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LONG RANGE LATERAL INTERACTION IN THE ON AND OFF VISUAL
PATHWAYS OF HUMANS

by

PATRICK J. CLARK

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A DISSERTATION

Submitted to the graduate faculty of the University of Alabama at Birmingham,
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ABSTRACT OF DISSERTATION
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Title Long Range Lateral Interactions in the ON and OFF Visual Pathways of Humans

The human periphery effect (PE) is characterized by changes in target thresholds when the luminance of retinal areas that are located remote from the target locus is modulated. This study sought to determine whether the PE occurred in the ON and OFF visual pathways in humans, whether the magnitude of the PE was similar in the two pathways, and whether the observed effects were retinal or cortical in origin. This was done by determining the effect of peripheral stimulation on thresholds for detecting of flicker in rapid ON and rapid OFF sawtooth temporal waveforms.

Five subjects set thresholds, in four different paradigms, for detection of flicker in rapid ON and rapid OFF luminance modulated foveal stimuli. Stimuli were 1.2° and presented on a 4° steady white background of 41.0 cd/m^2 . Surrounding the background was a luminance-matched $16.0^\circ \times 22.0^\circ$ field that was either unmodulated (uniform control) or a 0.25-cpd vertical square wave grating that was counterphase modulated at 7.5 Hz. In Experiment 1, the test stimuli were flickered rapid ON or rapid OFF sawtooth waveforms on top of the background, whereas, in Experiment 2, they were modulated around the mean luminance of the background. In Experiment 3, the surrounding grating and target were either presented to the same or opposite eyes in a dichoptic viewing situation. Finally, in Experiment 4, full field flicker in the periphery was used to

investigate the underlying neural organization of the lateral interactions in the ON and OFF pathways.

A PE of nearly equal magnitude is found in both the ON and OFF pathways in humans when the peripheral stimulus is a grating. However, there appears to be a slight asymmetry in the organization of the pathways involved in the PE, particularly when a pedestal presentation for the stimulus is used. The locus of the effects of remote stimulation on flicker thresholds at higher frequencies appears to be retinal in origin. Finally, all PE results varied by frequency and took on a band pass nature, with the most sensitive thresholds and larger PE effects occurring in the middle temporal frequencies.

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INTRODUCTION

It has been estimated that somewhere between one third and one half of the human brain is devoted to some function related to vision. For neurological purposes vision starts with the brain's visual receptor known as the retina. In years long past, the retina was merely thought to be a collector of photons whose main function was to create and relay action potentials to the cortex. As science delved deeper into the intricacies of the retina, it has come to be appreciated not as a passive collector of light stimuli, but as a complex processor of light stimulation well before it is ever transmitted deeper into the brain. Furthermore, if we think of the retina as being a forward projection of the brain, then insights into its nature and the nature of vision take on a particular importance. Among the disciplines that are used to study the function and nature of vision is psychophysics. Through careful observations and experiments, psychophysical investigators have greatly expanded upon our knowledge of the visual system. Physiological vision discoveries often have a psychophysical correlate, and almost anything found psychophysically will have a physiological etiology. The visual phenomena known as the human periphery effect (PE) represents a particularly interesting area of study for psychophysical and physiological relationships in the visual system. Studies of the human periphery effect have as their goal the expansion of knowledge concerning the nature of the human visual system and relationships among psychophysics and physiological observations.

Periphery Effect

The PE was first described physiologically in cat by James McIlwain (1964). McIlwain not only endeavored to describe the characteristics of the center and surrounds of retina neurons but also to define the extent of the surround organization. Using a tangent screen and circular stimuli ranging from 0.5° to 10.0° in diameter, he plotted centers and surrounds of optic tract axons and neurons in the lateral geniculate nucleus (LGN). While performing these experiments, he discovered that moving a 3° black disk at 50° in the periphery had an excitatory effect on the LGN cells he was recording from. Excitation of the cells was observed as an increase in action potentials (firing rate) above spontaneous levels. It was important that the disc was moving; a stationary disc had no effect. It appeared to McIlwain that the black disc was able to influence retinal neurons from well outside the cell's classical receptive field. He termed this influence the periphery effect.

However, McIlwain could not rule out the possibility that his findings were the result of stray or scattered light. Ruling out stray or scattered light was accomplished by Levick, Oyster, and Davis (1965). They reasoned that if the PE was caused by stray light, then its magnitude should decrease as the background illumination was reduced. They discovered that reducing background illumination by a substantial amount did not cause the periphery effect to diminish. They also found that shapes with sharp edges such as triangles, rhomboids, and rectangles provided a stronger response than did a black disc. McIlwain (1966) confirmed this finding by discovering that alternating black and white stripes, which comprised a grating, were very effective in generating the periphery effect. McIlwain's grating or *interrupted stimulus* has remained the most common means of inducing the periphery effect in both physiological and psychophysical studies.

After the initial studies by McIlwain (1964, 1966) other investigators discovered that the PE was not uniform across different cell types. Using a small (1.5°), bright (220 cd/m^2), flashing light as a target and a rotating sector disc of alternating black and white wedges as the peripheral stimulus, Ikeda and Wright (1972a) classified responses from cat optic (nerve or tract) axons as being either *transient* or *sustained*. They reported that a PE was obtained in about half of the transient cells and was never found in the sustained cells. A number of other investigators classified cat retinal ganglion cells as *X* or *Y* according to the criteria described by Enroth-Cugell and Robson (1966) and reported finding a PE in both cell types including the sustained or X type cells (Derrington & Felisberti, 1998; Fischer, Kruger, & Droll, 1975; Hamasaki & Hanada, 1983; Kruger, 1981; Kruger & Fischer, 1973; Passaglia, Enroth-Cugell, & Troy, 2001; Rapaport & Stone, 1988). However, the proportion of X cells exhibiting a PE was usually lower than that of Y cells. Furthermore, the PE finding of most research (the notable exception being Derrington & Felisberti, 1998) has shown that, in Y cells, the PE tended to be strong and brisk, whereas in X-cells, the PE was weak and sluggish. An example of the difference between the X and Y cells is shown in Figure 1 along with a depiction of the peripheral stimulus. The peripheral stimulus was a 30° inner diameter, 70° outer diameter annular grating. The receptive field of the cells was centered in the 30° blank area, and the grating that was shifted one half a period to elicit the periphery effect. In both X and Y cells, the peripheral stimulus increased the firing rate above baseline, but the effect is clearly greater in Y cells.

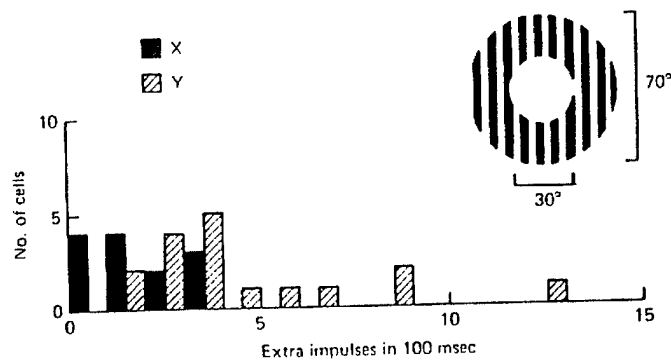


Figure 1. X and Y cells. Originally from Derrington, Lennie, & Wright (1979) The mechanism of peripheral evoked responses in retinal ganglion cells. Journal of Physiology, 289, page 301. Permission to reprint granted by Blackwell Publishing.

The stimulus configuration shown in Figure 1 is typical of PE studies. Flickering, drifting, or counterphasing gratings have been used to generate the PE, as have gratings that are shifted by a half cycle. The effect observed with shifting gratings is referred to as the *shift effect* which Fischer et al. (1975) advocated in order to avoid the misleading and perhaps confusing association with the periphery. The response generated in retinal ganglion cells and cells in the LGN by a grating shift is usually more robust than that found with gratings that are modulated over longer temporal intervals. However, the shift and periphery effects are generally thought to be nothing more than different manifestations of the same phenomenon (Kruger, 1980).

Retinal ganglion and LGN cells can also be classified as ON center or OFF center, depending on whether or not the receptive field center responds to the onset increases or offset decreases of light, respectively. This also applies to the X or Y classification because there are both ON-, and OFF-center cells of these two types. Studies in cat report a PE or shift effect in both ON-, and OFF-center cells (Cleland, Dubin, & Levick, 1971;

Derrington & Felisberti, 1998; Derrington, Lennie, & Wright, 1979; Felisberti & Derrington, 1999; Hamasaki & Hanada, 1983; Ikeda & Wright, 1972b; Kruger & Fischer, 1973; Levick et al., 1965; Passaglia et al., 2001). Furthermore, the magnitude of the response in the ON and OFF cells has usually been found to be similar (Hamasaki & Hanada, 1983; Kruger & Fischer, 1973; Passaglia et al., 2001), but see Fischer et al. (1975).

Although the periphery or shift effect was first studied in cat, it has also been found and studied physiologically in the rhesus monkey (Kruger, 1977; Kruger, Fischer, & Barth, 1975; Marrocco, McClurkin, & Young, 1982) and in a New-World monkey, the marmoset (Felisberti & Derrington, 2001). Kruger et al. (1975) found an excitatory shift effect in both ON and OFF-center retinal ganglion cells. However, they noted that the monkey's shift effect was smaller in amplitude and more sensitive to a stationary spatial pattern than that found in cat. They also found the shift effect was not restricted to regions beyond the receptive field or peripheral retina, but could be obtained from any part of the retina. Kruger (1977) and Marrocco et al. (1982) also recorded responses from cells located in the magnocellular and parvocellular layers of LGN of rhesus monkeys. Kruger found that 86% (73 of 81) of cells in the magnocellular layers showed a shift effect that he described as clear and excitatory. In contrast, only 31% (26 of 85) of cells in the parvocellular layers demonstrated a shift effect, and, in most cells, it was weak and inhibitory. These results were obtained in both ON and OFF-center cells. Similarly, Marrocco et al. found the PE was 5 times more prevalent in magnocellular cells (M cells) than in parvocellular cells (P cells). However, the overall percentage of M cells that showed the effect was found to be only 25%. This was a much smaller percentage than the 86% reported by Kruger (1977).

Results from a New-World monkey are somewhat different. In the marmoset, Felisberti and Derrington (2001) found that M and P cells were equally likely to show a shift affect. Furthermore, although the effect was stronger in M cells, the difference was not as great as reported in rhesus by Kruger (Kruger, 1977; Kruger et al., 1975). With respect to ON- and OFF-center cells, there appeared to be differences in the magnitude of the shift effect. The OFF-center M cells in marmoset showed a significantly stronger effect than ON- center M cells, ON-center P cells, and OFF-center P cells.

During the sequence of more than 30 years of physiological studies in cat and monkey, a number of properties of the PE have been described. Several of these have already been discussed, including the similarities in prevalence and strength of the PE in ON- and OFF-center cells as well as the differences between cat X and Y cells or monkey M and P cells. Two other properties of the physiological PE observed in cat are that it first appears at very low contrast of the peripheral stimulus and that the response saturates over a narrow contrast range (Fischer et al., 1975). The non-linear nature of the function is so robust in cat that it has been referred to as an "all-or-none" type phenomenon. These all or none phenomena are illustrated in Figure 2, in which the mean response peak discharge for two ON-center cat ganglion cells (open circles) and two OFF- center (closed circles) cat ganglion cells are illustrated. The number of times the neuron was tested is indicated to the right of the curves.

Additional characteristics of the PE are that it decreases in magnitude as a function of increasing distance between the peripheral stimulus and receptive field (Fischer et al., 1975), but, in general, the PE increases in magnitude with increasing eccentricity

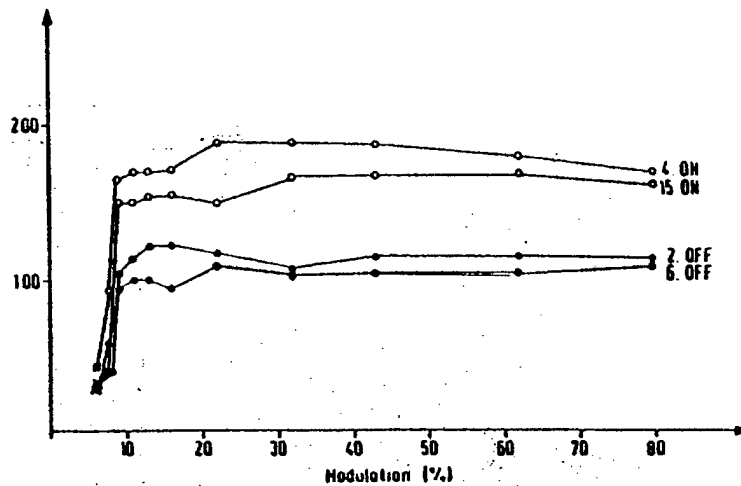


Figure 2. ON and OFF "all or none" Originally from Fischer, Kruger, and Droll (1975) Quantitative aspects of the shift-effect in cat retinal ganglion cells. *Brain Research*, 83, p. 396. Permission to reprint granted by Elsevier Science.

(Hamasaki & Hanada, 1983; Rappaport & Stone, 1988). Illumination levels at the receptive field center can also affect PE strength in ON- and OFF-center cells (Fischer et al., 1975; Ikeda & Wright, 1972b; Kruger & Fischer, 1973). It is more robust in ON-center cells when the receptive field is illuminated and in OFF-center cells when it is not (Kruger & Fischer.). As noted in several studies, the PE can be obtained anywhere in the retina (Kruger, 1980; McIlwain, 1966). It is also possible to stimulate retinal areas near and including the *area centralis* to generate a PE in cells located in the peripheral retina (McIlwain, 1964). Thus, the PE signal does not travel in just one direction, from the peripheral retina to more central locations, as the name seems to imply. In addition, the PE signal can cross over the vertical meridian (Fischer et al., 1975; Kuyk & Niculescu, 2001; McIlwain, 1964).

Periphery Effect in Human

It was not long after McIlwain's (1964) discovery that scientists began looking for psychophysical correlates to the physiological PE in man. Spillman and Gambone (1971) were the first to attempt this by using a disc with 72 alternating black and white stripes. Each stripe was 5.0° wide, and the disc was rotated at 40.0° per second. The disc consisted of a 15.7° inner diameter and an outer diameter of 61.6° . They tested the incremental threshold for a flash on the nasal horizontal meridian of one eye at various distances from the center of the disc and were unable to demonstrate the effect. This was perhaps because they used a dark background in the center blank area of the disc and created what Kruger would term inadequate *illumination*, in which he found that the shift effect was often abolished. (Kruger et al., 1975). Shortly after this failure to find a PE, Sharpe (1972) did find evidence of a PE in humans. He noticed that the entopic shadow of retinal blood vessels were not visible below scanning frequencies of 2 Hz, but if a black card was moved across the top half of the visual field, then the vessels could be seen below the scanning frequencies of 2 Hz.

More convincing evidence for a PE in humans came from a series of papers in 1979 and 1980 by Breitmeyer and colleagues (Breitmeyer & Valberg, 1979; Breitmeyer, Valberg, Kurtenbach, & Neumeier, 1980; Valberg & Breitmeyer, 1980). Their stimulus paradigm, shown in Figure 3, bears many similarities with those used in physiological studies.

The testing paradigm consisted of a 0.38° test spot, flashed for 100 ms on the center of a 7° steady white background, which was surrounded by a 26.0° by 19.5° grating. The grating (either a square or sine wave) had a spatial frequency of 0.53 cycles per

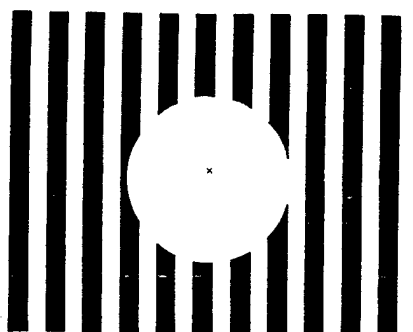


Figure 3. Breitmeyer stimulus. Originally from Breitmeyer, Valberg, Kurtenbach, and Neumeyer (1980), *Vision Research*, 20, p. 800. Permission to reprint granted by Elsevier.

degree and was temporally modulated in counterphase at varying frequencies. Breitmeyer et al. (1980) compared the threshold luminance of the test spot with and without a grating present. They determined that an approximately 0.3- to 0.4-log-unit decrease in sensitivity to the test flash resulted when either the square or sine wave gratings were present and modulated at 4 Hertz.

