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Aliasing in peripheral vision for counterphase gratings

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The study measured spatial detection and resolution acuity thresholds at 30 deg eccentricity for sinusoidal gratings of different contrast (10–90%) that phase reverse at different temporal frequencies (0–40 Hz). Resolution performance at any contrast displayed little deterioration with increasing temporal frequency up to 10 Hz, after which it declined smoothly, indicating no definable break where performance switched from being P-cell to M-cell mediated. Detection was measurably higher than resolution acuity for all temporal frequencies at 90%. At 50% contrast, detection and resolution performance converged at ~30 Hz. For 10% contrast, detection and resolution performance were the same at all temporal frequencies. These results indicate that resolution performance remains largely P-cell mediated and sampling limited over a large range of contrasts and temporal frequencies. © 1996 Optical Society of America.

1. INTRODUCTION

The work of Campbell and Gubisch[1] indicated that, under normal viewing conditions, spatial patterns beyond the resolution limit of the fovea (Nyquist frequency) are eliminated by the filtering properties of the eye's optical system. However, evidence exists that in the periphery, the neural resolution limit falls off faster than the optical quality,[2–4] which indicates that grating resolution is limited not by optics but by retinal sampling. Thibos *et al.* concluded that whereas central resolution for high-contrast stimuli is limited by optical filtering, peripheral pattern resolution is limited by "the spacing of the receptive fields of the coarsest array of the sequence, the ganglion cells,[5] (p. 1526)." Strong evidence that peripheral resolution is sampling limited arises from the perception of aliasing that arises for high-frequency grating stimuli in peripheral viewing. The sampling-limited nature of peripheral resolution means that it is possible to image a grating on the peripheral retina that can be detected but not resolved, which means that the minimum angle of detection is measurably smaller than the minimum angle of resolution, whether resolution is measured by means of grating orientation discrimination[4,6–9] or direction discrimination for drifting gratings.[10–12]

Thibos *et al.*[5] discussed the differences between minimum angle of detection and minimum angle of resolution and proposed that any retinal limit to detection acuity will be because of the size of the ganglion cell receptive field that is the largest in the sequence of retinal processing. This in effect means that resolution for high-contrast stimuli is determined by ganglion-cell spacing and that detection acuity is determined by ganglion-cell receptive field size.

Previous measures of peripheral resolution acuity have mostly used high-contrast stationary gratings (for orientation discrimination) or low-drift-velocity gratings (for direction discrimination), which are believed to selectively stimulate the ganglion cells that project to the parvocellular layers of the lateral geniculate nucleus (P cells). These cells respond tonically to visual stimuli,[13] constitute the large majority of retinal ganglion cells,[14] and play the major role in vision at high spatial frequencies and low temporal frequencies.[15] The minority group ganglion cells that project to the magnocellular layers of the lateral geniculate nucleus (M cells), on the other hand, generally display phasic responses to visual stimuli[16] and are more sensitive to low contrasts and high temporal frequencies.[17–19]

Anderson *et al.*[20] extended previous studies that used drifting gratings by measuring peripheral detection and direction discrimination thresholds for gratings that drifted at a number of different temporal frequencies and contrasts in order to measure the Nyquist limit of the ganglion cells that limited performance for these different stimuli. Interestingly, they concluded that P ganglion cells remain the limiting factor for motion direction discrimination even for targets with velocities as high as 24 Hz.

In this study I wished to extend previous research that measured detection and orientation discrimination performance for gratings in peripheral vision by using gratings of different contrast that phase reverse at different temporal frequencies. The main reason for using a counterphase grating is that it lends itself better than a drifting grating to orientation discrimination measurements, being free of directional cues that could be used to determine stimulus orientation. Watson *et al.*[21] proposed that detection of a counterphase grating may be mediated by

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mechanisms different from those for detection of a drifting grating. Although Watson *et al.* were measuring for foveal vision, it is possible that a difference in performance may also exist in peripheral vision, and so detection performance for a counterphase grating may be different from that observed by Anderson *et al.*[20] for drifting gratings. In addition, the fact that it is possible with a counterphase grating to measure detection and resolution performance beginning at 0 Hz allows a direct connection with previous studies that measured resolution using stationary gratings.

