Pergamon

Vision Res. Vol. 34, No. 6, pp. 799–802, 1994
Copyright © 1994 Elsevier Science Ltd
Printed in Great Britain. All rights reserved
0042-6989/94 $6.00 + 0.00

Research Note

Stereopsis and Positional Acuity under Dark Adaptation

MARGARET S. LIVINGSTONE,*† DAVID H. HUBEL*

Received 4 February 1993; in revised form 6 July 1993

Though experience tells us we can perceive depth in dim light, it is not so obvious that one of the chief mechanisms for depth perception, stereopsis, is possible under scotopic conditions. The only studies on human stereopsis in the dark adapted state seem to be those of Nagel [(1902) *Zeitschrift für Psychologie*, *27*, 264–266] and Mueller and Lloyd [(1948) *Proceedings of the National Academy of Science, U.S.A.*, *34*, 223–227], both of which used real objects or line stereograms. We tested stereopsis using both random-dot and line stereograms and, in agreement with these studies, found that stereopsis is indeed possible in dark adaptation. We also measured stereo acuity and positional acuity (both of which are examples of hyperacuity) and compared these with grating acuity at several levels of light and dark adaptation. At all illumination levels tested, acuities for stereopsis and relative line position were both higher than for grating acuity. As light levels decreased, positional and grating acuity declined in parallel fashion, whereas stereoacuity declined more steeply.

Stereopsis Dark adaptation Hyperacuity

EXPERIMENT 1. STEREOPSIS IN DARK ADAPTATION

Two previous studies have reported that stereopsis is possible in the dark adapted state: Nagel (1902) tested his own stereopsis by determining the threshold depth differences between a reference pair of rods and a center one whose distance could be adjusted. He made the determinations in bright light, dim light, and in clearly scotopic conditions as assessed by foveal blindness. Meuller and Lloyd measured stereo acuity for black-line triplets viewed stereoscopically. In this experiment we tested our stereopsis under scotopic conditions using dynamic random-dot stereograms (Julesz, 1971).

The two authors were subjects; both have corrected-to-normal acuity and normal stereopsis. Tests were conducted in a light-proof room. Before each test subjects were dark adapted for 40 min, and the order of testing began at the lower luminance level. Dynamic random-dot stereopairs (Julesz, 1960) were generated with a Silicon Graphics Iris Indigo XZ 4000 system, a fast color workstation capable of stereo displays using liquid crystal display lenses which block the left eye then the right eye, alternating with each refresh of the monitor. The monitor runs at a 120 Hz refresh rate, so that pairs of stereo images are displayed at 60 Hz. The liquid crystal lenses change transmittance by a factor of 15 between the open and closed states. Each stereogram was a square, 5 deg on a side, consisting of green and black checks. The size of the checks constituting the square, and hence the coarseness of the display, was variable.

To generate the dynamic random-dot patterns, first a large table of random black and green values was created using the Iris system random number generator drand48; then each display used another random number to choose where in the table to start gathering values for the checks. Identical arrays were drawn for the two eyes, except for a vertical bar of checks whose position in one display could be shifted horizontally by a variable number of checks, relative to its position in the other. Artificial pupils were not used. Luminance levels were determined with a Pritchard spot photometer, aligned to read through the liquid crystal lenses (note: 1 ft-L = 3.426 cd/m^2). The luminance of the checkerboard was taken as the average value of the green and black checks $(L_{Gr} + L_{Bkg})/2$. We tested our stereopsis at two scotopic levels: 8.8×10^{-5} and 2.6×10^{-4} ft-L (Shlaer, 1937). The green stimuli at both these levels of illumination appeared achromatic, and a 0.5 deg spot disappeared when viewed foveally.

The task was forced-choice in which the subject had to say whether the central 3.8 × 1.4 deg rectangular region of the random-dot pattern was in front of or behind the plane of the rest of the pattern. At 2.6×10^{-4} ft-L both of us correctly identified the direction of the disparity more than 90% of the time for a check size of 10 min arc and disparities of 10 min arc (10 trials at each disparity). At 8.8×10^{-5} ft-L both of us correctly identified the direction of the disparity for

---

*Department of Neurobiology, Harvard Medical School, 220 Longwood Avenue, Boston, MA 02115, U.S.A.

†To whom all correspondence should be addressed.

check sizes of 20 min arc and disparities of 20 min arc. Since the smallest disparity corresponded to the width of 1 check, it is not clear whether our stereo acuity in this experiment was limited by the disparity itself or the coarseness of the stereogram. But in either case, this result confirms previous reports that humans can detect binocular disparity using rod vision.