Since the initial studies by Breitmeyer et al. (1980), a number of investigators have conducted experiments on the periphery or shift effects in human observers. Some of the findings closely parallel what had been previously discovered physiologically. Furthermore, other findings contributed information about the human PE that did not so far have a physiological correlate. In the latter case, physiological correlates are lacking because what has been studied in humans has not been examined in other animals.

One of the findings reported by Breitmeyer and Valberg (1979) was that the human PE was restricted to the fovea. This finding was not consistent with physiological studies in which a PE could be obtained throughout the retina and in which the PE increased in strength with eccentricity. However, other psychophysical studies indicate a

PE can be obtained in humans outside the fovea and, like the physiological findings, that the magnitude of the effect increases with eccentricity (Brooks & Impleman, 1981; Cope & Kuyk, 2001; Kuyk, Elliott, & Fuhr, 1999). Furthermore, Mattingley and Badcock (1991) found that stimulating near the fovea with a shifting grating reduced sensitivity to peripheral targets. One difference between these studies and Valberg and Breitmeyer's is that smaller stimuli were used by Valberg and Breitmeyer. Stimuli size may explain why a PE is not always obtained outside the fovea.

Other physiological characteristics of the PE that have psychophysical correlates in humans are that the human PE has a non-linear contrast response function (Fuhr & Kuyk, 1998) and it crosses the vertical meridian (Kuyk & Niculescu, 2001). In addition, Breitmeyer et al. (1980) and later Kuyk and Fuhr (1993) reported that the shift effect diminished in magnitude as a function of the size of the background disc. In other words, the further the peripheral stimulus was from the test spot, the weaker the effect. Similar results were reported in cat by McIlwain (1964) and Fischer et al. (1975).

Studies of the human periphery and shift effects have also revealed characteristics of the phenomena that do not as yet have physiological correlates. Of particular interest are studies that have tied the human PE to a luminance mechanism but not to chromatic mechanisms. It has often been speculated that the luminance and chromatic channels correspond, respectively, to the M- and P-cell pathways that originate in retina and remain segregated into the visual cortex. He and Loop (1990) revealed through spectral sensitivity functions that detection thresholds for percepts that generated curves with a single peak at middle wavelengths were elevated by peripheral stimulation, whereas those that generated three peaked functions were not. The two forms of spectral sensitivity curves

have been associated with luminance and chromatic mechanisms, respectively. Subsequent studies have verified the findings of He and Loop (DeMarco, Brigell & Gordon, 1997; Kuyk & Fuhr, 1993; Kuyk & Fuhr, 1994). Other evidence supporting this association comes from studies reporting that low, but not high, spatial frequency gratings are affected by remote peripheral stimulation (Derrington, Krauskopf, & Lennie, 1984; Marrocco et al., 1982). Accordingly, M cells are more sensitive to low spatial frequencies than are P cells (Derrington & Lennie, 1984).

Mechanism of Action

Although much has been characterized about the nature of the PE, there exists no study that definitively demonstrates the retinal mechanism that allows the PE to occur. Given its lateral nature, it would appear that horizontal cells or amacrine cells would be primary candidates for carrying a PE signal laterally over a large retinal distance. Horizontal cell connections as mediating the periphery effect can almost certainly be eliminated due to their dependence on gap junctions to transmit signals laterally. Physiologic recordings have demonstrated that the periphery effect can occur by stimulation of well over 20° or more (Barlow, Derrington, Harris, & Lennie, 1977; Kruger & Fischer, 1973). Horizontal cells, either H1 or H2, do not appear to have the receptive field size to account for this long-range interaction. (Mills & Massey 2000, Piccolino, Neyton, & Gershenfeld, 1984). In fact, the largest peripheral dendritic field diameter of an H1 cell is less than 160 μm (Rodieck, 1998). This coverage falls far short of what is needed to account for the dendritic field, which would need to transverse distances that are beyond 20° (Drasdo & Fowler, 1974). Furthermore, the length constant of the horizontal cells being coupled by

gap junctions is also insufficient to mediate the spread. (Benda, Bock, Rujan, & Ammermuller, 2001)

Since the earliest studies, it has been widely suspected that the amacrine cells of the inner retina are responsible for mediating the periphery effect (Barlow et al., 1977; Dowling & Boycott, 1966; Hamasaki & Maguire, 1985). This would seem a plausible explanation because some amacrine cells have the ability to create and transmit action potentials or spikes (Dacey, 1999). Studies of polyaxonal cells in rabbits have revealed several different types and morphologic features, with some of the cells demonstrating bistratification, while others only stratify in the ON or OFF sublamina of the inner plexiform layer. (Famiglietti, 1992; Volgyi, Xin, Amarillo, & Bloomfield, 2001) Thus, it seems that the path for the periphery effect signal would most likely include amacrine cells.

Retinal vs. Nonretinal Origin of the PE

Although the origin of the PE in cat and monkey is obvious, a question that often arises in psychophysical studies of the PE is whether or not the changes observed with peripheral stimulation are retinal or cortical in origin. A method for making this distinction is to compare the results taken under monocular and dichoptic viewing conditions. In the monocular situation, in which the same eye views the target and the peripheral stimuli, it is possible to have interactions between them that are certainly retinal in origin. In the dichoptic condition, the target is presented to one eye and the peripheral stimulus to the other, creating a situation that precludes any retinal interactions. In the dichoptic condition, the signals are generated in different eyes by the target and the peripheral stimu-

lus, which remain separated until they reach visual cortex. If a visual signal is being processed primarily by the retina, then the subjects' monocular and dichoptic thresholds will reflect these differences. Specifically, if the PE is observed under monocular viewing and if the PE is of a retinal origin, then under dichoptic viewing, the PE should not be observed. Conversely, if a PE is observed under monocular and dichoptic conditions, the conclusion would be that the PE was not retinal in origin. Results from two experiments suggest the psychophysical PE has a retinal origin. Dortmann and Spillmann (1981) found both facilitation and inhibition in a shift-effect paradigm under monocular viewing, but no effects dichoptically. Similarly, He and Loop (1990) found no effect of a flickering surround on test flicker thresholds under dichoptic conditions, whereas there was a significant effect on test flicker thresholds under monocular conditions.

Masking

The periphery and shift effects are characterized and defined by a spatial separation between the peripheral stimulus and the target. In physiological studies, this distance can be upwards of 40° (McIlwain, 1964). In psychophysical studies, it is usually on the order of 1° to 10° . However, a number of studies have produced results that have been related to the periphery or shift effects even though the test conditions are not precisely those that define a true PE. Such studies have used stimulus conditions that qualify them as metacontrast or nonmetacontrast masking. Perhaps some of the confusion has arisen because the psychophysical periphery effect has been referred to as a masking phenomenon. In any event, results from such metacontrast and non-metacontrast masking experiments have not been included in this dissertation's discussion of the psychophysical PE.

Examples of the stimulus conditions that define the PE are shown in Figures 1, and 2. In contrast, Figure 4 illustrates the conditions that define many of the metacontrast and nonmetacontrast masking paradigms. In general, visual masking experiments fall into three types of masking. If the paradigm uses a condition in which the mask and the stimulus share a common border, then this is known as *metacontrast*. The stimulus target can either be enclosed by the mask or flanked by the mask. *Surround masking* can refer to either an enclosed or flanked stimulus. (Green 1983) If the mask overlaps the stimulus target, then the paradigm is termed *non-metacontrast* masking.

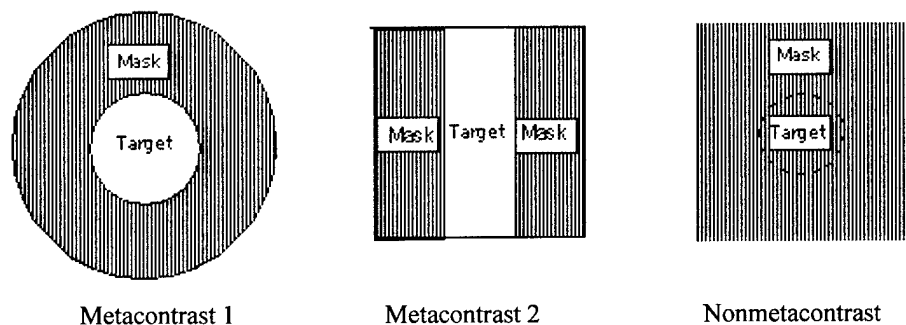


Figure 4. Masking paradigms. Of great importance are the details that in metacontrast 1 and 2, the target and mask share a border, whereas in nonmetacontrast they overlap. This is in contrast to the PE paradigm, where no border is shared.

The PE differs from the metacontrast paradigm in that there is a separation between the mask and the target. This is an important distinction, and one must be cautious when reading papers about the peripheral effect. Some of them use metacontrast masking and may, in fact, be quite different from a peripheral effect stimulus. In order to clarify and

avoid any confusion, Figure 5 is provided to illustrate the terms that will be used to describe the PE paradigm that will be most commonly discussed in the course of this study.

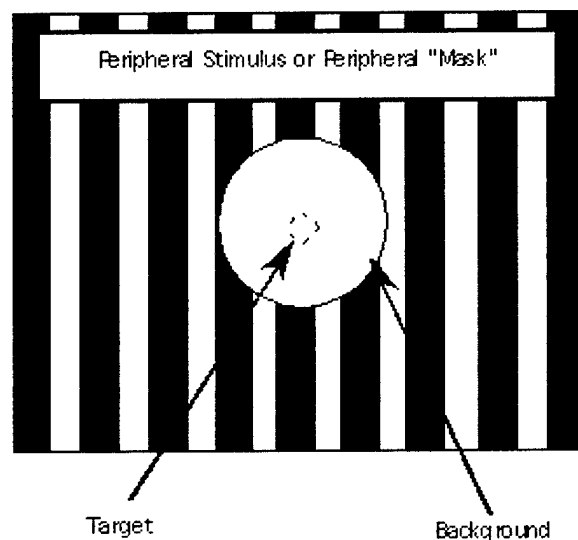


Figure 5. Periphery effect paradigm. Shown are Target, Background, and Peripheral Stimulus, otherwise often known as a peripheral mask.

A Gap in Knowledge

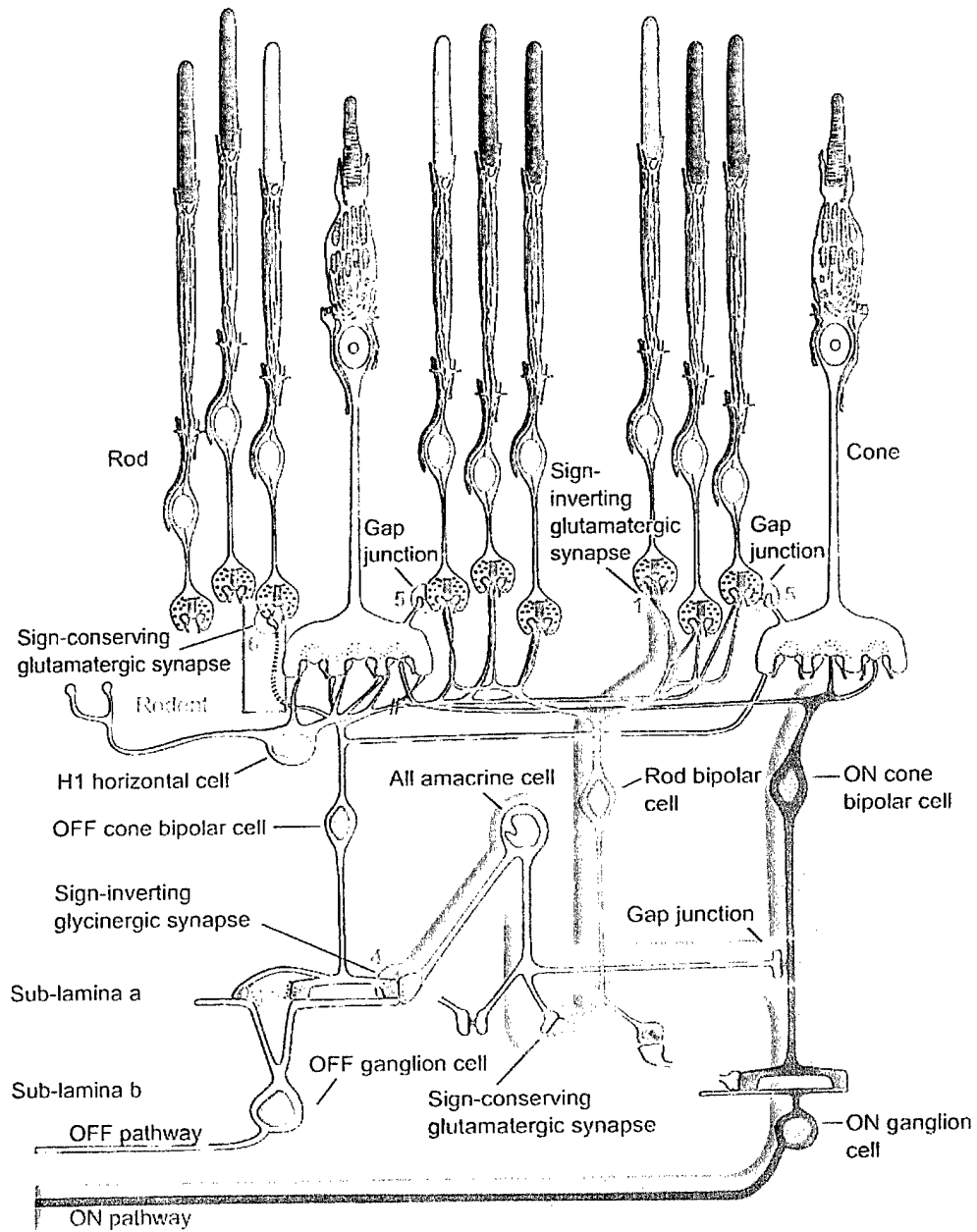
One feature of the physiological PE observed in both cat and rhesus monkey is that it occurs in both ON- and OFF-center cells with approximately the same magnitude. (Hamasaki & Hanada, 1983; Ikeda & Wright, 1972b; Kruger, Fischer, & Barth, 1975; McIlwain, 1966). However, beyond some pilot data (Clark & Kuyk, 2002), nothing was previously known about the effects of remote peripheral stimulation on discriminations mediated by the human ON and OFF pathways. The overall purpose of the experiments utilized in this study was to begin filling in this information gap. This was accomplished

by specifically using sawtooth waveforms as target stimuli and a peripheral stimulus consisting either of a grating or a full-field sawtooth.

ON and OFF Pathways

From the bipolar cells onward, some cells respond to increases in light, others to decreases. This separation into ON and OFF pathways is a critical feature of the visual system that has been studied both physiologically and psychophysically. The general organization of the ON and OFF pathways is illustrated nicely in Figure 6 from Sharpe and Stockman (1999). The pathways involve both rods and cones, but for now we will concern ourselves with only the cone pathways.

There is clear separation of ON and OFF signal processing within the retina. The cone ON pathway involves synaptic transmission from cones onto ON cone bipolar cells. In the dark, the cone is releasing glutamate, and activation of opsin ultimately results in the hyperpolarization of the cell, which, in turn, will stop the release of glutamate. The cone pedicle contacts the ribbon-associated, invaginating, sign inverting, metabotropic receptors on the cone ON bipolar cells. The ON cone bipolar cells then synapse with ON ganglion cells in sublamina *b* in the inner plexiform layer of the retina. The cones also contact the flat, sign-conserving, ionotropic OFF cone bipolar cells. The output of these bipolar cells is to the OFF ganglion cells via synapses located in sublamina *a* of the inner plexiform layers (Oyster, 1999).



trends in Neurosciences

Figure 6. ON and OFF pathways. Originally from Sharpe and Stockman (1999). Rod pathways: The importance of seeing nothing. Trends in Neurosciences, 22, p. 498. Permission to reprint granted by Elsevier Science.

Studying the ON and OFF Pathways

ON and OFF pathways have been studied physiologically and psychophysically with flashed increments and decrements of light as well as rapid-ON and rapid-OFF flicker. Flicker is the repetitive onset and offset of light, or put another way, the modulation of the intensity (contrast) of light stimuli over time. Flicker may have many different waveforms, including sinusoidal, square, or sawtooth. The sinusoidal and square waves are familiar concepts in vision science. A sinusoidal waveform and some of its characteristics are shown in Figure 7.

