Interindividual Variation in Human Visual Performance

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Abstract

■ The responses of 20 young adult emmetropes with normal color vision were measured on a battery of visual performance tasks. Using previously documented tests of known reliability, we evaluated orientation discrimination, contrast sensitivity, wavelength sensitivity, vernier acuity, direction-of-motion detection, velocity discrimination, and complex form identification. Performance varied markedly between individuals, both on a given test and when the scores from all tests were combined to give an overall indication of visual performance. Moreover, individual performances on tests of contrast sensitivity, orientation discrimination, wavelength discrimination, and vernier acuity covaried, such that proficiency on one test predicted proficiency on the others. These results indicate a wide range of visual abilities among normal subjects and provide the basis for an overall index of visual proficiency that can be used to determine whether the surprisingly large and coordinated size differences of the components of the human visual system (Andrews, Halpern, & Purves, 1997) are reflected in corresponding variations in visual performance. ■

INTRODUCTION

Although humans differ greatly in their talents and abilities, it is unclear how these idiosyncrasies are instantiated in the nervous system. One possibility is that quantitative differences in the amount of neural circuitry devoted to particular behaviors underlie such variations. Circumstantial support for this interpretation comes from comparisons across species, which show that proficiency in a particular behavior is reflected in a commensurate allocation of supporting neural circuitry (reviewed in Purves, 1994; Purves, White, Zheng, Andrews, & Riddle, 1996). Human vision is a particularly attractive context in which to explore whether this relationship holds among individuals of the same species. In a previous study (Andrews, Halpern, & Purves, 1997), we reported that the sizes of three components of the visual system—the optic tract, lateral geniculate nucleus (LGN), and primary visual cortex (V1)—varied two- to threefold between individuals. Importantly, this variation was coordinated within the visual system of any one individual. Thus, a large V1 was generally associated with a large LGN and a large optic tract. If the idiosyncratic talents of individuals are realized by the devotion of a greater (or lesser) amount of related neural space, this substantial interindividual variation in the size of the human visual system suggests a corresponding range of visual ability among the population. Whereas previous investigations of vision in normal subjects have noted that individuals vary greatly in their performance on several visual tasks (Benton, Varney, & Hamsher, 1978; Burbeck & Regan, 1983; Ginsburg, Evans, Cannon, Owsley, & Mulvanny, 1984; Roy, Podgor, Collier, & Gunkel, 1991; Yates, Harrison, O'Conner, & Balentine, 1987), no systematic evaluation of this behavioral variability has been reported.

The aim of this study, therefore, was to develop a battery of tasks to determine the range of visual ability among ophthalmologically normal, young adults. Our choice of tests was motivated by an assessment of the known physiology of the visual system. In the primary visual cortex, for example, neurons have been described that are selective for orientation, direction of motion, wavelength (Hubel & Wiesel, 1977), speed of movement (Orban, Kennedy, & Bullier, 1983), spatial frequency (Schiller, Finlay, & Volman, 1976), and luminosity (Kayama, Riso, Bartlett, & Doty, 1979). Accordingly, seven previously validated tests of visual function that discriminate aspects of form, color, orientation, contrast, and motion perception were administered in different parts of the visual field. Our immediate aim was to carry out a systematic analysis of individual variation in performance on a variety of visual tasks, with the goal of assessing whether such a battery provides an index of overall visual ability that could ultimately be used to assess the relationship between brain size and behavior.

RESULTS

Interindividual Variation in Performance for Different Visual Tasks

The performance of a representative subject in the visual tests from the battery we employed is shown in Figure 1. For the contrast, wavelength, velocity, and vernier acuity tests, sigmoidal functions were fit to the data. The goodness of fit is shown by the chi square values.

Marked variations in test scores were apparent among individual subjects (Table 1). Considering the tests in the order in which they were presented, orientation discrimination varied about 60% (normalized score range = 0.79 to 1.24), a range similar to that reported in previous studies (Benton, Hannay, & Varney, 1975; Benton et al., 1978). About a 100% interindividual variation was apparent for both the tests of wavelength sensitivity (normalized score range = 0.68 to 1.34) and contrast sensitivity (normalized score range = 0.68 to 1.35). The range of variation for these parameters also agrees with previous reports (e.g., Ginsburg et al., 1984; Roy et al., 1991; Yates et al., 1987). A larger (~1000%) interindividual variation was evident in the vernier acuity scores among subjects (normalized score range = 0.27 to 2.65). This variation is consistent with previous studies that show that vernier acuity declines rapidly as line separation exceeds a few minutes of arc, with relatively large differences between individuals (Berry, 1948; Westheimer & McKee, 1977). Interindividual variation in both the direction-of-motion detection (normalized score range = 0.64 to 1.35) and velocity discrimination (normalized score range = 0.67 to 1.36) tests was about 100%. Finally, the complex form identification scores varied by about 60% (normalized score range = 0.79 to 1.28).

Interindividual Variation in Overall Visual Performance

To assess overall differences in visual ability among our subjects, we combined the normalized scores from all the tests and expressed the composite score as a percentage, with the mean = 100. The combined scores expressed in this manner ranged from 81 to 122 and were normally distributed about the mean value (Figure 2). Evaluation by ANOVA showed that subjects differed significantly from each other in their overall visual ability ($p < 0.0001$); the specific differences between subjects are given in Table 2.

Performance across the Visual Field

As expected, visual performance declined as a function of eccentricity (Figure 3). The magnitude of this difference, however, varied from task to task. For example, orientation discrimination declined significantly between central and peripheral vision (0°, 7.5° $p < 0.0001$; 0°, 15° $p < 0.0001$), but the difference between performance at 7.5 and 15° was not significant ($p = 0.3$). Previous studies have reported a similar magnitude of decline in orientation discrimination with eccentricity (Rovamo, Makela, & Whitaker, 1993). Likewise, both direction-of-motion detection and velocity discrimination were more sensitive at 0° than at 7.5° (direction, $p < 0.0001$; velocity, $p < 0.05$) or 15° (direction, $p < 0.0001$; velocity, $p < 0.0005$), but no significant difference was apparent comparing performance at 7.5 and 15° (direction, $p = 0.69$; velocity, $p = 0.13$). Wavelength and contrast sensitivity in central vision were also significantly greater in central vision than in the periphery (0°, 7.5° $p < 0.0001$; 0°, 15° $p < 0.0001$).

When overall visual performance was evaluated in different parts of the visual field, a similar range of variation was apparent. Furthermore, the level of performance at one eccentricity was reflected in performance at other eccentricities. For example, performance in central vision correlated with performance at 7.5° ($r = 0.5$; $p < 0.05$) and 15° ($r = 0.6$; $p < 0.005$). Similarly, individual performance at 7.5° covaried with performance at 15° ($r = 0.6$; $p < 0.005$).

