Pergamon

0028-3932(95)00155-7

Neuropsychologia, Vol. 34, No. 7, pp. 637–646, 1996
Copyright © 1996 Elsevier Science Ltd. All rights reserved
Printed in Great Britain
0028-3932/96 $15.00+0.00

Nasotemporal overlap at the retinal vertical meridian: Investigations with a callosotomy patient

ROBERT FENDRICH, C. MARK WESSINGER and M. S. GAZZANIGA

Center for Neuroscience, University of California at Davis, Davis, CA 95616, U.S.A.

(*Received* 7 *June* 1995; *accepted* 19 *September* 1995)

Abstract—To evaluate nasotemporal overlap at the retinal vertical midline, we asked a callosotomy patient to compare the orientation of square wave gratings that were presented in his opposing visual fields. The gratings were horizontally or vertically oriented and had spatial frequencies ranging from 1 to 8 cycles per degree (cpd). Retinal stabilization ensured the gratings remained properly lateralized during sustained presentations. In accord with previous investigations, when the gratings were presented for only 200 msec, or their medial edges were 2° from the vertical meridian, performance was generally at chance. However, when presentations lasted 2 sec and the medial edges of the gratings were 1° from the vertical meridian, above chance performance was obtained. Accuracy rates were highest with 2 and 4 cpd gratings, and dropped at 1 and 8 cpd. Unexpectedly, the subject performed significantly better when the gratings were offset vertically from each other than when both were displayed on the horizontal meridian. Since this improvement did not occur when gratings were presented horizontally aligned above or below the horizontal meridian, it must be attributed to the relative offset between the gratings. The data suggest a narrow zone of nasotemporal overlap at the retinal vertical midline where very limited visual information is encoded by crossed temporal and uncrossed nasal retinal ganglion cells. An experiment in which only one grating in a pair was close to the vertical meridian indicates that this zone may be more pronounced in the nasal hemiretina. Copyright © 1996 Elsevier Science Ltd.

Key Words: nasotemporal; callosotomy; macular sparing.

Introduction

In primates, the left hemiretina of each eye projects to the left cerebral cortex while the right hemiretina projects to the right cerebral cortex. Each cerebral hemisphere therefore receives its visual input from the contralateral visual field. At the retinal vertical meridian, anatomical investigations in monkeys have demonstrated that there is a narrow zone of overlap in which ganglion cells projecting to the two cerebral hemispheres intermingle [7, 13, 20, 28]. It has been proposed that a similar median zone of nasotemporal overlap could account for macular sparing in human patients rendered hemianopic by unilateral damage to primary visual cortex [6, 7, 20]. However, psychophysical studies in normal human observers have consistently failed to find functional evidence of such a zone [17, 18, 22]. On the other hand, at least one electrophysiological study has produced data commensurate with the existence of a median zone of overlap in humans [31].

Investigations with human callosotomy patients have also failed to demonstrate nasotemporal overlap [11, 25, 29]. In one study, Fendrich and Gazzaniga [11] asked a callosotomy patient to compare target shapes presented 15′ to 1° from the vertical meridian with a reference shape presented 2.5° from the meridian in the same or opposite visual field. The subject reported whether the figures were the same or different. A Purkinje image eyetracker was used to ensure that the target stimulus was presented only when the subject was fixating accurately. When the target and reference were presented to the same visual field, they were readily compared. When they were presented to opposite fields, performance fell to chance. Thus, the patient's fovea appeared to be effectively split at the vertical meridian. In another study, Sugishita *et al.* [29] found that callosotomy patients with a normal left hemisphere dominance for language could not name letters presented to their left visual field if the medial edges of the letters fell 0.6° from the retinal vertical midline. Presentations were right eye monocular and the retinal placement of stimuli was monitored with a video system. The investigators note that their data is consistent with the possibility that there is 'no significant ... bilateral overlap' in the human temporal hemiretina.

However, the outcome of these experiments may have been determined by the character of the stimuli and presentation conditions that were employed. Fendrich and Gazzaniga [11] used small (0.5°) outline geometric figures, while Sugishita *et al.* [29] used small (0.16 to 0.27° wide) letters. If anomalously projecting ganglion cells in the zone of nasotemporal overlap are capable of conveying only attenuated or degraded visual information, they might not be able to encode the details needed to discriminate such stimuli. These cells might nevertheless be capable of encoding coarse stimulus attributes. In accord with this possibility, Bunt *et al.* [7] report that the density of anomalously projecting ganglion cells in the macaque median zone of overlap is only 1 in 14. Although Lines and Milner [22] failed to find evidence of nasotemporal overlap in normal observers using simple light flashes as stimuli, these investigators note that the flashes were quite dim and the signal conveyed to the hemisphere contralateral to each hemiretina may have been 'insufficiently strong to be separated from background noise'. In addition, all previous studies of nasotemporal overlap have made use of brief stimulus presentations (2–200 msec). Conceivably, longer presentations would provide more opportunity for a subject to retrieve useful information from a degraded visual representation.

It therefore seemed desirable to evaluate nasotemporal overlap using longer stimulus presentations, and stimuli likely to remain identifiable even when visually degraded. We report a series of experiments with a callosotomy patient in which this is done. In these studies, the stimuli are high contrast circular square wave grating patches with fundamental spatial frequencies ranging from 1 to 8 cycles per degree (cpd). It was expected that any degradation of visual information passing from each hemiretina to the ipsilateral cerebral hemisphere would entail a selective loss of high spatial frequency information, so that the low frequency gratings would be resistant to such degradation. In addition, image stabilization was employed to eliminate the retinal displacements produced by eye motions. This allowed us to use extended stimulus presentations in order to increase the subject's opportunity to utilize minimal information.

Method

Subject

Testing was conducted on callosotomy patient J.W., a 41-year-old male. In 1979, to treat intractable epilepsy, J.W.'s corpus callosum was sectioned in two stages with sparing of the anterior commissure. The completeness of the section has been magnetic resonance (MR) verified [14]. J.W. is one of a small subset of callostomy patients with demonstrable right hemisphere cognition. A patient history can be found in Sidtis *et al.* [27].