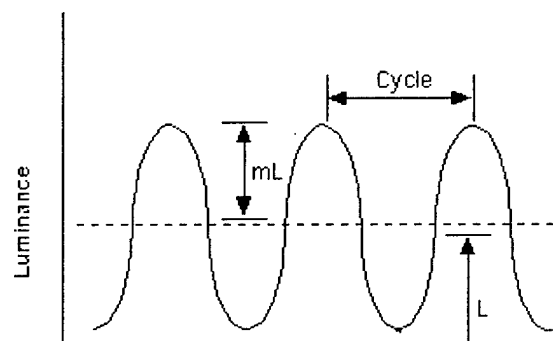


Figure 7. Sine waveform.

In Figure 7, L represents the average background luminance, and m varies between the value 0 and 1. The value m represents the ratio of the peak or trough height to L . Commonly, the modulated amplitude of the wave is termed mL . If psychophysical testing is done, and the subject is asked when he or she can see a luminous wave stimulus as flickering vs. when it is steady, we obtain functions like those depicted in Figure 8 of Kelly and DeLange (DeLange, 1958; Kelly, 1961, 1972).

In the curve on the left, Kelly used a large spot stimulus while DeLange's curve on the right used a small stimulus. Note the similarities between the two curves. In both sets of data, the curves for all retinal illuminance levels tend to converge to a common value at the lower frequencies. Since the modulation, m , is analogous to the Weber fraction, this low-frequency behavior is in accordance with the Weber-Fechner Law (Kelly, 1972).

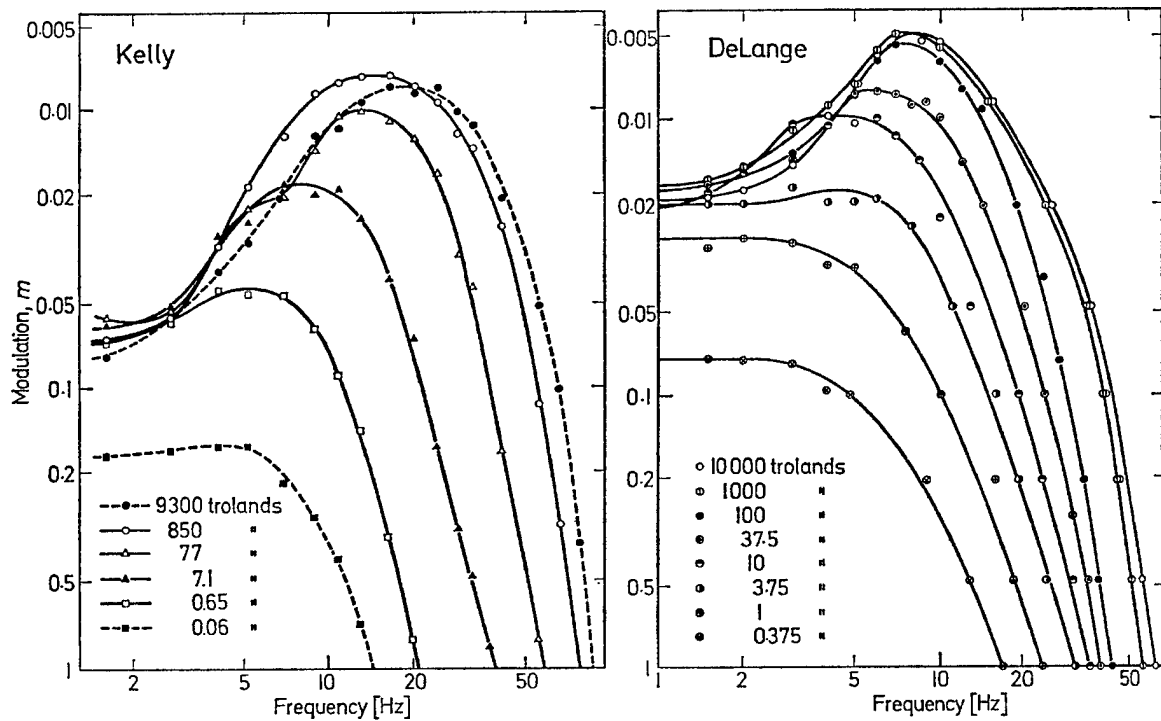


Figure 8. Kelly and DeLange. Originally from Handbook of Sensory Physiology VII/4, p. 280. Permission to reprint granted by Sterling-Verlag, Heidelberg, Germany.

In studies of the ON and OFF pathways, another flickering waveform, the sawtooth, has been used to generate response curves. The sawtooth can be defined by the Fourier series function $f(x) = 2a/\pi(\sin x + \sin 2x/2 + \sin 3x/3\dots)$. Where x is expressed in radians and a is the amplitude of the function (Bowen, Pokorny, & Smith, 1989). The rise and fall of the sawtooth can give us a rapid ON appearance or a rapid OFF appearance depending on whether the terms in the series are positive or negative. This waveform can be represented as such.



Figure 9. Rapid ON and rapid OFF.

The sudden onset of the rapid ON when presented could conceivably stimulate the ON visual pathway more than the OFF, and, similarly, the rapid OFF could stimulate the OFF pathway more than the ON. There is, in fact, experimental evidence consistent with this interpretation. Adaptation studies such as that by Hanly and MacKay (1979) and that of Purkiss, Hughes, and DeMarco (2001) have shown polarity sensitive adaptation that is consistent with there being separate ON and OFF pathways. In other words, a rapid-ON mask would have more of an effect on a rapid-ON target than it would have upon a rapid-OFF target. Similarly, DeMarco, Hughes, and Purkiss (2000), using a Gaussian mask, found that thresholds were elevated most when the mask and the stimuli had the same

sign. Other evidence of selectivity comes from studies such as that of Bowen, Porkorny, and Smith (1989), who found contrast sensitivities to sawtooth flicker depended on whether it was rapid ON or rapid OFF. Specifically, Bowen et al., measured contrast sensitivity to sawtooth flicker and were able to show that their observers were more sensitive to the rapid-OFF flicker across a range of 2-26 Hz. This is illustrated in Figure 10.

Also of note in Figure 10 is that the two observers were more sensitive to the rapid OFF at frequencies below 13 Hz. The advantage was about 0.1 log units for decremental stimuli (rapid-OFF) over incremental stimuli (rapid-ON). In addition, Purkiss, Hughes, and DeMarco (2001) examined the adaptation characteristics of three observers to sawtooth stimuli. Under photopic conditions, two observers were more sensitive to the rapid OFF than to rapid ON. However, one was more sensitive to rapid ON than to rapid OFF. After adapting to sawtooth waveforms, the thresholds for the rapid ON stimuli were raised more than the rapid OFF. Furthermore, rapid ON adaptation had the greatest effect on rapid ON stimulus detection. (Purkiss, Hughes, & DeMarco).

Experimental Overview

Four experiments were completed to test four hypotheses about the PE in human ON and OFF pathways. The first experiment was designed to determine whether a PE would be observed in both ON and OFF pathways in humans, and whether the PE would be of approximately the same magnitude upon both pathways. These predictions were based on physiological findings in cat and monkey ON and OFF center cells. The second experiment was designed to determine whether the method of presenting sawtooth wave-

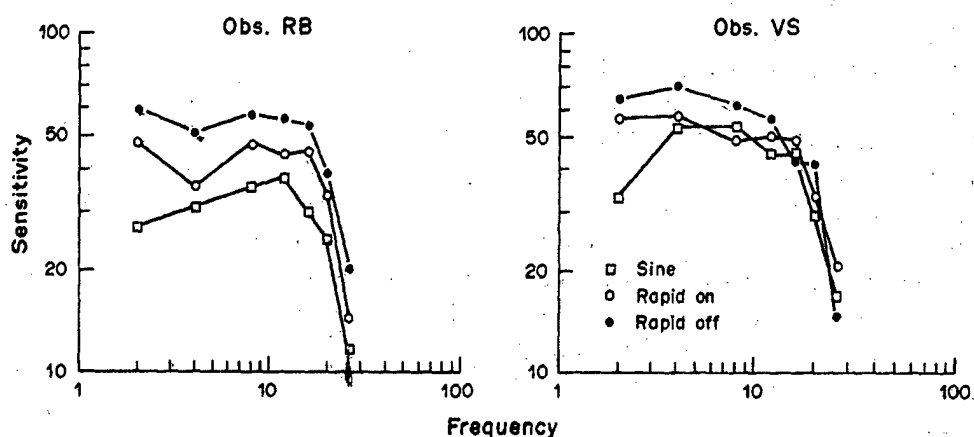


Figure 10. Bowen Rapid ON/OFF flicker. Originally from Bowen, Pokorny, & Smith, (1989) Sawtooth contrast sensitivity: decrements have the edge. *Vision Research*, 29, p. 1504. Permission to reprint granted by Elsevier Science.

forms, on top of the background or modulated around the luminance of the background, affects the results, in particular the magnitude of the PE in ON and OFF pathways. It was predicted that detection thresholds would be affected but that the PE would not be changed by the presentation. The third experiment was constructed in order to determine whether the PE measured in Experiments 1 and 2 is retinal or cortical in origin. It is predicted that the PE is retinal in origin and that no PE will be found under dichoptic viewing conditions. The aim of the fourth experiment was to investigate whether there is a general bistratified PE signal or whether there are specific ON layer and OFF layer PE signals. The prediction was that the PE signal would be a general one and that stimulating ON or OFF pathways in the periphery would not result in selective effects on foveal responses to rapid-ON or -OFF sawtooth flicker. In other words, regardless of which pathway is stimulated in the periphery, the effects on foveal thresholds for ON and OFF flicker would be the same.

MATERIALS AND METHODS

Subjects

Subjects were two experienced and three naïve psychophysical observers who participated in all four experiments. A brief eye health history was taken in order to screen for any color anomalies, binocular deficiencies, or any visual problems. Subjects were tested for distance and near visual acuities. In addition, an Ishihara plate discrimination test was performed. The Birmingham Veterans Administration Medical Center Institutional Review Board approved the project, and all subjects signed informed consent prior to participation in the study. The Birmingham Veterans Administration Institutional Review Board (IRB), Department of Veterans Affairs Medical Center, VA Research Services, approval may be found in Appendix A.

Apparatus

A Vision Works computer graphic system was used for the experiments (Vision Research Graphics, Inc., Durham, NH). The system uses a Cambridge Research Systems VSG 3/X controller. All stimuli were presented on a 21-in FlexScan FXE7S red, green, blue (RGB) monitor with a 1600 x 1200 resolution and a refresh rate of 110 Hz. The monitor had an ultra-short persistence p46 phosphor. A Tektronix J16 Digital Photometer with probe and a HP 1741A Oscilloscope (100MHz) was used to calibrate the system. Observers viewed the monitor from a distance of 75.0 cm in Experiments 1, 2, and 4, and from 57.3 cm in Experiment 3. A chin rest was used to stabilize observers' heads. A light-tight box, open at one end, was used to limit stray light from returning to the monitor after reflecting off laboratory room walls. For dichoptic viewing in Experiment 3,

subjects were moved to 57.3 cm from the screen, and the stimulus and mask were scaled appropriately. A silver prismatic mirror was used to create an overlapping image of the screen. All experimental data were collected using the psychophysical method of yes/no QUEST.

Subjects were instructed to respond to the perception of flicker. All subjects were asked to respond only if they perceived a flickering stimulus and not to respond if they only perceived that something might have appeared to only flash. Test conditions within an experiment were counterbalanced across test sessions. Most subjects were tested for about 2 hr a day with 5-min breaks every 30 min. It took subjects approximately 42 hr of testing time to complete all the experiments.

Procedures

Experiment 1 (Rapid-ON, Rapid-OFF Pedestal Experiment). The purpose of Experiment 1 was to determine whether detection of rapid-ON and rapid-OFF sawtooth flicker was affected by peripheral stimulation, and, if so, whether the magnitude of the effects for the two waveforms were the same or different. The expected outcome was that the thresholds for rapid-ON and -OFF flicker would be equally affected by peripheral stimulation. These are the first two hypotheses, and they are based on findings in monkey and cat ganglion and LGN cells. It was also anticipated that subjects would be more sensitive to the rapid-OFF flicker than to the rapid -ON flicker (Bowen et al., 1989).

The stimulus configuration consisted of a 1.2° achromatic test spot presented on a 41.0 cd/m², 4° achromatic background. The larger background served to separate the test spot from the peripheral stimulus and clearly establish the experiment as dealing with the

periphery effect and not metacontrast masking. The test spot was luminance modulated, rapid ON or rapid OFF, at 1.5, 3, 10, 20, or 24 Hz and was presented at the fovea.

Surrounding the 4.0° background was a 16.0° by 22.0° degree field of the same luminance as the background. It was either unmodulated (uniform, no peripheral stimulation condition) or was a 0.25-cycles-per-degree, vertical-square-wave grating that was counterphase modulated (pattern reversal) at 7.5 Hz (peripheral stimulation condition). A graphic representation of the target area, background, and the peripheral grating stimulus is depicted in Figure 11.

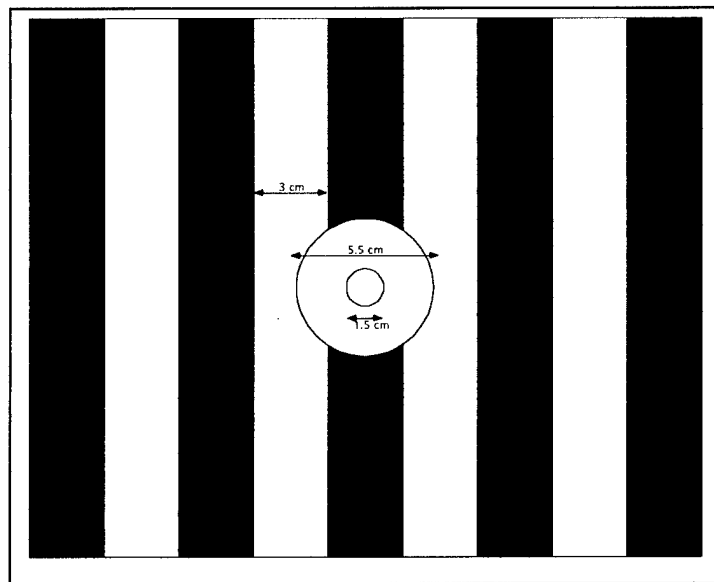


Figure 11. Periphery effect target and stimulus.

In all experiments, onset of the peripheral stimulus grating preceded presentation of the test spot. The sequence of the presentation of the peripheral grating stimulus and test spot

are depicted in Figure 12. The test spot was presented in a pedestal fashion on top of the background. Thus the general nature of the luminance appearance of the target is shown in graphic form in Figure 13.

Because the grating, which is the peripheral stimulus, was expected to have a similar effect on both the rapid-ON and the rapid-OFF targets, results were expected to look something like those depicted in the hypothetical graph of Figure 14. In Figure 14, *OFF Constant* and *ON Constant* refer to the condition when the peripheral grating was not present. *OFF Modulated* and *ON Modulated* refer to the condition in which the periphery effect was being induced by a grating. The graph also shows the expected overall higher sensitivity to the rapid-OFF waveform, which had been previously predicted and found by others.

Experiment 2 (Rapid-ON, Rapid-OFF Counterphase experiment). This experiment utilized the same testing conditions and procedures as Experiment 1, except the target waveforms were counterphase modulated around the mean luminance of the background rather than presented as pedestals on top of the background. This is illustrated in Figure 15. It had been found that luminance pedestal targets differ from mean modulated targets in that the thresholds for the pedestal targets are higher because the average luminance is higher. Additionally, at low flicker frequencies, luminance pedestal thresholds are elevated by edge contrast produced by the pedestal and the surround (Anderson & Vingrys, 2000). If this had occurred in Experiment 2, it would have been revealed by lower thresholds for the mean modulated target than those obtained in Experiment 1. However, even if thresholds for mean modulated targets are lower, one

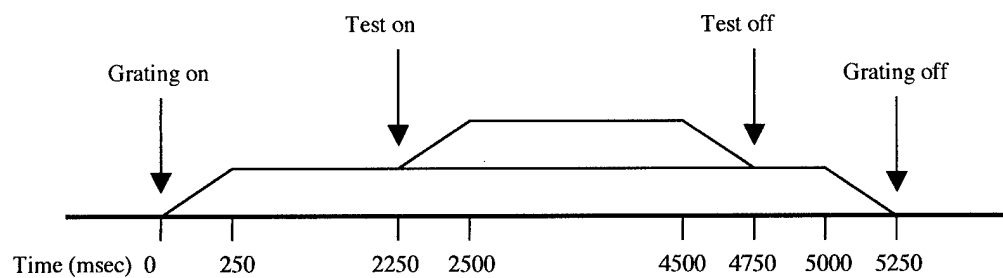


Figure 12. Stimulus and target onset and offset.