Correlation of Visual Performance in Different Tests

To determine whether the marked differences in individual performance apparent in the specific visual tests and in overall visual ability were coordinated within an individual, we examined the degree of covariance in the scores of the different tests using principal components analysis (Table 3). This evaluation demonstrates that a proportion of the variation in the contrast sensitivity, orientation discrimination, wavelength discrimination, and vernier acuity tests can be explained by one factor, meaning that proficiency in these tests is indeed coordinated within subjects. A lesser proportion of the variance in the complex form identification and velocity discrimination tests was also explained by this factor. Despite this interrelationship, a proportion of the variance in test performances did not covary. For example, the direction-of-motion test showed little correlation with the other tests. Evidently the neural circuitry underlying performance on different tests can in some degree operate autonomously—a conclusion that accords with the modular organization of the primary visual cortex.

Figure 1. Visual performance on six of the tests in the battery from a representative subject. Sigmoidal functions were fit to all tests except the orientation and direction-of-motion tests. The parameters for the sigmoidal function were varied until they generated the lowest possible chi square value, thus giving a best-fit curve. The degrees of freedom for the individual tests are 11 for contrast, 16 for wavelength, 8 for velocity, and 11 for vernier acuity. Psychometric functions could be fit to the data in all 20 subjects examined.

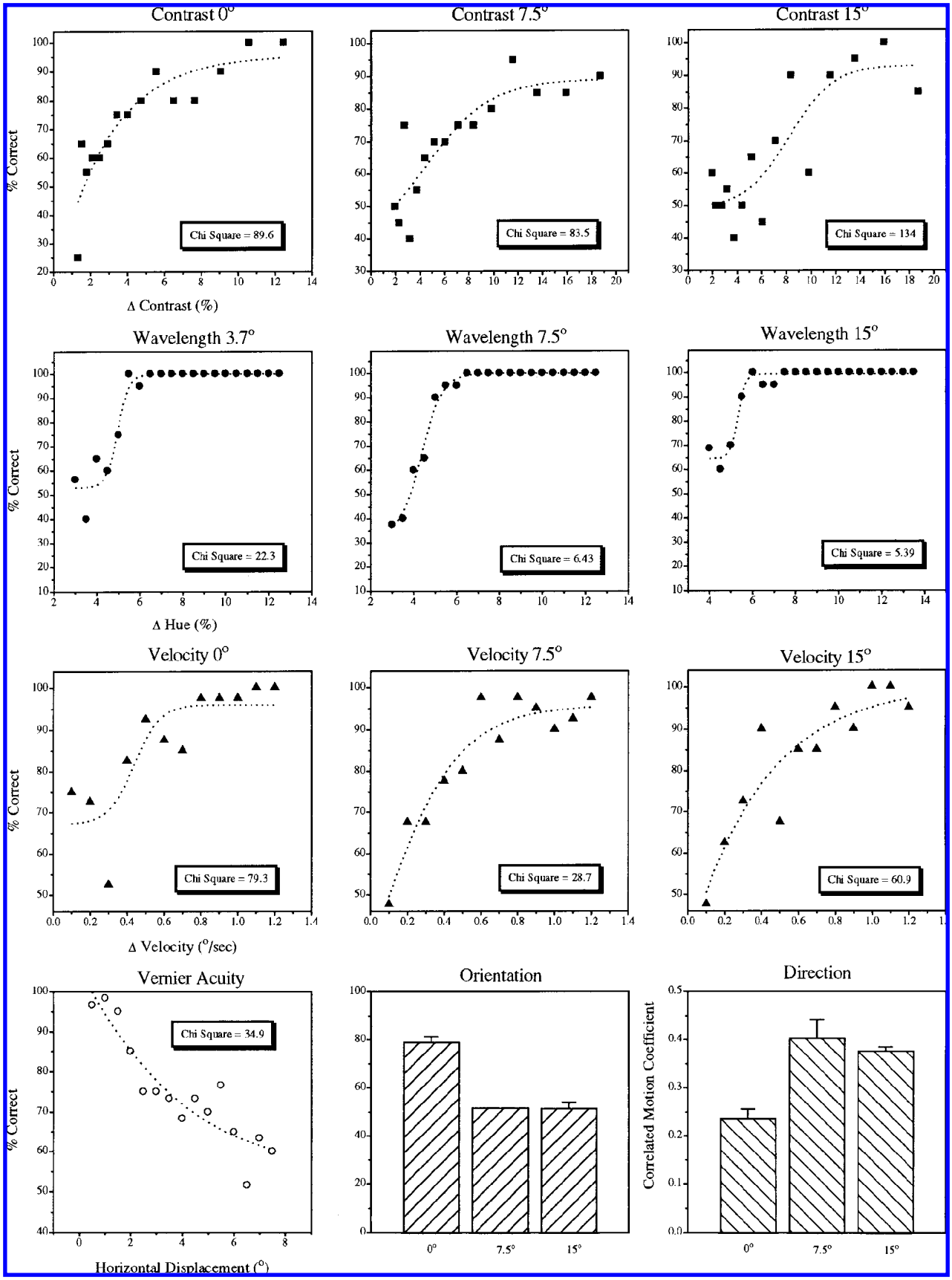
Contrast 0°
Contrast 7.5°
Contrast 15°
% Correct
Chi Square = 89.6
Chi Square = 83.5
Chi Square = 134
Δ Contrast (%)
Wavelength 3.7°
Wavelength 7.5°
Wavelength 15°
% Correct
Chi Square = 22.3
Chi Square = 6.43
Chi Square = 5.39
Δ Hue (%)
Velocity 0°
Velocity 7.5°
Velocity 15°
% Correct
Chi Square = 79.3
Chi Square = 28.7
Chi Square = 60.9
Δ Velocity (°/sec)
Vernier Acuity
Orientation
Direction
% Correct
Chi Square = 34.9
Correlated Motion Coefficient
0°
7.5°
15°
0°
7.5°
15°
Horizontal Displacement (°)

Table 1. Individual Normalized Scores[a] on the Different Visual Tests

Subject No.	*Orientation Discrimination*	*Wavelength Discrimination*	*Contrast Sensitivity*	*Vernier Acuity*	*Direction-of-Motion Detection*	*Velocity Discrimination*	*Complex Form Identification*
1	1.02	1.04	0.93	0.72	1.07	0.77	1.08
2	1.02	1.34	1.13	1.82	1.12	1.30	1.21
3	1.13	1.09	1.17	1.71	1.10	1.11	0.90
4	1.01	1.06	0.84	0.95	0.64	1.02	1.10
5	0.96	1.29	1.22	0.68	1.05	0.82	1.03
6	1.07	1.16	1.24	1.02	0.83	1.11	1.03
7	1.10	0.90	1.04	1.63	0.94	0.81	0.90
8	0.95	1.07	0.79	1.29	0.98	0.67	1.08
9	1.16	1.33	1.14	0.30	0.90	1.36	1.06
10	0.94	0.85	1.12	0.99	0.80	1.09	1.23
11	1.24	1.10	0.74	0.45	0.98	1.15	0.93
12	0.84	0.69	0.74	0.72	0.80	0.99	0.81
13	1.02	0.84	1.13	0.98	1.36	0.93	0.79
14	0.79	0.84	0.95	0.61	0.80	1.33	0.88
15	0.81	1.01	0.98	0.87	1.13	1.13	0.99
16	1.02	0.93	0.85	1.44	1.14	0.87	0.93
17	0.86	0.92	0.68	0.27	1.24	0.75	0.99
18	1.11	0.68	1.24	2.65	1.16	0.99	1.28
19	0.92	0.80	0.71	0.27	1.05	0.92	1.06
20	0.99	1.08	1.35	0.60	0.90	0.89	0.79

[a] Note that due to normalization of scores, mean score for each test is 1.0.

