

Motion perception at scotopic light levels

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Although the spatial and temporal properties of rod-mediated vision have been extensively characterized, little is known about scotopic motion perception. To provide such information, we determined thresholds for the detection and identification of the direction of motion of sinusoidal grating patches moving at speeds from 1 to 32 deg/s, under scotopic light levels, in four different types of observers: three normals, a rod monochromat (who lacks all cone vision), an S-cone monochromat (who lacks M- and L-cone vision), and four deuteranopes (who lack M-cone vision). The deuteranopes, whose motion perception does not differ from that of normals, allowed us to measure rod and L-cone thresholds under silent substitution conditions and to compare directly the perceived velocity for moving stimuli detected by either rod or cone vision at the same light level. We find, for rod as for cone vision, that the direction of motion can be reliably identified very near to detection threshold. In contrast, the perceived velocity of rod-mediated stimuli is reduced by approximately 20% relative to cone-mediated stimuli at temporal frequencies below 4 Hz and at all intensity levels investigated (0.92 to $-1.12 \log \text{cd m}^{-2}$). Most likely, the difference in velocity perception is distal in origin because rod and cone signals converge in the retina and further processing of their combined signals in the visual cortex is presumably identical. To account for the difference, we propose a model of velocity, in which the greater temporal averaging of rod signals in the retina leads to an attenuation of the motion signal in the detectors tuned to high velocities.

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1. INTRODUCTION

Our visual world is vastly reduced at night, when perception is mediated by the rod, or scotopic, visual system. Compared with the cone-mediated, or photopic, visual system, its spatial and temporal resolution is relatively poor, contrast sensitivity is diminished, and color vision is totally in abeyance. Of course, aided by artificial lighting, the disadvantages of rod-mediated vision can largely be avoided, so that most tasks can be performed as well by night as by day. But there are important exceptions. While steering a car, plane, or ship at night, we do not exclusively rely on cone-mediated vision. Rather, we depend to a large degree on our rod vision and usually have to cope with rapid changes between rod and cone vision. This is especially true for judging distances and for estimating the directions and speeds of moving objects. Surprisingly, however, little information is available about the perception of motion under scotopic conditions. Although other aspects of rod vision have been studied in great detail, including spectral, contrast, and incremental sensitivity (for an overview, see Hess *et al.*),¹ only a couple of recent studies²⁻⁴ have treated motion perception.

What is known about dynamic vision under scotopic conditions mostly pertains to flicker fusion and not to motion perception *per se*. For instance, the highest critical flicker fusion frequency of rod-mediated vision is significantly lower (28 Hz) than that for cone-mediated (50 Hz) vision.⁵⁻⁷ Such flicker phenomena are probably determined by peripheral factors—mainly the rods them-

selves—whereas selectivity for direction of motion and speed arises in the visual cortex in primates.⁸⁻¹⁰ Granted, a reduced peripheral temporal resolution will have direct consequences for central motion perception. For example, very fast moving objects will simply be invisible, because they fall outside the window of visibility of the rod system.¹¹ But less obvious effects are also of interest. Do central factors, in particular the way in which rod signals are processed in the visual cortex, influence our motion perception at night under scotopic conditions?

Centrally, at least two mechanisms for motion perception have been identified in photopic vision.¹²⁻¹⁴ They differ mostly in their temporal frequency preferences. The fast mechanism has a high sensitivity for luminance-defined stimuli. Its color sensitivity is negligible, and speed coding is contrast invariant and highly precise. The neuronal substrate of this mechanism is presumably the magnocellular retino-geniculo-cortical pathway, including the extrastriate middle temporal area (MT), which predominantly receives inputs from the magnocellular retino-geniculo-cortical pathway.¹⁵ In contrast, the slow-motion mechanism has an extremely high sensitivity for chromatic inputs, but the coding of speed is dependent on contrast and therefore quite impaired. The neuronal substrate of the slow pathway is probably the inferotemporal pathway, which receives inputs from both the magnocellular and parvocellular retino-geniculo-cortical pathways of the lateral geniculate nucleus (LGN).¹⁶

Do rod signals contribute to both of these motion systems or only to one of them? Based on the low temporal frequency preference of rod vision, one might expect a dominance of the slow-motion pathway in scotopic vision. However, contrast gain and heterochromatic modulation sensitivities in macaque monkeys reveal rod input in both magno- (M-) and parvo- (P-) system cells, although it is much more apparent and less variable in M- than in P-pathway cells (see, e.g., Virsu and Lee,¹⁷ Virsu *et al.*,¹⁸ Purpura *et al.*,¹⁹ and Lee *et al.*²⁰). Thus the physiological evidence could be interpreted to mean that the fast-motion pathway dominates in scotopic vision. On the other hand, psychophysical measurements²¹ indicate that the spatial resolution of the rod system is clearly above that of the M-pathway, suggesting that the rods also contribute importantly to the P-system and presumably to the slow-motion pathway.

Any analysis of the distribution of rod inputs to motion perception is further complicated by questions about the correlation between the two retinocortical systems and the two retinal pathways involved in the processing of rod signals. Anatomical and physiological studies indicate that at least two pathways are available for the transmission of rod signals through the mammalian retina: one through the rod bipolar that predominates at low intensities and the other through rod-cone gap junctions and cone bipolar that predominates at higher intensities.^{22–26} Psychophysical and electrophysiological studies in man support an analogous rod duality in the human visual system; the clearest signature of which is a loss of flicker visibility and a corresponding reduction in electroretinographic response amplitude at frequencies near 15 Hz and at intensities near 0 log scotopic td caused by destructive interference between slow (low intensity) and fast (high intensity) rod signals.^{5,27–33} Are these slow and fast rod flicker signals correlated with the two cortical motion systems? Does the rod visual system at low intensities, at which only the slow retinal pathway is functioning, have access to the fast cortical motion system?