Apparatus

Stimuli were presented by a Macintosh IIcx computer and displayed on a Macintosh II color monitor. Eye motions were monitored with a Fourward Technologies double Purkinje image eyetracker, which has a resolution of 1 arcmin [8]. Subjects viewed the Macintosh screen through the optics of a Fourward Technologies image deflector which was coupled to the eyetracker. This device (which we will term the 'stabilizer') uses the tracker's horizontal and vertical output signals to deflect two mirrors. Consequently, scenes viewed through the stabilizer move in tandem with an observer's eyes, holding a constant retinal position despite changes in the observer's gaze direction. A beam splitter allowed the non-stabilized image of a Hewlet–Packard 1310 x–y monitor to be superimposed on the stabilized image of the Macintosh screen. An IBM PC-AT computer was interfaced to the eyetracker and the x–y display via a Data Translation analog to digital (AD) and digital to analog (DA) converters.

To calibrate retinal stabilization, a matrix of five fixation points (center, and 3° left, right, up and down) and a 1° outline square were presented on the non-stabilized x–y display. The position of the square on the monitor screen was controlled by the eyetracker outputs. These outputs were adjusted so that the square surrounded each point of the fixation matrix when the subject looked at that point. This square was taken to be retinally stabilized. The stabilizer gains and offsets were then adjusted so that a 1° circle on the Macintosh screen superimposed on the square and remained superimposed on it as the subject looked around the matrix. Calibration was checked periodically during the course of each testing session.

General procedures and display characteristics

Circular square wave grating patches 2° in diameter were always employed as the stimuli. The spatial period of the gratings (grating frequency) was 1, 2, 4 or 8 cpd. The dark bars of the gratings had a luminance of 1.6 cd/m^2 and the bright bars had a luminance of 104 cd/m^2 (on the Macintosh screen), yielding a contrast close to 1. Gratings were presented against a uniform background with a luminance of 38 cd/m^2. Viewed through the stabilizer optics, luminances were reduced to approximately one-third of these values. The subject viewed the gratings monocularly with his right eye through the stabilizer in a darkened room, with his head positioned by a bite plate and forehead rest. His left eye was occluded. The effective distance of the Macintosh screen through the stabilizer optics was 57 cm, so that 1 cm (28 pixels) on the monitor screen equaled 1°.

Grating orientations were either horizontal or vertical. In all the reported experiments, two grating patches with the same spatial frequency were presented on each trial and the subject's task was to report whether their orientations were the same or different. The probability that the orientations would be the same was 50%. A single fixation point was always present on the non-stabilized screen to act as an anchor for the subject's gaze. Two-tailed binomial tests were used to compare obtained accuracy rates with an expected chance rate of 50%, or compare obtained accuracy rates with each other.

Preliminary within-field testing

Initially, we appraised J.W.'s ability to make within-field grating comparisons. Gratings were presented simultaneously with their medial edges 2° from the vertical meridian. In separate trial blocks, grating pairs were presented in the subject's left visual field (LVF) or right visual field (RVF). The grating patches were vertically aligned, with one centered 2° above the horizontal meridian and one centered 2° below that meridian. Presentations lasted 20 msec without masking. J.W. responded by pressing one of two keys on the Macintosh keyboard (V or same, N for different). His response hand was ipsilateral to the field of the display. Four blocks of 96 trials were run, two in the RVF and two in the LVF, yielding a total of 48 presentations in each field at each grating frequency.

In his left visual field, J.W.'s accuracy rates for the four frequencies (listed from 1 to 8 cpd) were 98, 96, 92 and 98%. In his right visual field, the corresponding accuracy rates were 98, 92, 94 and 79%. Thus, both of the subject's cerebral hemispheres understood the comparison task and performed it well. The modest dropoff in performance with the 8 cpd gratings in the RVF is in accord with previous within-field testing carried out with this subject using sinewave gratings [10].

Between-field testing

Experiment 1

In the first between-field experiment, the grating patches were presented on the horizontal meridian with one in the RVF and one in the LVF. In separate trial blocks, grating patches were presented with their medial edges 1° 'close' or 2° 'far' from the vertical meridian. For each of these conditions, separate blocks of trials were run with 200 msec 'fast' or 2 sec 'slow' presentations. Figure 1(A) illustrates the near and far stimulus arrangements.

Data was collected over several sessions. J.W. responded "same" or "different" verbally in this experiment, and in Experiments 2 and 3 below. The experimenter initiated trials and entered J.W.'s responses. Initially, three blocks of 96 trials were run for each speed–distance combination. Two additional blocks were run in the close–slow condition to confirm the reliability of the results obtained in this condition. Presentation at each grating frequency were randomized within each block.

Results are presented in Table 1 as percentage correct responses. Data from both the initial three blocks (n = 72) and the full five blocks (n = 120) of the close–slow condition are shown. Subsequent data descriptions are based on the five block values.

When the medial grating edges were 2° from the vertical meridian *or* the presentations were 200 msec, J.W. almost always performed at chance. The sole exception is marginally significant accuracy rate in the far–slow condition with the 4 cpd gratings [$z = 2.00$, $P < 0.05$]. However, this outcome did not replicate with an identical stimulus configuration in a subsequent experiment (see Experiment 3, supplemental far–slow condition).

In contrast, when the medial grating edge was 1° from the vertical meridian and the presentations were slow, J.W. performed significantly better than chance at every grating frequency. Going from 1 to 8 cpd, binomial tests comparing his accuracy rates in the close–slow condition to 50% yield respective z scores of 2.46 ($P < 0.02$), 6.48 ($P < 0.0001$), 4.10 ($P < 0.0001$) and 2.64 ($P < 0.01$). These data suggest that J.W. is able to cross-compare stimuli in his left and right visual fields if the stimuli are 1° from the vertical meridian and the stimulus presentations are extended in time. J.W.'s accuracy rates are highest for the central range of grating frequencies, dropping off at 8 and (unexpectedly) at 1 cpd.