As the temporal frequency of the grating increases, we may reasonably expect the stimulus to selectively stimulate a different population of retinal ganglion cells. Although Anderson *et al.*[20] found that P cells limited direction discrimination up to 24 Hz, it may be that M cells play a larger role beyond this temporal frequency. Specifically, as temporal frequency increases and contrast decreases, P cells could respond less and the contribution of M cells to the task could become more prominent. Since P cells are more numerous than M cells, this increase in temporal frequency should result in an overall decrease in resolution performance, because resolution is related to the density of the responding cells as long as the task is sampling limited. To this end, therefore, we need to determine that resolution is still sampling limited for higher temporal frequencies and lower contrasts. A finding of higher performance for detection acuity than for resolution acuity and/or the observation of aliasing would be strong evidence that resolution is sampling limited. This means we must measure detection performance as well as resolution performance for each stimulus to determine which stimuli yield sampling-limited performance and can therefore be used to estimate the density of the underlying ganglion cells.

There is another motivation for undertaking this study. The M and P pathways are commonly referred to as being parallel in that they follow similar paths through the visual system but are anatomically segregated, projecting to different layers of the lateral geniculate nucleus and higher centers and are believed to carry separate information. If there is minimal overlap in their functional characteristics, we can expect that a change in temporal frequency or contrast will result at some point in an M/P break similar to the rod/cone break observed in the dark-adaptation curve, which would indicate a temporal frequency where the task shifts from being P-cell to M-cell dominated. However, even though the pathways are parallel anatomically, it does not necessarily follow that there is no overlap in their functional characteristics. The absence of such a feature would indicate a greater degree of overlap in function between the two pathways than is commonly conceded.

2. METHODS

An experienced psychophysical observer (the author), who is also an emmetrope, was the subject. A natural pupil size of 4–5 mm was used throughout. Peripheral acuity was measured for the right eye, and the left eye was patched. The subject rested his head on a chin rest and fixated a cross at 1.5 m in front while peripherally viewing the stimulus on the monitor, which was also at 1.5 m but at 30 deg in the horizontal nasal field. Refractive error at this eccentricity was determined by an experienced optometrist using retinoscopy, and the appropriate lenses were placed in a lens holder in front of the eye in line with the peripheral stimulus (Rx: $+2.25/-2.50 \times 90$).

A. Stimuli

A Visual Stimulus Generator VSG2/3 (Cambridge Research Systems) was used to generate 4-deg circular patches of sine-wave grating on a high-resolution monitor (Eizo). The gratings had the same mean luminance as the surround, which was verified for each session by the subject's viewing foveally through a positive blur lens. No difference in luminance between stimulus and surround was observable. Stimulus orientation was one of two oblique orientations (45 or 135 deg). The reason for using these orientations is that acuity is similar for gratings oriented obliquely with respect to the fovea, unlike for horizontal or vertical gratings, which produce a higher acuity for the horizontal orientation.[22] This higher acuity for horizontal gratings may have given a cue for deciding which orientation was presented.

Stimulus contrasts ranged from 10 to 90%, and stimulus temporal frequency (sinusoidal phase reversal) ranged from 0 to 40 Hz. It was verified that no loss of effective contrast occurred at high temporal frequency, owing to temporal persistence of the monitor in the following way. A Frame Rate Photometer, obtained from the Visual Stimulus Generator manufacturers, was capable of making relative photometric measurements at a rate of up to 400/s. The photocell of this device was placed on the screen on top of a peak of the sine-wave stimulus at high contrast (90%). The sine wave was then made to counterphase at 1 Hz, and luminance readings were taken at a rate of 400/s over a time interval of 1 s, and the maximum and minimum values were noted. The grating was then made to phase reverse at 40 Hz, and luminance readings were taken at a rate of 400/s over a time interval of 1 s. This gave only ten readings per cycle, meaning that a reading may not exactly coincide with the maximum or minimum luminance points, so to increase the temporal sampling rate the procedure was performed four times, and the maximum and minimum luminance values of the four were noted. Contrast measured at 1 and 40 Hz by this method differed by less than 1%, the contrast being, if anything, higher for the 40-Hz stimulus.