DISCUSSION

The main results of this study are that (1) ophthalmologically normal adults differ markedly in visual proficiency on tests that assess form, color, orientation, contrast, and motion perception and (2) when test performances are combined, significant interindividual differences in overall visual ability are apparent. The fact that an individual's performances on most of these tests covaried suggests a common denominator of visual performance. What might this factor be?

Although variation in test scores might reflect individual differences in nonvisual factors such as attention, one obvious possibility is the widely varying amount of visual circuitry devoted to visual processing in different individuals. Two- to threefold differences have been described in peak foveal cone density (Curcio, Sloan, Packer, Hendrickson, & Kalina, 1987), retinal ganglion cell number (Curcio & Allen, 1990), optic nerve area (Balazsi, Rootman, Drance, Schulzer, & Douglas, 1984; Johnson, Miao, & Sadun, 1987; Repka & Quigley, 1989), optic tract area (Andrews et al., 1997), LGN volume (Zworykin, 1980; 1981; Andrews et al., 1997), V1 surface area (Andrews et al., 1997; Brodmann, 1918; Filiminoff, 1932; Putnam, 1926; Smith, 1904, 1906; Stensaas, Eddington, & Dobelle, 1974) and V1 volume (Andrews et al., 1997; Klekamp, Riedel, Harper, & Kretschmann, 1991; Leuba & Kraftsik, 1994; Murphy, 1985). Because these structural differences tend to be correlated within a given hemisphere or brain (Andrews et al., 1997), some individuals possess substantially more neural circuitry related to processing visual information than others.

It is attractive to suppose, therefore, that interindividual variation in the amount of neural circuitry devoted to vision gives rise to differences in human visual ability. Indirect evidence indicates that this hypothesis is plausible. Comparisons across species have shown that proficiency in visual behavior is indeed reflected in the amount of underlying circuitry. For example, the proportion of visual cortex specialized for the perception of form and color is larger in diurnal monkeys than in nocturnal ones (Kaas, 1993). Variations in visual cortical space have also been related to differences in visual acuity among primates (Cowey & Ellis, 1967; Rolls &

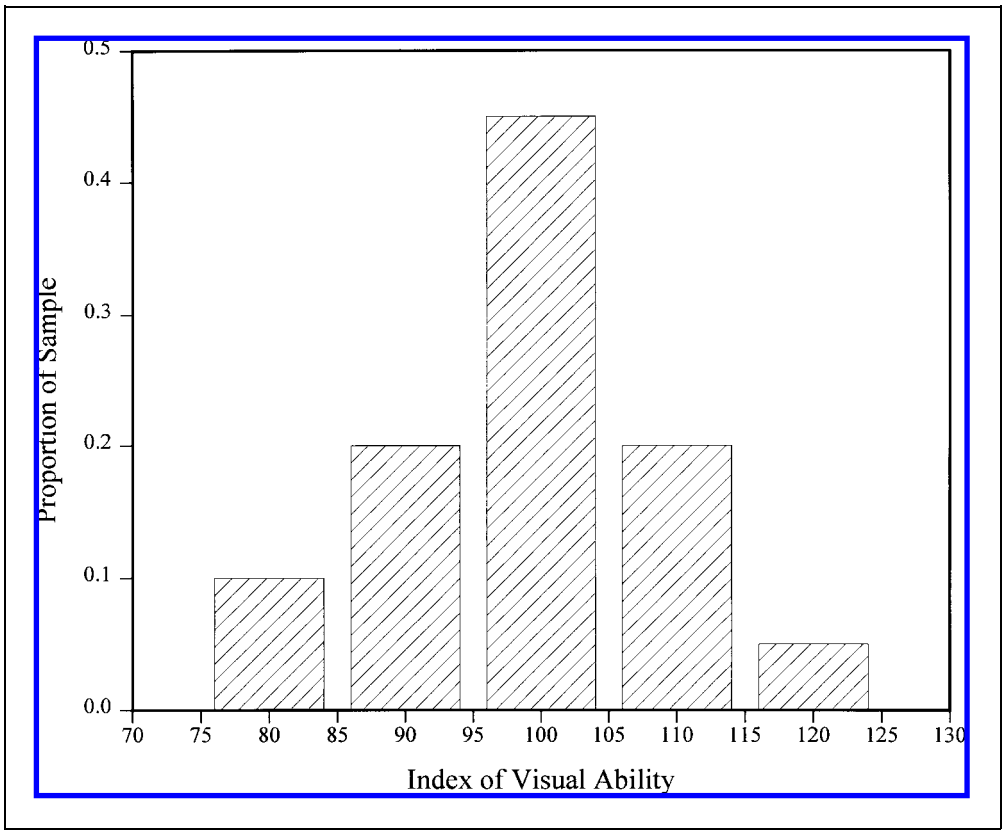

Figure 2. Histogram showing the range of scores in overall visual ability for the 20 subjects studied. The composite score was generated as the unweighted sum of the normalized scores from all tests expressed as a percentage (i.e., mean = 100). Because we had no a priori hypotheses about which tests would best reflect overall performance, an unweighted composite was deemed most appropriate. The scores are normally distributed. Interestingly, we found no correlation between overall visual ability and Snellen ratio ($r = 0.05$; $p = 0.83$).

Cowey, 1970). The relationship between the allocation of neural space and visual performance is further apparent in species in which a particular ability diminished or never fully developed in the course of phylogeny. For example, most subterranean mammals (e.g., moles and mole rats) and some bats have limited visual abilities, presumably because vision is of less use than other sensory modalities in a life spent underground or hunting in darkness. In such animals, the visual centers are markedly reduced in size compared to related species who make more use of information conveyed by light (Burda, Burns, & Muller, 1990; Cooper, Herbin, & Nevo, 1993).

Circumstantial evidence for a relationship between the amount of visual circuitry and visual ability in humans is provided by the amount of cortical space allocated to visual processing at different eccentricities. Thus the cortical space devoted to each degree of visual space in humans increases systematically from peripheral to central vision (Holmes, 1945; Drasdo, 1977; Horton & Hoyt, 1991; McFadzean, Brosnahan, Hadley, & Mutlukean, 1994; see also Daniel & Whitteridge, 1961). This variation correlates well with changes in performance for the variety of visual tasks we employed. Indeed, previous studies have also shown that thresholds for orientation discrimination (Paradiso & Carney, 1988; Rovamo et al., 1993), contrast sensitivity (Virsu & Rovamo, 1979), vernier acuity (Levi, Klein, & Aitesbaomo, 1985; Virsu, Nasanen, & Osmoviita, 1987), motion detection (Levi, Klein, & Aitesbaomo, 1984), and pattern sensitivity (Saarinen, Rovamo, & Virsu, 1989) all vary with eccentricity, performance being best in central vision where each degree of visual space is accorded much more processing circuitry.

