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Cortical Components of the Westheimer Function

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The Westheimer function in human cone vision was measured in normal observers under dichoptic conditions and in observers with naturally acquired amblyopia. Results show interocular transfer of both desensitization and sensitization under either "sustained" or "transient" stimulus conditions if binocular rivalry is eliminated. The spatial sensitization branches of the amblyopic functions are considerably broadened as compared with those of the non-amblyopic function. Our results are consistent with cortical components for the Westheimer function which probably reflect the behavior of cortical spatial filters. © 1997 Elsevier Science Ltd

Westheimer function   Perceptive field   Spatial filter   Interocular transfer   Amblyopia

INTRODUCTION

When a small spot target is centered on a circular background of various sizes, the detection threshold first increases (desensitization) until reaching a peak, then decreases (sensitization) until reaching an asymptote as the size of the background increases (Crawford, 1940; Westheimer, 1965, 1967). This effect, known as the Westheimer function, is generally interpreted as mirroring the center/surround organization of the retinal cell receptive fields (e.g., Enoch, 1978; Hayhoe, 1979a,b; Spillmann *et al.*, 1987; Westheimer, 1965, 1967), with desensitization matching spatial summation of the excitatory receptive field center, and sensitization

did not reduce, but actually slightly elevated the threshold. Similar results were also replicated in later studies (Fiorentini *et al.*, 1972; Sturr & Teller, 1973). Failure to observe interocular transfer of sensitization was explained on the basis that the Westheimer function occurs before the binocular convergence of visual inputs, and thus is organized precortically (Westheimer, 1967).

Dichoptic tests have also been conducted in which the spot target is presented to one eye and the entire background to the other eye. These tests, however, have produced mixed results. Under "transient conditions", i.e., the target and background have the same onset, interocular transfer has been observed (Fiorentini *et al.*, the inner retina and before the LGN, such as retrobulbar optic neuritis and sharp chiasmal lesion caused by tumor, had no effect. These and other findings led Enoch *et al.* to conclude that the Westheimer function is organized at the inner retina outer plexiform layer (see Enoch (1978) for a review). However, in our opinion, although these studies suggest a role for the retina in the organization of the Westheimer function, the conclusion is not exclusive. As Sturr and Teller (1973) suggested, the retinal diseases investigated by Enoch *et al.* would not only disturb the information processing within the retina, but also distort the information passed upstream to the visual cortex. There still exists the possibility that a distorted Westheimer function is the output of cortical processing on distorted input from the diseased retina. Thus, the role of the visual cortex in the Westheimer function cannot be completely excluded before it is directly examined.

Lawwill *et al.* (1973) tested one anisometropic amblyopic patient with the Westheimer paradigm and reported a function which had a moderately enlarged desensitization branch and a greatly enlarged sensitization branch. Based on the retinal theory of the Westheimer function, these results were interpreted as indicating a retinal anomaly in the amblyopic visual system (Lawwill, 1978). However, this interpretation has [redacted]

study we measure the Westheimer function dichoptically and in humans with naturally acquired amblyopia. We demonstrate interocular transfer of both desensitization and sensitization under either "sustained" or "transient" stimulus conditions if measurements are not interfered with by binocular rivalry. We also demonstrate that amblyopia alters the Westheimer function in that it moderately broadens the desensitization branch and greatly enlarges the sensitization branch of the function. Taken together, these results suggest that the Westheimer function is more likely a cortical effect, probably reflecting the behavior of cortical spatial filters.

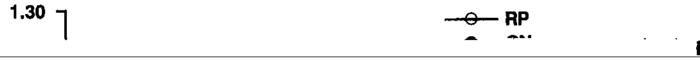
GENERAL METHODS

Observers

Normal observers. Three females aged 19–24 yr served in all dichoptic experiments. One male served in Experiment 3 only. All were slightly myopic and wore appropriate lenses to correct the vision of each eye to 20/20 or better. Their stereopsis, examined with the Randot Stereotest (Stereo Optical Co., Inc., Chicago, IL), was normal (20 sec). They had no prior psychophysical experience and were naïve as to the purpose of the study.

Amblyopic observers . Two amblyopes, highly experi- [redacted]

out), dichoptically transferred information (if any) could



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GENERAL DISCUSSION

impaired retinal structure in amblyopic eyes, their inference is problematic since the processing locus of the Westheimer function itself is still open to question. Furthermore, recently many lines of evidence have suggested that the retinal structures of amblyopic eyes of humans and primates are basically intact and the

1992; Yu & Essock, 1996a), like elongated receptive fields found in cortical area V1. The functions measured with either circular or rectangular stimuli not only share the same desensitization and sensitization ranges, but also have identical E_2 values when measured across the visual field (Yu & Essock, 1996b), as well as similar fields, to represent the responses of retinal ganglion cells. The experiments and modeling discussed above suggest that a simple retinal based model is unlikely. The main contribution of the present paper is to show that: (1) when the substantial and significant effects of rivalry and fixation disparity are carefully controlled, the Westheimer effect shows interocular transfer; and (2) that the Westheimer effect is abnormal in observers with amblyopia. In combination, we argue below that these results provide strong qualitative evidence for a cortical locus.

Interocular transfer provides clear evidence that a cortical locus is sufficient, but does it imply that a cortical locus is necessary? For example, one could argue that sensitization can occur both retinally and cortically. In this view, in the monoptic case, sensitization could be retinal, reducing threshold, and in the dichoptic case some central process could take place which also reduces threshold. We believe that this is unlikely. The striking similarity between the monocular and dichoptic effects (see Fig. 1) suggests that the same processes are active in

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