Our experiments were devised to address such questions, while characterizing sensitivity to direction of motion and to speed at low light levels. To simplify the interpretation of the data, the experiments were conducted in individuals lacking partially (dichromats and a blue-cone monochromat) or totally (a rod monochromat) the function of the photopic, or cone, visual system. The use of dichromats, in particular, allows us to determine rod and cone sensitivities at the same light levels in the same individuals.

Preliminary reports of some of these data have been presented in Mayser *et al.*³⁴ and in Gegenfurtner *et al.*³

2. GENERAL METHODS

A. Subjects

In total, nine subjects participated in the experiments. Three of the subjects, TE, CF, HM, had normal or corrected-to-normal visual acuity and normal color vision. The remaining six subjects had color vision deficiencies. Subject KN is a typical, complete achromat, or rod-monochromat, for whom extensive psychophysical and electroretinographic investigations have established that

he has no functioning cone vision (for a review, see Ref. 35). Molecular genetic analysis has revealed that he is homozygous for a mutation—a C→T transition at nucleotide 887, causing an arginine-to-tryptophan replacement at codon 283—in the CNGA3 gene, which encodes the α -subunit of the cone photoreceptor cGMP-gated cation channel, a key component of the phototransduction pathway.³⁶ Subject PS is an S-cone (or blue-cone) monochromat, who has only functioning rods and S cones. He is known to lack M- and L-cone functions on both psychophysical and molecular genetic grounds.^{37–39} He has two X-chromosome opsin genes but has an upstream deletion in the region that controls their expression. The four other subjects, AZ, MM, SH, and GE, are deuteranopes, lacking the M-cone function. All are single-gene dichromats, with a solitary L-cone pigment gene in the opsin gene array on their X chromosome, as confirmed by their Rayleigh matches, by their psychophysically measured spectral sensitivities, and by the amino acid sequences of their single X-linked cone pigment as deduced from its gene sequences (for details, see Sharpe *et al.*⁴⁰ and Jägle *et al.*⁴¹).

B. Equipment

The stimuli were displayed on a Sony 560 SE color CRT monitor that was driven by a Cambridge Research VSG 2/3 graphics board with a refresh rate of 120 Hz noninterlaced. The images were generated on the monitor by reading through the picture memory in a raster scan and then interpreting the numbers in each location as a color defined in a 256-element color look-up table. The numbers in the look-up table had an intensity resolution of 12 bits and were used, via two combined 8-bit digital-to-analog converters, to control the intensity of each of the three monitor primaries. The luminances of each of the phosphors were measured at various output voltage levels with a Graseby Optronics Model 370 radiometer with a Model 265 photometric filter. They were subsequently checked and confirmed with a second photometer (P-9710-1, VL-3701-2, Gigahertz Optik, Munich). A smooth function was used to interpolate between the measured points, and look-up tables were generated to linearize the relationship between voltage output and luminance. We also made sure that additivity of the three phosphors held over the range of intensities used in these experiments.⁴² All the displays in the present experiments had a space-time averaged luminance of 8.35 cd m^{-2} ($0.92 \text{ log cd m}^{-2}$), corresponding to a retinal illuminance of $2.44 \text{ log photopic td}$ or $2.83 \text{ log scotopic td}$ calculated for a mean pupil diameter of 6.5 mm and a correlated color temperature of 6500 K. A Photo Research PR 650 spectroradiometer was used to measure the spectra of the red, green, and blue phosphors at their maximum intensity setting. The spectra were multiplied with the CIE 1931 color matching functions, as revised by Judd [see Wyszecki and Stiles,⁴³ Table 1(5.5.3)], to derive CIE x, y chromaticity coordinates and the luminance Y of the phosphors.⁴⁴ All further references to luminance and photometric luminance refer to the photopic luminous efficiency function $V(\lambda)$ as modified by Judd.⁴³ The primaries of our monitor had x, y, Y coordinates of 0.613, 0.343, 5.144 (red); 0.283, 0.599, 13.19 (green); and 0.155, 0.067, 1.602 (blue). The moni-

tor spectra were multiplied with the Smith and Pokorny⁴⁵ cone fundamentals to calculate absorptions and contrasts in the L, M, and S cones.

C. Stimuli

The stimuli in all experiments were drifting one-dimensional 1 cycle/degree (c/deg) sine-wave gratings of different color, direction, and temporal frequency. Since all stimuli had a fixed spatial frequency of 1 c/deg, the values for temporal frequency in Hz and speed in deg/s are identical. All stimuli were symmetric modulations around a neutral white point ($x, y, Y = 0.335, 0.368, 8.35$) along various directions in color space chosen to excite differentially various classes of photoreceptors. For the experiments with the color normals and the rod monochromat (KN), stimuli were modulated along the luminance axis. For blue-cone monochromat observer PS, two color directions were chosen that modulated the S cones and rods, exclusively, achieving 82% contrast in the rods and 6% contrast in the S cones for maximum modulation in the rod direction and 76% contrast in the S cones and 1.2% in the rods for maximum modulation in the S-cone direction. For the deuteranopes, two different color directions were chosen that modulated rods and L cones exclusively (without any S-cone modulation). For them, the highest possible contrasts were 27.5% L-cone modulation (at 0.29% rod contrast) and 24.7% rod modulation (at 0.08% L-cone contrast).

The stimuli were displayed to the observers in an otherwise dark room. Viewing was with natural pupils. In addition to regular viewing, the stimuli were also presented while the observers were wearing custom-modified skiing goggles equipped with neutral-density filters (Göttingen Farbfilter, Göttingen). The goggles did not restrict the peripheral or central viewing fields. The filters reduced the light level by 1.02 (producing a space-time average luminance of $-0.10 \log \text{cd m}^{-2}$), 2.04 ($-1.12 \log \text{cd m}^{-2}$), 3.17 ($-2.25 \log \text{cd m}^{-2}$), or 4.12 ($-3.20 \log \text{cd m}^{-2}$) log units.

