BINOCULAR SUMMATION IN HUMANS: EVIDENCE FOR A HIERARCHIC MODEL

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SUMMARY

1. Binocular summation was studied in human subjects using a battery of vision tests. Two tests assessed detection, another three acuity, one hyperacuity and one pattern recognition.

2. The magnitude of summation was consistent with, or exceeded, the level predicted from quadratic summation for both detection tests.

3. The summation factor was significantly smaller in the resolution tests than in the detection tests. Hyperacuity showed a large individual variation.

4. Spatial filtering of acuity targets did not influence summation.

5. No summation was found in the pattern recognition test.

6. It is argued that the degree of summation is related to the complexity of the visual task. A simple task yields a larger binocular summation than a more complex one. This may be related to the level of processing in the primary visual cortex.

INTRODUCTION

Binocular summation designates a superiority of binocular over monocular visual performance. Previous studies have generated rather conflicting results. It seems clear that there are substantial individual differences in the magnitude of the summation factor as well as discrepancies between different tests. It has not yet been possible to propose a model of summation capable of reconciling the different findings in previous studies (see Blake & Fox, 1973, for a review).

The best prediction of binocular sensitivity is $\sqrt{S_{R^2}+S_{L^2}}$, where S_R and S_L are the sensitivities for the right and the left eye, respectively. This model has been termed the quadratic summation model (Legge, 1984*b*), and has its origin in the theoretical work of Green & Swets (1966). For two identical eyes the expected summation factor equals $\sqrt{2}$. This indeed approximates the observed summation effect in many studies of different aspects of vision.

Probability factors have been claimed responsible for binocular summation. The theory of probability summation (Pirenne, 1943) states that if the two eyes are considered as independent detectors, the probability of seeing with both eyes equals $(p_{\rm R} + p_{\rm L}) - (p_{\rm R} \times p_{\rm L})$, where $p_{\rm R}$ and $p_{\rm L}$ are the probability of seeing with the right and the left eye, respectively. It is now known that a substantial proportion of visual cortical neurones are binocularly driven in higher primates (Hubel & Wiesel, 1968,

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1972). Thus there exists true interaction between visual neurones from the two eyes which makes it impossible to accept the probability model as the sole explanation for summation.

In an attempt to reconcile the different results reported by previous investigators, we studied summation with a battery of tests of central vision in one and the same group of test subjects. The battery included tests of differential light sensitivity (DLS), minimum visible (MV), optotype acuity (both in and out of focus), acuity for high-pass spatial frequency-filtered targets ('vanishing optotypes', VO), hyperacuity (HA) and pattern recognition (PR). We did not include sine-wave gratings, which already have been studied extensively. The summation factor for these stimuli typically approximates $\sqrt{2}$ (see e.g. Campbell & Green, 1965).

METHODS

Differential light sensitivity

Differential light sensitivity was measured in a Haag-Streit Goldmann clinical perimeter with 1 decibel (dB, 0.1 \log_{10} unit) steps between target luminance levels. After a verbal cue, the target (0.43 deg visual angle) was exposed for 0.2 s in the centre of the built-in four-dot fixation mark. Background illumination was 10 cd/m².

Minimum visible

'Minimum visible' was measured as the smallest vertical black bar (height 16 times width) that could be detected against a white background. Size was varied in steps of approximately 1 dB. Subjects responded to seen targets only. In this and the following tests targets were generated on a cathode ray tube (CRT) by a personal computer. Unless otherwise stated, target exposure was 1 s, contrast $((L_{\max}-L_{\min})/(L_{\max}+L_{\min}))$, where L is luminance) was 0.90, background luminance was 350 cd/m², room illumination was 14 lx, and test distance was 13 m. All light measurements were made with a Hagner S2 Universal Photometer.

Visual acuity

Minimal angle of resolution was determined with two different acuity tests.

Broken ring ('Landoll's C'). Gap size equalled 'stroke' width and outer ring diameter was 5 times larger (Fig. 1). Gap sizes were scaled to approximately 1 dB and the gap was positioned at random. The task was to locate the gap, answering 'up', 'down', 'right', 'left' or 'not seen'.