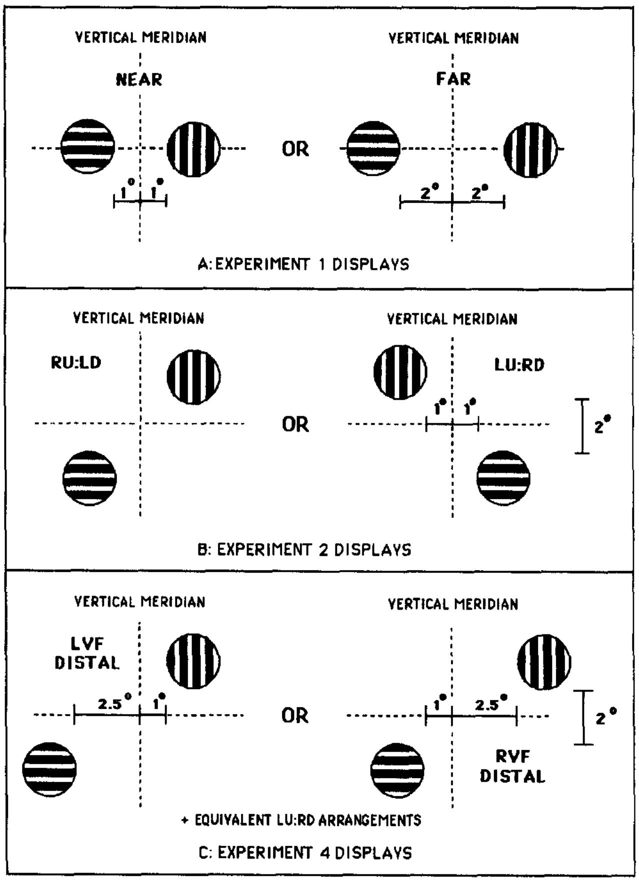

Fig. 1. Stimulus arrangements used in (A) Experiment 1, (B) Experiment 2, and (C) Experiment 3. All illustrations depict a 'different' presentation with 4 cpd gratings.

Table 1. Results of Experiment 1

Condition		Grating frequency (cpd) 1	2	4	8
Far–fast	(n = 72)	51	44	43	56
Far–slow	(n = 72)	43	54	62*	47
Close–fast	(n = 72)	49	56	50	56
Close–slow	(n = 72)	57	79†	67†	65*
Close–slow	(n = 120)	62*	80‡	69‡	63†

* $P < 0.05$; † $P < 0.01$; ‡ $P < 0.0001$.
Values are percentage correct performance.

Experiment 2

Following a run of close–slow presentations in Experiment 2, J.W. was asked if he felt he could actually 'see' both of the grating patches. He responded that he felt that he could, but that they were difficult to discriminate because they "got mixed up with each other". This made us wonder about the possible consequences of separating the gratings spatially along the vertical axis. We evaluated the effect of this manipulation in Experiment 2.

Stimuli and procedures were identical to those employed in the close–slow condition of Experiment 1, save that the gratings were not presented on the horizontal meridian. Instead, one grating was always displaced vertically upwards by 2° and the other displaced downwards by 2°. The bottom of the upper grating and top of the lower were therefore separated by 2°. On half the trials the RVF grating was displaced upwards and LVF grating downwards (RU : LD); on the other half these directions were reversed (LU : RD). Seventeen blocks of 96 trials were run. Figure 1(B) illustrates the stimulus arrangements. Results are given in Table 2.

With both grating alignments (RU : LD and LU : RD), J.W.'s accuracy rates exceed chance at the 0.0001 level at every grating frequency. However, he was consistently better with the RU : LD alignment. In this alignment condition, his performance was close to ceiling and comparable to his within-field performance.

Even in the weaker LU : RD alignment condition, J.W.'s accuracy rates with a vertical offset between the gratings are higher at all grating frequencies than his accuracy rates in the close–slow condition of Experiment 1. This improvement reaches statistical significance with the 1 and 4 cpd gratings ($P < 0.002$ and $P < 0.001$, respectively). In the stronger RU : LD alignment condition, his accuracy rates are significantly higher than the corresponding values in the close-slow condition of Experiment 1 at all grating frequencies ($P < 0.0001$ for the 1, 2 and 4 cpd gratings; $P < 0.002$ for the 8 cpd gratings). To facilitate a comparison of the two experiments, data from both are plotted in Fig. 2.

Supplementary conditions. The improved performance obtained when the gratings were vertically offset from each other made us wonder if an offset between the gratings would allow J.W. to perform above chance with either faster presentations or gratings more distant from the vertical midline. Experiment 2 was therefore repeated using 200 msec second presentations with the medial grating edges 1° from the midline (close–fast) and 2 sec presentations with the medial edges 2° from the midline (far–slow). Six runs of 96 trials were conducted in each condition. Results are given in Table 3.

In the far–slow condition, J.W.'s accuracy rates did not differ significantly from chance at any spatial frequency with either the LU : RD or RU : LD grating alignments. Thus, even with extended presentations and a vertical offset between the gratings, J.W. was unable to compare gratings in his opposing visual fields when their medial edges were 2° from the midline. The slightly elevated accuracy rates in the RU : LD condition with the 1 and 2 cpd gratings raise the possibility, however, that some vestige of his ability to make same–different comparisons may have remained.

In the close–fast condition, J.W. also did not perform better than chance with the LU : RD alignment. With the RU : LD alignment, on the other hand, he exceeded chance accuracy rates with the 1, 2 and 4 cpd gratings [$z = 3.41$, $P < 0.001$, $z = 2.23$, $P < 0.05$, and $z = 3.18$,

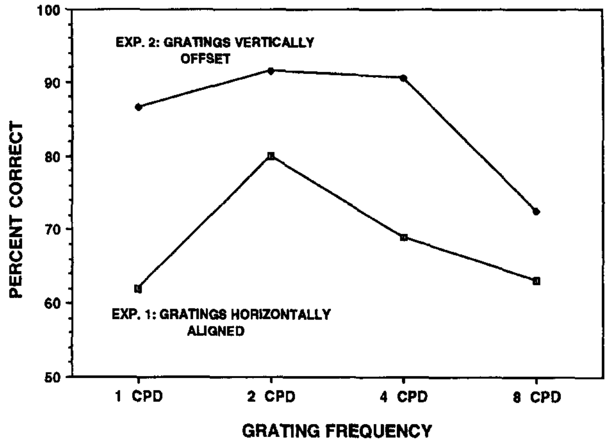

Fig. 2. Percentage correct matches for the four grating frequencies in Experiment 1 and Experiment 2. Presentation conditions were identical, save that in Experiment 2 the gratings were displaced vertically away from each other (see Fig. 1). The Experiment 2 data combines the LU : RD and RU : LD alignment conditions.

