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HEMISPHERIC PROCESSING OF SPATIAL FREQUENCIES IN TWO COMMISSUROTOMY PATIENTS

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Abstract—To test the hypothesis that in humans the left brain hemisphere is specialized for processing high spatial frequencies while the right hemisphere is specialized for processing low spatial frequencies, pairs of Gaussian windowed sinusoidal gratings were presented for 167 msec within the left and right visual fields of two commissurotomy patients. The gratings employed had spatial frequencies ranging from 1 to 8 cycles per degree, and horizontal or vertical orientations. The two gratings in each pair were identical in spatial frequency but could differ in orientation. Subjects reported if their orientations were the same or different. Twelve normal controls were also run.

Accuracy data provides no indication of a relative advantage for high frequencies in the RVF or low frequencies in the LVF. One commissurotomy subject showed a trend in the reverse direction; the other was better with LVF presentations for all spatial frequencies. Control subjects failed to show a spatial frequency × visual field interaction. These outcomes suggest that at the processing stages required by the task, the hemispheres are not specialized for particular ranges of spatial frequencies.

INTRODUCTION

WITH NORMAL human observers, degrading visual stimuli by blurring them [9, 11, 21], increasing their retinal eccentricity [15, 20], decreasing their exposure duration [14, 17, 20], or lowering their luminance [19], impairs performance more in the right visual field (RVF) than in the left visual field (LVF) (see SERGENT [23] for a recent review of these findings). Reductions in stimulus size, on the other hand, sometimes impair performance more in the left than right visual field [20]. To account for these observations, SERGENT has proposed that the left cerebral hemisphere (LH) is specialized for the processing of high spatial frequencies, and that the right hemisphere (RH) is specialized for the processing of low spatial frequencies [17, 18, 19, 20, 21, 22, 23]. This model of hemispheric specialization is generally commensurate with data from both normal and brain lesioned patients which suggest the left hemisphere preferentially processes "local" stimuli while the right hemisphere processes "global" stimuli [10, 16, 18, 24].

We tested for a hemispheric specialization in the processing of spatial frequencies in two commissurotomy patients. In such patients, it is possible to study the capabilities of each hemisphere in relative isolation from the other, due to the separation of the hemispheres at the level of the cortex.

SERGENT argues that the hemispheres may have different capacities for processing high and low spatial frequencies, yet not differ in their detection thresholds for those frequencies [18]. We presented pairs of Gaussian windowed sinusoidal gratings (Gabor functions [51]), with spatial frequencies ranging from 1 to 8 cycles per degree (cpd), to the RVF and LVF of our subjects. The gratings within each pair were always the same spatial frequency but could differ in orientation. Subjects were required to judge if their orientations were the same or different. Thus, simple detection of the gratings was not sufficient to perform the experimental task; a comparison of the gratings was required. It was predicted that a LH advantage for processing high spatial frequencies would result in better RVF than LVF performance with the high frequency gratings. Likewise, it was predicted that RH advantage for processing of low frequencies would produce better LVF than RVF performance with the low frequency gratings.

METHOD

Subjects

Commissurotomy patients J.W. and V.P. served as subjects. J.W., a 35-year-old male, underwent two stage callosal surgery with sparing of the anterior commissure in 1979, for the treatment of intractable epilepsy brought on by a concussive head trauma at the age of 13. V.P., a 36-year-old female, underwent two stage commissurotomy with sparing of the anterior commissure in 1979, for the treatment of intractable epilepsy brought on by febrile illness at the age of 6.* Both V.P. and J.W. have previously been shown to have right hemispheres capable of understanding simple verbal instructions, which permitted both hemispheres to be tested in the present experiment. However, the left hemisphere of both subjects remains dominant for language [25]. Case histories of these patients can be found in SIDTIS *et al.* [25].

In addition, data were obtained from 12 control subjects, seven female and five male, with normal or corrected to normal vision. Control subjects were volunteer medical school students or clerical staff. All controls were consistently right-handed by self report.

Displays

Sinusoidal gratings were presented with an Apple Macintosh II computer configured to generate 256 grey levels, and displayed on a Macintosh color monitor. Gratings with spatial frequencies of 1, 2, 4 and 8 cpd were presented.† The orientation of the gratings was either horizontal or vertical. The gratings had a mean luminance of 31 cd/m^2, which matched the background luminance, and were windowed by a circular Gaussian which yielded a visible grating patch about 1.5° across. Grating contrast was 66% prior to Gaussian modulation.