Broken line. The nasal and temporal visual hemifields have slightly different sensitivities. This may interfere with interpretation of results obtained with laterally extensive targets, e.g. broken rings. Therefore, the broken ring optotype was straightened and presented as a vertical line. Gap size and stroke width equalled those of the corresponding ring target. The gap could be placed at 1/4, 2/4 or 3/4 of the line length (Fig. 1). The test task was to localize the gap, the alternatives being 'up', 'centre', 'down' or 'not seen'.

To simulate low-pass spatial frequency filtering, resolution was measured also after defocusing both eyes with 0.25, 0.5 and 0.75 dioptres (D) plus sphere, respectively.

High-pass spatial frequency-filtered ring targets

High-pass spatial frequency-filtered ring targets were used as a complement to defocused (low-pass-filtered) line targets (Fig. 1). The rings had a light core and dark borders balanced so that the space-average luminance equalled that of the background. They have closely similar detection and resolution thresholds, meriting the name 'vanishing optotypes' (Frisén, 1986).

In this test, exposure time was 0.2 s and test distance was 6 m. Within-target contrast was 0.25, and background luminance was 20 cd/m^2 . Target size was changed in steps of 0.5 dB (Frisén, 1987).

Hyperacuity

Hyperacuity was measured as the smallest detectable horizontal displacement between two vertical bars (Fig. 1) (height 11 min of arc, width 1.6, vertical separation 2.6). The upper bar could be displaced 1, 2 or 3 units to the right or left (1 unit = 4.8 seconds of arc or a multiple thereof). Hyperacuity threshold was defined as the arithmetic mean of the 25 and 75% thresholds, i.e. the average of the thresholds for right and left displacement (Westheimer & McKee, 1977).



Fig. 1. Test displays used to study binocular summation. A, vanishing target. B, broken ring. C, hyperacuity test (note horizontal displacement of upper rod). D, broken line. A, B, and D are shown with approximately correct relative sizes while C is smaller. Note how the vanishing target abruptly disappears from view with an increase in viewing distance.

Pattern recognition

Pattern recognition was used as an example of a complex visual task. Sets of three digits (drawn at random) were shown on the CRT, superposed on a randomly scrambled black and white checkerboard background (Fig. 2). Check size was $6\cdot 2 \times 6\cdot 2$ min of arc at 1 m test distance. Each digit (height 4.3 deg, width 2.6 deg) was built up by 100 white checks. The experimental variable was the number of checks actually shown for each digit. This was set to 45, 50, 55, 60 or 65 units, distributed at random along the digit's outline, with clustering constraints (L. Frisén, in preparation). Ten presentations were made at each level, in a predetermined order, and each time with a new background. All three digits had to be correctly read to count as a correct response. The threshold was defined as the number of checks required for 50% correct responses.

Test procedures

In all tests the sequence was right eye-both eyes-left eye, or vice versa, to avoid learning and fatigue bias. In monocular testing, a central occluder was put before the non-tested eye, allowing background illumination to reach the eye peripherally. Natural pupils were used. The subjects were refracted to the nearest 0.12 D for each test distance.

All tests started with a bracketing procedure under the examiner's control. Frequency-of-seeing curves were then generated by the computer, except in the DLS test where stimuli were presented manually. Presentation order was unpredictable. Feed-back was given.



Fig. 2. Pattern recognition test. Three digits are shown against a random checkerboard background. The number of checks comprising each digit was variable. A, 65% of checks shown. Digits 246 can be read with difficulty. B, 90% of checks shown, allowing easy reading of digits.

Unless otherwise stated, thresholds were obtained as follows. Five neighbouring stimulus levels straddling the preliminary threshold were used. Each stimulus was presented ten times, for a total of fifty presentations. Thresholds were defined as 50% correct responses and were determined from the frequency-of-seeing curves by probit analysis, without correction for guessing (Finney, 1971; Lieberman, 1983). To facilitate comparison with previous studies, threshold values were inverted to provide measures of 'sensitivity'. Relational values were then transformed to decibel units.

Statistical significance was defined as P < 0.05 in the two-tailed Student's t test.



Fig. 3. Mean binocular summation for eight test subjects compared to square root of summed squares of monocular sensitivity (A) and highest monocular sensitivity (B). Interrupted line represents expected level in quadratic summation model for two identical eyes. Vertical bars show 95% confidence intervals. DLS = differential light sensitivity, MV = minimum visible, HA = hyperacuity test, VO = vanishing optotype, Line = broken line acuity test, PR = pattern recognition test.

Subjects.