Table 2. Results of Experiment 2

Alignment	Grating frequency (cpd) 1	2	4	8
LU : RD	79	87	86	65
RU : LD	94	96	95	80
Combined	86	92	91	73

Values are percentage correct performance. Alignment (left up: right down, right up: left down) is expressed in terms of visual field. Each value is based on 204 trials (408 for the combined data). All values are significant beyond 0.0001.

Table 3. Supplementary conditions: Experiment 2

Alignment	Grating frequency (cpd) 1	2	4	8
Far–slow				
LU : RD	54	51	54	49
RU : LD	58	61	53	51
Close–fast				
LU : RD	46	56	47	51
RU : LD	71‡	64*	69†	54

* $P < 0.05$; † $P < 0.01$; ‡ $P < 0.001$.

Data are percentage correct performance for far–slow and close–fast conditions with a vertical offset between the gratings. Alignment is expressed in terms of visual field. Each value is based on 72 trials.

$P < 0.01$, respectively]. His accuracy rates do not, however, approach the levels previously achieved with either the close–slow RU : LD or LU : RD presentations (see Table 2). Thus, although a vertical offset between the gratings allowed J.W. to make some cross-field comparisons between briefly presented gratings 1° from the vertical meridian, the brevity of the presentations acted to impair his performance substantially.

Experiment 3

The improvement in J.W.'s accuracy rates when the gratings were vertically offset from each other could be attributed either to the relative offset between the gratings or to the absolute offset of the gratings from the horizontal meridian. Experiment 3 was designed to evaluate the latter possibility.

All procedures and stimuli were the same as in the close–slow condition of Experiment 1, save that on one-third of the trials grating pairs were presented with their centers 2° above the horizontal meridian, and on one-third of the trials grating pairs were presented with their centers 2° below that meridian. On the remaining trials, gratings were presented on the horizontal meridian, as in Experiment 1. Presentations at the three vertical levels were randomly intermixed within each run. Twenty-two runs of 96 trials each were conducted. Results are presented in Table 4.

With grating presentations on the horizontal meridian, J.W. performed above chance with the 1, 2 and 4 cpd gratings [respectively, $z = 3.39$, $P < 0.001$; $z = 5.80$, $P < 0.0001$ and $z = 3.84$, $P < 0.0002$], confirming the above chance performance obtained in the slow–close condition of Experiment 1. With the 8 cpd gratings, his performance only exceeds chance at the 0.1 level [$z = 1.73$]. His accuracy rates do not differ significantly from the values found in Experiment 1 at any grating frequency.

Above the horizontal meridian, his performance declined at all grating frequencies, and significantly exceeds change only with the 2 cpd gratings [$z = 3.69$, $P < 0.001$]. Below the horizontal meridian, his performance is similar to or better than his performance at that meridian. Collapsed across the four grating frequencies, the high–low difference is significant beyond 0.0001 [$z = 4.27$]. These data suggest that for J.W. the zone of nasotemporal overlap is more pronounced below the horizontal meridian than above that meridian. However, even below the horizontal meridian where his accuracies were best, J.W. performed less well at every grating frequency than he had in the weaker LU : RD condition of Experiment 2. This drop in performance is significant for the 2, 4 and 8 cpd gratings [$z = 3.42$, $P < 0.001$; $z = 4.00$, $P < 0.0001$ and $z = 1.99$, $P < 0.05$, respectively]. This outcome argues that the relative offset between the gratings, not their absolute offset from the horizontal meridian, is the main contributing factor to the enhanced performance obtained in Experiment 2.

Table 4. Results of Experiment 3

	Grating frequency (cpd)			
Vertical Position	1	2	4	8
Above horiz. merid.	56	64*	56	47
On horiz. merid.	63*	72†	65*	57
Below horiz. merid.	72†	73†	69†	55

* $P < 0.001$; † $P < 0.0001$.

Data are percentage correct performance for close–slow presentations, with horizontally aligned gratings presented on the horizontal meridian, or offset 2° above or below that meridian. Each value is based on 176 trials.

Supplementary conditions. Both anatomical observations in monkeys [13] and theoretical considerations [33] suggest a zone of nasotemporal overlap may be narrowest at the fovea and wider along extra foveal portions of the vertical meridian. Supplementary experiment runs were conducted to address this possibility specifically. The presentation conditions were identical to those used in the far–slow condition of Experiment 1, save that the grating patches were randomly presented 2° above, 2° below, or on the horizontal meridian. To reduce the trial load, only the 4 cpd gratings were presented.

J.W. consistently performed at chance with these displays. Based on 96 trials, his accuracy rates for presentations above, on and below the horizontal meridian were 52, 51 and 42%, respectively. There was therefore no indication of above chance performance 2° from the vertical meridian on the horizontal meridian, or of a spatial spread of the zone of nasotemporal overlap above or below that meridian. However, the vertical offsets which we employed were quite small. A lateral spread of the zone of nasotemporal overlap may occur at larger vertical eccentricities. The outcome of experiment 3 (Table 4) suggests there is more likelihood of this occurring in the inferior visual field.

Experiment 4

In the preceding experiments, the LVF and RVF stimuli were positioned equidistant from the vertical meridian and J.W. responded verbally. Although the use of verbal responses could have created a bias in favor of our subject's (speech dominant) left hemisphere, J.W.'s right hemisphere has shown an increasing ability to access the speech apparatus [1]. It is therefore uncertain which hemisphere was the source of J.W.'s responses in these experiments. Experiment 4 was designed to allow us to assess and compare the ability of J.W.'s left and right hemisphere to utilize information from the contralateral hemiretina.