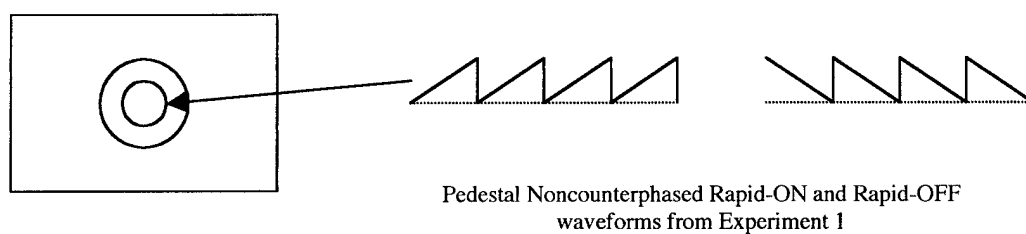


Figure 13. Experiment 1.

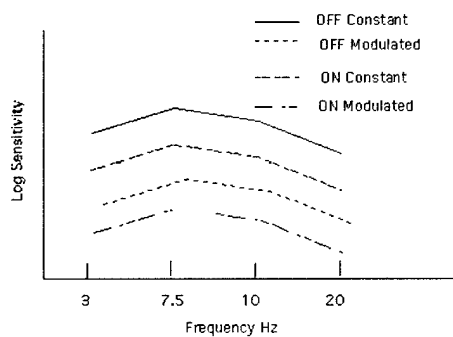


Figure 14. Hypothetical results experiment 1.

would expect to find the same pattern of results that were obtained in Experiment 1-a PE of equal magnitude in both ON and OFF pathways. The reason for the expectation was that the PE signal generated in both experiments would be the same. Therefore, the effects on test flicker thresholds would also be the same regardless of the form of the flicker presentation. Three test frequencies, low (3.0 Hz), medium (10.0 Hz), and high (24.0 Hz) were used to determine the counterphase results.

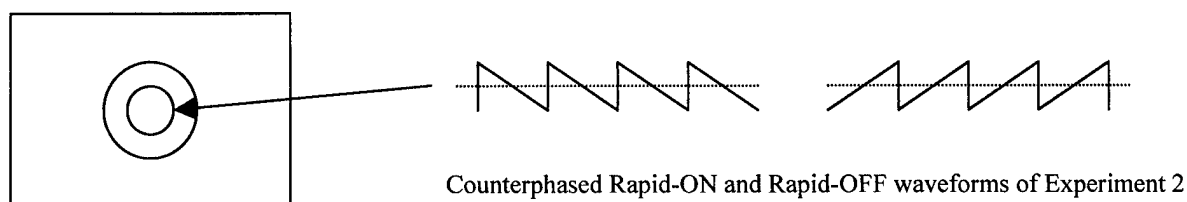


Figure 15. Experiment 2.

Experiment 3 (Dichoptic Viewing). Experiment 3 was similar in its protocol to Experiment 2, with the following modifications. The subjects were moved from 75.0 cm to a distance of 57.3 cm in order to maximize the field of view of the stimulus within the limited constraints of the apparatus. A dividing septum was introduced inside the light-tight box in order to split the computer screen into two equal sections. A silver prismatic mirror was placed in front of the left eye and the viewing situations depicted in Figure 16 were presented.

The purpose of Experiment 3 was to determine whether the origin of the PE was retinal or cortical. A retinal origin was hypothesized; thus, the expected result was that

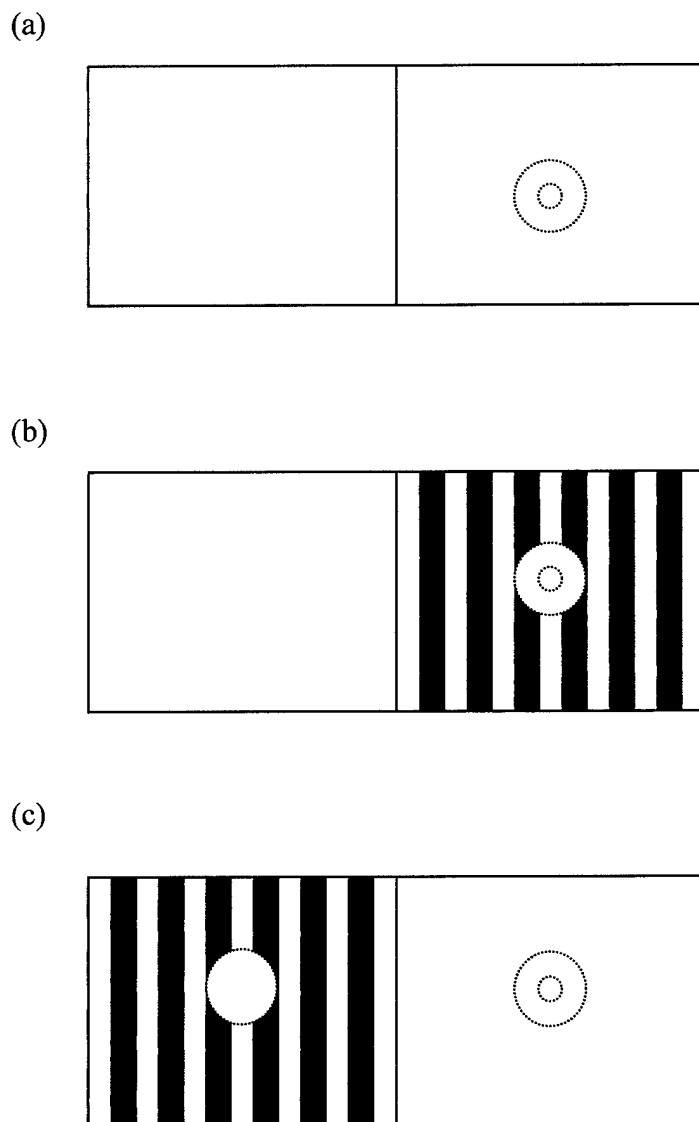


Figure 16. Experiment 3. (a) Condition 1. Left eye sees mean luminance screen. Right eye views the target stimulus on background via mirrored prism. (b) Condition 2. Left eye sees mean luminance screen. Right eye sees target stimulus, surrounded by background and peripheral stimulus. Presentation of right side was similar to Figure 11. (c) Condition 3. Left eye sees peripheral stimulus. Right eyes sees target stimulus. Images are superimposed by prism and give the same cortical appearance as the right side of condition two.

subjects would show the most sensitivity to dichoptic condition 1 and the least sensitivity (highest expected results) to dichoptic condition 2. Dichoptic condition 3 should yield sensitivities like those of condition 1 if the effect was retinal in origin (see Figure 17 for expected results). If it yielded thresholds like those of condition 2, the effect would be cortical in origin. Without this demonstration of the retinal nature of the periphery effect, it would be difficult to implicate amacrine cells or some other retinal cells as being responsible. Subjects were tested at the same test flicker frequencies as in Experiment 2.

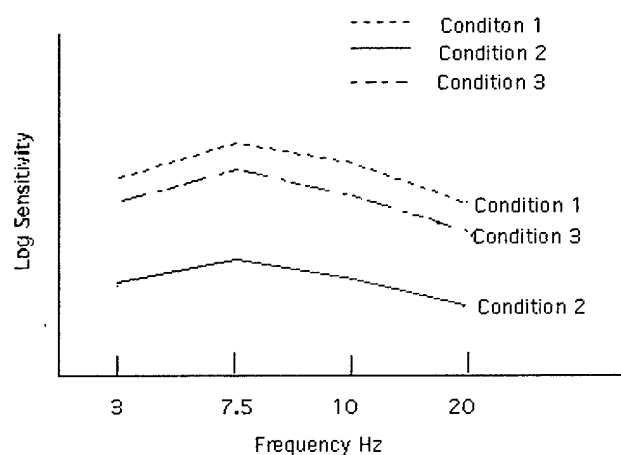


Figure 17. Hypothetical results Experiment 3.

Experiment 4 (Cross-modal). In this experiment, the peripheral grating was replaced by full-field flicker that was either a rapid-ON or Rapid-OFF waveform modulated at 7.5 Hz around the same mean luminance (41.0cd/m^2) of the grating it replaced. Thresholds for detection of flicker in the foveal targets (rapid-ON and rapid-

OFF of varying frequency) were determined as before, with and without peripheral stimulation present. The purpose of this experiment was to determine whether the ON and OFF layers in retina are segregated with respect to the PE signal that is transmitted from the periphery to the fovea. In other words, are there ON and OFF PE signals that selectively effect ganglion cells in the ON and OFF layers of the retina. Assuming the ability to selectively activate ON and OFF pathways in the periphery with appropriate sawtooth flicker, if PE signals are segregated (see Figure 18), we would expect detection thresholds to be most affected when the target and peripheral stimulus have the same waveform (e.g., both are rapid ON or both are rapid OFF). When the waveforms of the target and peripheral stimulus differ, (e.g., one rapid ON the other rapid OFF or vice versa) detection thresholds should be minimally affected. In contrast, if the PE signal is transmitted equally to both ON and OFF layers (see Figure 18), then the difference in the sign of the peripheral stimulus will have a rather unimportant significance.

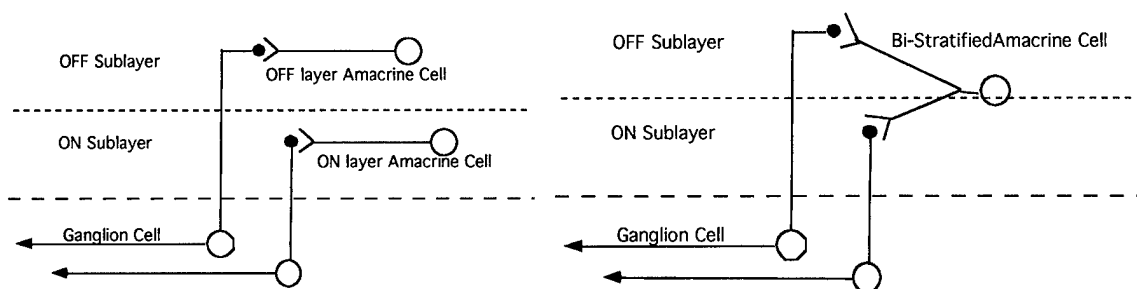


Figure 18 ON/OFF amacrine cell. The illustration on the left represents a monostratified or segregated arrangement. The right side represents a bistratified possibility.

A third alternative is that both monostratified and bi-stratified amacrine cells are involved and that would be expected to yield some asymmetry, but not of the same extent and magnitude if the PE signals are segregated.

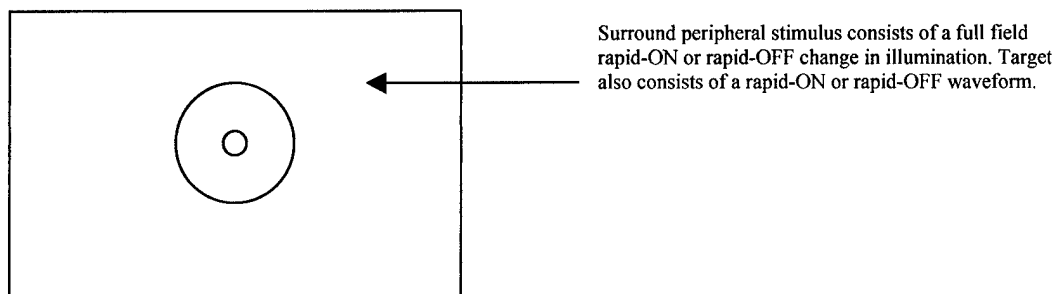


Figure 19. Experiment 4

It was anticipated that three representative test frequencies were sufficient to demonstrate the nature of full-field flicker and its relationship to ON and OFF long-range interaction pathways.

RESULTS

All threshold results were printed out, tabulated, and filed. The mean and variance were calculated for all data points as appropriate. Both collective and individual data were presented as log graphs for comparison between various conditions. Parametric methods (t -tests or analysis of variance) were used to compare and contrast sensitivities for control or to compare PE magnitudes.

Experiment 1 (Rapid-ON, Rapid-OFF Pedestal Experiment).

Figure 20 presents the results of Experiment 1 averaged across all subjects. In Figure 20, contrast sensitivity functions for detecting rapid-ON and rapid-OFF flicker with and without peripheral stimulation present are plotted. From these plots, it readily appears that contrast sensitivities to both ON and OFF flicker were reduced in the presence of surround stimulation. This was verified statistically using a paired sample t -tests. The average reduction across temporal frequencies between the mask and no mask conditions was 0.192 log units for the ON stimulus ($t = 2.57, p < 0.0002$) and 0.148 log units for the OFF stimulus ($t = 2.57, p < 0.0004$). These differences support the first hypothesis for Experiment 1, which was that surround stimulation would reduce sensitivity to both rapid-ON and rapid-OFF flicker. Another prediction was that the reductions in sensitivity would be equal for the two pathways. However, the experiment showed that reductions were statistically significantly larger for the rapid-ON than rapid-OFF stimuli ($t = 2.57, p < 0.0002$). The inset for Figure 20 has plotted for each test flicker frequency the log unit

amounts that surround stimulation-reduced contrast sensitivity for rapid-ON and -OFF flicker.

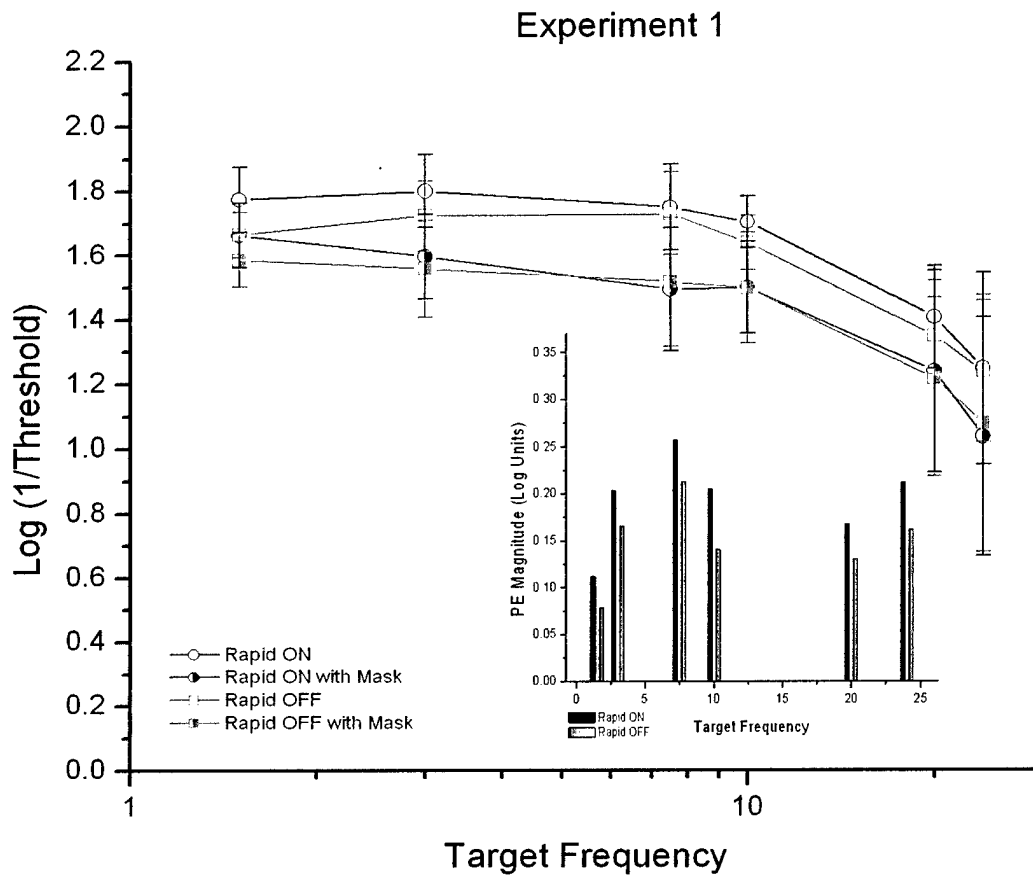


Figure 20. Experiment 1 results.

Inspection of the inset reveals that there are variations in the magnitude of the PE size as a function of target flicker frequency. The magnitude of the PE was statistically significant ($p < 0.05$) for the ON frequencies of 1.5 Hz, 3.0 Hz, 7.5 Hz, 10.0 Hz, and 24.0 Hz (See Table 1). Similarly, the PE effect was statistically significant ($p < 0.05$) for 1.5

Hz and 3.0 Hz for the OFF frequencies. Although threshold changes at 20.0 Hz for ON, and 7.5, 10.0, 20.0, and 24.0 Hz for OFF were in the direction of sensitivity loss, the magnitudes were not statistically significant (p values ranging from 0.06 to 0.19).