The eight healthy subjects, aged 25-36, had no ophthalmological or neurological abnormalities. None had anisometropia exceeding 1 D or astigmatism exceeding 0.5 D.

RESULTS

While the quadratic summation model has theoretical merit as the best baseline for binocular comparisons, it is intuitively easier to compare binocular to best monocular performance. In the following, both alternatives will be used.

Mean summation factors for the different tests are presented in Fig. 3, both in relation to the expected quadratic summation value (Fig. 3A), and in relation to the best monocular value (Fig. 3B). Because no significant difference was found for the summation factors in the broken ring and broken line tests only the latter is shown. The different test results are shown in Table 1.

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Table 2 shows a statistical significance analysis comparing the different tests. In summary, both detection tests showed significantly higher summation values than the resolution tests and the PR test. The detection tests did not differ significantly from each other. Both resolution tests showed a small but statistically significant binocular superiority over best monocular performance (P < 0.05 for line, P < 0.02 for VO).

TABLE 1. Binocular summation (in dB) in the different tests for eight subjects. Binocular performance is compared to the predicted value from the quadratic summation model (A) and to the best monocular sensitivity (B). For abbreviations see legend to Fig. 3

Test	Mean	Range (A)	S.D.
DLS	+0.42	-0.21 to $+1.13$	0.46
MV	-0.05	-0.47 to $+1.04$	0.51
HA	-0.31	-1.94 to $+1.05$	1.15
VO	-0.92	-1.49 to -0.39	0.39
Line	-1.05	-1.44 to -0.31	0.42
PR	-1.48	-1.79 to -0.98	0.30
		(B)	
DLS	+1.82	+1.12 to $+2.52$	0.42
MV	+1.21	+0.65 to $+2.11$	0.42
HA	+0.58	-0.81 to $+1.52$	0.94
VO	+0.46	+0.22 to $+0.91$	0.40
Line	+0.37	-0.19 to $+1.07$	0.44
\mathbf{PR}	-0.02	-0.46 to $+0.51$	0.32

TABLE 2.	Results	of a	statist	ical sig	nificance	analysis	compar	ring	different	visual	tests;	expe	ected
quadratic	summa	tion	value	used a	s baselin	e. Numb	ers are	P	(probabili	ty) va	lues.	n.s. =	= not
significant	t. For ab	brev	iations	see leg	gend to H	Figure 3							

	DLS	MV	HA	vo	Line	\mathbf{PR}
DLS		n.s.	n.s.	< 0.001	< 0.001	< 0.001
MV			n.s.	< 0.01	< 0.05	< 0.002
HA		—		n.s.	n.s.	n.s.
VO	_	_			n.s.	n.s.
Line						n.s.
\mathbf{PR}				—		

Describing binocular summation in terms of mean values for a group of subjects is potentially misleading because of the large individual variations. However, all subjects showed higher summation ratios in the two detection tests than in the two resolution tests, except one subject who had a slightly larger summation factor in the broken line test compared to MV. Further, all subjects had higher summation ratios in the detection tests than in the PR test. Thus, summation factors varied in a hierarchic fashion so that more complex visual stimuli evidenced less binocular summation.

Mean monocular resolution in the broken line test was 0.57 min of arc compared to 0.68 min of arc in the broken ring test. This corresponds to decimal acuities of 1.8 and 1.5, respectively, and Snellen acuities of 20/11 and 20/13 (P < 0.01). Summation did not differ significantly for the two acuity tests, however (P > 0.1). Summation

was also determined with the broken line acuity test after defocusing to simulate lowpass spatial frequency filtering. Summation did not change significantly from the optimal corrected state, but the minimum angle of resolution increased, as expected, with increasing defocus. The effect of high-pass filtering was illuminated by means of vanishing optotypes. These had a crisp border between resolution and invisibility, necessitating a scaling factor of only 0.5 dB. The minimum angles of resolution were larger in this test than in the other acuity tests, because of the lower contrast. The summation ratios, however, were closely similar to those of the high-contrast resolution tests. Hence, neither low-pass nor high-pass filtering of the test targets influenced binocular summation.

There was a large variability in the hyperacuity test result, frequently necessitating use of both 4.8 and 9.6 seconds of arc step sizes (Table 1).

The influence of guessing was studied for the broken line acuity test in a twoalternative test design. The two subjects were asked to indicate whenever a gap was seen in the optotype, but to disregard its position. Thresholds were slightly smaller compared to the regular four-alternative test, but the summation factor remained unchanged.