3. EXPERIMENT 1: DIRECTION DISCRIMINATION

The discrimination of direction of motion is one of the most basic requirements for a motion-detecting mechanism. It has been shown in the past that observers are able to tell the direction of motion of a sine-wave pattern, even when the contrast of the stimuli is close to detection threshold.^{46,47} This indicates that the detection mechanism involved in this task is also able to signal direction of motion. Interestingly, this is not always the case. If stimuli are defined by color, then the threshold for detection is significantly lower than the threshold for identification of direction of motion.⁴⁸⁻⁵⁴ This is particularly the case for slowly moving stimuli, for stimuli displayed in the peripheral visual field, or for briefly presented stimuli. Chromatic signals seem to feed through different mechanisms for pattern and motion.

Are rod-detected moving stimuli also processed by different mechanisms? To find out, we performed detection and identification experiments, analogous to those that

have been performed under photopic conditions, under conditions of scotopic vision. If rod signals are processed in a manner identical to cone-based luminance signals, then we would expect equal thresholds for detection and identification for rod-detected stimuli over the whole range of temporal frequencies.

A. Methods

Methods were as described in Section 2, save for the following details. In the first series of experiments, we used the method of constant stimuli to measure detection and identification thresholds simultaneously. Stimuli were circular patches of sine-wave gratings moving at different temporal frequencies between 0.5 and 32 Hz. The aperture window had a diameter of 2 deg and was presented at a retinal eccentricity of 4 deg. At the beginning of each trial, a fixation spot was displayed briefly, followed by the presentation of the grating, which was drifting within the window for a duration of 500 ms. The observer had to make two successive button presses, indicating whether the grating appeared in the right or in the left half of the monitor (the detection task) and whether the grating moved to the right or to the left (the identification task). We fitted a cumulative Gaussian function to the resulting choice proportions, and the mean of the Gaussian was used as a threshold estimate. Rod monochromat observer KN, blue-cone monochromat observer PS, and color normal observers TE, HM, and CF participated in this experiment.

In the second series of experiments with deuteranopic observer AZ, we measured detection and identification thresholds separately. The stimulus was a vertically oriented 1-c/deg sine-wave grating displayed foveally in a circular aperture with a diameter of 10 deg. The grating drifted within the window for a duration of 1 s. Its contrast was multiplied by a Gaussian temporal envelope with a time constant of 250 ms. In the identification task a fixation spot was displayed briefly, turned off, and followed by the presentation of the grating. The observer's task was to indicate whether the grating drifted rightward or leftward by pressing one of two buttons. In the detection task there were two presentation intervals, each one marked by an audible burst of noise. In one of the two intervals the drifting grating was presented; in the other, the uniform gray background. The observer had to indicate by a button press which one of the two intervals contained the grating. An up-down staircase procedure⁵⁵ was used to measure the threshold levels at which the grating could be detected or its direction of motion identified in 79% of the trials.

B. Results

Figure 1 shows thresholds for detection and identification for rod monochromat KN. The x axis indicates temporal frequency and the y axis indicates sensitivity as the inverse of contrast at threshold. The open symbols indicate thresholds for detection, the solid symbols, thresholds for identification. Squares indicate thresholds without any neutral-density filters ($0.92 \log \text{cd m}^{-2}$); triangles, thresholds with a 2.04 log unit neutral-density filter ($-1.12 \log \text{cd m}^{-2}$). In accordance with his previous

flicker measurements made under similar conditions,⁶ his temporal contrast sensitivity curve (i.e., for threshold detection) is bandpass at the higher light level (0.92 log cd m⁻²) and becomes lowpass and shifted toward lower temporal frequencies at the lower light level (-1.12 log cd m⁻²).

Generally, thresholds for detection are slightly lower than thresholds for identification. The average detection/identification threshold ratio was 1.59 at 0.92 log cd m⁻² ($t = 7.57, p < 0.001$) and 1.48 at -1.12 log cd m⁻² ($t = 4.687, p < 0.001$). This seems particularly the case at the lower temporal frequencies. In both cases, the maximal detection/identification ratio was reached at the lowest temporal frequency of 0.5 Hz. These trends were confirmed for two other types of observer: the blue-cone monochromat and the color normals.

Figure 2 shows data from blue-cone monochromat observer PS. Detection and identification thresholds were measured at -1.12 log cd m⁻² (triangles) and at -2.25 log cd m⁻² (circles). As described in Section 2, stimuli for him were chosen by silent substitution to isolate rod vision. As for observer rod monochromat KN, thresholds for detection are slightly lower than thresholds for identification. The mean ratio of detection/identification sensitivities was 1.79 at -1.12 log cd m⁻² ($t = 8.905, p < 0.001$) and 1.23 at -2.25 log cd m⁻² ($t = 5.779, p < 0.01$). Again, the maximal ratios were achieved at the lowest temporal frequency of 0.5 Hz.

We also performed the experiment with the three color-normal observers, HM, CF, and TE. Only data from TE are shown here. Data from CF and HM were similar in all aspects. In color-normal observers, rod and cone responses cannot be completely distinguished. It can only be assumed that cones dominate at the highest light levels and rods become more effective as light level decreases. Figure 3 shows detection and identification sen-

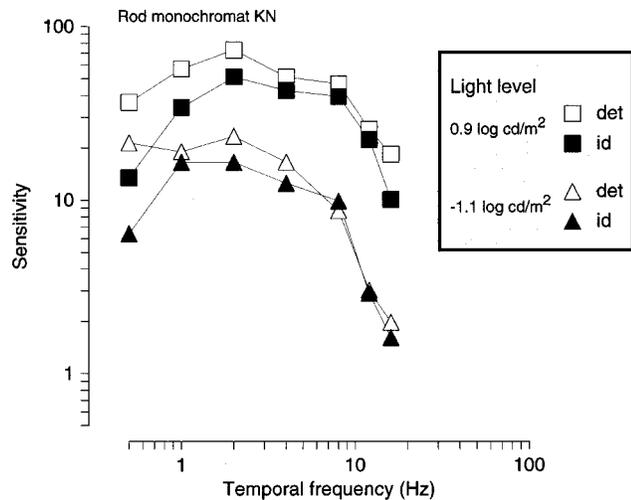


Fig. 1. Thresholds for detection and identification of 1-c/deg moving-grating stimuli for observer KN, a rod monochromat. The x axis plots temporal frequency, and the y axis plots sensitivity as the inverse of contrast at threshold. Open symbols, thresholds for detection; solid symbols, thresholds for identification. Squares, thresholds measured at a space-time-averaged luminance of 0.92 log cd m⁻²; triangles, thresholds measured at -1.12 log cd m⁻².