Another prediction was that sensitivity would be greater to rapid-OFF flicker than to rapid-ON. However, close examination of the control condition contrast sensitivity data in Figure 20 suggests the opposite. The data points for rapid-OFF flicker are often below those for rapid-ON flicker. Comparing rapid ON and OFF thresholds at each frequency and across individuals yields 29 points of comparison (4 subjects multiplied by 6 frequencies plus 1 subject multiplied by five frequencies). For 23 of the 29 comparisons, data points for rapid ON lay above those for rapid OFF, a statistically significant difference (sign test, $p = 0.0012$). A separate analysis was conducted to determine whether the ON and OFF sensitivity differences were significant at each frequency tested. The results indicate that sensitivity to rapid ON was somewhat greater than to rapid OFF at 1.5, 3.0, and 20 Hz (see Table 1), but not at 7.5, 10, and 24 Hz.

Further inspection of the data concerning the nature of adding peripheral stimulation yielded additional insight upon the PE effect of ON and OFF. Specifically, adding peripheral stimulation had the effect of diminishing the ON versus OFF difference. The number of times ON sensitivity exceeded OFF was reduced to 17 of 29 (sign test, $p = 0.22$) and a significant sensitivity difference was found at only one frequency, 7.5 Hz.

What Figure 20 does not reveal are individual differences among subjects in the size of the effects of peripheral stimulation on sensitivity to rapid ON and OFF flicker. Appendix A, Figures A-1 to A-5, present the data for each of the subjects in the experiment. The data is plotted in the same format as in Figure 1. All of the individual contrast

Table 1.

Experiment 1 Sensitivity Results.

Frequency	PeripheryEffect		ON vs. OFF	
	ON vs ON+Mask	OFF vs OFF+Mask	ON vs OFF	ON+Mask vs OFF+Mask
1.5	$\Delta = 0.1120$ ($p = 0.034$)*	$\Delta = 0.0787$ ($p = 0.002$)*	$\Delta = 0.1099$ ($p = 0.020$)*	$\Delta = 0.0767$ ($p = 0.100$)
3	$\Delta = 0.2034$ ($p = 0.001$)*	$\Delta = 0.1654$ ($p = 0.010$)*	$\Delta = 0.0767$ ($p = 0.038$)*	$\Delta = 0.0387$ ($p = 0.194$)
7.5	$\Delta = 0.2567$ ($p = 0.048$)*	$\Delta = 0.2129$ ($p = 0.064$)	$\Delta = 0.0200$ ($p = 0.524$)	$\Delta = -0.0237$ ($p = 0.048$)*
10	$\Delta = 0.2050$ ($p = 0.005$)*	$\Delta = 0.1407$ ($p = 0.142$)	$\Delta = 0.0652$ ($p = 0.247$)	$\Delta = 0.0008$ ($p = 0.966$)
20	$\Delta = 0.1674$ ($p = 0.082$)	$\Delta = 0.1307$ ($p = 0.192$)	$\Delta = 0.0582$ ($p = 0.039$)*	$\Delta = 0.0215$ ($p = 0.238$)
24	$\Delta = 0.2121$ ($p = 0.017$)*	$\Delta = 0.1614$ ($p = 0.115$)	$\Delta = 0.0086$ ($p = 0.850$)	$\Delta = -0.0420$ ($p = 0.526$)

The table shows the difference (" Δ ") between the log (1/Threshold) values for four comparative conditions. These conditions are noted at the top of each column. The first two columns represent the Periphery Effect for the peripheral mask upon ON- and OFF-flicker waveforms. The last two columns represent the differences between the nature of ON and OFF waveforms with and without a mask. The number in parentheses indicates the P value. "*" $P < 0.05$.

sensitivity functions share some common attributes. They tend to be band pass to low-pass, with the highest sensitivity at lower frequencies, and show a sharp decline in sensitivity above 10 Hz. All subjects, except FZ, showed a significant PE at most flicker frequencies tested, with a tendency for the larger PE to be associated with the mid frequencies. In contrast, subject FZ, produced inconsistent results, showing suppression with peripheral stimulation for some conditions and facilitation for others.

Experiment 2 (Rapid-ON, Rapid-OFF Counterphase experiment).

In Experiment 1, the rapid-ON and rapid-OFF waveforms were presented on top of a steady background in what amounted to an increment pedestal of a magnitude equal to the mean luminance of the sawtooth waveform at threshold. Since it is known that this condition elevates flicker thresholds as compared to when waveforms are modulated around the mean of the background, it was necessary to determine whether the condition had any effect on the magnitude of the periphery effect. It was expected that the sensitivity to the target stimulus would be higher when utilizing the mean-modulated stimuli rather than the pedestal-modulated stimuli. Furthermore, it was predicted that the effects of surround stimulation would be similar for the two.

To test these predictions, flicker thresholds for sawtooth waveforms were measured while they were counterphased about the mean luminance of the background with and without surround stimulation. These results were then compared with the results obtained in Experiment 1. Sensitivity to rapid-ON and-OFF flicker was measured at 3.0 Hz, 10.0 Hz, and 20.0 Hz. The average results are plotted in Figure 21.

As in Experiment 1, the presence of surround stimulation significantly reduced sensitivity to both rapid-ON and-OFF flicker. The sensitivity reductions averaged across frequencies were 0.26 and 0.27 log units for rapid ON and OFF, respectively (ON $t = 4.30$, $p < 0.03$ and OFF $t = 4.3$, $p < 0.04$). Additional analysis revealed that the threshold-elevating effect of peripheral stimulation was significant at all frequencies tested for both the ON and OFF waveforms (see inset Figure 21 and Table 2). Furthermore, the amount of change was similar for both waveforms, with the largest PE occurring at 10 Hz. This is illustrated graphically in Figure 21 and numerically in Table 2.

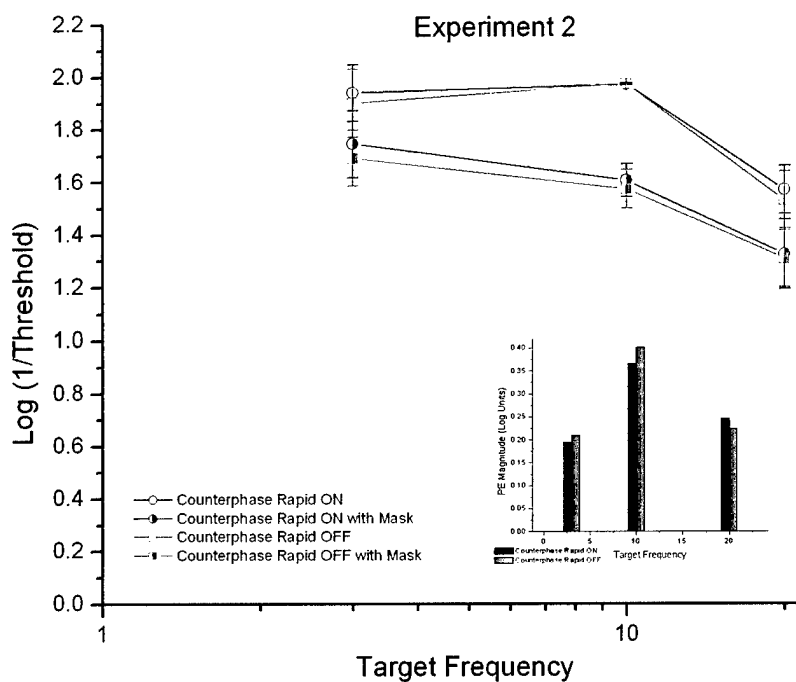


Figure 21. Experiment 2 Results.

Table 2. Experiment 2 sensitivity results.

Frequency	Periphery Effect		ON vs OFF	
	ON vs ON+Mask	OFF vs OFF+Mask	ON vs OFF	ON+Mask vs OFF+Mask
3	$\Delta = 0.195$ $p = (0.033)^*$	$\Delta = 0.209$ $p = (0.005)^*$	$\Delta = 0.039$ $p = (0.135)$	$\Delta = 0.053$ $p = (0.042)$
10	$\Delta = 0.366$ $p = (0.001)^*$	$\Delta = 0.401$ $p = (0.001)^*$	$\Delta = 0-0.002$ $p = (0.398)$	$\Delta = 0.032$ $p = (0.100)$
20	$\Delta = 0.245$ $p = (0.001)^*$	$\Delta = 0.223$ $p = (0.0001)^*$	$\Delta = 0.038$ $p = (0.014)^*$	$\Delta = 0.016$ $p = (0.377)$

Note. The table illustrates the difference (" Δ ") between the log(1/Threshold) values for four comparative conditions. These conditions are noted at the top of each column. The first two columns represent the Periphery Effect for the periheral mask upon ON- and OFF- flicker counterphase waveforms. The last two columns represent the differences between the nature of ON and OFF counterphase waveforms with and without a mask. The number in parentheses indicates the p value. "*" $P < 0.05$.

Comparing results of Experiments 1 and 2 reveals that not only was the sensitivity to mean modulated stimuli greater than to pedestal stimuli, but the magnitude of the PE was also greater. The first result was expected, but the second one was not. However, as already noted, other changes with surround stimulation were similar for the two presentation modes. Surround stimulation was effective with either ON or OFF, and the effects were approximately the same for rapid-ON and -OFF flicker.

As in Experiment 1, there seemed to be a tendency for the subjects to be more sensitive to the rapid-ON than to the rapid-OFF waveform. However, this was not substantiated by frequency analysis (sign test, $p < 0.09$), nor was it substantiated by direct comparison of sensitivities at different frequencies. In contrast, in the presence of a peripheral mask, subjects were frequently more sensitive to the rapid-ON stimulus than to the rapid OFF (sign test, $p < 0.01$). On the other hand, direct comparison yielded only one significant difference out of the six possible comparisons of similar conditions (see Table 2).

Reminiscent of Experiment 1, the individual subjects' experimental results looked largely similar to the overall results. That is to say that the individual contrast sensitivity functions have the same general shape, and they have significant PEs at most test frequencies. Interestingly, the standard deviation of the thresholds was significantly reduced with the counter phase stimulus, with a clearer separation between stimuli without the peripheral mask and those with the peripheral mask.

Experiment 3 (Dichoptic Viewing)

Experiment 3 was designed to determine whether the human psychophysical periphery effect was retinal or cortical in origin. The results of testing all subjects under the three conditions described in the Methods and illustrated in Figure 18, are shown in Figure 22.

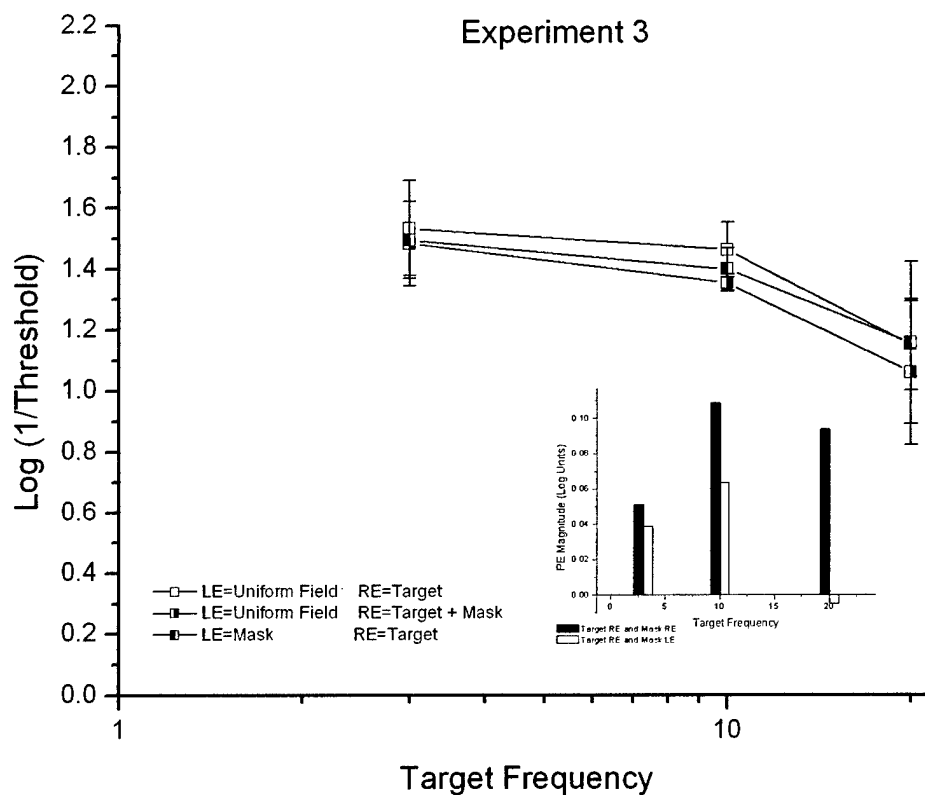


Figure 22. Experiment 3 results.

When thresholds for the control, target, and mask in the same eye were compared, the only significant difference occurred at 10 Hz ($t = 3.18, p < 0.042$). Although the black

bars in the inset graph suggest differences at the other frequencies, a high degree of individual variation prevented the differences from reaching statistical significance. Similarly, when thresholds for the control, target, and mask in opposite eyes were compared, a significant difference was again found only at 10.0 Hz ($t = 0.042$) The average PE (across frequencies) for the target and mask on the same side was greater, 0.08 log units, than when the mask was presented to one eye and the target to the other, 0.03 log units ($t = 2.16, p < 0.02$). Comparisons at each frequency indicated the PE was significantly larger for the same eye condition at 10.0 and 20.0 Hz. However, the magnitude of the effects of the peripheral stimulus on the target threshold when the target and mask were presented to the same eye was overall much smaller than those obtained in Experiments 1 and 2.

Although the results from Figure 22 indicate that presenting the mask to a different eye than the target was less effective than when both were presented to the same eye, not all individual data reflected this (see Appendix B). Results for subjects TK and PC were consistent with the average data whereas subjects, JR and YY showed no difference between the two viewing conditions. Subject FZ, produced mixed results depending on the test flicker frequency including facilitation at 3.0 and 10.0 Hz.

A statistical analysis of the results demonstrates that only at 3.0 Hz, (when comparing the sensitivities to *a*) the condition of a uniform field in the left eye and target presented right eye and *b*) to the condition of left eye seeing uniform field and the right eye seeing the target with the peripheral mask) did the study achieve a statistical significance ($p < 0.05$). All the other data points have mentionable overlap. As with Experiments 1 and 2, Experiment 3 follows the expected result of the human psychophysical temporal-contrast-sensitivity curve. The nature of the curve is band pass, with a sharp decline near

the higher frequencies. As with Experiments 1 and 2, conditions without the peripheral mask resulted in greater sensitivity, notably at frequencies 3.0 Hz and 10.0 Hz. The average PE for the target and mask on the same side was much greater (0.08 log units) than that for the mask presented to one eye and the target to the other (0.03 log units). In fact, at 20 Hz, the presence of the mask presented on the opposite eye lead to a slight facilitation. Experiment 3, as did Experiments 1 and 2, attained the most PE in the mid-frequency range.

Individual variations are more pronounced in Experiment 3 than in the first two experiments (see Appendix B). Generally, the curves looked similar to the overall data. More specifically, JR, TK and PC demonstrated a presumably strong retinal effect. However, YY demonstrated what might be cortical. Finally FZ, as with Experiment 1, demonstrated facilitation to the stimulus, particularly at low and high frequencies.

Experiment 4(Rapid-ON, Rapid-OFF Pedestal Experiment).

Experiment 4 was similar to Experiment 2 with respect to the nature of the target being a mean modulated rapid-ON or rapid-OFF sawtooth flicker. However, the peripheral stimulus, which in all previous experiments had been a mean modulated grating, was replaced with homogenous counterphased flicker that was either a rapid-ON or rapid-OFF sawtooth. This allowed for four different test conditions: Target ON, Surround ON; Target OFF, Surround ON; Target ON, Surround OFF; Target OFF, Surround OFF (see Figure 23).

The control condition for Experiment 4 was derived from the data of Experiment 2, utilizing the steady surround. The results of Experiment 4 are plotted in Figure 23. Statis-

tical analysis revealed that all four flicker surround conditions resulted in significant changes in test flicker thresholds when compared to control condition thresholds.