In experiment 4, one grating patch was placed with its medial edge 1° from the vertical meridian (the 'proximal grating'), while the other was placed with its medial edge

2.5° from that meridian (the 'distal grating'). Since the distal grating was sufficiently far from the vertical meridian to be outside the zone of nasotemporal overlap (found in our previous experiments), only the hemisphere which was presented with the distal grating had the information necessary to perform the matching task. To reduce the total trial load only 4 cpd gratings were presented. Four blocks of 96 trials were run in a counterbalanced order, two with the distal grating in the LVF and two with that grating in the RVF. J.W. responded by pressing the N key on the Macintosh keyboard to indicate 'different' and the V key to indicate 'same', using his left hand when the distal grating was in the LVF and his right hand when the distal grating was in the RVF. As in Experiment 2, the gratings were vertically offset from each other; on half the trials the RVF grating was displaced 2° upwards and the LVF grating 2° downwards (LU : RD); on the remaining trials these offset directions were reversed (RU : LD). LU : RD and RU : LD trials were randomly intermixed within each block. The stimulus arrangements are illustrated in Fig. 1(C).

Because this experiment entailed a switch from verbal to manual responses, we initially allowed J.W. to practice making manual responses with the Macintosh V and N keys when both gratings were presented 1° from the vertical meridian. Left- and right-handed practice blocks were run, using only the 4 cpd gratings. Following an initial period of adjustment, J.W.'s accuracy rates at this task were similar to his accuracy rates in Experiment 2: 83% for the LU : RD condition and 94% for the RU : LD condition. Accuracy rates did not differ for left- and right-handed responses. Results are presented in Table 5.

Both of J.W.'s cerebral hemispheres were able to perform the matching task significantly better than chance ($P < 0.0005$ or better). Since the subject was run monocularly, this outcome implies that the midline zone where information is conveyed to both his cerebral hemispheres extends into both his nasal and temporal hemiretina.

When the distal stimulus was placed in J.W.'s LVF so that the matching task could only be performed by his right hemisphere, his accuracy rates were similar to those obtained in Experiment 2. When the distal grating was placed in his RVF so that the task could only be performed by his left hemisphere, he performed less well than he had with the 4 cpd gratings in Experiment 2. This decline in performance is significant for both the LU : RD and RU : LD conditions [$z = 3.20$ and $z = 3.37$, $P < 0.002$]. These results suggest that despite the use of verbal responses, J.W.'s strong performance in Experiment 2 was mediated primarily by his right hemisphere.

Table 5. Results of Experiment 4

Alignment	Field of distal grating	
	LVF	RVF
LU : RD	88	69
RU : LD	98	81
Combined	93	75

LVC = left visual field; RVF = right visual field.

Data are percentage correct performance, using 4 cpd gratings. The medial edge of distal grating was 2.5° from the vertical midline; the medial edge of the proximal grating patch was 1° from the midline. Alignment is expressed in terms of visual field. Each value is based on 96 trials (192 for the combined data.) All values are significant beyond 0.0005.

Discussion

In Experiment 1, callosotomy patient J.W. performed above chance when comparing the orientation of square wave gratings presented to mirror symmetric locations in his right and left visual fields. This occurred only if the grating medial edges were presented 1° from the vertical meridian and the stimulus presentations lasted 2 sec. His accuracy rates were best with 2 and 4 cpd gratings, and dropped off with 1 and 8 cpd gratings. Experiment 2 showed that the subject's ability to make interfield comparisons is significantly improved if the gratings are displaced vertically away from one another. The observed improvement was most pronounced when the RVF grating was displaced upwards and the LVF grating downwards, but remained robust when these directions were reversed. Experiment 3 demonstrated that this improvement is attributable to the relative offset between the gratings, rather than to their absolute offset from the horizontal meridian. When gratings were presented horizontally aligned, J.W.'s performance declined above the horizontal meridian and remained essentially unchanged below that meridian. Finally, Experiment 4 showed that when the information needed to perform the matching task was restricted to J.W.'s left or right cerebral hemisphere by presenting the grating in that hemisphere's visual field outside the zone of nasotemporal overlap, each hemisphere was capable of performing the task. However, the performance of the right hemisphere was superior to that of the left.

These results indicate that there is a narrow zone along the retinal vertical meridian where retinal information from both of J.W.'s visual fields is available to each of his cerebral hemispheres. Data from cats and monkeys suggest that the anatomical substrate of this zone is a median strip where contra and ipsilaterally projecting retinal ganglion cells intermingle [7, 13, 20, 28]. Following Stone [28] we will refer to this zone as the 'median strip of overlap'.

J.W.'s ability to compare grating orientations was attenuated or eliminated when the stimulus presentations lasted only 200 msec. One way to account for this outcome is to assume that each hemisphere has only a weak or degraded representation of the contraretinal portion of the median strip of overlap. In this case, prolonged stimulus presentations might be required for useful amounts of information to be retrieved from that representation. Initially, we were prone to think of any stimulus degradation in terms of a loss of high spatial frequencies, with a consequent loss of stimulus detail. It was this consideration that initially led us to employ a range of grating frequencies in our test stimuli. We expected that if there was a degraded representation, matching accuracies would be poorest with the 8 cpd gratings and best with the 1 cpd gratings. The data support only part of this prediction. Accuracy rates clearly fall with the 8 cpd gratings, suggesting a loss of high frequency information. Part of the performance drop with the 8 cpd gratings may be due to the normal loss of sensitivity for high spatial frequencies, although during initial within-field testing there was no loss of accuracy with the 8 cpd gratings in the LVF and only a small loss in the RVF. J.W.'s performance did not, however, peak with the 1 cpd gratings. In Experiment 1 and to a lesser extent in Experiments 2 and 3, accuracy rates are highest at 2 or 4 cpd and drop at 1 cpd. With respect to the effect of grating frequency, J.W.'s performance profile bears some resemblance to a normal contrast sensitivity profile. This suggests that the representation of the contralateral retina in each hemisphere might be better construed as low in contrast rather than low-pass filtered, i.e. as faint rather than blurred. If this is the case, one would predict that with actual low-contrast stimuli little or no evidence of nasotemporal overlap would be found. Of course, an overall loss of contrast *and* low-pass filtering could *both* be serving to degrade the representation of the contralateral hemiretina in each hemisphere. Finally, it should be noted that Savoy *et al.* [26] have reported the contrast threshold of low frequency sine wave gratings depends upon the number of cycles presented. With the 1 cpd square wave gratings we employed, relatively little oriented contour was present within the narrow zone of overlap. This may have made orientation matching more difficult with these gratings than with the higher frequency gratings.

