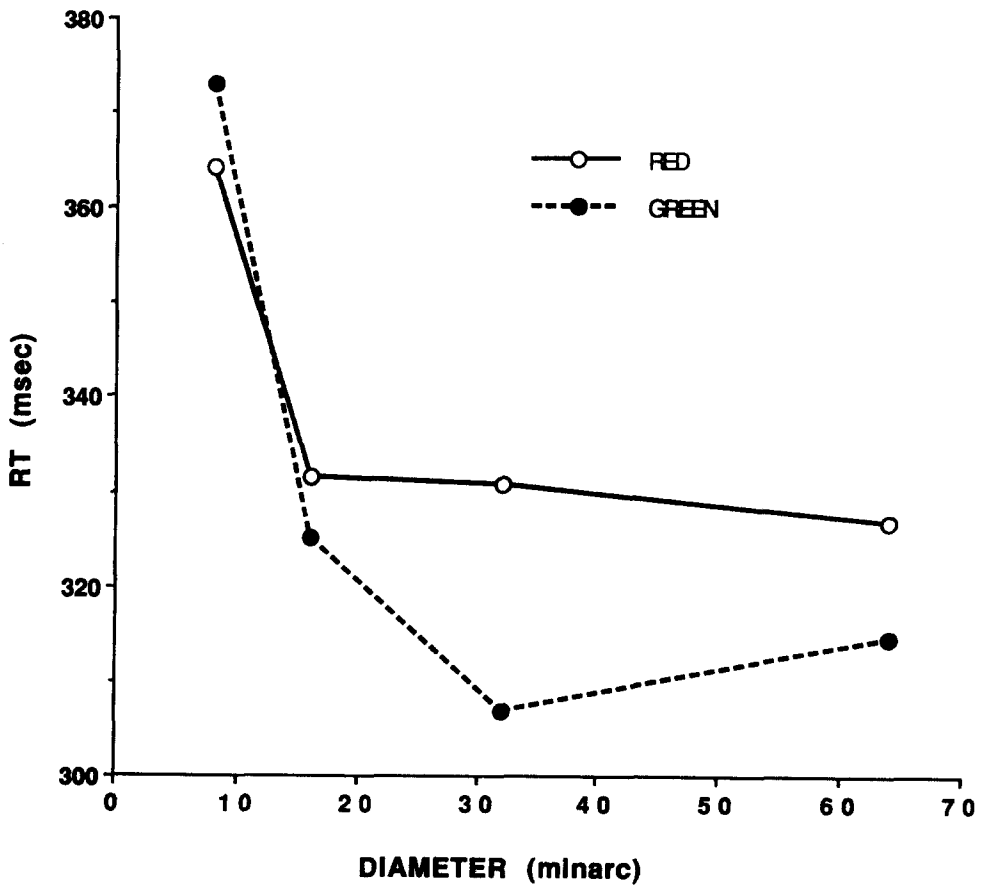

FIGURE 3. Reaction time (RT) to onsets of luminance increment stimuli flashed on red or green backgrounds as a function of stimulus diameter.

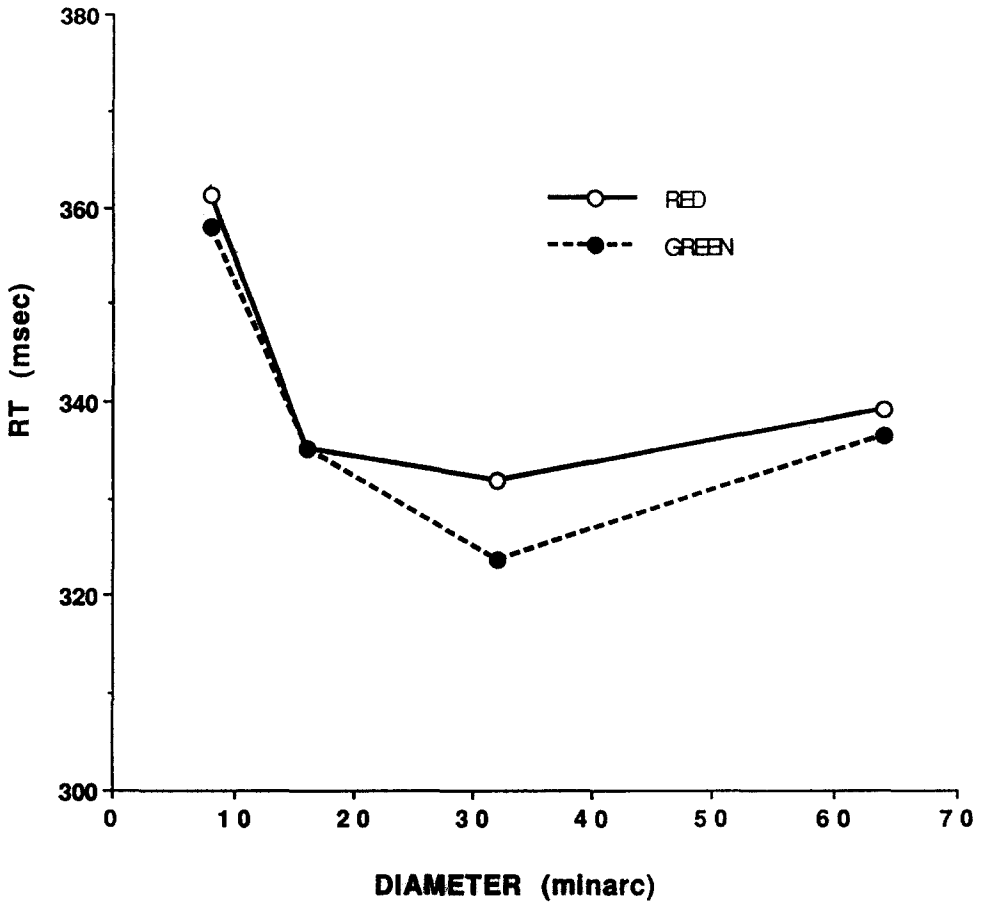

FIGURE 4. Reaction time (RT) to onsets of luminance decrement stimuli flashed on red or green backgrounds as a function of stimulus diameter.

or green backgrounds should be evident mainly in those M-pathway neurons specialized to detect luminance increments. Such neurons, as shown by Schiller (1982) and Schiller, Sandell and Maunsell (1986), comprise the ON channels consisting of cells with on-center receptive fields in the visual tract. This explanation, although consistent with the present psychophysical findings, is *post hoc*, and we are designing experiments to test its validity more directly.

Finally, in three of the experimental results the RTs to the smallest 8 min arc dia stimulus were faster on red as compared to blue or green backgrounds. Our assumption, outlined in the Introduction, was that the P channels ought to dominate RT performance at the smallest stimulus diameter. If this is so, the present results suggest that, relative to blue or green backgrounds, a red one may enhance the activity of the P channel. Such enhancing effects of diffuse red light have been found in cells of the P layers of monkey lateral geniculate nucleus (J. Krueger, personal communication). However, a wider range of stimulus sizes, with several stimuli smaller than the ones used in the present experiments, would have to be employed in order to test the validity and generalizability of this tentative interpretation.

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