B. Detection

Detection acuity was measured in cycles per degree (c/deg) for stimuli of four different contrasts (90%, 50%, 20%, or 10%) which phase reversed at seven different temporal frequencies (0, 5, 10, 15, 20, 30, or 40 Hz). For each session, contrast and temporal frequency of the stimulus were fixed and gratings were presented in one of two intervals using a forced-choice paradigm (temporal two-alternative forced choice). The other interval contained a uniform field of the same mean luminance as the grating. The grating was randomly presented at either orientation in either of the two oblique orientations. Presentation time for each interval was 1 s, and the two intervals were separated by 1 s. The observer indicated which interval contained the stimulus by pressing one of

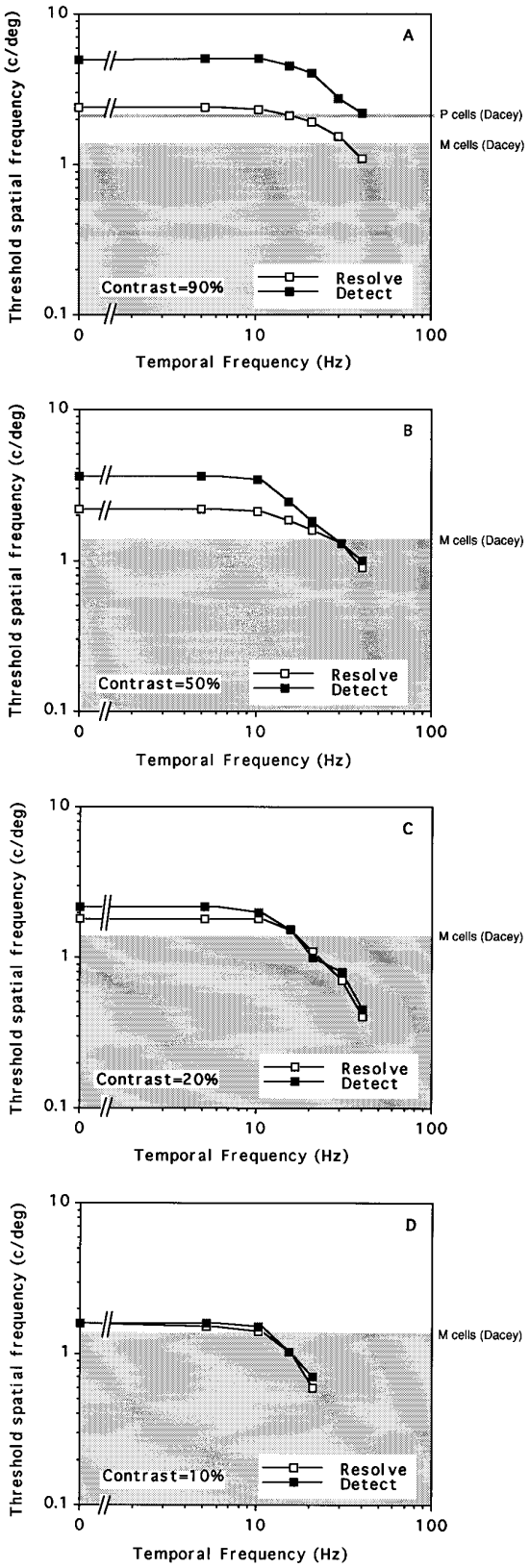

Fig. 1. Threshold spatial frequency (c/deg) for detection and resolution versus temporal frequency for stimuli of different contrast. The horizontal line in plot A represents the Nyquist limit for P cells based on the anatomical data of Dacey. The shaded area in plots A–D represents the spatial-frequency range that is theoretically resolvable by the M-cell population (Dacey).

two buttons. This response then triggered the next pair of presentations. Each session consisted of 50 presentations of the stimulus. Three correct responses caused a 10% increase in spatial frequency, and one incorrect response caused a 10% decrease in spatial frequency. This gave, on average, six or seven reversals per session. Threshold spatial frequency for detection was calculated as the mean of the reversal values.

C. Resolution

Resolution was measured for stimuli of the same fixed contrasts (90%, 50%, 20%, or 10%), which phase reversed at each of the same fixed temporal frequencies (0, 5, 10, 15, 20, 30, or 40 Hz). For each session, contrast and temporal frequency of the stimulus were fixed, and gratings were randomly presented at one of the same two oblique orientations, with a single-interval two-alternative–forced-choice paradigm. Presentation time for each stimulus was 1 s, and the observer indicated by pressing one of two buttons which orientation of the stimulus was perceived. This response then triggered the next presentation. Each session consisted of 50 presentations of the stimulus. Three correct responses caused a 10% increase in spatial frequency, and 1 response caused a 10% decrease in spatial frequency. This, again, gave, on average, six or seven reversals per session. Threshold spatial frequency for resolution was calculated as the mean of the reversal values.