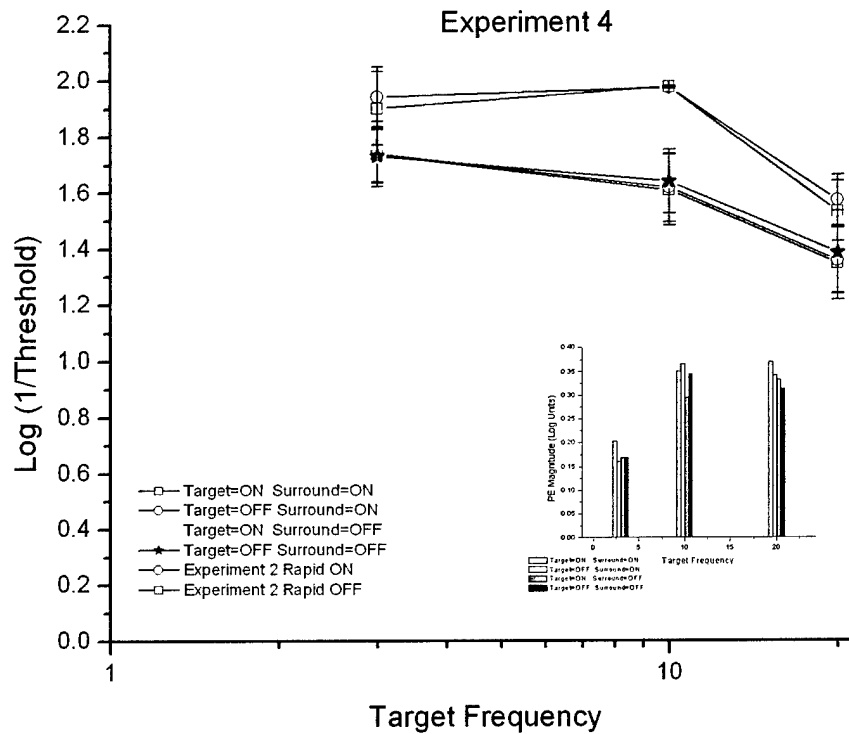


Figure 23. Experiment 4 results.

This is summarized in Table 3. Specifically, the PE magnitude was 0.27 log units for target ON and surround ON, 0.23 log units for target ON and surround OFF, 0.24 log units for target OFF and surround ON, and 0.23 log units for target OFF and surround OFF. These values are similar to the PE magnitudes obtained in Experiment 2 with a grating surround. Specifically, Experiment 2 revealed an average PE magnitude of 0.26 log units with the rapid ON target and 0.27 log with the rapid OFF target.

Table 3.

Experiment 4 Sensitivity Differences in Log Units.

Frequency	Target ON Surround ON	Target ON Surround OFF	Target OFF Surround ON	Target OFF Surround OFF
3	$\Delta = 0.203$ ($p < 0.006$)*	$\Delta = 0.168$ ($p < 0.028$)*	$\Delta = 0.160$ ($p < 0.014$)*	$\Delta = 0.168$ ($p < 0.013$)*
10	$\Delta = 0.388$ ($p < 0.010$)*	$\Delta = 0.324$ ($p < 0.027$)*	$\Delta = 0.386$ ($p < 0.007$)*	$\Delta = 0.360$ ($p < 0.008$)*
20	$\Delta = 0.225$ ($p < 0.001$)*	$\Delta = 0.187$ ($p < 0.001$)*	$\Delta = 0.176$ ($p < 0.003$)*	$\Delta = 0.147$ ($p < 0.007$)*

Note. The difference " Δ " is between the control without a grating obtained via Experiment 2 and test conditions described in Experiment 4.

Examination of the curves of Figure 23 and the PE Magnitudes plotted in the inset suggests a close similarity between test conditions. However, statistical analysis indicated there was a difference in the effectiveness of the ON and OFF surrounds in reducing sensitivity to rapid ON targets. The results of these comparisons are summarized in Table 4.

Table 4.

Experiment 4 sensitivity results.

Frequency	Target ON Surround ON	Target ON Surround OFF	Target OFF Surround ON	Target OFF Surround OFF
3	$\Delta = -0.003$ ($p < 0.893$)	$\Delta = 0.039$ ($p < 0.165$)	$\Delta = -0.034$ ($p < 0.045$)*	$\Delta = 0.008$ ($p < 0.720$)
10	$\Delta = -0.004$ ($p < 0.429$)	$\Delta = 0.033$ ($p < 0.369$)	$\Delta = -0.064$ ($p < 0.023$)*	$\Delta = -0.025$ ($p < 0.166$)
20	$\Delta = -0.010$ ($p < 0.441$)	$\Delta = -0.001$ ($p < 0.973$)	$\Delta = -0.037$ ($p < 0.039$)*	$\Delta = -0.0028$ ($p < 0.207$)

The difference " Δ " is between the control with a grating obtained via Experiment 2 and test conditions described in Experiment 4.

Examination and analysis of individual data (see Appendix B) revealed that all subjects produced similar results. All subjects showed a PE at all frequencies, with the one exception; subject PC showed facilitation at 3.0 Hz for the target ON mask OFF condition.

DISCUSSION

Reductions in sensitivity to numerous visual stimuli presented to the fovea can be achieved by stimulating retinal areas located some distance away from the target with counter-phased or shifted gratings and homogeneous flicker. Experimental evidence suggests that some underlying visual mechanisms, but not others, are affected by peripheral stimulation. This includes transient but not sustained mechanisms, luminance but not color, and magnocellular but not parvocellular. All of these mechanisms and systems can be further broken down into ON and OFF subdivisions. This separation into ON and OFF pathways is one of the most fundamental in vertebrate retina. This study investigated the effect of peripheral stimulation on these pathways. From physiological research in cat, monkey, and rabbit, several hypotheses were formulated. The first of these was addressed in Experiment 1.

Experiment 1

Studies in cat, monkey, and rabbit indicated that the periphery or shift effect is found with approximately equal vigor in ON and OFF responding neurons. Consequently, it was hypothesized that peripheral field stimulation in humans would affect their responses to both the onset and offset of light and that those affects would be equal in magnitude. From studies in humans, it was further hypothesized that subjects would be more sensitive to light offset than onset.

Experiment 1 combined two psychophysical issues. These are investigations into the human periphery effect and investigations into the nature of ON and the OFF psychophysical pathways. To study the PE, retinal areas were peripherally stimulated. A background spatially separated the peripherally stimulated retinal areas from the foveal target area. The peripheral stimulation was done with a counterphased grating and compared to test thresholds obtained under conditions when the grating was not present. Rapid-ON and rapid-OFF sawtooth flicker was used to selectively stimulate the ON and OFF pathways.

The results of Experiment 1 support the first hypothesis. Peripheral stimulation with a counterphased grating resulted in elevated thresholds for both rapid-ON and rapid-OFF flicker. However, when averaged across test flicker frequencies, the magnitude of the PE was significantly larger for the ON pathway than for the OFF pathway.

This has important implications, especially that the ON and OFF are affected by the periphery effect. Perhaps then this lateral interaction could be accomplished by analogous or even the same gamma-aminobutyric acid mediated amacrine cells that Roska and Werblin (2003) suspect are responsible for rapid global shift inhibition. They suggest that the neural components that provide the inhibition are not independent. This is in contrast to research by Pang, Gao and Wu (2003), who suggest that increment and decrement light responses of ganglion cells are composed of different sets of bipolar cells and amacrine cells. An interesting finding of Experiment 1 was that the average PE reduction for the rapid ON target was 0.19 log units whereas that for the rapid OFF was 0.15 log units. It would be tempting to speculate why the rapid ON was affected more than the rapid OFF. The myriad of possibilities that exist within the retina, with over

eight different bipolar inputs and possibly 28 different amacrine cells, precludes any meaningful insight at this time. It may be as simple as the fact that the ON ganglion cells have a higher resting spike rate and thus are more prone to the PE effect than are the OFF ganglion cells. Or it may be a complex, asymmetrical physiological and anatomical relationship that exists within the inner plexiform layer of the retina.

The third hypothesis, that subjects would be more sensitive to light offset (rapid-OFF flicker) than to onset was also not supported by the data. If anything, some of the findings suggested the opposite--that subjects tended to be more sensitive to light onset. If a person's preference for ON as opposed to OFF is treated as an event, much like flipping a coin has the result of either "heads" or "tails," then a simple sign test can be applied to the results. Inspection of Experiment 1 reveals that ON seemed to be preferred 23 out of the 29 data points tested. However, one must be careful to draw the inference that subjects are more sensitive to ON than OFF from this result. Direct comparison of contrast sensitivity to rapid-ON and -OFF flicker revealed significant differences in favor of ON at only three of six frequencies tested. Nevertheless, despite the inherent subject variability, such results may in fact yield significant future discernment.

This leads to an interesting discussion on whether or not asymmetries exist with the ON and OFF pathways. It is held by many that ON and OFF pathways are opposite in sign but otherwise equal in kinetics and sensitivity (Zaghloul, Boahen, & Demb, 2003). Some have said that incremental tests are detected at threshold by the ON system and decremental tests are detected by the OFF system (Sinai, Essock, & McCarley, 1999). Some have held that, psychophysically, humans are slightly more sensitive to decrements (Bowen et al., 1989). Still others have suggested that, at least physiologically, primates in

low-contrast conditions have ON cells that give a faster kinetic response than do OFF cells. Thus, in low contrast conditions, the ON cells are better suited to signal decrements, whereas OFF cells can do little in the way to signal an increment (Chichilnisky & Kalmar, 2002). Past and present physiological and psychophysical experiments have tried to find asymmetries between the ON and OFF pathways within the visual system. However, there is no agreement as to the exact nature of the asymmetries that may exist between ON and OFF. The results of Experiment 1 suggest that if any asymmetry exists psychophysically, then it would tend to be minor.

Experiment 2

Experiment 2 was designed to determine whether presenting flicker as an increment pedestal influenced the PE results, perhaps biasing them in favor of one pathway or the other. The results of Experiment 2 indicate that this may have been the case. Although we found a PE in both pathways, consistent with Experiment 1 results, the significantly larger PE for the ON pathway found in Experiment 1 was not confirmed with the mean modulated stimuli. In contrast, PE magnitude was the same in both pathways, indicating that the pedestal presentation in Experiment 1 may have favored the ON pathway.

The results of Experiment 2 also add additional data that address the hypothesis that subjects would be more sensitive to light offset. In Experiment 1 there was some evidence that sensitivity to onsets was greater than that to offsets--the opposite of what was hypothesized to occur. However, the same type of analysis of the Experiment 2 results indicated no difference in ON and OFF sensitivity. This was further supported by frequency-specific comparison of contrast sensitivity to rapid ON and OFF flicker. In sum-

mary, the combined data from Experiments 1 and 2 suggest that the presenting sawtooth waveforms as increment pedestals may bias things in favor of the ON pathway. However, this bias was removed with mean modulated presentation and when the results for ON and OFF pathway in terms of PE magnitude and overall sensitivity are equivalent.

Experiment 3

Experiment 3 was designed to determine whether the human psychophysical periphery effect was retinal or cortical in origin. Although the physiological PE in mammals has been well established as being retinal via recordings from ganglion and LGN cells, this does not necessarily mean that what the human subjects have reported psychophysically represents the retinal process and only the retinal process in its entirety. In fact, there are those who maintain that the periphery effect is entirely cortical. The results of the experiment yielded only one point, 10.0 Hz, that showed a significant difference that would indicate the PE was retinal in origin. Most points demonstrated that the remote masking is more effective and thus retinal when presented in the same eye as the target, than when the target and mask are presented in opposite eyes. The difference between the cortical masking and the retinal masking was within the standard deviations for the points tested. Thus, we did not see such clear distinction between monocular and dichoptic conditions as Dortman and Spillmann (1981) and He and Loop (1990) found in their experiments. Rather, our results are similar to the binocular experiments of Schieting and Spillmann (1987) who suggested a 65% retinal and 35% cortical involvement with their binocular experiments. Of note is that our experiment, like that of Schieting and Spillmann compared results that were seen binocularly across all the testing conditions in Ex-

periment 3. Such testing conditions may tend to minimize the difference seen when the test is monocular verses binocular.

None of the subjects in Experiment 3 reported problems with suppression or an inability to fixate. However, one subject, YY, in the ocular history noted that he had a moderately large degree of exophoria. Testing with a Titmus stereo test yielded normal results, and the subject was allowed to participate in the study. Inspection of YY data and graph reveal that he obtained nearly identical results when the target and mask were presented in the same eye (retinal) as opposed to when they were presented in different eyes (cortical). Additionally, two subjects showed some facilitation when the target was presented in one eye and the mask in the other. This is thought to be simply a result of the somewhat dynamic nature of the testing conditions. In other words, the subjects had to maintain fixation of the crosses and ensure the target was in the middle of the surround. The condition of having the target viewed by one eye with a grating surround viewed by the other eye was a little more exciting than having a target and surround viewed by the same eye and an blank field by the other. This would have contributed to an increased cognitive awareness of the test and thus to decreased thresholds, especially because the difference between experimental PE thresholds in Experiment 3 was so much lower than those in Experiments 1 and 2.

Although Experiment 1, with its raised pedestal stimulus, looked to the observers to be practically identical to condition one and condition two of Experiment 3, a meaningful comparison cannot be made. Indeed, comparison of the uniform and mask results of the aforementioned experimental conditions revealed that they were statistically different. This is not surprising when one considers that the test distances were different (75.0

cm vs 57.3cm), and although the spatial degree parameters of the target, background, and spatial frequency were scaled appropriately, the area of the mask, although similar, was different because of restraint conditions attributed to monitor size. This, in effect, then is consistent with findings of Woods, Nugent, and Peli (2002) that lateral interactions with flankers (masks) will change noticeably with size.

However, the design and intent of Experiment 3 was not to compare it with Experiment 2 as the control condition. Nevertheless, the results of Experiment 3 show that the PE had a similar effect on the subjects contrast sensitivity curves. Specifically, they tended to be band pass in nature, most sensitive in the mid frequencies, and have a sharp decline around 20.0 Hz. The magnitude of the PE was smaller in Experiment 3, which was always done binocularly, than in Experiments 1 and 2, which were always performed monocularly. Experiment 3 reveals that at least part of the PE effect is probably retinal in origin and although PE lateral interaction may originate in the inner plexiform layer. The results most certainly appear to have a cortical modification to them.

Experiment 4

Experiment 4 differed from the previous experiments in that the grating was replaced by a full-field flicker that was either rapid ON or rapid OFF at 7.5 Hz. This paradigm led to some interesting interactions. It was thought that perhaps an interaction similar to that found by Purkiss, Hughes, and DeMarco (2001) and Purkiss and DeMarco (2002) might be elicited. Specifically, they found that adapting to a rapid-ON waveform would elevate the threshold to a rapid-ON target that was presented in the same location as the adapting waveform had been. Similar results were found when rapid ON was re-

placed with rapid OFF for both the adapting wave form and target. They did not find any elevation in threshold when the adapting waveform and target were of opposite sign.

The results of Experiment 4 show the PE magnitude effects of the full-field flicker were similar to the PE magnitude effects of Experiment 2 with the grating. All PE effect magnitudes fell within a log-unit range of 0.22 to 0.27. An asymmetry does seem to exist, however, when comparing the effects that a rapid-ON, full-field surrounding waveform has on the threshold of a rapid-ON target. Interestingly it appears to statistically elevate it, whereas the reciprocal paradigm of a rapid-OFF surround with a rapid-OFF target appear to not elevate the threshold any different than a rapid ON surround would. This leads to the interesting possibility that maybe a rapid-ON wave form that has a transient ON component is asymmetrically different in its PE affects than a rapid OFF with its transient OFF component. In short, Experiment 4 indicates that there may be a PE difference elicited by a transient ON signal that is more inhibitory than a transient OFF signal.

CONCLUSIONS AND THE FUTURE

The results of all four experiments show that the ON and OFF pathways appear to be, for the most part, equally or symmetrically affected by peripheral stimulation under a human PE paradigm. This symmetry was shown to exist with both pedestal target stimuli and counterphased target stimuli. It was also shown to exist under binocular dichoptic conditions and has a significant component that appears to be retinal in origin. Only with a full-field flicker did we find what may be an asymmetrical finding, with a rapid-ON surround eliciting a greater PE magnitude than the rapid OFF surround on a rapid-ON target.