Measuring the extent of the primary (or other areas) of the visual cortex, if done in conjunction with behavioral testing of the sort we describe, would allow a direct assessment of the quantitative relationship between neural circuitry and visual performance. The solution to this central issue in cognitive neuroscience may soon be possible as continued improvements in noninvasive brain imaging make accurate measurements of the human visual cortex increasingly practical. The battery of tests we describe here thus provides a first step toward the establishment of a comprehensive "visual IQ test" that would allow the relationship between brain space and behavior to be assessed in a definitive manner.

METHODS

Subjects

We solicited volunteers between 20 and 30 years of age (students, faculty, and staff from Duke University) who did not require corrective lenses and had no history of ophthalmological disease. After obtaining informed consent, subjects were screened using a Snellen letter chart and Ishihara's Tests for Color Deficiency

Table 2. P Values from the Post Hoc Analysis of the ANOVA Used to Determine Differences in Overall Visual Ability between Subjects

	#1	*#2*	*#3*	*#4*	*#5*	*#6*	*#7*	*#8*	*#9*	*#10*	*#11*	*#12*	*#13*	*#14*	*#15*	*#16*	*#17*	*#18*	*#19*	*#20*
#1																				
#2	**<0.0001***																			
#3	**<0.005**	0.14																		
#4	0.52	**<0.0001**	**<0.0005**																	
#5	0.15	**<0.005**	0.08	**<0.05**																
#6	**<0.05**	**<0.01**	0.24	**<0.01**	0.55															
#7	0.53	**<0.0001**	**<0.05**	0.21	0.41	0.16														
#8	0.57	**<0.0001**	**<0.0005**	0.94	**<0.05**	**<0.01**	0.23													
#9	**<0.01**	0.06	0.69	**<0.001**	0.17	0.44	**<0.05**	**<0.001**												
#10	0.74	**<0.0001**	**<0.005**	0.33	0.26	0.09	0.77	0.37	**<0.05**											
#11	0.51	**<0.0001**	**<0.05**	0.19	0.43	0.17	0.97	0.22	**<0.05**	0.75										
#12	**<0.01**	**<0.0001**	**0.0001**	**<0.05**	**<0.0001**	**<0.0001**	**<0.001**	**<0.05**	**<0.0001**	**<0.005**	**<0.001**									
#13	0.18	**<0.001**	0.62	**<0.05**	0.91	0.48	0.48	0.06	0.14	0.31	0.50	**<0.0001**								
#14	0.47	**<0.0001**	**<0.0001**	0.93	**<0.05**	**<0.01**	0.18	0.87	**<0.0005**	0.29	0.16	**<0.05**	**<0.05**							
#15	0.45	**<0.0001**	**<0.05**	0.16	0.49	0.19	0.90	0.19	**<0.05**	0.67	0.93	**<0.001**	0.56	0.14						
#16	0.60	**<0.0001**	**<0.01**	0.24	0.35	0.13	0.91	0.28	**<0.05**	0.85	0.88	**<0.005**	0.41	0.21	0.81					
#17	0.08	**<0.0001**	**<0.0001**	0.27	**<0.005**	**<0.0005**	**<0.05**	0.24	**<0.0001**	**<0.05**	**<0.05**	0.33	**<0.005**	0.31	**<0.05**	**<0.05**				
#18	**<0.05**	0.16	0.93	**<0.0001**	0.06	0.21	**<0.01**	**<0.0005**	0.62	**<0.005**	**<0.01**	**<0.0001**	**<0.05**	**<0.0001**	**<0.05**	<0.01	**<0.0001**			
#19	0.06	**<0.0001**	**<0.0001**	0.22	**<0.005**	**<0.0001**	**<0.05**	0.20	**<0.0001**	**<0.05**	**<0.05**	0.39	**<0.005**	0.26	**<0.01**	**<0.05**	0.91	**<0.0001**		
#20	0.47	**<0.0001**	**<0.05**	0.17	0.47	0.18	0.92	0.20	**<0.05**	0.69	0.96	**<0.001**	0.54	0.15	0.97	0.87	**<0.05**	**<0.05**	**<0.05**	

* Numbers in bold represent significant differences.

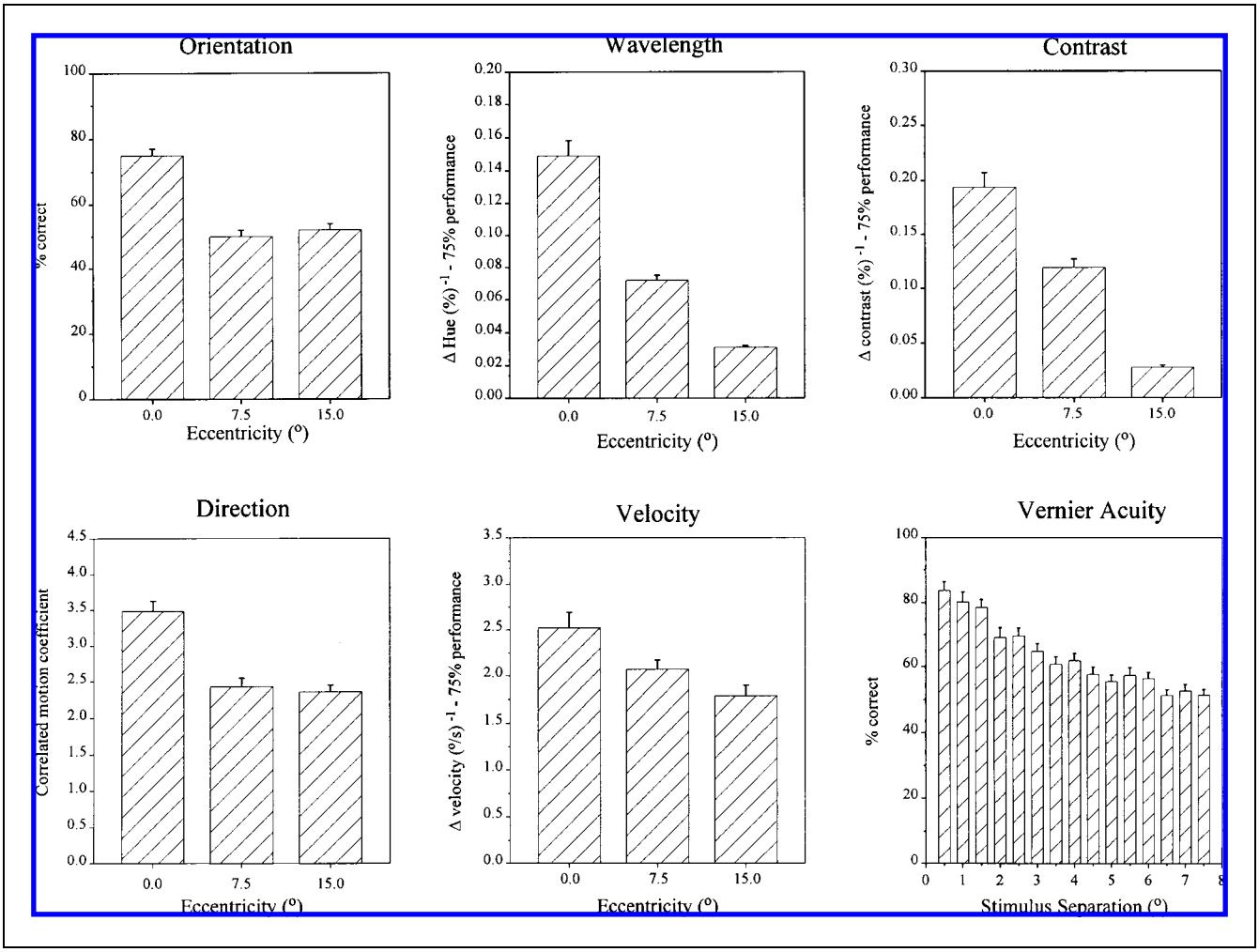

Figure 3. Differences in performance as a function of eccentricity for orientation discrimination, wavelength sensitivity, contrast sensitivity, direction-of-motion detection, velocity discrimination, and vernier acuity. Columns represent the mean scores ±*SD* for the 20 subjects. Note that the rate of decline in visual performance with eccentricity varies from task to task.