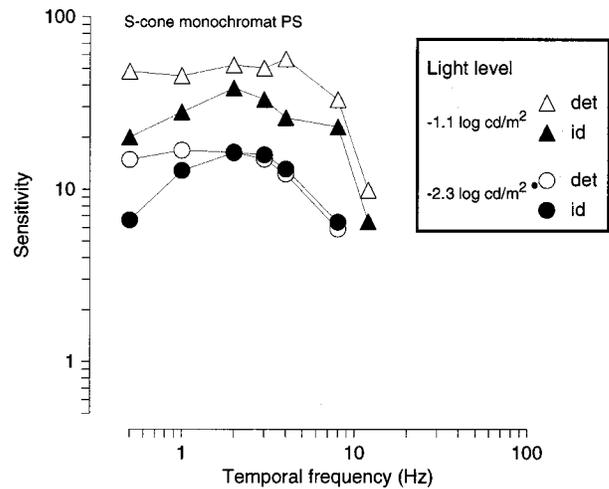


Fig. 2. Detection and identification thresholds for S-cone monochromat PS, who has only functioning rods and S cones. Triangles, thresholds measured at -1.12 log cd m⁻²; circles, those measured at -2.25 log cd m⁻². Otherwise, symbols as in Fig. 1. As described in Section 2, stimuli for PS were modulated so as to isolate rod vision by the silent substitution technique.

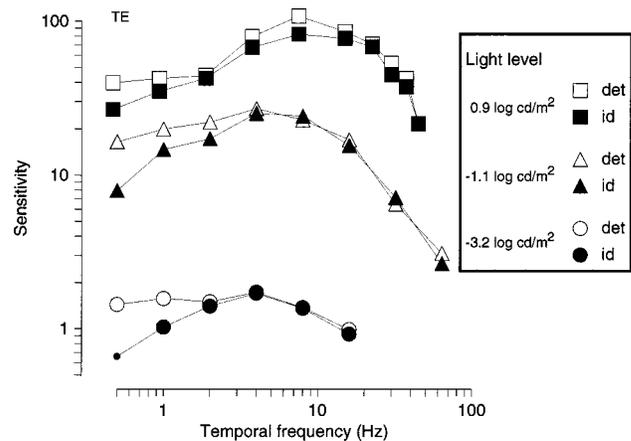


Fig. 3. Detection and identification thresholds for color-normal observer (TE). Squares, triangles, and circles, thresholds measured at 0.92, -1.12, and -3.20 log cd m⁻², respectively. Otherwise, symbols as in Fig. 1. The smaller solid circle at 0.5 Hz indicates that this threshold was extrapolated from responses to contrasts lower than 100%.

sivities at 0.92 (squares), -1.12 (triangles), and at -3.20 (circles) log cd m⁻². At photopic light levels (squares), detection and identification sensitivities are quite close with a mean ratio of 1.16. That ratio increases slightly to 1.236 (-1.12 log cd m⁻²) and to 1.313 (-3.20 log cd m⁻²). Again, the only pronounced differences between detection and identification occur at the lowest temporal frequencies.

In all the above experiments, we found small differences between detection and identification thresholds. However, the differences seem to exist not only for the conditions mediated by rods (Figs. 1 and 2) but also to some extent in the conditions probably mediated by cones (Fig. 3, top curves). Furthermore, the interpretation of all the above results suffers from the problem that the photopic and scotopic luminance systems were not compared under identical conditions. For the color-normal

observers, there is no way to stimulate rods and cones in our experiments selectively. We can achieve only three degrees of freedom on our monitor display system, whereas normal observers have four different types of photoreceptors. One can only assume that vision at low light levels reflects the activity of the rods and vision at higher light levels reflects the activity of the cones. However, even if isolation for a single photoreceptor type is achieved, the difference in the absolute light level itself will have a profound effect on visual processing speed (see, e.g., Stockman *et al.*).^{29,32} On the other hand, rod monochromats allow perfect, selective stimulation of scotopic vision but not direct comparison with cone vision. For the S-cone monochromat, it is possible to compare rod with S-cone vision at the same light level. However, functional magnetic resonance images from the motion-selective cortex in the same S-cone monochromat observer suggest that the S-cone-mediated contrast sensitivity is far smaller than L- and M-cone-mediated contrast sensitivity to luminance signals in the normal observer.⁵⁶ Such differences are potentially confounding. A solution is to resort to dichromatic observers, who have rods and intact L- (deuteranopes) or M-(protanopes) cones, and therefore only three degrees of freedom owing to the loss of the other X-chromosome-linked cone photopigment.

Figure 4 shows detection and identification thresholds for one typical deuteranope (AZ), measured at four different light levels, for his L cones and for his rods. Note that these experiments were carried out with large, foveally presented targets. Under these conditions, there

are no significant differences between detection and identification thresholds. Interestingly, the rod thresholds for observer AZ are fairly constant over the whole range of different light levels, whereas sensitivity for his L cones varies by a factor of ~ 200 . At the lowest light level, $-2.25 \log \text{cd/m}^2$, L-cone thresholds could no longer be measured. This makes it quite likely that the thresholds shown in Fig. 3 for the normal observer at that and lower light levels are solely mediated by rod vision.