Although this research was not concerned with practical or clinical aspects of its findings, there exist numerous possibilities in which it may be employed in the future. For example, diabetic retinopathy is a difficult disease to diagnosis in its early presentation. Some researches have shown that an abnormal electroretinogram is able to be obtained on patients well before the characteristic microhemorrhages of the disease are apparent. This is because the disease leads to apoptosis of ganglion cells and the inner nuclear layer (Gardner, Antonetti, Barber, LaNoue, & Levision, 2002) Because there are so few amacrine cells that presumably are modulating the PE, it might be possible to quickly detect an abnormality of the inner plexiform layer by using a test that would employ a person's sensitivity to a psychophysically presented PE. Absence of a normal PE result would indicate early problems with the inner plexiform layer, such as is found in early

diabetic retinopathy. In short, further study of the PE and of ON and OFF pathways can lead to exciting relationships, understanding, and possible uses for such findings.

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APPENDIX A
INSTUTUTIONAL REVIEW BOARD APPROVAL FORMS

 Department of Veterans Affairs		REPORT OF SUBCOMMITTEE ON HUMAN STUDIES	
Project/Program Title <u>Reinforce Masking in Human Vision</u>			
Principal Investigator <u>Kuyk, Thomas K., Ph.D.</u>			
VAMC <u>Birmingham (621)</u>		Review Date: <u>2/7/00</u>	

COMMITTEE FINDINGS:

1. The information given in the Informed Consent Under the Description of Research by Investigator is complete, accurate, and understandable to a research subject or a surrogate who possesses standard reading and comprehension skills.
 YES
 NO

2. The informed consent is obtained by the principal investigator or a trained and supervised designate under suitable circumstances.
 YES
 NO

3. Every effort has been made to decrease risk to subject (s)?
 YES
 NO

4. The potential research benefits justify the risk to subject(s)?
 YES
 NO

5. If subject is incompetent and surrogate consent is obtained, have all of the following conditions been met; a) the research can't be done on competent subjects; b) there is no risk to the subject, or if risk exists the direct benefit to subject is substantially greater; c) if an incompetent subject resists, he/she will not have to participate; d) if there exists any questions about the subject's competency, the basis for decision on competency has been fully described.
 YES
 NO

6. If the subject is paid the payment is reasonable and commensurate with the subject's contribution.
 YES
 NO
 NA

7. Members of minority groups and women have been included in the study population whenever possible and scientifically desirable.
 YES
 NO

8. Comments: (Indicate if Expedited Review)

 RECOMMENDATION: APPROVED DISAPPROVE/REVISE

Signature of Chairman 	Date <u>3/8/00</u>
--	-----------------------

**Birmingham VA Institutional Review Board (IRB)
Department of Veterans Affairs Medical Center**

VA Research Service (151) • Campus Mail 0001, VAMC Rm. 2-R-28 • 205-933-8101 • Fax: 205-933-4471

CONTINUING REVIEW SUBMISSION FORM

Date: January 6, 2004
Investigator: **Patti Fuhr, O.D., Ph.D.**
Protocol: Remote Masking in Human Vision
ID: 00820 Prom#: 0009 Protocol#: N/A

Initial IRB Approval Date: 01/31/2000
Previous Continuing Reviews: 03/06/2001, 01/14/2002, 12/09/2002, 10/20/2003
Approval Expiration: 10/19/2004

Submission Form Due Date: 08/26/2004
Continuing Review Date: 08/30/2004

FDA Regulations specify that Continuing Review is required for all IRB approved human studies. Failure to comply will result in suspension or termination.

Please provide the following information:

- (1) Continuing Review Form - see attached questions; also include:
 - (a) Names and SSNs of Birmingham subjects enrolled in the study (original packet only)
 - (b) Use study I.D. number to identify subjects who withdrew consent and reason for withdrawal
 - (c) Use study I.D. number to identify subjects who received study drug, for cross-tabulation with Investigational Pharmacy
 - (d) Has any information been communicated to subject as suggested by the Data Monitoring Board?
 - (e) Were all study prescriptions dispensed by the VA Pharmacy?
 - (f) Any changes regarding conflict of interest since last review? If Yes, please explain.
 - (g) Explain how confidentiality of records is being maintained (e.g., storage of records, etc.)
- (2) Progress Report - see attached
- (3) Copy of currently approved consent form
- (4) List of all AEs and SAEs (both local and off-site)
- (5) Protocol (if revised since initial submission)
- (6) Clean copy of consent form for approval stamp

Please assemble the packets in the order listed above. With the exception of the clean copy of the consent form, the required number of packets is 10.

Attach the following items when submitting this form:


1. **A copy of the consent form currently in use.**

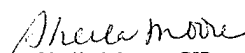
UAB THE UNIVERSITY OF
ALABAMA AT BIRMINGHAM

Institutional Review Board for Human Use

MEMORANDUM

TO: Mr. Patrick Clark

FROM: 
Ferdinand Urthaler, M.D.
Chairman, IRB


Sheila Moore, CIP
Director, IRB

RE: "Remote Masking in Human Vision" VA Project/ Graduate Dissertation

DATE: July 2, 2004

As requested this memorandum should serve as notification that the UAB IRB is in receipt of your letter regarding the above-mentioned research project. The UAB OIRB has reviewed your letter and copies of the VA IRB approval for this project. The OIRB understands that all work involved in the project was conducted at the VA with VA IRB approval, however UAB IRB approval was never obtained. The OIRB is in receipt of approved consent forms, approvals and IRB continuing review from the VA IRB's office.

As a UAB student, all research involving human subjects must be submitted to the UAB IRB office for approval. It appears that you were under the impression that since this had VA IRB approval, UAB IRB was not necessary. The UAB IRB cannot retrospectively approve projects. However, in this case it appears that VA IRB approval was obtained and UAB IRB approval would have been granted for this project had it been submitted to the UAB IRB for review. The OIRB is also aware that an appropriate change has been made within the Vision Science Research Center to avoid this from happening in the future.

A copy of this memorandum will be sent to the graduate school and should serve as final paperwork needed for your dissertation.

Cc: Randy Seay, Graduate School
Dr. Patti Fuhr, VA
Dr. Kent Keyser, UAB Vision Science Research Center

470 Administration Building
701 20th Street South
205.934.3789
Fax 205.934.1301
irb@uab.edu

The University of
Alabama at Birmingham
Mailing Address:
AB 470
1530 3RD AVE S

APPENDIX B
SUBJECT GRAPHS

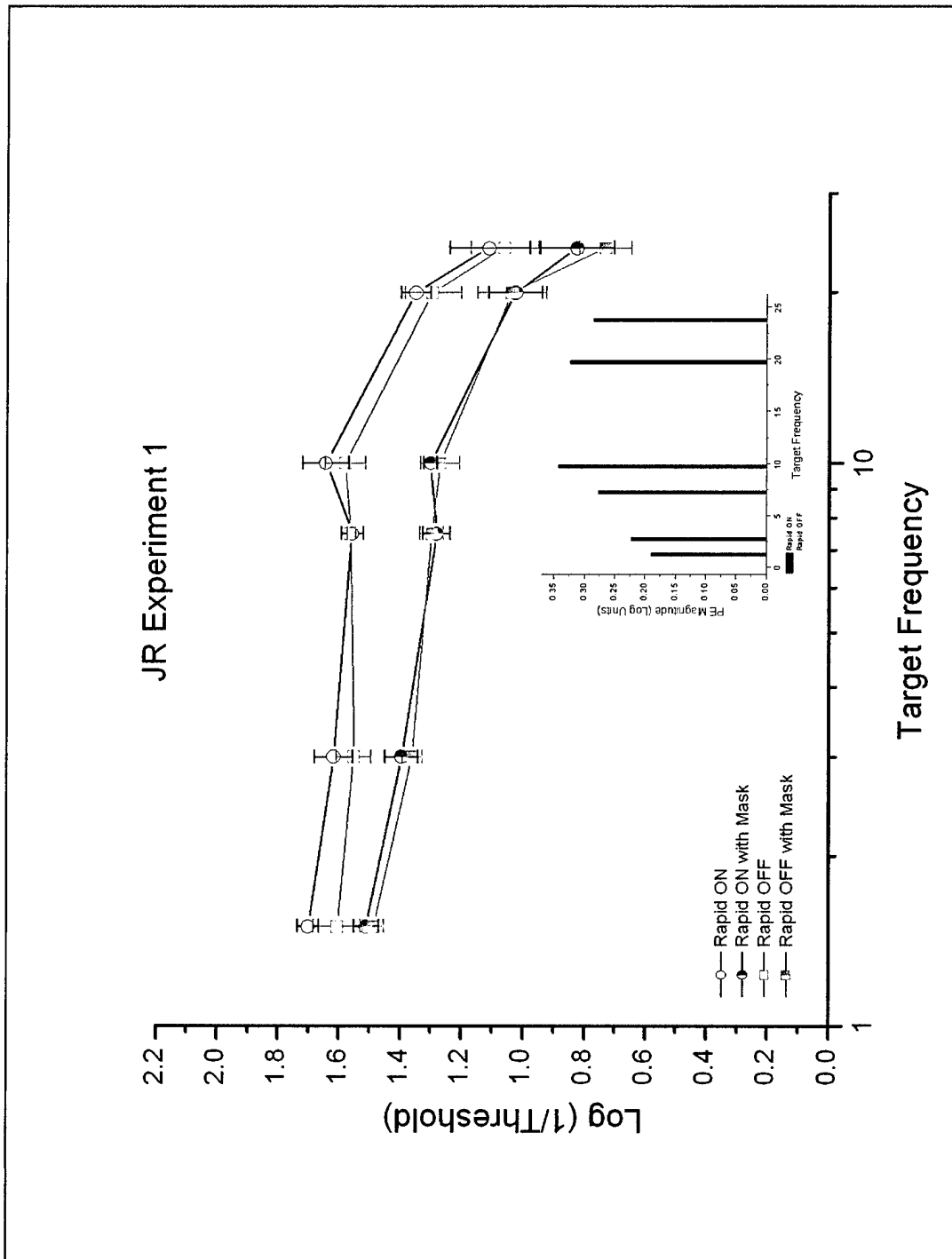


Figure B-1, JR Experiment 1.

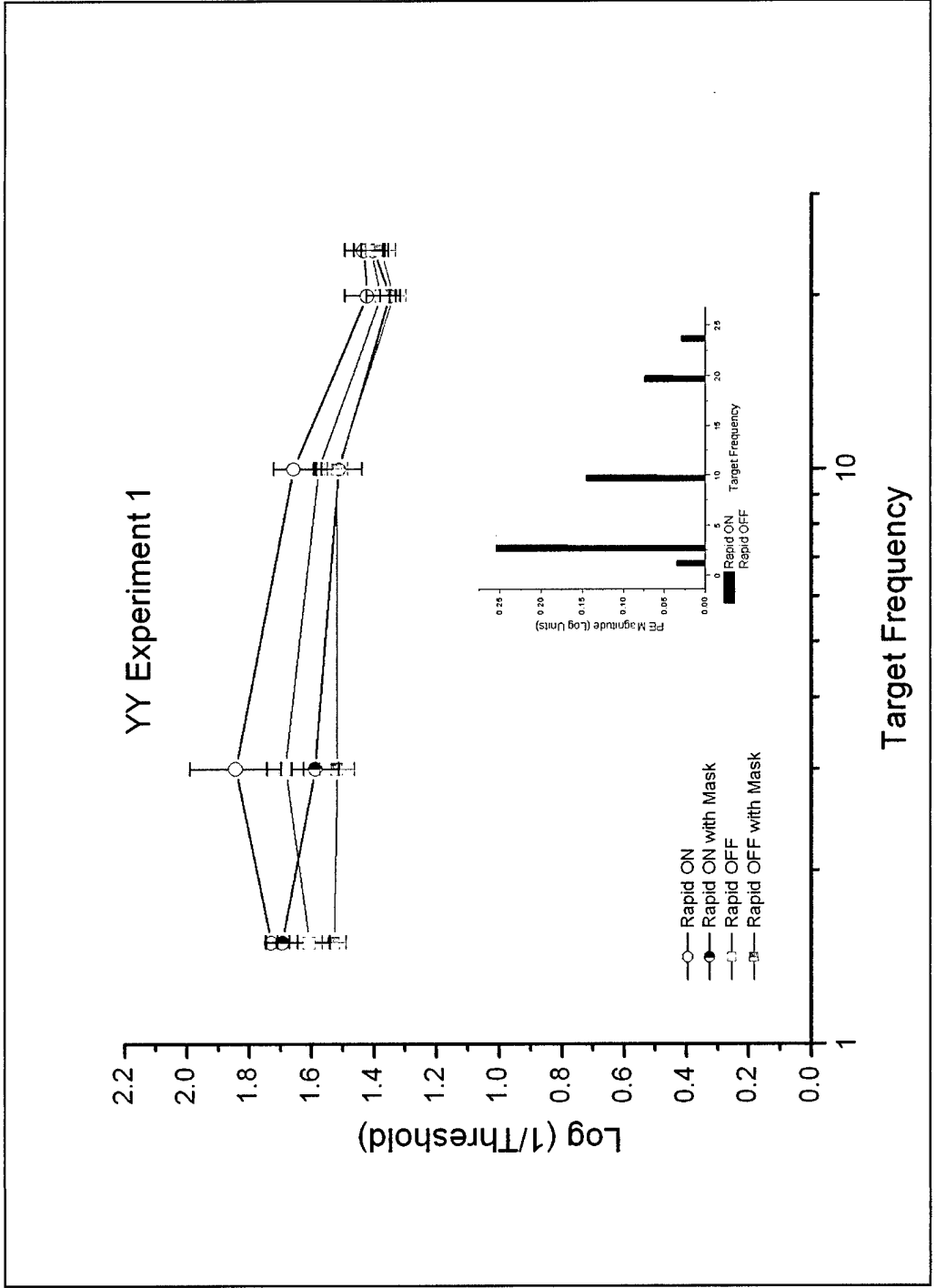


Figure B-2, YY, Experiment 1.

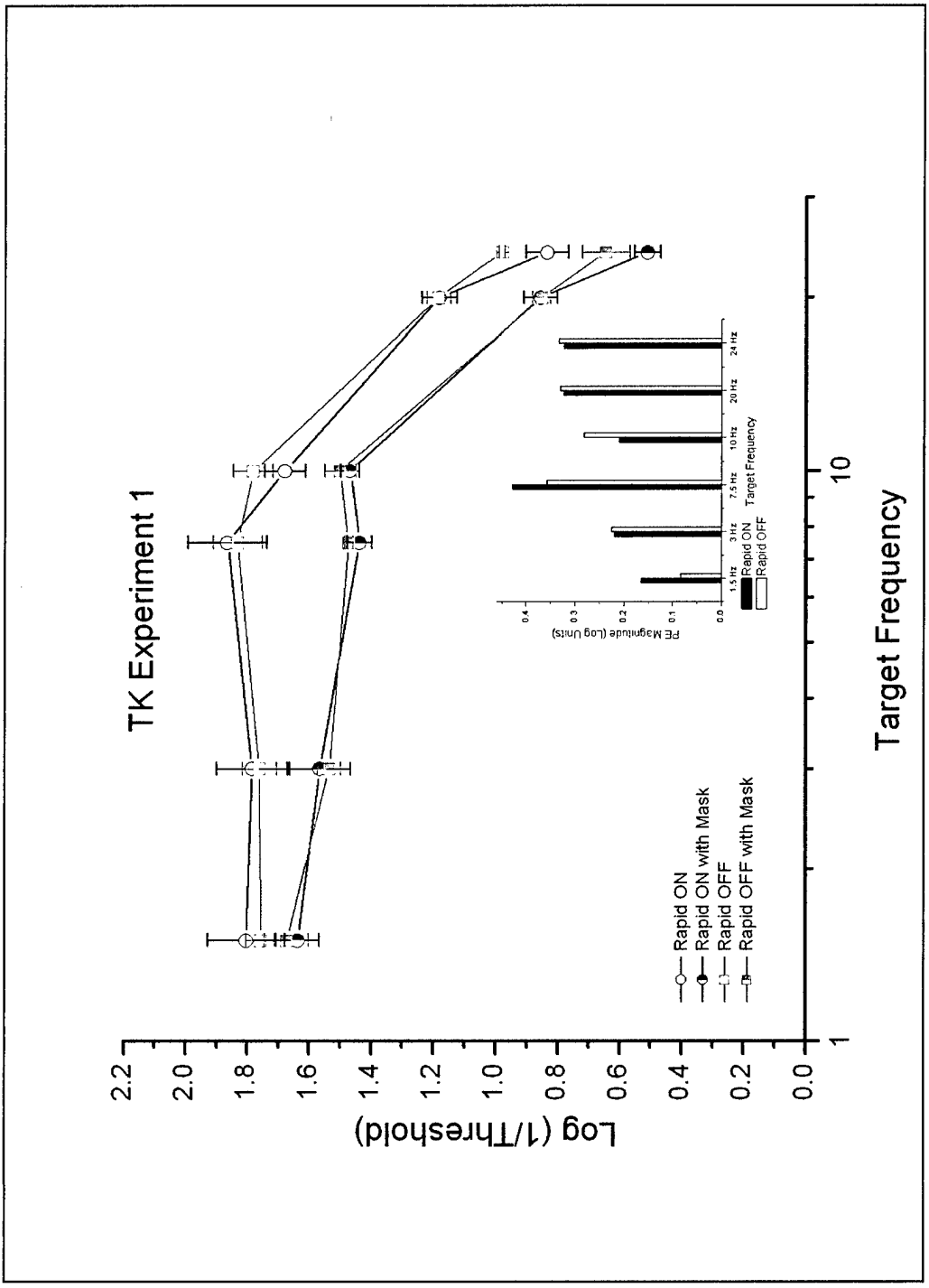


Figure B-3, TK Experiment 1.

