A CHOLINERGIC-SENSITIVE CHANNEL IN THE CAT VISUAL SYSTEM TUNED TO LOW SPATIAL FREQUENCIES
(Reprint)

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A Cholinergic Sensitive Channel in the Cat Visual System Tuned to Low Spatial Frequencies

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Physostigmine
Carbamate
Visual Evoked Response
Cat

See Back of Form
Visually evoked responses to counterphased gratings were recorded from the cat visual cortex before and after physostigmine administration. Physostigmine markedly reduced the responses to low spatial frequencies, but minimally affected the response to high frequencies. This effect is considered cholinergic since it could be reversed by atropine. These results support at least a two-channel model of spatial frequency responsivity.
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A Cholinergic-Sensitive Channel in the Cat Visual System Tuned to Low Spatial Frequencies

Abstract. Visually evoked responses to counterphased gratings were recorded from the cat visual cortex before and after physostigmine administration. Physostigmine markedly reduced the responses to low spatial frequencies, but minimally affected the response to high frequencies. This effect is considered cholinergic since it could be reversed by atropine. These results support at least a two-channel model of spatial frequency responsivity.

The application of Fourier theory to the analysis of the visual system has revealed quantitative and systematic information about its dynamics and organization. Campbell and Robson (1) suggested that the human visual system contains channels that are sensitive to different bands of spatial frequency (2). Since then, numerous psychophysical (3) and single-unit electrophysiological (4, 5) experiments have been conducted to elucidate the existence and nature of the channels.

According to the multichannel model, psychophysically obtained contrast sensitivity functions (6) are thought to represent the sensitivity of more than one detection mechanism and not the output of a single detector channel. In support of this model, visual cortical cells have been shown to be tuned relatively narrowly to spatial frequency (5). Problems are encountered, however, in trying to extrapolate single-unit response characteristics to their role in visual perception, for perception presumably represents the combined activity of populations of cells. Stronger agreement is observed between psychophysical results and results from experiments with visual evoked responses (VER's), which represent the “sum of massed neural events. For example, psychophysically obtained contrast sensitivity functions are positively correlated with curves derived from VER measures (7).

Cholinergic influences have been found at various stages of processing within the primary visual pathway (8). Altering the normal cholinergic activity at these stages and measuring a physiological response which is correlated with results from a psychophysical detection task may provide clues to the types of cells involved in the perceptual task. We wish to show that the carbamate physostigmine, which binds acetylcholinesterase (AChE) and thus prevents the hydrolysis of acetylcholine (ACh) at synaptic sites, preferentially reduces the response to low spatial frequencies. We used the VER as a measure of responsivity.

Anesthesia was induced in adult cats by ventilation of 3 to 4 percent halothane in a 3:1 gas mixture of nitrous oxide and carbogen and maintained with 1 to 2 percent halothane during surgical preparation. Cannulas were inserted into the trachea, one of the femoral arteries, and the two saphenous veins. To reduce eye movements, the two sympathetic trunks were cut and the animal was paralyzed by an infusion of Flaxedil (30 mg kg⁻¹ hour⁻¹) in an isotonic glucose solution. End-tidal CO₂ was maintained near 4 percent by adjusting the stroke volume of the respirator. The cat was held in a stereotaxic headholder, and core temperature was maintained at 37°C. During the experiment, halothane was removed from the gas mixture. Heart rate, blood pressure, lung resistance, and electroencephalogram (EEG) were continuously monitored. Arterial blood gas and cholinergic

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![Fig. 1. Peristimulus histogram averages (120-second collection period with a 1-msec sampling interval) for two spatial frequencies from a single experiment (cat 24). (A) Baseline VER's. (B) VER's after an injection of physostigmine (0.5 mg/kg). (C) Recovery VER's after injection of atropine sulphate (0.5 mg/kg). The bottom row depicts the 2-Hz square-wave alternation of the grating pattern. All response averages were collected with sine-wave gratings of 0.40 contrast \((L_{max} - L_{min})/(L_{max} + L_{min})\), where \(L\) is luminance.](image-url)
The influence of an abundance of cholinergic receptor sites on spatial frequency. Responses to low spatial frequencies were completely abolished (Fig. 2B). The effect was the same whether sine-wave (Fig. 1) or square-wave (Fig. 2) gratings were used.

The VER reduction could be due to secondary effects of AChE inactivation (for example, facilitated or inhibited release of other neurotransmitters that mediate the primary response). Since atropine reverses the VER depression (Fig. 1), excessive cholinergic stimulation within a pathway must mediate the effect.

It is tempting to describe our results in terms of a change in the response properties of a particular class or classes of cells that function in a detector-response channel, either in the cortex or subcortically. Kirby and Enroth-Cugell (13) have shown a pharmacological distinction in the receptive field properties between the X and Y retinal ganglion cells of the cat (14). Ikeda and Sheardown (15) have suggested that ACh enhances retinal Y cell responses while simply altering the maintained discharge of X cells. In a histochromic study of the cat lateral geniculate nucleus, Dean et al. (16) reported an abundance of AChE in layers A and Al where X cell terminations are predominantly found. Finally, Kemp et al. (17) have reported preliminary data showing that 94 percent of the cortical cells studied responded to ACh.

Lacking further information concerning cholinergic influences on functional cell classes in the cat and cortical cell contributions to the VER, we cannot ascribe our results to a loss of a subcortical input or to changes in response properties of a cortical cell class. However, our results do provide evidence for the existence of at least two detector-response channels located in the cat visual system and differentially sensitive to spatial frequency. Similarly, Snyder and Shapley (11) showed that the monocularly deprived eye of kittens had cortical VER's that were more depressed to low spatial frequencies than the VER's of the nondeprived eye. Although the selective depression caused by developmental manipulation was less pronounced than that reported here, consideration of the combined results suggests that cholinergic synapses failed to develop in the path-way from the deprived eye to the cortex.

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Spatial frequency is defined as the number of luminance varying periods (sinusoid or square wave) per unit of visual angle.


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