C. Discussion

None of our observers showed large differences between detection and identification thresholds for rod vision. However, for most of the observers (the rod monochromat, the S-cone monochromat, and the normal observers), we found small but significant differences at low temporal frequencies, where thresholds for detection were slightly lower than thresholds for identification of direction of motion. Does this discrepancy resemble the differences that have been reported between detection and identification for isoluminant stimuli?^{48–54} Clearly not; there are qualitative differences between chromatically detected (cone) motion and rod-detected motion. The threshold ratios we observed for rod stimuli of ~ 2.0 for 0.5-Hz stimuli are similar to what is found for foveal isoluminant stimuli,^{53,57} not for peripheral isoluminant stimuli. Indeed, at the retinal eccentricities used in our experiments, much higher ratios—between 3 and 10 rather than between 1 and 1.8—are typically observed for chromatic motion.^{48,49,51} The differences found between rod-

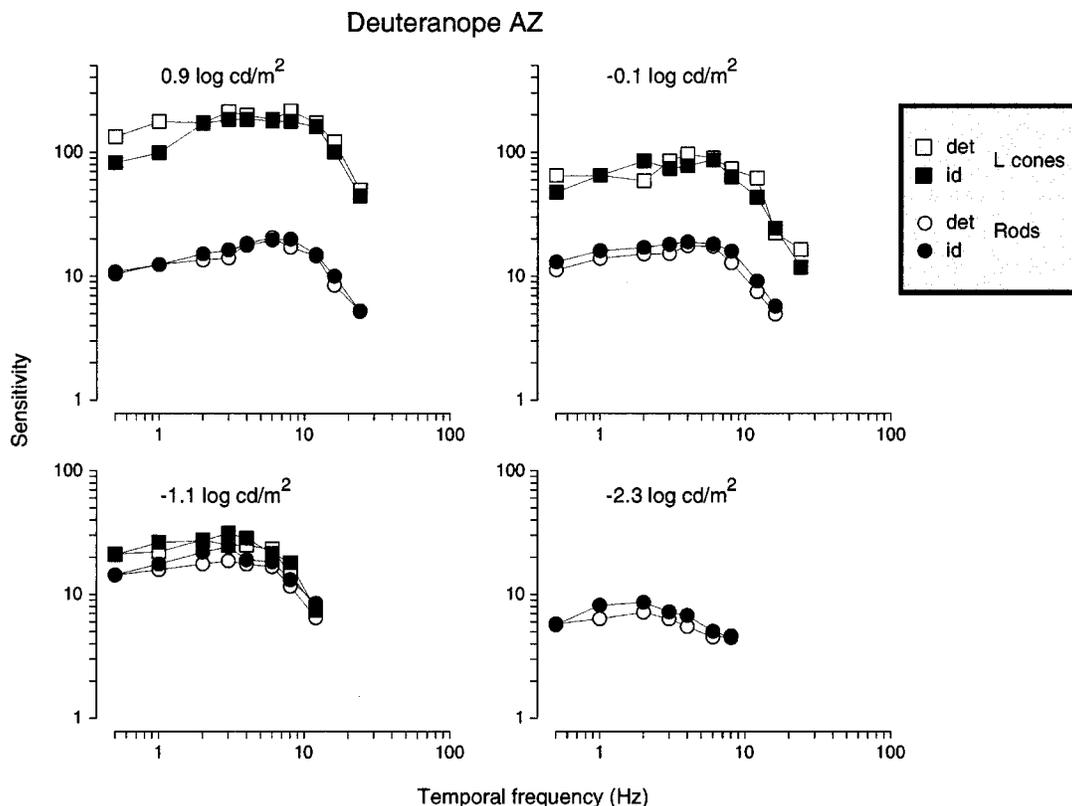


Fig. 4. Detection (open symbols) and identification (solid symbols) thresholds for deuteranope AZ for four different space-time-averaged luminances: 0.92, -0.10 , -1.12 , and -2.25 cd m^{-2} . L-cone-activating and rod-activating stimuli are indicated by squares and circles, respectively.

detected motion perception and cone-based luminance motion detection are small in comparison with those found between cone-based luminance and chromatic motion detection, and they are unlikely to influence motion perception very much. Finally, for large, foveally presented stimuli, the differences between detection and identification thresholds disappear almost completely (Fig. 4).

4. EXPERIMENT 2: PERCEIVED SPEED

Besides identifying an object's direction of motion, a basic component of motion perception is judging its speed. Recently, it has been shown that, for a large variety of stimuli, the perception of speed is far from veridical.^{58–62} In particular, at slow temporal frequencies, stimuli defined by color or flicker appear to move much slower than luminance-defined stimuli of the same physical speed. Moreover, for color- or flicker-defined stimuli, the speed percept is significantly dependent on their contrast. It is unknown whether similar departures from veridicality occur for rod motion perception. We therefore decided to determine the relative perceived speed of gratings under scotopic conditions. In such experiments, it is critically important that the cones are not stimulated and that only rods detect the gratings. Otherwise, any residual cone activation will significantly influence the velocity judgments. This is impossible to achieve in color-normal observers because in the design of silent substitution experiments, the quantal absorptions in three separate cone classes and in the rods must be taken into account. We therefore chose once again to conduct the perceived speed experiments in dichromatic observers, who are missing one of the X-chromosome-linked cone photopigments. To achieve the maximal contrast in the rods, we used deuteranopes who lack functional M cones. As described in Section 2, it is possible to devise high-contrast stimuli for these observers that differentially activate L cones or rods. It is known that luminance-based motion perception of deuteranopes behaves essentially normal⁴⁹ and is presumably driven by the L cones exclusively. These properties not only allowed us to isolate rod stimulation, but they also allowed a direct comparison of the perceived speed of stimuli as seen through the rod and the cone visual systems.

A. Methods

Methods were as described in Section 2, with the following exceptions. The objective of the experiments was to determine the speed required for observers to make a perceptual match between a comparison and a standard stimulus. On each trial, the observer's task was to judge which one of two simultaneously presented moving 1-c/deg sine-wave gratings moved faster. Each stimulus presentation consisted of two viewing windows, 21 deg wide by 7 deg high, juxtaposed vertically. One window contained the standard target, which always had a fixed temporal frequency. The other window contained the comparison target; the temporal frequency of which was determined with a staircase procedure. The central horizontal border of each window was positioned at 0.5 deg from the center of the screen. To avoid systematic bias of

speed judgements by motion aftereffects, we randomly assigned the direction (left or right) and the position (upper or lower window) of the standard. The two gratings always moved in opposite directions, and the spatial starting phase of the two gratings was randomized.