3. RESULTS AND DISCUSSION

Figure 1A is a plot of threshold spatial frequency for detection and resolution versus stimulus temporal frequency for gratings of 90% contrast. It can be seen that as temporal frequency increases, there is no change in resolution performance until close to 10 Hz, after which performance declines steadily for both. However, the decline in performance beyond 10 Hz is smooth, and there is no obvious M/P break that would indicate a sudden switch from P-cell-mediated performance to M-cell-mediated performance. This pattern is similar for detection in that there is no observable decline in performance in the range 0–10 Hz. This would indicate that there is no increase in either the receptive field size or the spacing of the responding ganglion-cell population up to this critical temporal frequency; this finding leads us to conclude that the responding cell population does not change significantly, either. The above performance is observed for all other stimulus contrasts tested (Figs. 1B–1D) in that there is no abrupt M/P break. The fact that no break is observable at any contrast implies that there is no point at which resolution suddenly switches from being P-cell mediated to being M-cell mediated. The horizontal line on Fig. 1A represents the resolution limit of the P-cell population from the anatomical data of Dacey.[23] This line lies close to the measured resolution for gratings of high contrast and low temporal frequency, which we may expect to be P-cell mediated; the psychophysical measurement is slightly higher, since resolution measurements that use grating orientation methods tend to overestimate the sampling density slightly.[24] It is clear that resolution between 0 and 30 Hz is too good to be mediated by M