A bright 1 pixel fixation point was displayed at the center of the computer screen. Each pair of gratings was presented 1.5° to the left or right of this fixation point. The two gratings in each pair were presented simultaneously for 167 msec. The gratings were vertically aligned, with one grating 1.5° above the level of the fixation point and the other 1.5° below that level. All grating presentations were terminated by a composite grating mask. This mask was a square 2° on a side, formed by superimposing all of the test gratings employed. Visually, it appeared to be a complex plaid-like pattern. The mask was presented for 167 msec.

Procedure

The subjects viewed the video display from a distance of 61 cm, with their heads positioned by a chin rest. They were cautioned frequently to keep their eyes on the fixation point. Trials were initiated by the experimenter; subjects responded by pressing the "v" key on the computer keyboard if the two gratings had the same orientation (i.e. if both were horizontal or both were vertical) and the "*n*" key if their orientations were different (i.e. if one was horizontal and one vertical). The probability that the grating orientations would be the same was 0.5 on each trial.

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*MRI scans of V.P. have revealed small regions of fiber sparing in both the splenium and rostrum of the corpus callosum [7]. However, in a wide variety of visual tasks, V.P. has not shown any ability to integrate visual information across her hemispheres. Moreover, when the gratings used in the present experiment were presented to her opposing visual fields, V.P.'s same–different orientation judgements were completely at chance for all the spatial frequencies employed.

†There were 32 pixels to a degree of visual angle in the experimental displays. Because of pixel size limitations, the 8 cpd gratings were poor approximations to sine waves. However, since the distortion of these waves was produced by the presence of higher frequency harmonics, this distortion did not compromise the value of these gratings as high frequency test stimuli. An analysis of the harmonic content of the stimuli indicates that the low frequency gratings were not meaningfully contaminated by high frequencies. In general, the "boxcar" representation of the sinusoids generated low amplitude harmonics at multiples 32 cpd $\pm$ the frequency of the fundamental. With the 1 and 2 cpd gratings, the lowest frequency (and highest amplitude) harmonics were at 31 and 30 cpd respectively, with effective contrasts of 2.1% and 4.4%. These contrast levels are well below reported detection thresholds for gratings of these frequencies [4], a fact commensurate with the informal observation that the low frequency gratings appeared completely smooth to the investigators.

Trials were run in blocks of 64. Each block contained 16 grating pairs at each of the four spatial frequencies. In half of these grating pairs the grating orientation was the same. Within each block, all of the presentations were to the same visual field, and the hand used by the subject to respond was ipsilateral to that field. With the commissurotomy patients, a counterbalanced sequence of eight blocks was run, four in each visual field, yielding a total of 64 trials for each spatial frequency in each visual field. With the control subjects, two blocks of trials were run in each visual field, yielding a total of 32 trials for each spatial frequency in each visual field. The presentation order was randomized within each block.

Prior to the experimental trials, subjects were trained using displays in which grating pairs were presented for a full second. Training was terminated when subjects performed without an error in a sequence of eight trials in each visual field. Subjects were instructed that accuracy was more important than speed, and accuracy was the dependent variable.

RESULTS

Graphs of the accuracy data for subject J.W., subject V.P., and the normal controls are presented as Figs 1, 2 and 3. With the commissurotomy patients, two-tailed binomial tests were used to evaluate whether the obtained accuracy rates differed from a chance value of 50%. In the following data presentation, accuracies exceed chance at the 0.001 level or better unless otherwise indicated.

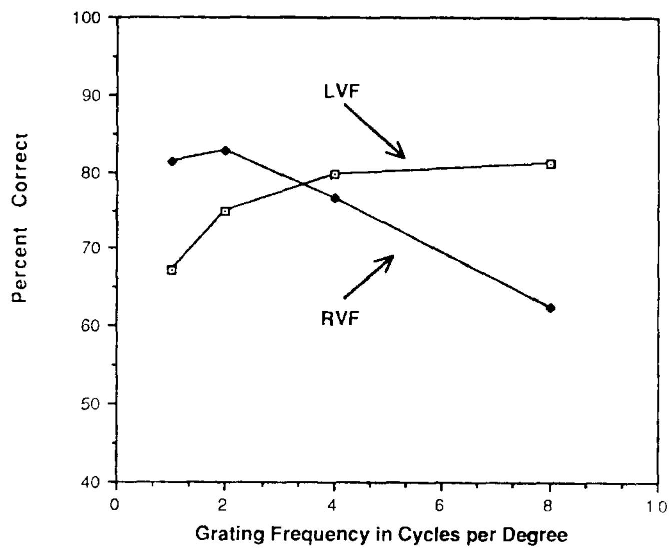

Fig. 1. Accuracy as a function of grating frequency. Subject J.W.