The present evidence that each hemisphere has at best a weak representation of the contralateral hemiretina can account for the failure of previous investigations to find evidence of nasotemporal overlap. As previously noted, these investigations have generally used stimuli likely to be vulnerable to visual degradation. Such stimuli were low in luminance [22] or required the resolution of small letters [18, 29] or geometric forms [11] and were always briefly presented. In addition, previous studies have often attempted to reduce the RT delays associated with interhemispheric transfer times by presenting stimuli close to the retinal vertical midline [17, 18, 22]. Lines and Milner [22] and Harvey [17] looked for a reduction of the increase in manual RTs which occurs when the visual field of a stimulus is contralateral to the responding hand; Haun [18] looked for a reduction in a delay in letter naming that occurs when the letters are presented to the LVF. In these cases, any information reaching a hemisphere via projections from the contralateral hemiretina may simply not have had sufficient salience to produce a RT advantage.

An unexpected outcome in the present investigation was the improvement in accuracy rates that occurred when the gratings were vertically displaced from one another. One way to interpret this result is in terms of an inhibitory process acting at short distances across the vertical meridian between horizontally symmetric locations. Presumably, the weaker contraretinal representation in each hemisphere would be suppressed by the stronger ipsiretinal representation. Alternatively, excitatory processes spreading across the vertical meridian might allow a strong stimulus in one visual field to mask a weak signal in the other visual field. The strongest variant of this hypothesis would argue that masking occurred because the representation of the grating in the contralateral hemiretina was effectively superimposed on the stronger representation from the ipsilateral hemiretina. This strong form of the masking hypothesis has the virtue of fitting J.W.'s phenomenal report that when the gratings were side by side they somehow "got mixed up with each other". To the best of our knowledge, however, normal observers do not experience ghostly representations of stimuli presented close to the vertical meridian in the opposing visual field.

Short range interactions between mirror symmetric regions close to the vertical meridian have been reported previously. Bernardi and Fiorentini [3] have reported that perceptual learning which is normally location specific can transfer from a locus in one visual field to a horizontally mirror symmetric locus in the opposing visual field. Bernardi *et al.* [2] have reported that cortical visual evoked potentials produced by a grating in one visual field can be reduced by the simulateneous presentation of a counterphase grating to a mirror symmetric location in the opposing field. In accord with the present findings, these effects occur only if the stimuli are presented less than 2° from the vertical meridian, and do not occur if the stimuli are displaced vertically away from each other. In the present case, the presentation of stimuli in locations that were horizontally mirror symmetric with respect to the retinal vertical midline reduced the ability of each hemisphere to access information from the contralateral hemiretina. A masking hypothesis would permit interactions of the kind reported by Bernardi *et al.* [2, 3] to account for this outcome. Bernardi *et al.* attribute their effects to neural interactions across the corpus callosum, but acknowledge that a zone of nasotemporal overlap could provide an alternative pathway for these interactions. If the effects we observe and those reported by Bernardi *et al.* are mediated by the same neural pathway, their presence in a callosotomy patient is a strong argument for this alternative. Interactions via J.W.'s intact anterior commissure (or some subcortical pathway) cannot, however, be ruled out. It should also be noted that Fiorentini *et al.* [12] found that in a patient with callosal agenesis the interference effect reported by Berardi *et al.* was limited to region within 15′ of the retinal vertical meridian, which provides support for the premise that this effect is at least in part callosally mediated. Of course, hemispheric interactions at the vertical midline could normally be mediated by *both* nasotemporal overlap *and* callosal connections.

The fact that above chance performance occurred almost entirely when presentation times were long raises the possibility that information transferred between our subject's hemispheres via some complex route. If so, conceptual rather than truly perceptual information could have been conveyed. However, it is difficult to reconcile this premise with the fact that above chance performance was limited to regions proximal to the vertical meridian, or the other observed effects of the spatial arrangement of stimuli.

Bunt *et al.* [6, 7] and Leventhal *et al.* [20, 21] have argued that ipsilaterally projecting ganglion cells around and within the macaque fovea could produce a bilateral representation of the entire fovea. However, Tootell *et al.* [30] did not find a double representation of the vertical midline when they used ^{14}C-2-deoxy-d-glucose to map the projection of the retina onto macaque striate cortex. In addition, when Dow *et al.* [9] used single cell recording to map the projection of the fovea onto macaque striate cortex, they found no receptive field centers more than 5′ into the visual field ipsilateral to each hemisphere. This apparent discrepancy between the retinal and cortical data gives some credence to the idea that uncrossed nasal and crossed temporal retinal ganglion cells may project to cortical neurons with their primary receptive fields in the opposing hemiretina. Bishop [4] and Blakemore [5] have proposed that the information conveyed by these ganglion cells could be used to facilitate midline stereopsis.* It is interesting to speculate in this regard whether the inhibitory or masking effects we report might be related to the mechanisms which maintain the singleness of vision in the presence of disparity.

The right hemisphere advantage found in Experiment 4 could reflect differences in the spatial processing capabilities of the hemispheres [15], but a more peripheral explanation is also possible. Since all our investigations were carried out monocularly with our subject's right eye, uncrossed ganglion cells projected to our subjects right hemisphere. Both Leventhal *et al.* [20] and Fukuda *et al.* [13] have reported that in monkeys the incidence of uncrossed nasal ganglion cells exceeds the incidence of crossed temporal ganglion cells. Victor *et al.* [31] have argued from electrophysiological data that a similar pattern is present in the human retina. If this is the case, our subjects's right hemisphere would have had more access to the left visual field than his left hemisphere had to the right visual field. This explanation predicts that if monocular testing could be conducted with the subject's left eye, the advantage would switch to his left hemisphere. However, the fact that J.W.'s accuracy did not fall to chance when the distal stimulus was in his RVF indicates that the zone of overlap is not limited exclusively to the nasal hemiretina in humans. Recent data on residual vision at the vertical midline in hemispherectomy patients are consistent with this conclusion [32].