A spatial, two-alternative, forced-choice procedure was used to drive the staircase, which adjusted the temporal frequency (or speed) of the comparison stimulus. Twelve reversals of the staircase were obtained for each comparison, resulting in six threshold estimates.⁵⁵ In each experiment, five comparison stimuli were interleaved, and two separate staircases were run for each comparison. The contrast of the comparison stimuli was varied both above and below the contrast of the standard, in half-octave steps. In each session the standard could be a rod-isolating or a L-cone isolating stimulus, and the comparison stimuli were all either rod- or L-cone isolating. The standard L-cone stimulus had a contrast of 10.68%. The L-cone comparison stimuli had contrasts of 5.33%, 8.01%, 10.68%, 21.36%, and 27.5%. The standard rod stimulus had a contrast of 9.68%; the rod comparison stimuli had contrasts of 4.84%, 7.26%, 9.68%, 19.36%, and 24.69%. The mean velocity of the comparison at the match was determined from six experiments, each representing the mean of six estimates. Thus each data point is based on a total of 36 estimates.

B. Results

Figure 5 shows the results for deuteranope observer AZ for three different luminance levels: 0.92 (no filter condition), -0.10 (1.02 log unit filter condition), and -1.12 (2.04 log unit filter condition) $\log \text{cd m}^{-2}$. The temporal frequency was 1 Hz. Absolute contrast (in % rod contrast or % L-cone contrast) is plotted on the x axis. Relative speed (standard/comparison) is plotted on the y axis. The symbols correspond to conditions in which a rod (circles) or L-cone (squares) standard stimulus was used. Solid symbols indicate conditions in which the standard and comparison stimuli activated the same class of photoreceptor (i.e., either rods or cones); open symbols, conditions in which they activated different ones.

Especially at higher light levels, a small but significant dependence of perceived speed on contrast is observed. That is, higher contrasts lead to an increase in perceived speed, as has been reported in other studies for comparable conditions.^{58–62} Furthermore, when the standard and comparison stimuli activate the same type of photoreceptor, the ratio of perceived velocities is close to unity, which indicates equivalent motion perception. However, when a rod-detected moving stimulus is compared with a cone-detected standard (open squares), it appears to move significantly slower than the standard. For the data depicted in Fig. 5, the rod comparison stimuli having the same contrast as the L-cone standard (10%) are perceived to move at 72% ($0.92 \log \text{cd m}^{-2}$), 79% ($-0.10 \log \text{cd m}^{-2}$), and 86% ($-1.12 \log \text{cd m}^{-2}$) of the speed of the standard. Vice versa, the L-cone comparison stimuli, when compared with the 10% contrast rod standard (open circles), are perceived to move significantly faster at $\sim 135\%$ ($0.92 \log \text{cd m}^{-2}$), $\sim 114\%$ ($-0.10 \log \text{cd m}^{-2}$), and $\sim 112\%$ ($-1.12 \log \text{cd m}^{-2}$) of the speed of the rod standard. Note that these results cannot be explained by sensitivity differ-

ences between rods and cones. The differences in relative perceived speed between rods and cones are fairly stable over the three different light levels, whereas their relative sensitivity changes by approximately a factor of 20.

Figure 6 shows average data from all four deuteranopic observers for four temporal frequencies (0.5, 1, 2, and 4 Hz) and for three light levels (0.92, -0.10, and -1.12 log cd m⁻²). Perceived speed of 10% contrast rod stimuli is shown compared with that of a 10% contrast L-cone stimulus (open symbols), and vice versa (solid symbols). The dashed lines at a perceived speed of 1.0 indicates where rod motion perception would be veridical (i.e., equal to that of the cone-detected standard). An analysis of variance revealed significant main effects of receptor type ($F_{1,3} = 7.66, p < 0.05$), temporal frequency ($F_{3,9} = 11.4, p < 0.01$), and a highly significant interaction between receptor type and temporal frequency ($F_{3,9} = 32.107, p < 0.001$). At low temporal frequencies, the

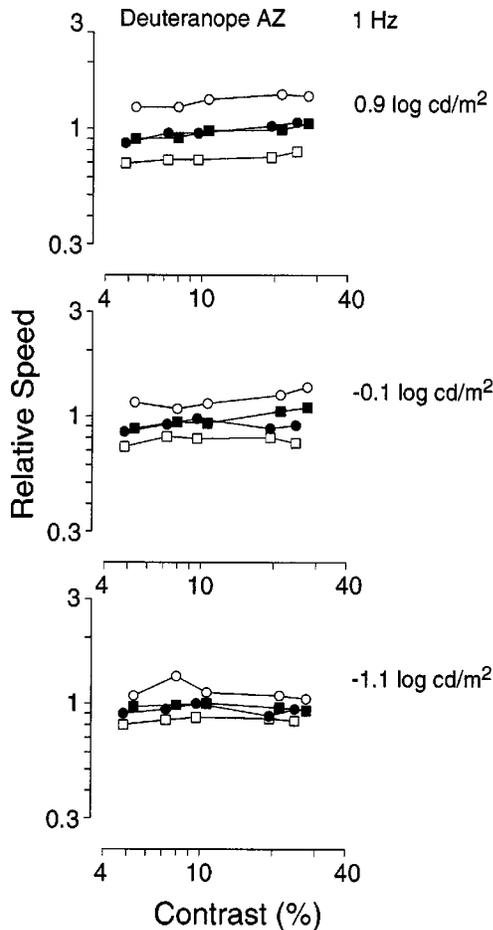


Fig. 5. Perceived speed as a function of contrast for deuteranope AZ for three different space-time-averaged luminances: 0.92, -0.10, and -1.12 log cd m⁻². Temporal frequency was 1 Hz. Absolute contrast (in % rod or % L-cone contrast) is plotted on the x axis. Relative speed (standard/comparison) is plotted on the y axis. Circles, conditions for which a rod standard stimulus was used; squares, conditions for which a L-cone standard stimulus was used. Solid symbols, conditions for which standard and comparison stimuli activated the same classes of photoreceptor (i.e., either rods or L cones); open symbols, conditions for which standard and comparison stimuli activated different classes of photoreceptor.