Going from 1 to 8 cpd, J.W.'s accuracy rates are 81, 83, 77 and 63% ($P<0.07$) for RVF presentations, and 67% ($P<0.01$), 75, 80 and 81% for LVF presentations. Collapsed across all spatial frequencies, his accuracy is 76% in both his LVF and RVF. However, in the RVF data there is an increase in accuracy with the low frequency gratings, while in the LVF there is an increase in accuracy with the high frequency gratings. These trends are the reverse of what the spatial frequency hypothesis would predict. In his RVF, J.W. is 18% more accurate with 1 cpd gratings than with the 8 cpd gratings ($z=2.27$, $P<0.03$). In his LVF, he is 14% more accurate with the 8 cpd gratings than with the 1 cpd gratings ($z=1.82$, $P<0.07$). Comparing across the visual fields, at 1 cpd J.W. performs 14% better in his RVF than LVF while at 8 cpd he performs 18% better in the LVF than RVF.

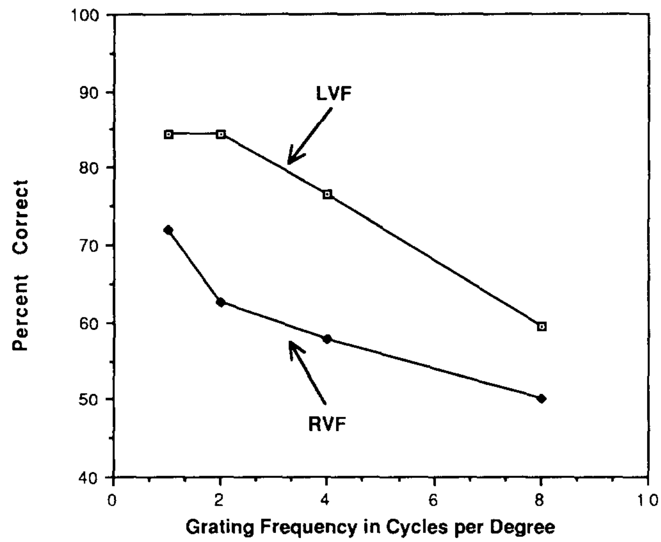

Fig. 2. Accuracy as a function of grating frequency. Subject V.P.

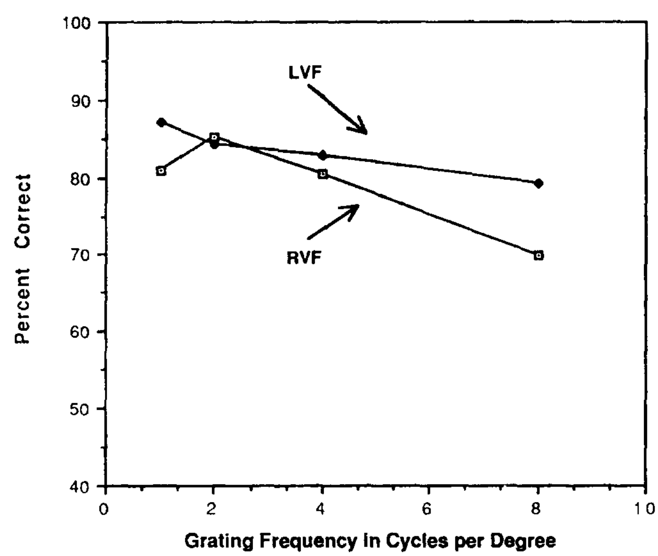

Fig. 3. Accuracy as a function of grating frequency. Controls.

Going from 1 to 8 cpd, V.P.'s accuracy rates are 72, 63% ($P < 0.07$), 58% (NS) and 50% (NS) in her RVF, and 84, 84, 77 and 59% (NS) in her LVF. Thus, V.P. performed better with LVF presentations for all the spatial frequencies tested. The LVF advantage reaches statistical significance with the 2 and 4 cpd gratings ($z = 2.69$, $P < 0.01$ and $z = 2.29$, $P < 0.05$). Collapsed across spatial frequencies, her right field accuracy is 61% and her left field accuracy is 76%. The difference between these values is highly significant ($z = 3.65$,

$P<0.0002$). In both visual fields, her performance declines as grating frequency increases. In her RVF, she is 22% less accurate with the 8 cpd gratings than with the 1 cpd gratings ($z=2.55$, $P<0.02$); in her LVF, the corresponding drop in accuracy is 25% ($z=3.13$, $P<0.002$).