(Kanehara and Co., Ltd., Tokyo). The first 20 subjects with a Snellen ratio of 1 (i.e., 20/20) or greater at viewing distances of both 20 and 10 ft and normal color vision were enrolled in the study. The age, gender, education, and Snellen ratios of our sample are shown in Table 4. Subjects were financially compensated for their time.

Stimulus Presentation

Subjects viewed a 20-in., high-resolution, color monitor using an adjustable chin rest and forehead bar to stabilize the head at a viewing distance of 30 cm. All stimuli were generated on a PowerComputing 9500/120 computer using Morphonome 2.7 (C. W. Tyler et al., Smith-

Table 3. Principal components analysis of the variation in performance on the different tests used. The values represent the correlation of each variable with a derived visual performance factor. With the exception of direction, a single factor predicts a proportion of the performance variation in all the tests. The proportion of the overall variance accounted for by the visual performance factor is 0.3. It is important to note that Snellen acuity did not covary with the visual system factor, implying that this factor is not influenced by optical resolution.

	Contrast Sensitivity	*Orientation Discrimination*	*Wavelength Discrimination*	*Vernier Acuity*	*Complex Form Identification*	*Velocity Discrimination*	*Direction-of-Motion Detection*	*Snellen Ratio*
Visual performance factor	0.70	0.68	0.57	0.53	0.51	0.47	–0.01	–0.04

Table 4. Age, Education, Gender and Snellen Acuity Ratio of Subjects, All of Whom Had Normal Color Vision

Subject No.	*Age (years)*	*Education Level*[a]	*Gender*	*Snellen Acuity Ratio (at 20 ft)*[b]	
				Right Eye	*Left Eye*
1	20	1	M	1.54	1.00
2	29	3	F	1.54	1.54
3	28	3	M	1.00	1.00
4	25	3	F	1.33	1.33
5	25	3	F	1.33	1.00
6	23	2	F	1.33	1.54
7	27	3	M	1.54	1.54
8	24	3	F	1.54	1.33
9	28	3	M	1.54	1.54
10	20	1	M	1.00	1.00
11	21	3	M	1.00	1.00
12	25	2	F	1.33	1.54
13	26	3	M	2.00	2.00
14	26	2	F	1.54	1.54
15	30	3	F	1.00	1.00
16	21	1	M	1.54	1.54
17	23	3	M	1.54	1.54
18	29	3	M	1.33	1.33
19	21	1	M	1.00	1.00
20	23	3	M	1.54	1.54

[a] Education level: 1 = current undergraduate; 2 = bachelor's degree obtained (current employee); 3 = bachelor's degree obtained (current graduate student).
[b] All subjects also had a Snellen Ratio ≥1.0 at 10 ft.

Kettlewell Eye Research Institute), MacLaboratory for Psychology Research 3.0 (D. L. Chute, Drexel University), and Shell 2.2/Macglib 2.0 (R. Comtois, Harvard University) software. The testing was carried out in a room in which the computer monitor was the only source of illumination. Luminance determinations were made with an appropriately filtered photodiode (PIN 10AP, UDT Sensors, Inc., 12525 Chadron Avenue, Hawthorne, CA 90250). Viewing was binocular, and all tests (except vernier acuity and complex form) were performed in both central (0°; 3.7° for wavelength discrimination only) and peripheral (7.5 and 15°) vision. Because the central 15° of the monocular visual field is represented by approximately two-thirds of the neurons in both the retina (Perry, Oehler, & Cowey, 1984), LGN (Schein & de Monasterio, 1987), and in V1 (Daniel & Whitteridge, 1961; Drasdo, 1977; Horton & Hoyt, 1991; McFadzean et al., 1994), this provides a reasonable assessment of overall visual system function. A video camera attached to a display monitor allowed the supervisor to track the subject's eye position to ensure that proper fixation was maintained throughout testing. Responses were indicated by pressing a keypad during five 2 to 3 hr sessions that were completed on nonconsecutive days over a 3-week period. To avoid fatigue, each test session was divided into three parts separated by 10 min intervals; moreover, a 3-min rest was required between each trial within a session. A practice trial of each test was carried out before data collection began to acclimate the subjects to the demands of each task. All tests employed criterion-free psychophysical methods in a forced choice format. Test-retest reliabilities for the visual abilities assessed in this battery have been documented in previous studies (Benton et al., 1978; Benton, Sivan, Hamsher, Varney, & Spreen, 1994; Simpson & Regan, 1995; Yu, Falcao-Reis, Spileers, & Arden, 1991).

Tests

Orientation Discrimination

In this task, the subject had to discriminate the orientation of two briefly presented (100 msec) lines at 0, 7.5,

or 15° eccentricity. The test lines, oriented between 0 and 180°, were followed by a response screen showing all 14 possible lines; the screen remained visible until the subject had indicated which pair of these reference lines corresponded to the test lines (Figure 4). When testing in the periphery, stimuli were presented in all four quadrants of the visual field, with the response screen always centered about the fixation point. All possible line pairs were presented in random sequence during each test block. Results from two test blocks at each eccentricity were summed, and the orientation discrimination score calculated as the mean number of correct responses. Although a component of this task involves recognition and memory, it has been widely used as an indicator of orientation discrimination in normal subjects, with deficits in performance being related to specific lesions of the visual cortex (Benton et al., 1975, 1978).

Wavelength Sensitivity

In this component of the test battery, subjects were asked to discriminate changes in the wavelength of emitted light (Yu et al., 1991). To test wavelength sensitivity at different eccentricities, a blue annulus with an outer radius of either 3.7, 7.5, or 15° was presented on an isoluminant background square that varied in its ratio of blue (CIE $x = 0.15, y = 0.06$) and green (CIE $x = 0.21, y = 0.71$) (Figure 5). Isoluminance was determined using a photometer but was not corrected for individual subjects. (Although blue/green combinations were used in this study, it has been shown that performance with this combination is predictive of other color combinations; see Yu et al., 1991). Subjects were instructed to fixate on a black spot in the center of the screen while a portion of one quadrant of the annulus was made to disappear by briefly making it identical in hue to the background. The subject was asked to indicate the quadrant in which the change occurred. Trial blocks were repeated five times at each eccentricity. Wavelength discrimination was determined by fitting a sigmoidal function to the data and assessing performance at the 75% correct level. Although other color tests that involve categorizing colors according to hue could have been employed (e.g., the Farnworth-Munsell 100 Hue Test), we chose to use this color discrimination task because it is a reliable, criterion-free, forced-choice test that was easily incorporated into our computerized battery.