Fukuda [13] also reports that in the Japanese macaque the median strip of overlap widens with increasing distance from the horizontal meridian, and does so more in the upper hemiretina than in the lower hemiretina. If a median strip of overlap is likewise more pronounced in the upper hemiretina in humans, one would expect more evidence of nasotemporal overlap in the lower than in the upper visual field. This was, in fact, the pattern we observed in Experiment 3. Such a weighting of a median strip of overlap toward the lower visual field could have functional advantages; in humans, stereopsis is more likely to be useful in the lower visual field. One caveat should be noted: the upper-lower hemifield difference we observed in J.W. was due more to a performance *drop* in the upper visual field than an improvement in the lower field. Nevertheless, Fukuda's finding raises the possibility that the asymmetry in J.W.'s performance with respect to the horizontal meridian is related to upper and lower hemiretina differences in the density of the median strip of overlap. Additional testing using larger vertical eccentricities will be needed to address this issue.

A puzzling aspect of the present data is the relatively strong performance in the RU : LD offset condition relative to the LU : RD condition. We are not able to suggest an anatomical basis for this outcome, although there is one potential artifact that could have contributed to it. We address this point below.

Potential artifacts

Eccentric fixation. In all the experiments described, the stimuli were retinally stabilized so that their lateralization would not be altered by subject eye motions. However, eccentric fixation during the calibration of the eyetracker would have produced a bias of the subject's retinal vertical midline to the left or right of the fixation point. Such a bias could allow gratings presented to the RVF to fall within the LVF, or vice-versa, allowing the matching task to be performed. Several considerations argue against such an artifact. In all the reported experiments, fixation

---

* It has been argued that the corpus callosum mediates midline stereopsis in humans, since it can be impaired in commissurotomy and callosotomy patients [16, 19, 25] and cases of callosal agenesis [12]. However, the data on this matter has been inconsistent. For example, Mitchell and Blakemore [25] failed to find midline stereopsis in one commissurotomy patient using line stimuli and large (2°) disparities, whereas Hamilton and Vermeire [16] report it was unimpaired in the same patient using random dot stereograms and disparities from 5′ to 40′. Lassonde [19] reports that the absence of a corpus callosum impairs midline stereopsis when stimulus presentations are rapid (120 msec), but has little effect on stereopsis with slightly longer presentations (300 msec). Fiorentini *et al.* [12] have reported nearly normal stereopsis in a patient with callosal agenesis with small disparities, but deficient stereopsis for large crossed disparities. At present, the possible contributions of callosal and non-callosal pathways to midline stereopsis therefore have not been clearly established.

eccentricities up to 1° could have been present without displacing a grating into the wrong visual field. More important, eccentric fixation cannot account for the improvement in performance produced by an offset between the gratings, or the difference between upper and lower field performance. Finally, in Experiment 4, J. W. would have had to have fixated eccentrically in different directions on different runs, depending on the field of the distal grating. We therefore do not believe that eccentric fixation can account for our results.

Tilt of the vertical meridian. If the vertical meridian of our subject's right retina was tilted clockwise with respect to vertical on the stimulus display screen, this would have biased upper right and lower left stimuli towards that meridian. Such a tilt could account for the relative advantage for RU : LD presentations over the LU : RD presentations which we observed in Experiments 2 and 4. However, given the 2° vertical offsets we employed, a tilt of more than 26° would have been needed to displace the medial edges of our grating patches to the retinal vertical meridian. Although a tilt of this magnitude should have been conspicuous, we did not observe any tilt of our subjects head or the images viewed through the stabilizer optics. Moreover, in Experiment 2 J.W. showed a significant improvement in the LU : RD condition, relative to his performance in Experiments 1 and 3 where the gratings were horizontally aligned, although a clockwise tilt of the vertical meridian would have biased the grating patches *away* from the vertical meridian in this condition. A tilt of the vertical meridian also cannot account for the upper field–lower field differences or the above chance performance found when gratings were presented on the horizontal meridian. Therefore, while we do not rule out the possibility that a small tilt of this kind contributed to the RU : LD–LU : RD differences we observed, it cannot provide a general explanation for our results.

Macular sparing

The present investigations contrast with previous psychophysical investigations of nasotemporal overlap in that they do find evidence of median strip where the retinal information is conveyed to both cerebral hemispheres. However, the information conveyed to each hemisphere from the parafoveal contralateral hemiretina appears to be quite tenuous, and is confined to a region narrower than 2°. Macular sparing can provide vision of good quality over a substantially larger spatial extent [24]. The present investigation is therefore in accord with previous investigations in that it indicates nasotemporal overlap is not an adequate explanation for macular sparing. It is therefore commensurate with alternative explanations, such as one based on redundancy in the blood supply to the regions of striate cortex representing the fovea [23].

Acknowledgements—Supported by NIH/NINDS P01 NS17778, NIH/NINDS R01 NS22626 and the McDonnell-Pew Foundation.