Going from 1 to 8 cpd, mean accuracies for control subjects are 82% (SD = 17%), 85% (SD = 11%), 82% (SD = 14%) and 73% (SD = 18%) in the RVF, and 86% (SD = 16%), 83% (SD = 17%), 83% (SD = 15%) and 79% (SD = 16%) in the LVF. Overall, accuracy was 81% in the RVF and 83% in the LVF. The data were analyzed with a two way ANOVA with visual field and spatial frequency as repeated measures factors. A significant main effect was found for spatial frequency [F (3, 33) = 4.15, $P<0.05$]. This reflects the drop in response accuracy that occurred in both visual fields in the 8 cpd condition. It seems likely this drop in accuracy can be attributed to the drop in the human spatial frequency sensitivity function that occurs at 8 cpd. There was no effect for visual field [F (1, 11) = 1.78, NS], and no visual field × spatial frequency interaction [F = (3, 33) = 2.02, NS]. At 8 cpd, seven of the twelve controls performed better in the LVF, three performed better in the RVF, and two performed identically in the two fields. For two subjects, the LVF advantage reached statistical significance ($z=2.65$ and $z=2.01$), and for one the RVF advantage was significant ($z=2.08$). Likewise, at 1 cpd seven controls performed better in the LVF, three performed better in the RVF, and two performed identically in both fields. However, none of the differences at 1 cpd reached significance.

DISCUSSION

The data provide no support for the hypothesis that the left hemisphere is specialized for processing high spatial frequencies and the right hemisphere is specialized for the processing of low spatial frequencies. The results from J.W. suggest the reverse pattern of specialization. The results from V.P. suggest a right hemisphere advantage for processing both high and low spatial frequencies (although at the highest frequency tested, neither hemisphere performed above chance, so a comparison must be treated cautiously). In addition, control subjects failed to show a significant interaction between visual field and spatial frequency. The largest visual field difference present for the control subjects is a 6% advantage with the 8 cpd gratings in the LVF. If this reflects a valid trend in the data, its direction is the reverse of what the model being tested would predict.

The hypothesis of a left hemisphere specialization for processing of high spatial frequencies and right hemisphere specialization for processing of low spatial frequencies does account for a wide body of data. However, a number of investigations, in addition to the present one, have failed to support it. Several studies in which the size of stimuli was varied have yielded mixed or negative results [11, 13, 14]. For example, with lateralized random dot stereograms PITALBO [13] found evidence of the reverse pattern of specialization; there was a right hemisphere advantage with small dots and left hemisphere advantage with large dots. In a face recognition task, HELLIGE *et al.* [8] found increased retinal eccentricity (which produces a loss of high frequencies) was more detrimental in LVF than RVF. MOSCOVITCH and RADZINS [12] found that high and low spatial frequency masks were equally effective in the RVF and LVF. SZELAG *et al.* [26] had subjects judge whether successive square wave gratings had the same spatial frequencies, and found that high and low frequency gratings were processed with the same efficiency in both visual fields. BOLES and MORELLI [3] had subjects perform a similar task, and also estimate the number of bars in square wave gratings.

These investigators found a LVF advantage with both high and low grating frequencies. With hierarchical stimuli and normal subjects, neither ALIVISATOS and WILDING [1] nor BOLES [2] was able to demonstrate a left hemisphere advantage for local processing or right hemisphere advantage for global processing. In addition, VAN KLEEK *et al.* [27] recently failed to find this pattern of global/local specialization in two commissurotomy patients. Sergent has argued that in certain of the failures to support her spatial frequency hypothesis inappropriate stimuli or presentation procedures were employed, but with low pass filtered faces she has also failed to confirm some predictions of that hypothesis [22].

Some potential limitations on the generality of the present data should be noted. (1) The pattern of hemispheric specializations present in commissurotomy patients may not be typical of normal subjects, due to their preoperative pathologies and/or to cortical rearrangements occurring in response to their surgery. However, the present control and patient data are essentially in agreement. (2) In the present experiment, the perceptual judgement was a simple one, although subjects often reported they found it difficult. It is possible another task—one requiring more elaborate cognitive processing, or a finer discrimination, or a different type of discrimination—would have revealed the predicted pattern of specialization. (3) It is possible that a reaction time measure would have revealed differences not apparent in the accuracy data. For some controls, ceiling effects could have limited the sensitivity of the accuracy measure with the low spatial frequencies. (4) The range of spatial frequencies used in the present experiment was constrained by practical considerations. Had very low and high frequencies been used, effects in the predicted direction might have appeared.

The present results nevertheless underscore the need to consider alternatives to the hypothesis that spatial frequency processing is lateralized. JONSSON and HELLIGE [9], for example, have pointed out that manipulations which reduce the high spatial frequency content of stimuli also tend to decrease their "perceptibility"; conceivably any increase in the difficulty of visual processing favors the right hemisphere. This might be related to the allocation of left hemisphere resources to attempts at verbal processing [6]. Even if the hemispheres can be specialized for different ranges of spatial frequencies, the present data indicate, at least, that there will be substantial individual variations in the character of this specialization.

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