EXPERIMENT 2. HYPERACUITY UNDER DARK ADAPTATION

Under optimal conditions the smallest resolvable object subtends about 1 min arc, a resolution corresponding to the separation between individual foveal cones. Grating acuity is a measure of such resolution. Nevertheless one can judge the relative positions of objects with much higher accuracy: for several kinds of visual spatial discriminations human subjects can exhibit acuities in the range of a few seconds of arc (Westheimer, 1979). This is about an order of magnitude finer than would be expected from photoreceptor size or spacing and is therefore termed hyperacuity. Examples of hyperacuity include vernier line displacement, motion detection, relative position judgment, and stereoscopic depth. We wished to learn whether these kinds of tasks show higher acuity than grating acuity even under dark adaptation. Mueller and Lloyd (1948) compared stereo acuity at low and high light levels, but did not compare these results to other kinds of acuity tasks. We therefore compared our ordinary acuity as tested with gratings with two types of acuity that under photopic conditions fall into the hyperacuity range: stereopsis and relative line position (or bisection).

Tests were again presented with an Iris Indigo system, using the green phosphor on a black background. All three tests were performed with the subjects wearing the liquid crystal goggles. These tests were also conducted in a light-proof room. Each subject was dark adapted for 40 min before testing, and the order of testing began at the lowest luminance level. The stimulus for testing positional and stereo acuity was three parallel bars. Both stereo and positional acuity were measured by the method of adjustment (Graham, 1965), in which the subject turned a knob to vary the position of the central bar until it appeared centered between the flanking bars for the positional test or in the same plane as the two flanking bars for the stereo test. (The only difference between the two tests was that in the stereo test as the knob was turned the images of the central bars presented to the two eyes moved in opposite directions, and for the position test the movement for the two eyes was concordant.) Because we needed high resolution at the high luminance levels and large stimuli at the lowest levels, we carried out the tests at two different distances: 6 m for the two highest luminance levels and 3 m for the rest. For the tests at the lowest light levels, the bars were 6 × 0.1 deg, and for the two highest luminances the bars were 2 × 0.1 deg. The flanking bars were separated by 0.5 deg. The bars were long enough to extend well outside the foveas even for fixation on their center points, so that at least some part of them would be seen by the part of the retina having the greatest resolution at every light level. Acuity was taken as the standard deviation for 15 trials of the adjusted position (or

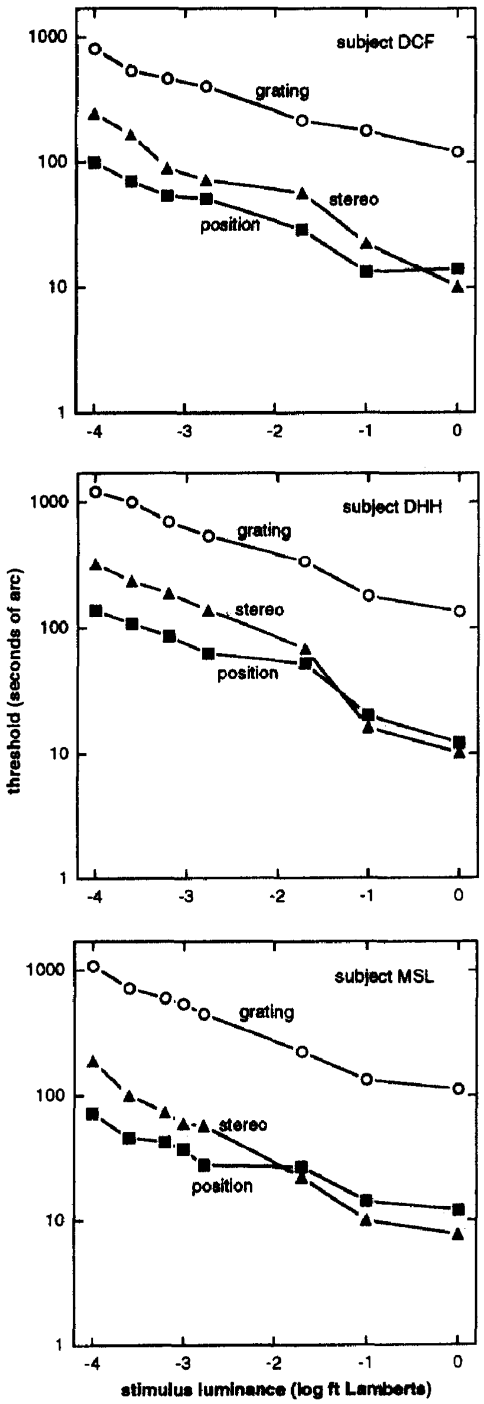

FIGURE 1. Results of three visual acuity tests at different luminance levels. The open circles show acuity thresholds for square-wave gratings viewed binocularly, measured by a forced-choice test. The threshold is given as the angle subtended by one cycle of the finest resolvable grating. The solid squares indicate accuracy in centering one line between two flanking lines; values are the standard deviation of 15 trials at each luminance level. The solid triangles show the accuracy with which the subject could set a central bar at the same disparity as two flanking bars; the values given are the standard deviation of 15 trials at each luminance level.