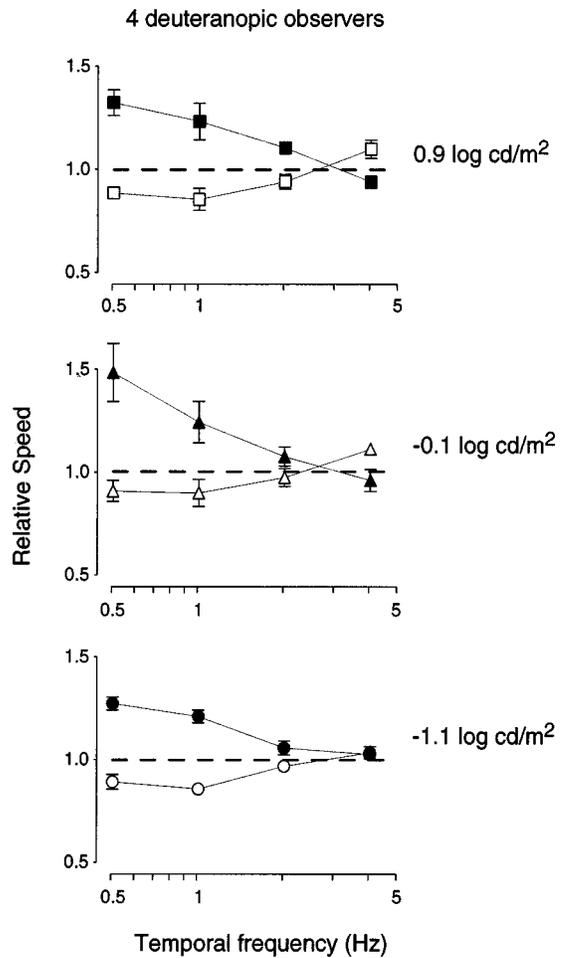


Fig. 6. Perceived speed averaged across deuteranopes, AZ, MM, GE, and SH, for temporal frequencies of 0.5, 1, 2, and 4 Hz. Perceived speed for a 10% contrast rod stimulus is compared with the perceived speed for a 10% contrast L-cone stimulus. Error bars, ± 1 standard error of the mean. Dashed lines at a perceived speed of 1.0 indicates where rod motion perception would be veridical (i.e., identical with cone motion perception).

data are clearly different from veridical, with the rod stimuli appearing slower by ~20–30%. For medium and high temporal frequencies, this is no longer the case. With increasing temporal frequency, the difference diminishes, so that at ~4-Hz rod and cone stimuli are perceived veridically and equally fast. At higher temporal frequencies, there seems to be a small trend in the opposite direction, with rod stimuli appearing to move slightly faster. This resembles an analogous finding for cone stimuli that at high temporal frequencies stimuli of lower contrast appear to move slightly faster than stimuli of higher contrast.^{47,60} Interestingly, the results are basically identical for three different light levels, which indicates that the finding is not based on relative sensitivity differences between rods and cones. At 0.92 log cd/m², cones are ~20 times more sensitive than rods, whereas at -1.12 log cd/m², cones and rods are about equally sensitive (see Fig. 4). Also, rods are more sensitive at the lower temporal frequencies, but it is at the high temporal frequencies at which both rod and cone stimuli appear to move veridically.

5. GENERAL DISCUSSION

Our results show that motion perception is handicapped at scotopic light levels. Thresholds for detecting moving stimuli are negligible or unaffected, but the perception of the speed of moving stimuli is severely impaired at low temporal frequencies. The same stimuli when activating rods appear to move ~20–25% slower than when activating cones. This perceptual slowing could have consequences, when one relies solely on rod vision or when one shifts between rod and cone vision; for example, while driving at night.

A. Comparison with Isoluminant Stimuli

At first sight, the deficits of rod motion perception appear quite similar to those for the perception of isoluminant motion stimuli. Isoluminant stimuli also appear to move slower than luminance stimuli of comparable contrast, and there are also differences in the thresholds for motion detection and identification (e.g., Gegenfurtner and Hawken¹⁴). But there are marked differences between the results for rod-detected motion stimuli and for isoluminant motion stimuli. First, the perceived slowing is much more dramatic for isoluminant stimuli than for rod-detected stimuli. High-contrast isoluminant gratings moving at a physical speed of 1 deg/s appear to move ~50% slower than a 10% contrast luminance grating; whereas rod-detected stimuli appear to move ~20% slower. Second, speed perception for isoluminant stimuli is highly dependent on contrast.⁶⁰ Rod motion is only slightly contrast dependent and certainly not more than cone-based luminance motion (see Fig. 5). This second observation suggests that the rod deficit might be due to distal factors, rather than central factors.

The question is then how differences in the spatial and temporal filtering in the rods and cones could indirectly influence motion perception. It is relevant to note that any spatial or temporal preprocessing *per se* will not influence the preferred velocity of a single elementary motion detector,^{63–66} since the preferred velocity depends only on the spatial distance between the two receptive fields of the detector and on the time delay between the two receptive fields. In other words, the velocity preferred by any one motion detector would be the same for rods and cones. But the output signal of any elementary motion detector (EMD) will also heavily depend on the contrast of the input signal, and this relationship is nearly linear over a wide range of contrasts. Therefore, attenuating high spatial and high temporal frequencies will reduce the output of the EMD's tuned to these frequencies, whereas EMD's tuned to low spatial and low temporal frequencies will not be affected.