Contrast Sensitivity

In this test, the ability of subjects to detect changes in luminance contrast of a grating stimulus was measured. The stimulus was a vertical sinusoidal grating of 2 cycles/degree with a mean contrast of 30% (the luminance difference between peak and trough). These baseline contrast and spatial frequency values were chosen to fall within the range of peak performance for human contrast sensitivity (Yates et al., 1987). The average luminance of the stimulus was maintained at 30 cd/m^2, and the luminance of the rest of the screen was 15 cd/m^2. In central vision, the stimulus was presented as a circular patch (radius = 2°), whereas in peripheral vision, the stimulus was an annulus with an identical grating and luminance profile (inner radius = 7.5°, annular width = 2°; or, inner radius = 15°, annular width = 4°). The range of contrast modulations of the stimulus varied between 1.2 and 18.7%. Each presentation had a duration of 2.7 sec, during which time a tone sounded at 0, 1, 1.7 and 2.7 sec. Subjects were asked to indicate whether an increase in contrast occurred in the first (0 to 1 sec) or

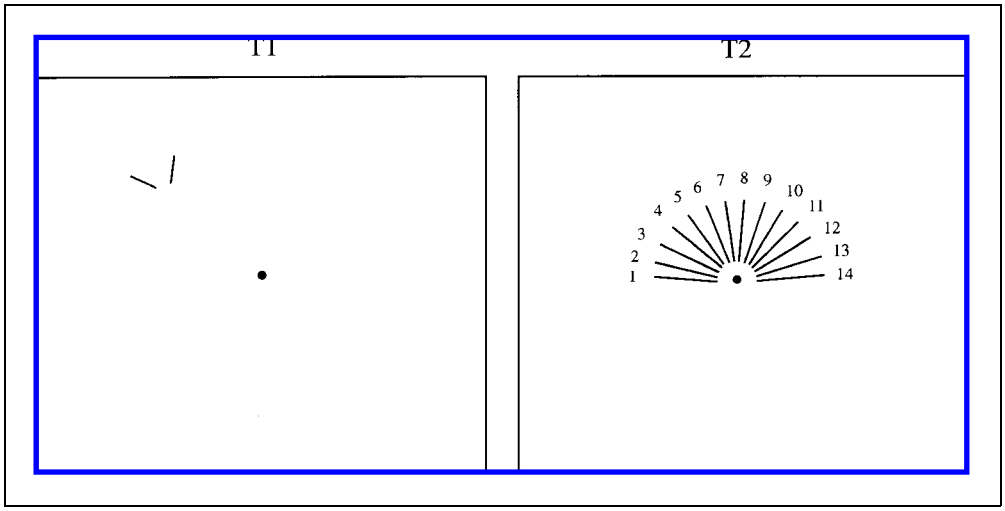

Figure 4. Orientation discrimination test at 15° eccentricity. Two test lines (1.25° in length) were initially presented for 100 msec (T1). The lines were oriented between 0 and 180° at 13° intervals. This presentation was followed by a response screen (T2) showing 14 reference lines, which remained visible until the subject indicated which of the reference lines corresponded to the test lines. The lines on the 14-choice response screen were twice as long (2.5°) as the test lines. The correct responses in the example shown here are 3 and 8. When testing more peripherally in the visual field, subjects fixated on a spot in the center of the screen while stimuli were flashed in one quadrant of the visual field (determined at random). The response screen always appeared centered about the fixation point. Data were collected in blocks of 91 presentations (182 responses) at each eccentricity, allowing all possible test pairs to be presented once in a random sequence. The luminance of the test lines was 1.5 cd/m^2, and the luminance of the background was 70 cd/m^2.

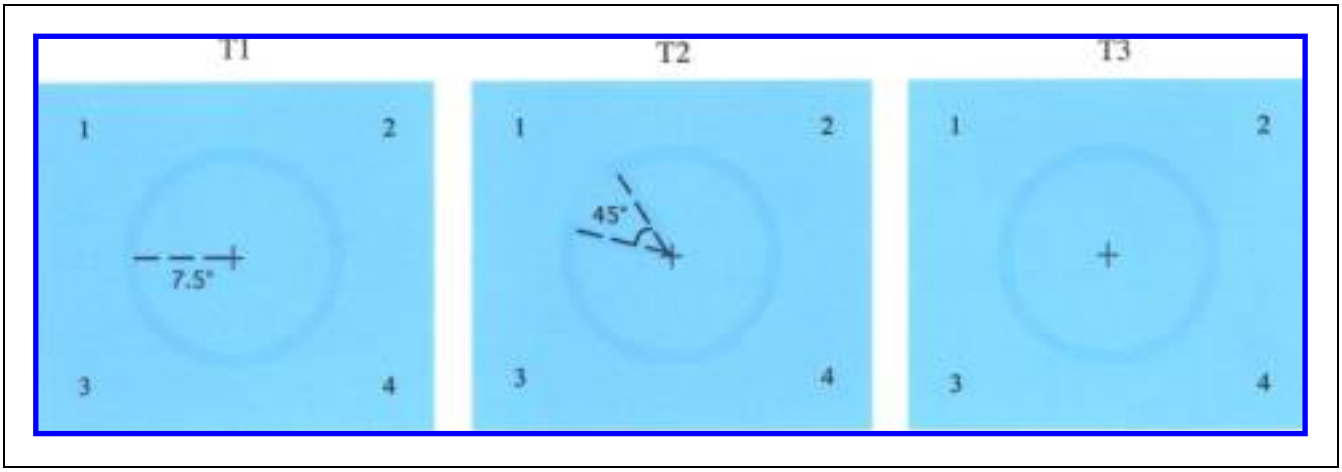

Figure 5. Wavelength sensitivity test at 7.5° eccentricity. Subjects fixed a central black cross in the center of a 1°-thick blue annulus (with an outer radius of 3.7, 7.5, or 15°) on an isoluminant background square (T1). After 1 sec, a 45° portion of the annulus in one quadrant (1 to 4) was made identical in hue to the background for 100 msec (T2) and then restored (T3). The subject then indicated the affected quadrant; in this example the correct response is quadrant 1. The annulus was always 100% blue, whereas the background square was composed of a combination of blue/green that varied between 97.5/2.5% to 86.5/13.5%. The combination of the two hues ensured that the annulus and background were always equiluminant. The luminance of the stimulus was 55 cd/m^2. Each quadrant was tested with 11 hue combinations in a random sequence repeated twice, resulting in a total of 88 presentations per test session.

the second (1.7 to 2.7 sec) interval. A change in contrast occurred in only one interval; between intervals (i.e., from 1 to 1.7 sec) the stimulus was maintained at baseline contrast (30%). Data were collected in trial blocks of 30 presentations each, with 10 blocks of data being collected at each eccentricity. A sigmoidal function was fit to the data; the change in contrast at which performance was 75% correct was used as the measure of contrast sensitivity.