DISCUSSION

The effect of binocular interaction has been studied in many types of visual tasks. These include absolute visual threshold (Thorn & Boynton, 1974), differential light sensitivity (Cogan, Silverman & Sekuler, 1982; Cogan, 1983), brightness summation (DeSilva & Bartley, 1930), flicker fusion (Thomas, 1955), grating contrast (Campbell & Green, 1965; Nachmias & Sansbury, 1974; Legge 1984a, b) and visual acuity (Bárány, 1946; Horowitz, 1949). Also more complex visual tasks have been investigated, e.g. letter identification (Townsend, 1968) and text reading (Sheedy, Bailey, Buri & Bass, 1986). Reported summation factors varied from 1 (i.e. no summation) to about 2. Summation has been shown to vary with test contrast (Cogan et al. 1982), but not with spatial frequency (Holopigian, Blake & Greenwald, 1986), in accordance with the present study. Nachmias & Sansbury (1974) and Legge (1984a) found that binocular summation was larger for detection than for suprathreshold discrimination of sinusoidal gratings. Complex visual tasks generally have yielded lower summation factors than tasks of low complexity, as pointed out by Blake & Fox (1973). In general, summation factors approximating $\sqrt{2}$ have been reported for sine-wave gratings, which can be considered to be uniquely simple visual stimuli.

The influence of guessing has been highlighted by Ericsen (1966). In the present study, this potential source of error was not found to be able to explain the discrepancies between the tests. Thus, it was conclusively shown that summation factors differed between different test tasks. Detection tests yielded higher summation factors than resolution tests, and the complex PR test showed no summation at all. Hence, there was a hierarchy of summation: the more complex the visual task, the lower was the summation factor.

As Westheimer (1979) has made clear, 'minimum visible' is a brightness threshold and is expected to show the same degree of summation as DLS. The small difference observed here may be attributable to small vergence errors preventing the two eyes from aligning perfectly (so-called fixation disparity, Ogle, 1950; Schor, 1983). The summation factor in the DLS test exceeded the value predicted from quadratic summation.

In some aspects the present study confirms earlier work. Bárány (1946) showed that binocular visual acuity exceeded best monocular acuity by about 11%. Similarly, Horowitz (1949) found an acuity summation factor of about 8%. Both values agree with the present results: 8.8% in the broken line test. Cogan (1983) found a mean binocular summation of 1.46 in a DLS task. With similar calculations, the present DLS test result was 1.56.

Attempts to compare psychophysical data with experimental neurophysiological data require extreme caution. Nevertheless, the following proposal for a summation model may have some merit, although it must be considered as no more than a first step towards a better understanding of binocular summation mechanisms.



Fig. 4. Model to explain different magnitudes of binocular summation. See text for explanation. Open circles represent monocularly driven cells in the visual cortex and closed circles binocularly driven cells.

It has been shown that in the primary visual cortex of the macaque, cells in layer IVc, which receive input from the lateral geniculate body, are almost exclusively monocularly driven (Hubel & Wiesel, 1972). Cells in other cortical layers, on the other hand, respond to a greater extent primarily to binocular stimulation. If visual tasks of low complexity, for example mere detection of light, primarily utilize signals from monocularly driven cells, a high degree of binocular summation can be expected since the two eyes then can be regarded as independent detectors (level 1 in Figure 4). On the other hand, if more complex visual tasks, e.g. resolution, utilize signals from higher order cells, binocular summation is expected to be less prominent since a high proportion of these cells are driven by both eyes (level 3 in Fig. 4 shows the extreme case where 100% of the cells are binocularly driven). In this case, the magnitude of summation should depend on the relative response of the individual cells to binocular and monocular stimulation, respectively. In a mixed-drive population the result should be intermediate to the two extremes (level 2 in Figure 4). Our model of hierarchic binocular summation predicts that the more complex the visual stimulus, the higher the level of cortical processing, and the less binocular summation.

Interindividual variation of the summation factors in the present tests are substantial (Table 1). This may be attributable to individual differences of the proportion of binocularly driven cortical cells in different cortical layers.

Many conflicting findings in the domain of binocular summation can be resolved by realizing that there is no single summation constant. Rather, the magnitude of the summation factor depends on the task complexity and probably on the level of cortical visual processing.

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