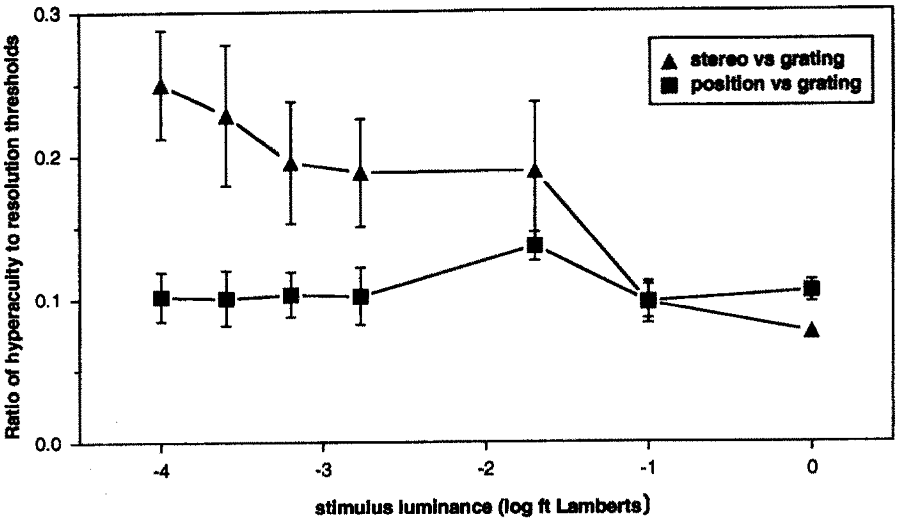

FIGURE 2. Comparison of the ratios of stereo and positional acuities to grating acuity (mean for all three subjects, ±SEM). This graph shows that at all luminances tested, both stereo and positional acuity are several-fold better than grating acuity, and that stereo acuity is degraded relative to both positional and grating acuity with decreasing luminance.

disparity), in seconds of arc. To measure grating acuity we used square-wave gratings, 2 × 2 deg for the two highest light level measurements and 7.5 deg on a side for the rest. Threshold was taken as the highest grating frequency giving over 75% correct responses in a forced-choice between horizontal and vertical.

All phosphor levels were set at zero for the background. At the five lowest luminance levels tested the room was dark, and the background luminance was 3×10^{-6} ft-L. For the two highest luminance levels tested the room lights were raised so that the background was 10^{-2} ft-L and the green lines or gratings appeared clearly colored green. In Fig. 1 light levels are based on the average of the light and dark luminances: $(L_{Gr} + L_{Bkg})/2$. We used this definition of luminance so that values for the gratings and checkerboards would be comparable to the line stimuli.

For this experiment, a third subject participated; he has corrected-to-normal acuity, and was ignorant of the hypothesis being tested. As shown in Fig. 1, for all three subjects the stereopsis and positional judgments were several-fold more accurate than grating acuity, and thus can be considered hyperacuities, at all luminances tested. Also, for all three subjects, although stereo and positional acuity are roughly similar to each other when compared with grating acuity, stereo acuity deteriorates relative to positional acuity with decreasing light levels. This can be seen more clearly in Fig. 2, where we have plotted the ratios of positional and stereo acuity to grating acuity; the ratio of positional to grating acuity remains constant over the luminance range tested, whereas stereo acuity deteriorates relative to grating acuity with decreasing luminance.

CONCLUSIONS

This study confirms earlier ones (Nagel, 1902; Mueller & Lloyd, 1948) in showing that stereopsis is possible in the dark adpated state, and extends those findings by establishing that depth can be seen in scotopic random-dot stereograms. We also found that in the dark adapted state, as in light adaptation, acuities for both position and stereopsis are higher than grating resolution. It has been suggested that grating acuity reflects the resolution of the ganglion-cell mosaic, and that hyperacuities reflect cortical averaging mechanisms (Levi, Klein & Aitsebaomo, 1985). The fact that the ratio of the values for position and grating acuity remains constant at all light levels is consistent with this, and suggests that such cortical averaging mechanisms can use either cone or rod inputs. That stereo acuity seems to suffer more, with decreasing light levels, than positional hyperacuity could reflect a different rod/cone ratio for that function, or it could mean that stereopsis requires more complicated cortical processing, and is degraded more when input is compromised. Previous studies agree in showing that vernier and stereo acuity are differentially affected by decreased visibility: Berry, Riggs and Duncan (1948) found that stereo acuity decreased more than vernier acuity with decreasing luminance. They used only foveal stimuli, however, and their lowest luminance levels were in the mesopic range (0.13 cd/m^2 or 0.04 ft-L). Similarly, Westheimer and Pettet (1990) found that stereopsis deteriorates more rapidly than vernier acuity with decreasing contrast and with shorter stimulus duration.