Vernier Acuity

A standard abutting lines test was used to investigate interindividual differences in vernier acuity (Levi, Klein & Aitesbaomo, 1985; Westheimer & McKee, 1977). Subjects indicated the position of a test line relative to a reference line (above, below, or aligned) by pressing one of three buttons on a keypad (Figure 6). A trial block consisted of six presentations at 15 different horizontal separations of the test and reference line, and each block was repeated 10 times. Performance at 75% correct was determined from a sigmoidal function fit to the data.

Direction-of-Motion Detection

To assess proficiency in motion detection, subjects were asked to discern the direction of movement as an increasing percentage of the randomly moving dots migrated in one of four directions (Figure 7). A correct response generated a tone, followed by a 700-msec interstimulus interval before the next stimulus presentation. An incorrect response was signaled by a different sound, and the presentation was aborted. To penalize premature guessing, which would obscure the subject's true directional sensitivity, only three incorrect responses were allowed per trial block. Each trial block consisted of 20 correct responses. Scores from three blocks were averaged for each eccentricity, and the correlated motion coefficient was defined as the mean proportion of dots moving coherently required for detecting the correct direction (i.e., from 0 for random motion to 1 for all dots moving in the same direction). When direction-of-motion sensitivity was tested in the periphery (7.5 or 15° eccentricity), a central fixation spot was added to the display. The entire stimulus was then presented to one of the four quadrants of the visual field. This test has been previously used with humans and monkeys as a reliable indicator of direction-of-motion discrimination (Newsome & Pare, 1988; Williams & Sekuler, 1984).

Velocity Discrimination

Velocity discrimination in human subjects is a U-shaped function, with best performance (i.e., smallest detectable differences) in the range of 4 to 32°/sec (Orban, de Wolf, & Maes, 1984). Moreover, judgments of line velocity appear to be genuine, rather than indirect inferences based on the duration or distance traversed by the stimulus (McKee, 1981; Orban et al., 1984). The task we used tested subjects' abilities to discriminate differences in the velocity of a moving (vertical) line (McKee, 1981). For testing in central vision, a fixation dot was presented in the center of the screen for 500 msec. A reference line (2.5 × 0.06°) then appeared to the left of the fixation point and moved to the right for 1 sec at a constant

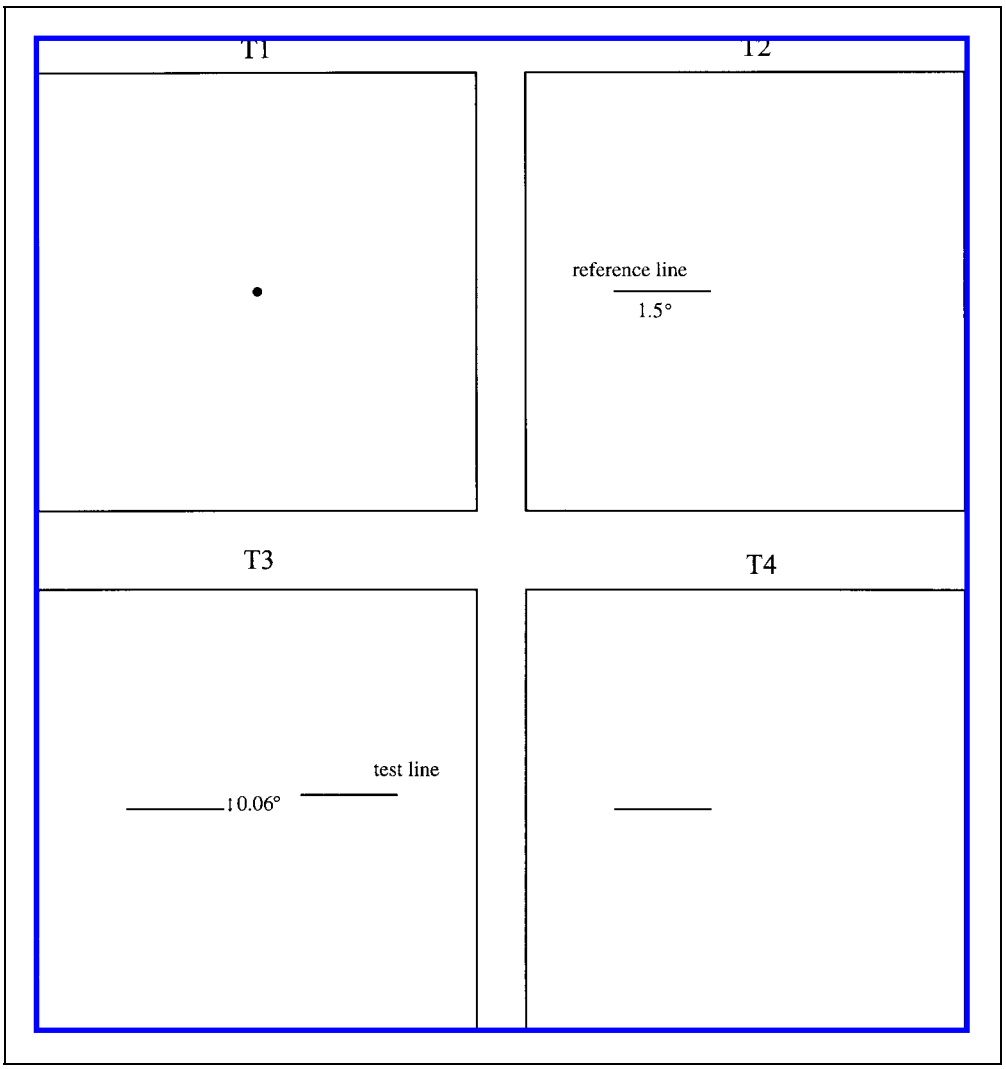

Figure 6. Vernier acuity test. Four consecutive frames (T1 to T4) were viewed by the subject prior to each response. The stimulus presentation began with subjects fixed on a black dot (0.1° in diameter), which was presented for 1 sec (T1) and then disappeared. This frame was replaced by a horizontal reference line (1.5° long, 0.06° wide) that appeared for 500 msec to the left of where the fixation dot had been located (T2). An identical test line was then flashed to the right of the reference line (T3) for 150 msec (roughly equal to saccadic latency—see Westheimer, 1954—thus preventing eye movements between lines), which then disappeared (T4). The distance between the test line and the reference line varied between 0.5 and 7.5°. The test line was randomly displaced in the vertical direction so that in a given trial it appeared either aligned 0.06° above or 0.06° below the reference line. The location of the initial fixation point varied randomly between trials so that subjects could not predict upcoming stimulus locations or complete the task by comparing the position of the test line with their memory of the location of the previous test line. The correct answer in the example shown here was Up. The luminance of the lines was 1.5 cd/m^2, and the luminance of the background was 70 cd/m^2.

velocity of 6.0°/sec. This reference target was followed by an identical test line moving in the same direction, but at a different velocity. The velocity of the test line varied from 4.8 to 7.2°/sec in 0.1°/sec increments. After each presentation, the subject indicated whether the test line had moved faster or slower than the preceding reference line. When testing velocity discrimination in the periphery (7.5 and 15°), subjects maintained fixation on a permanently placed dot while the reference and test lines were presented to one of the quadrants of the visual field. The luminance of the test line was 1.5 cd/m^2 and the luminance of the background was 70 cd/m^2. Data were collected in five blocks of 96 presentations at each eccentricity. The threshold for velocity discrimination was determined by plotting a sigmoidal function to the data. The minimum difference in velocity that the subject could identify at a level of 75% correct was taken as the velocity discrimination score.