There is, of course, strong spatial and temporal low-pass filtering in the rod visual system. Extensive psychophysical evidence implies that the retinal spatial summation area and temporal integration time are much larger for rod signals than that for cone. Although many factors must be taken into account, including retinal eccentricity, background intensity, stimulus duration, and whether the summation is truly complete or not, it can generally be said that, for dark-adapted peripheral rod vision, Riccò's area of total spatial summation is valid up to

2 deg in diameter, decreasing with light adaptation.^{67–74} In contrast, for foveal cone vision, Riccò's area holds only up to between 2–8 min of arc^{72,75,76} and does not seem to change much with light adaptation (see Chen *et al.*⁷⁷).

Likewise, depending upon stimulus configuration and retinal eccentricity, Bloch's Law of total temporal summation is valid up to 200–270 ms for fully dark-adapted peripheral rod vision, decreasing with light adaptation to ~100 ms.^{68,72,78–83} In contrast, for dark-adapted foveal cone vision, Bloch's Law holds up to ~100 ms, decreasing with light adaptation to 30–60 ms.^{68,81,83–86}

Larger spatial and longer temporal summation for rod vision will result in severe low-pass filtering of the input signal, both in the temporal and in the spatial domain. This will reduce the responses of EMD's with a short distance and a short time delay between their two receptive fields or, equivalently, EMD's highly sensitive to high spatial and high temporal frequencies. Given that the spatial frequency of all our stimuli was constant at 1 c/deg, we have to consider only temporal properties here. Thus, for rods, the signal in the low-velocity (long time delay) detectors relative to the signal in the high-velocity detectors will be higher than for the cones. If perceived speed is determined from the population response of all motion detectors (e.g., Heeger⁸⁷), then rod stimuli should appear to move slower whenever the low-velocity detectors are contributing significantly. Note that this explanation involves only distal (retinal) processing differences between rod and cones and assumes identical central processing.

B. Magno- and Parvo-Pathways

Rod signals are fed through the same ganglion cells that are used by the cones. Physiological evidence from the primate seems to support a dominant rod input to the magnocellular retino-geniculate pathway.^{19,20,88} In comparison, the rod input to P-pathway cells is weak but does not differ in latency from the stronger input to the M-pathway cells.²⁰ In psychophysical experiments in humans,²¹ it was found that at eccentricities beyond 15 deg, visual acuity under scotopic conditions was significantly higher than that of the magnocellular system. The researchers concluded that the basis of this higher acuity must therefore be the summation over many P-pathway cells, which receive rod input. However, Lee *et al.*²⁰ argue that the rod input to P-pathway cells is so weak—in their experiments 100% modulation delivered only a few spikes—that it is unlikely that it could be the substrate for scotopic spatial vision.

Like the psychophysical results of Lennie and Fairchild,²¹ our psychophysical results at a first glance seem to rule out the possibility that rods send signals only to magnocellular ganglion cells, because rod motion appears somewhat similar to motion at isoluminance and different from motion under photopic conditions. But the differences we observe between scotopic vision and vision at isoluminance make it clear that the similarities are superficial. Since rod motion is only slightly dependent on contrast, it seems likely that rod signals are processed in the same manner as photopic, cone-based motion signals. Therefore no conclusion can be drawn, on the basis of our

data, as to whether the rod substrate for motion perception is mainly through parvocellular or through magnocellular channels.

C. Two Retinal Pathways

It is interesting that no effect of light level on rod-detected velocity was observed, even though rod flicker signals are processed by two separate systems with different temporal characteristics: a slow system dominating at low luminances and a fast system at high.^{5,27–33} However, psychophysical investigations suggest that there is little or no difference between the spatial extents of the neural excitation pools of the two signals.^{28,31} Moreover, if the differences between rod and cone motion is largely due to filtering by the rod photoreceptors themselves or to the early spatial and temporal summing of their signals (or both), rather than to the subsequent retinal pathway characteristics, then no change of perceived velocity with a change in luminance should be expected. At the intensity levels we tested (see Fig. 6), both rod pathways are active. The faster pathway, which is shared more intimately with the cones, however, would be expected to dominate at higher temporal frequencies, at which the effect of contrast on perceived speed is no longer present.

D. Comparison with Other Studies

Our results agree well with the few published studies of scotopic motion processing. Takeuchi and De Valois⁸⁹ found some impairment of scotopic motion processing. In a recent conference paper, Turner *et al.*⁹⁰ also described a slowing of rod motion, albeit only by 5–10%. However, the smaller effect they report might have been caused by the method they used to differentiate rod and cone responses. Subjects wore a neutral-density filter over one eye, and a septum was used to separate the right and left visual field. Such a procedure might lead to only partial separation of the responses, because it is known that some of the relevant motion areas (e.g., area MT) receive inputs from both hemispheres.^{91–93} An interaction might have caused some degree of “correction” to the impaired rod motion signal. Also, given that Turner *et al.*⁹⁰ looked at speeds from 2.83 to 5.65 deg/s, they might have missed some of the effect, which is largest at low speeds. More recently, Grossman and Blake⁹⁴ have shown that coherent motion detection is affected little at scotopic light levels. They did find impaired perception of biological motion and of form-from-motion at scotopic light levels. However, in both of these studies, light level was a confounding factor, which could have contributed to the results. This is not the case in our experiments with deuteranopic observers.

6. CONCLUSIONS

Our results show that motion perception is deficient at low light levels. Although detection of motion is still possible, low temporal frequency stimuli predominantly activating the rods appear to move slower than those predominantly activating the cones. As a result of the contrast dependence of perceived speed, departures from veridicality will occur under conditions in which the rod visual system works alone; seriously impairing finely

tuned and accurate motor activity and responding. More important, failures of synchronization will occur under conditions where both the rod and the cone visual systems work simultaneously, and these can have important consequences. For example, when one is driving at night the region illuminated by the headlights of the car is processed mostly by the cones. The remaining visual field is in the dark and is processed mostly by rods. This region typically includes the outermost parts of the visual fields where translatory motion signals are largest (see, e.g., Warren and Kurtz⁹⁵). This might lead to an underestimation of the speed of our movement through the environment, which in turn might elicit a compensatory and possibly fatal speeding up of the movement.⁹⁶

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