Our findings comparing positional and grating acuity are consistent with previous studies: Waugh and Levi (1993) recently compared line detection thresholds with vernier acuity and found a constant relationship for these two tasks over a 2000-fold range of retinal illumination. Yap, Levi and Klein (1989) found that two-dot positional thresholds (a form of hyperacuity) were better than two-dot resolution in both scotopic and photopic conditions.

On the other hand, Geisler and Davila (1985) found that at low light levels separation discrimination was no better than two-dot resolution; i.e. they failed to find hyperacuity performance at low light levels. The reason for these differences is not clear; it may be related to the fact that at the low light levels at which Geisler and Davila failed to measure hyperacuity their subjects were just at threshold for detecting the tiny (0.2 min arc) foveal stimuli, so quantal levels may limit performance, whereas in our study and that of Yap *et al.* (1989) the dimmest stimuli were well above threshold and were viewed eccentrically.

The results reported here may not be too surprising given one's impression that, except for color and resolution, night vision is qualitatively similar to day vision. Single-cell recordings in monkeys, especially from the lateral geniculate body, have shown that some cells receive both rod and cone inputs, and for these cells the center and surround arrangements are the same under both scotopic and photopic conditions (Wiesel & Hubel, 1966); other cells can be driven only by cones. Wiesel and Hubel found that cells with both rod and cone inputs occur both in the parvocellular and magnocellular subdivisions, but a recent study by Purpura, Kaplan and Shapley (1988) found that at eccentricities from 1 to 13 deg most if not all magnocellular cells had rod input, whereas very few parvocellular cells did. Thus in the scotopic state stereopsis and other forms of hyperacuity must depend either on magnocellular mechanisms or on the very small number of parvocellular cells that have rod inputs. Consistent with this, a recent study by Lee, Wehrhahn, Westheimer and Kremers (1993) reports that responses of magnocellular, but not parvocellular, macaque ganglion cells can account for motion hyperacuity perception.

REFERENCES

Berry, R. N., Riggs, L. A. & Duncan, C. P. (1948). The relation of vernier and depth discriminations to field brightness. *Journal of Experimental Psychology*, *40*, 349–354.

Geisler, W. S. & Davila, K. D. (1985). Ideal discrimination in spatial vision: Two point stimuli. *Journal of the Optical Society of America*, *2*, 1483–1497.

Graham, C. H. (1965). Visual space perception. In *Vision and visual perception* (pp. 504–547). New York: Wiley.

Julesz, B. (1960). Binocular depth perception of computer-generated patterns. *Bell Systems Technical Journal*, *39*, 1125–1161.

Julesz, B. (1971). *Foundations of cyclopean perception*. Chicago, Ill.: University of Chicago Press.

Lee, B. B., Wehrhahn, C., Westheimer, G. & Kremers, J. (1993). Macaque ganglion cell responses to stimuli that elicit hyperacuity in man: Detection of small displacements. *Journal of Neuroscience*, *13*, 1001–1009.

Levi, D. M., Klein, S. A. & Aitsebaomo, P. (1985). Vernier acuity, crowding and cortical magnification. *Vision Research*, *25*, 963–978.

Mueller, C. G. & Lloyd, V. V. (1948). Stereoscopic acuity for various levels of illumination. *Proceedings of the National Academy of Science, U.S.A.*, *34*, 223–227.

Nagel, W. A. (1902). Stereoskopie und Tiefenwahrnehmung im Dämmerungssehen. *Zeitschrift für Psychologie*, *27*, 264–266.

Purpura, K., Kaplan E. & Shapley, R. M. (1988). Background light and the contrast gain of primate P and M retinal ganglion cells. *Proceedings of the National Academy of Science, U.S.A.*, *85*, 4534–4537.

Shlaer, S. (1937). The relationship between visual acuity and illumination. *Journal of General Physiology*, *21*, 165–188.

Waugh, S. J. & Levi, D. M. (1993). Visibility, luminance, and vernier acuity. *Vision Research*, *33*, 527–538.

Westheimer, G. (1979). The spatial sense of the eye. *Investigative Ophthalmology and Visual Science*, *18*, 893–912.

Westheimer, G. & Pettet, M. W. (1990). Contrast and duration of exposure differentially affect vernier and stereoscopic acuity. *Proceedings of the Royal Society of London B*, *241*, 42–46.

Wiesel, T. N. & Hubel, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *Journal of Neurophysiology*, *29*, 1115–1156.

Yap, Y. L., Levi, D. M. & Klein, S. A. (1985). Peripheral positional acuity: Retinal and cortical constraints on 2-dot separation discrimination under photopic and scotopic conditions. *Vision Research*, *29*, 789–802.