Complex Form Identification

This component of the test battery assessed subjects' abilities to recognize a complex form (see Benton et al., 1994). The presentation entailed the initial display of a form for 1 sec followed by a response screen containing four similar forms, only one of which was identical to the test form (Figure 8). A total of 30 forms were presented per trial block; each block was presented three times. The subject's form-identification score was taken as the mean number of correct responses in the three trials.

Statistical Analysis

To evaluate individual variation in proficiency for these tests, normalized scores at the different eccentricities on each component of the test battery were combined to

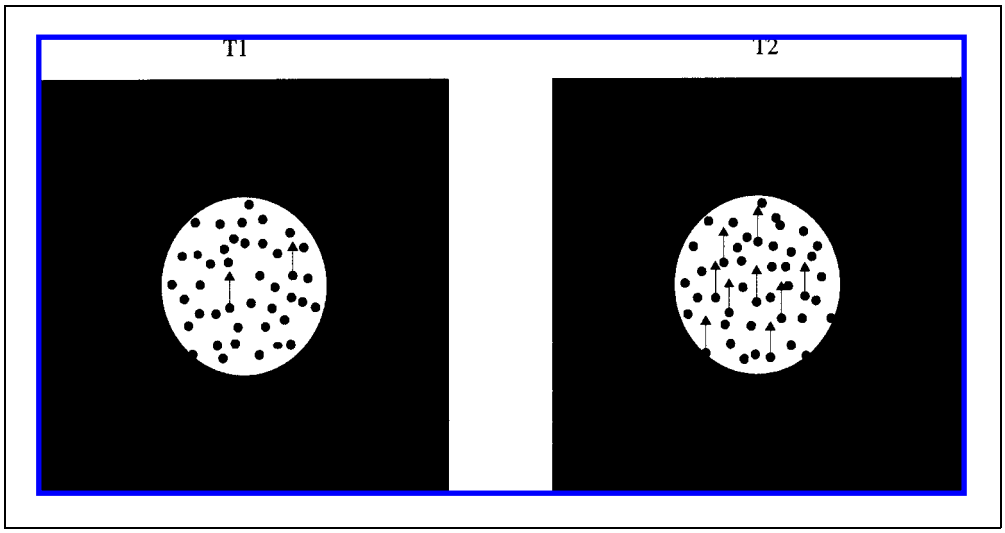

Figure 7. Direction-of-motion test in central vision. The stimulus consisted of high-contrast dots moving within a 5° circle on an otherwise dark computer screen. The direction of all dots without arrows was random. The dot density was 6 dots/degree^2 and their luminance was 1.5 cd/m^2; the luminance of the circle was 70 cd/m^2. Each dot subtended 0.2° and moved at a constant velocity of 2.5°/sec. The stimulus presentation began with all the dots moving randomly. An increasing percentage of the dots then began to move coherently in one of four discrete directions: right (0°), up (90°), left (180°), or down (270°), as shown in T1 and T2 here. The percentage of dots moving coherently increased at a constant rate of 1.5%/sec. Subjects were asked to indicate when a distinct direction of motion was perceived (i.e., Up in the example illustrated here). When testing in the periphery, subjects fixated a central dot while the random dot stimulus was presented in one of the quadrants of the visual field.

give an average score. Because a lower score on the wavelength, contrast, velocity, and direction tests reflects better performance, the inverse of the final threshold score was used as a measure of sensitivity. Normalized scores were derived by dividing each subject's score on a given test by the mean of all subject scores on that test. The scores for the various tests were then added together for each individual and expressed as a percentage (mean = 100) to provide an index of their overall visual ability. The normalization of scores does not affect the relative differences between individual performances; rather, it makes all the tests numerically equivalent, allowing them to be combined into a single, unweighted index. A two-way ANOVA (with test and individual as factors) was then used to determine whether interindividual differences in overall performance were evident. Principal components analysis was also used to assess how performances on the different tests covaried. This latter analysis specifically evaluated whether variance in test performances was coordinated for an individual.

To assess differences in visual performance as a function of eccentricity, scores had to be adjusted for stimulus size. This adjustment was achieved by dividing the test score by the size of the stimulus and was necessary because the size of the stimulus on some tests (wavelength discrimination and contrast sensitivity) varied as a function of eccentricity. A one-way ANOVA was then used to determine the effect of eccentricity on visual performance in each test. To further assess performance

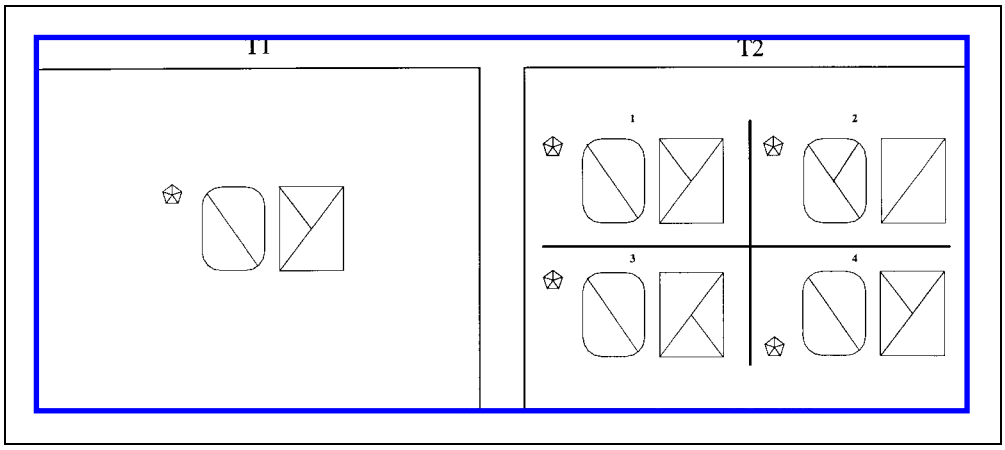

Figure 8. Complex form test. In each stimulus presentation, a target form of three shapes was presented for 1 sec (T1), followed by a response screen on which four reference forms were shown (T2). Only one of the four choices was identical to the target form, the three incorrect choices having been altered by rotation, displacement, or distortion. The correct answer in this case is 1. The subject had an indefinite amount of time in which to select the right answer; the next trial began 1 sec after each response. The luminance of the forms was 1.5 cd/m^2, and the luminance of the background was 70 cd/m^2.

in different parts of the visual field, the covariance of individual scores at different eccentricities was measured. This further measurement allowed us to determine whether individuals' proficiency in vision at one eccentricity reflected their proficiency at other eccentricities.

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