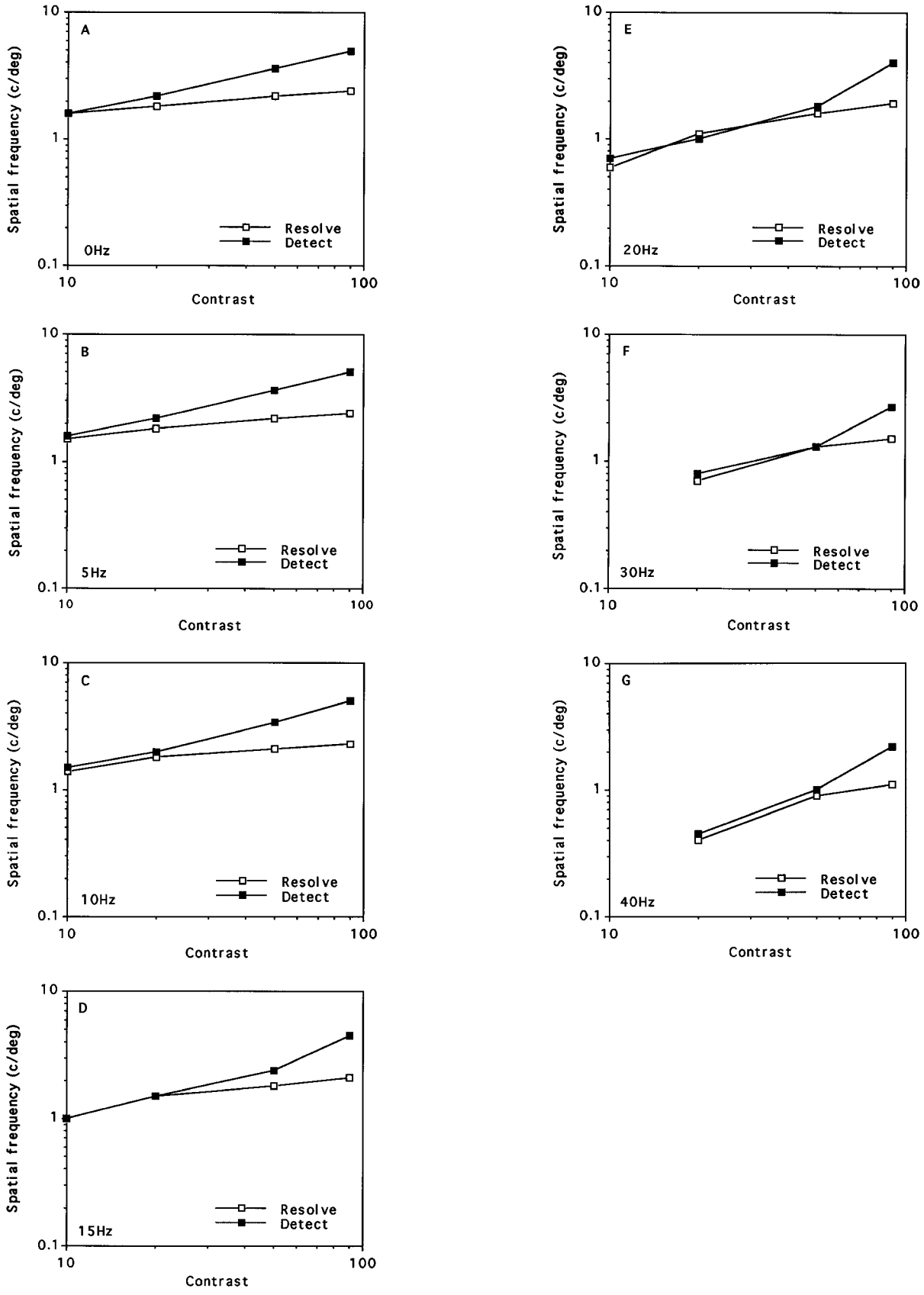

Fig. 2. Threshold spatial frequency (c/deg) for detection and resolution versus contrast for sinusoidal gratings of temporal frequency ranging from 0 to 40 Hz.

cells alone. However, even though there is no observable M/P break in the curve and resolution acuity is better than would be expected from an M-cell population, it does not follow that M cells do not contribute in part to the task, particularly as temporal frequency increases and contrast decreases. The shaded region at the bottom of Figs. 1A–1D indicates the spatial-frequency range that is resolvable by the M-cell population (based on an M-cell population of 20% of the total ganglion cell population at 40 deg eccentricity[25]). It can be seen that for a contrast of 50–90%, gratings of temporal frequency greater than 30 Hz are theoretically resolvable by the M-cell population alone, and we cannot rule out the possibility that M cells alone are responding at this point. At lower contrasts the M-cell Nyquist limit is reached even sooner. Although we do not know the exact composition of the effective sampling array within this shaded area we can, however, say that the transition from P-cell function to M-cell function is a smooth one and that there is likely a considerable overlap in their functional characteristics.

At high contrast (90%), detection performance is markedly higher than resolution performance for all temporal frequencies, which indicates that resolution is sampling limited throughout, although the curves converge somewhat at higher temporal frequencies. As stimulus contrast decreases, the difference between detection acuity and resolution acuity becomes smaller. For 50% contrast, detection and resolution converge at ~30 Hz. For 20% contrast this convergence occurs at ~10 Hz, and for 10% contrast there is no noticeable difference between detection and resolution performance at any temporal frequency, which implies that resolution performance is no longer sampling limited at low contrast but is contrast limited, as is detection performance. This convergence of detection and resolution performance can in part be attributed to the low-pass temporal filtering properties of the responding ganglion cells. Increases in temporal frequency yield an apparent loss of contrast in the target so that the target becomes undetectable by the underlying ganglion cells and spatial frequency must be decreased to render the stimulus detectable again. As temporal frequency increases further, stimulus detection performance decreases to a point where it is no longer superior to resolution performance. At this point, resolution acuity changes from being sampling limited to being contrast limited and decreases along with detection acuity.

Figure 2 plots threshold spatial frequency for detection and resolution versus contrast for stimuli of different temporal frequency. At 0 Hz (Fig. 2A), as contrast increases, detection performance increases steadily but resolution performance remains quite flat. These results agree with the findings of Thibos *et al.*[9] for stationary gratings. They found that although peripheral detection performance increased continuously with increasing contrast, no improvement in peripheral resolution was measurable as stimulus contrast increased above 10%. This is further evidence that performance is sampling limited in that increases in contrast yield little or no improvement in performance. For higher temporal frequencies (Figs. 2B–2G) the picture is very similar in that any increase in resolution performance with contrast is observable only before the point where detection and resolution performance split, i.e., where aliasing begins to occur; after this, resolution performance is quite flat. However, the size of the aliasing zone is seen to diminish with increasing temporal frequency up to the point where detection and resolution acuity yield the same performance. The resolution results are also in broad agreement with those of Anderson *et al.*[20] over the range of temporal frequencies (1–24 Hz) and contrasts (10–90%) that they tested, in that resolution was largely independent of temporal frequency between 0 and 15 Hz and of stimulus contrast between 20% and 90%. (Upon closer observation of the data of Anderson *et al.*, it seems that their claim that resolution is independent of temporal frequency between 1 and 24 Hz and contrast between 10 and 90% is a little overoptimistic.)

The current study also has clinical implications. Recent reports that M cells appear to be damaged earliest in glaucoma have led to numerous attempts to isolate M-cell function in order to detect the condition at an earlier stage. The above results indicate that resolution performance may never be M-cell dominated for any stimulus parameters used in this study. Also, since resolution is probably sampling limited only at higher contrasts or lower temporal frequencies, it may not be possible to estimate M-cell density directly by use of resolution measurements within the present stimulus parameter range.

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