References

1. Baynes, K.,Wessinger, C. M., Fendrich, R. and Gazzaniga, M. S. The emergence of the capacity to name left visual field stimuli: Implications for functional plasticity. *Neuropsychologia* **33,** 1225–1242, 1995.
2. Berardi, N., Bodis-Wollner, I., Fiorentini, A., Giuffre, G. and Morelli, M. Electrophysiological evidence for interhemispheric transmission of visual information in man. *J. Physiol.* **411,** 207–225, 1989.
3. Berardi, N. and Fiorentini, A. Interhemispheric transfer of visual information in humans: Spatial characteristics. *J. Physiol.* **384,** 633–647, 1987.
4. Bishop, P. O. Binocular vision. In *Adler's Physiology of the Eye*, R. A. Moses and W. M. Hart (Editors), pp. 619–689. Mosby, St. Louis, 1987.
5. Blakemore, C. Binocular depth discrimination and the nasotemporal division. *J. Physiol.* **205,** 471–497, 1969.
6. Bunt, A. H. and Minckler, D. S. Foveal Sparing. New anatomical evidence for bilateral representation of the central retina. *Arch. Opthalmol.* **95,** 1445–1447, 1977.
7. Bunt, A. H., Minckler, D. S. and Johanson, G. W. Demonstration of bilateral projection to the central retina of the monkey with horseradish peroxidase neuronography. *J. comp. Neurol.* **171,** 619–630, 1977.
8. Crane, H. D. and Steele, C. M. Generation-V dual Purkinje-image eyetracker. *Appl. Optics* **24,** 527–537, 1985.
9. Dow, B. M., Vautin, R. G. and Bauer, R. The mapping of visual space onto foveal striate cortex in the Macaque monkey. *J. Neurosci.* **5,** 890–902, 1985.
10. Fendrich, R. and Gazzaniga, M. S. Hemispheric processing of spatial frequencies in two commissurotomy patients. *Neuropsychologia* **28,** 657–663, 1990.
11. Fendrich, R. and Gazzaniga, M. S. Evidence of foveal splitting in a commissurotomy patient. *Neuropsychologia* **27,** 273–281, 1989.
12. Fiorentini, A., Berardi, B., Falsini, B. and Porciatti, V. Interhemispheric transfer of visual perceptual learning in callosal agenesis. *Clin. Vision Sic.* **7,** 133–140, 1992.
13. Fukuda, Y., Sawai, H., Watanabe, M., Wakakuwa, K. and Morigiwa, K. Nasotemporal overlap of crossed and uncrossed retinal ganglion cell projections in the Japanese monkey (*Macaca fuscata*). *J. Neurosci.* **9,** 2353–2373, 1989.
14. Gazzaniga, M. S., Holtzman, J. D., Deck, M., Benjamin, C. P. and Lee, C. P. MRI assessment of human callosal surgery with neuropsychological correlates. *Neurology* **35,** 1763–1766, 1985.
15. Gazzaniga, M. S. *The Bisected Brain.* Appleton-Century-Crofts, New York, 1970.
16. Hamilton, C. R. and Vermeire, B. A. Localization of visual functions with partially split-brain monkeys. In *Two Hemispheres—One Brain: Functions of the*

Corpus Callosum, F. Lepore, M. Ptito and H. Jasper, (Editors), pp. 385–401. Alan A. Liss, New York, 1986.

17. Harvey, L. O. Jr. Single representation of the visual midline in humans. *Nueorpsychologia* **16,** 601–610, 1978.
18. Haun, F. Functional dissociation of the hemispheres using foveal visual input. *Neuropsychologia* **16,** 725–733, 1978.
19. Lassonde, M. The facilitatory influence of the corpus callosum and intrahemispheric processing. In *Two Hemispheres—One Brain*: *Functions of the corpus Callosum*, F. Lepore, M. Ptito and H. Jasper (Editors), pp. 385–401. Alan A. Liss, New York, 1986.
20. Leventhal A. G., Ault, S. J. and Vitek, D. J. The nasotemporal division in primate retina: The neural basis of macular sparing and splitting. *Science* **240,** 66–67, 1988.
21. Leventhal A. G., Thompson, K. G. and Liu, D. Retinal ganglion cells within the fovealo of new world (*Saimiri Sciureus*) and old world (*Macaca fascicularis*) monkeys. *J. comp. Neurol.* **338,** 242–254, 1993.
22. Lines, C. R. and Milner, A. D. Nasotemporal overlap in the human retina investigated by means of simple reaction time to lateralized light flash. *Exp. Brain Res.* **50,** 166–172, 1983.
23. McFadzean, R., Brosnahan, D., Hadley, D. and Mutluken, E. Representation of the visual field in occipital straite cortex. *Br. J. Ophthalmol.* **78,** 185–180, 1994.
24. Miller, N. R. *Walsh and Hoyt's Clinical Neuro-Ophthalmology*, Vol. 1, pp. 145–147. Williams and Wilkins, Baltimore, 1982.
25. Mitchell, D. E. and Blakemore, C. Binocular depth perception and the corpus callosum. *Vision Res.* **10,** 49–53, 1970.
26. Savoy, R. L. and McCann, J. J. Visibility of low-spatial frequency sine wave targets: Dependence on number of cycles. *J. Opt. Soc. Amer.* **65,** 343–350, 1975.
27. Sidtis, J. J., Volpe, B. T., Wilson, D. H., Rayport, M. and Gazzaniga, M. S. Variability in right hemisphere language function after callosal section: Evidence for a continuum of generative capacity. *J. Neurosci.* **1,** 323–331, 1981.
28. Stone, J., Leichester, J. and Sherman, S. M. The naso-temporal division of the monkey retina. *J. comp. Neurol.* **150,** 333–348, 1973.
29. Sugishita, M., Hamilton, C. R., Sakuma, I. and Hemmi, I. Hemispheric representation of the central retina of commissurotomized subjects. *Neuropsychologia* **32,** 399–415, 1994.
30. Tootell, R. B. H., Switkes, E., Silverman, M. S. and Hamilton, S. L. Functional anatomy of Macaque striate cortex. II. Retinotopic organization. *J. Neurosci.* **8,** 1531–1568, 1988.
31. Victor, J. D., Conte, M. and Ladecola, C. Ocular dependence of hemifield visual evoked potentials: Relevance to bilateral cortical representation of central vision. *Clin. Vis. Sci.* **6,** 261–276, 1991.
32. Wessinger, C. M., Fendrich, R., Ptito, A. and Gazzaniga, M. S. Residual vision in the blind field after partial or complete hemispherectomy. *Soc. Neurosci. Abs.* **20,** 1579, 1994.
33. Wyatt, H. J. Nasotemporal overlap and visual field sparing. *Invest. Ophthalmol. Vis. Sci.* **17,** 1128–1130, 1978.