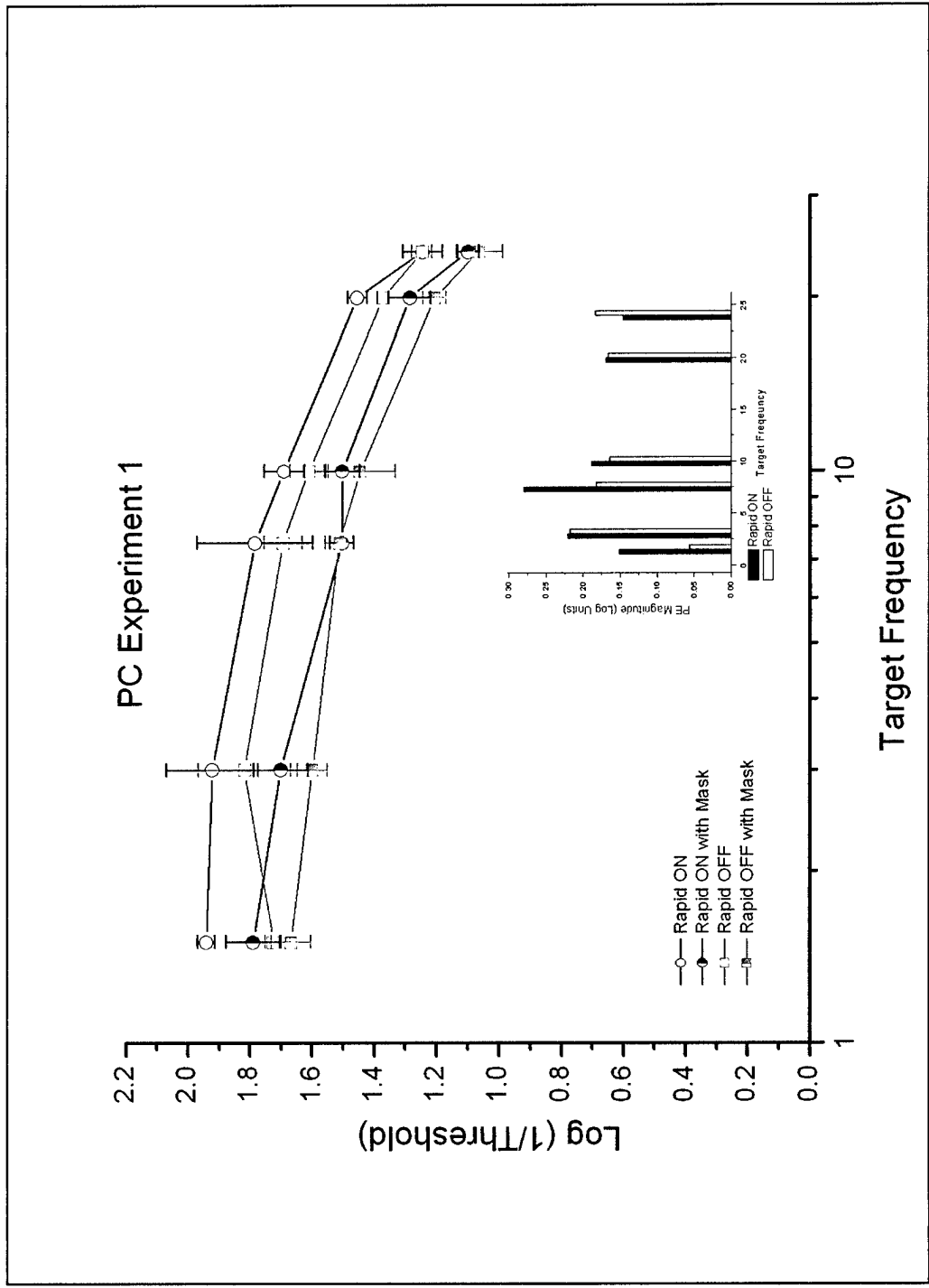


Figure B-4, PC Experiment 1.

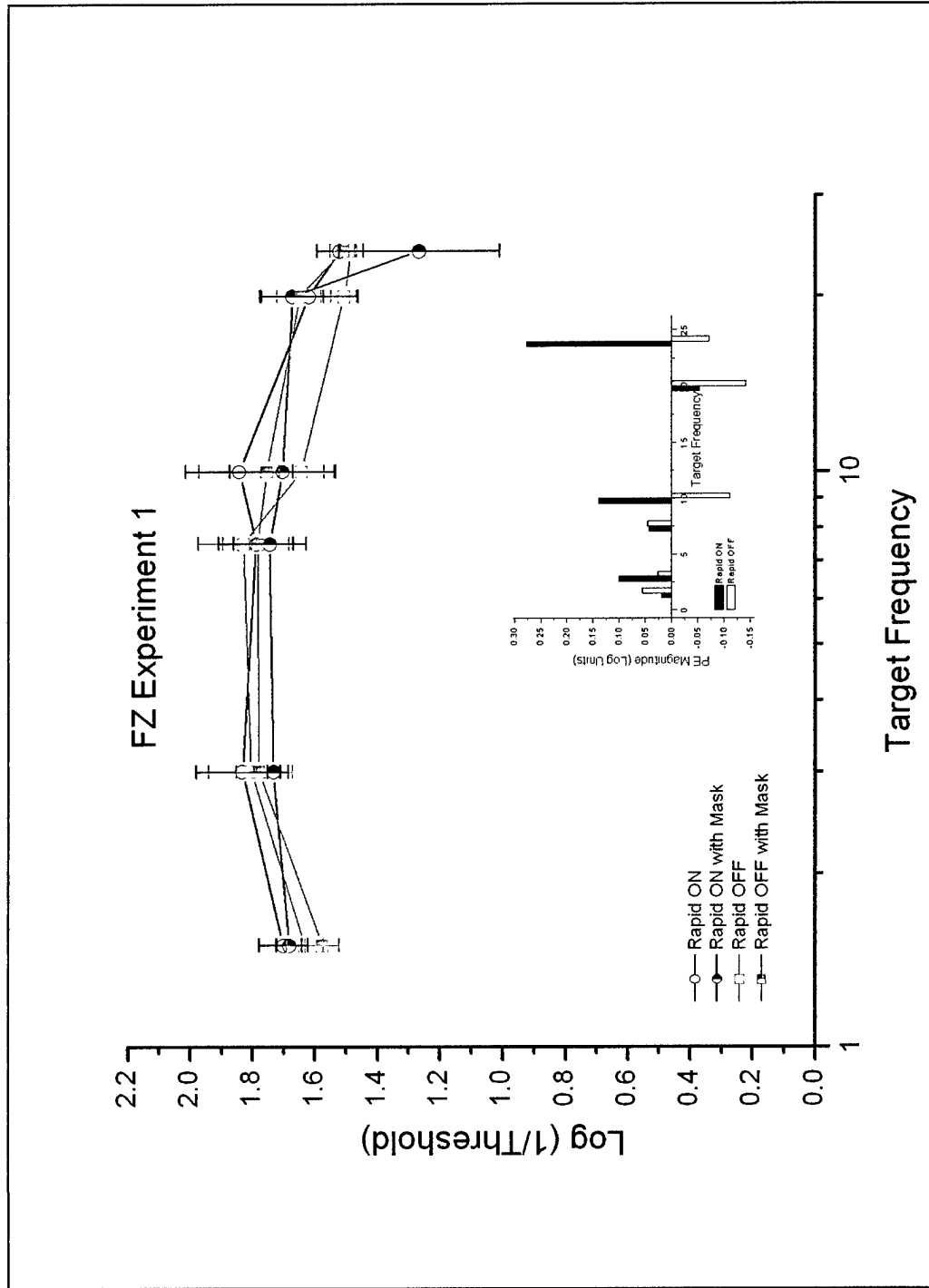


Figure B-5, FZ Experiment 1.

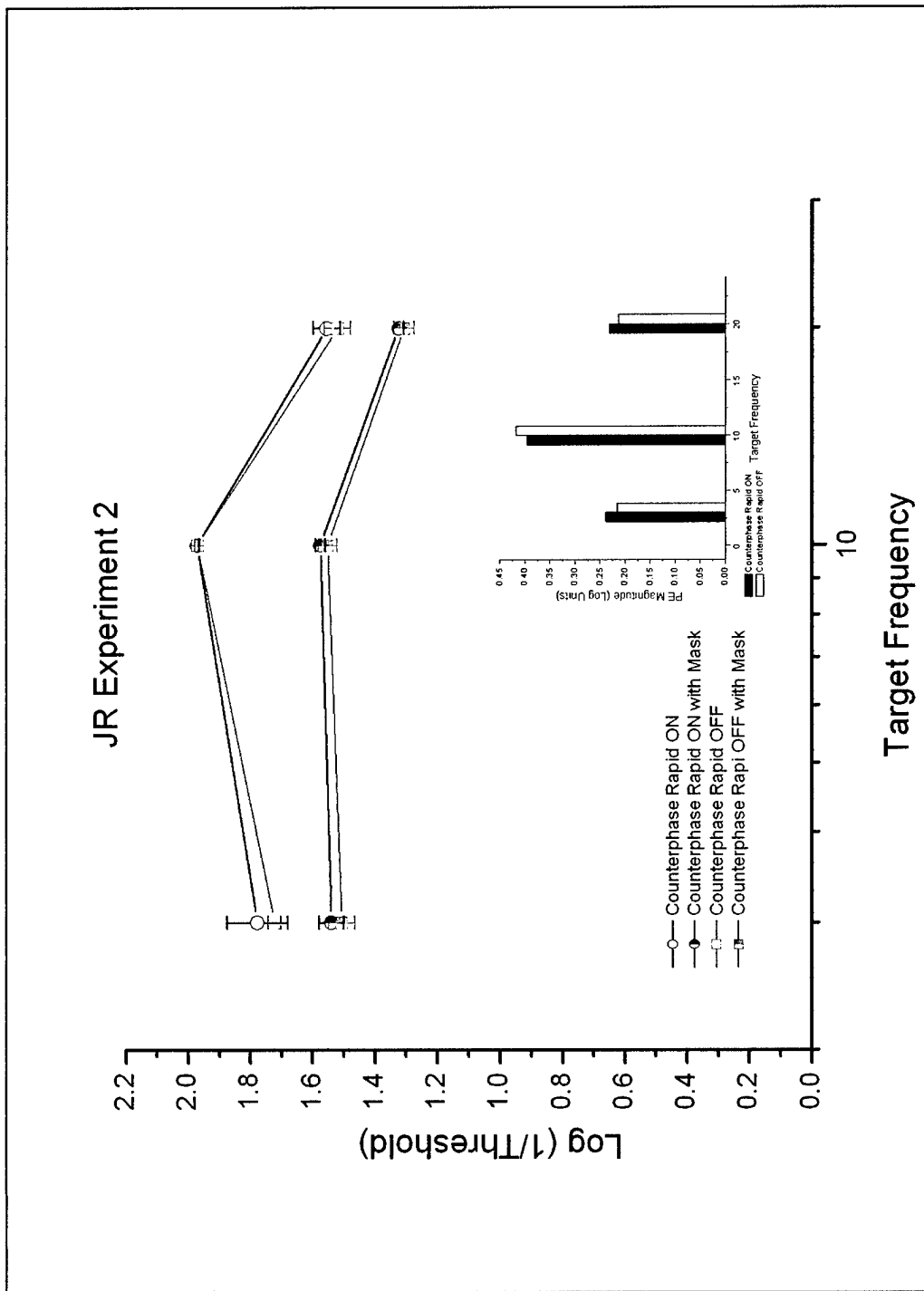


Figure B-6, JR Experiment 2.

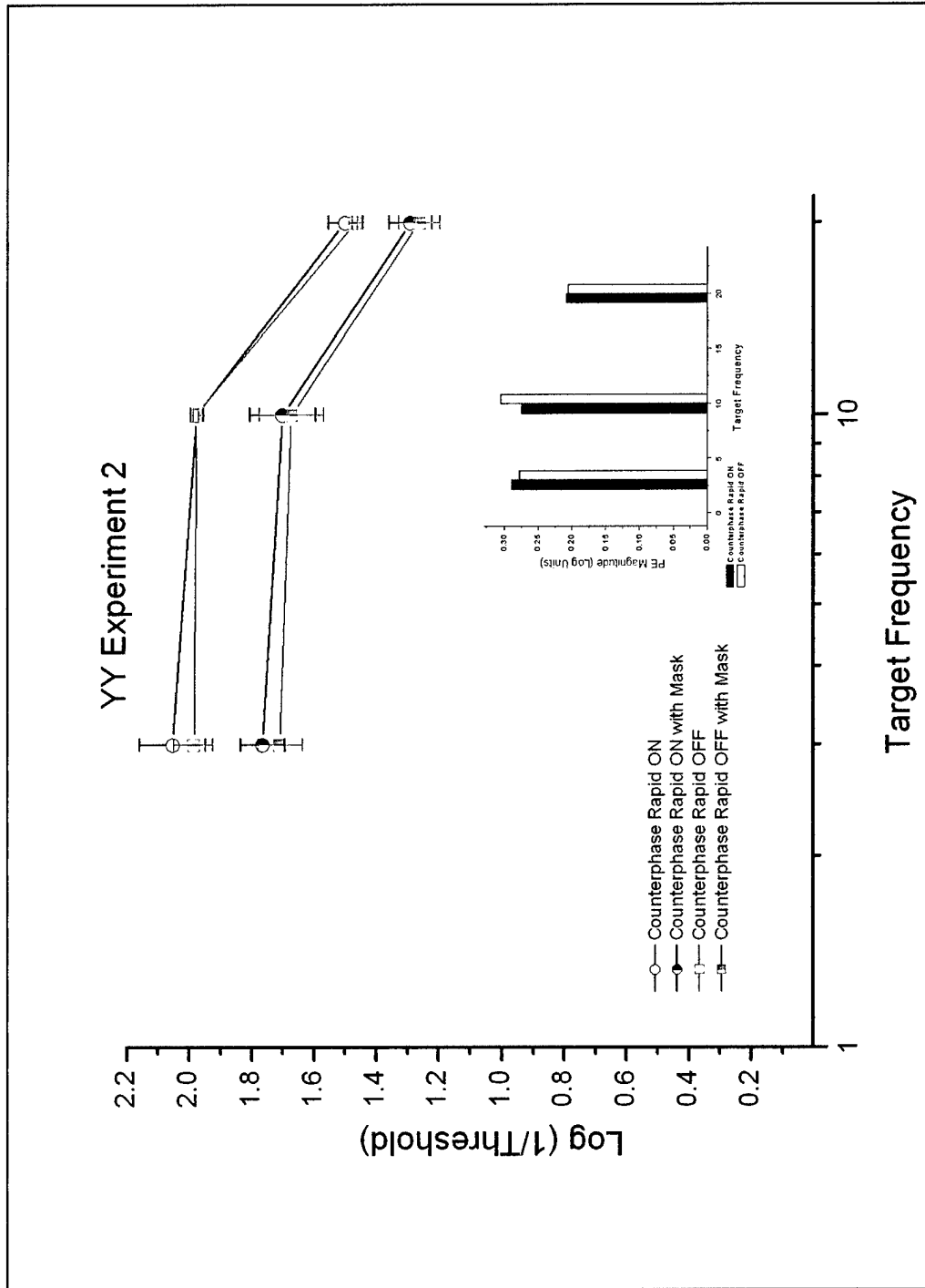


Figure B-7, YY Experiment 2.

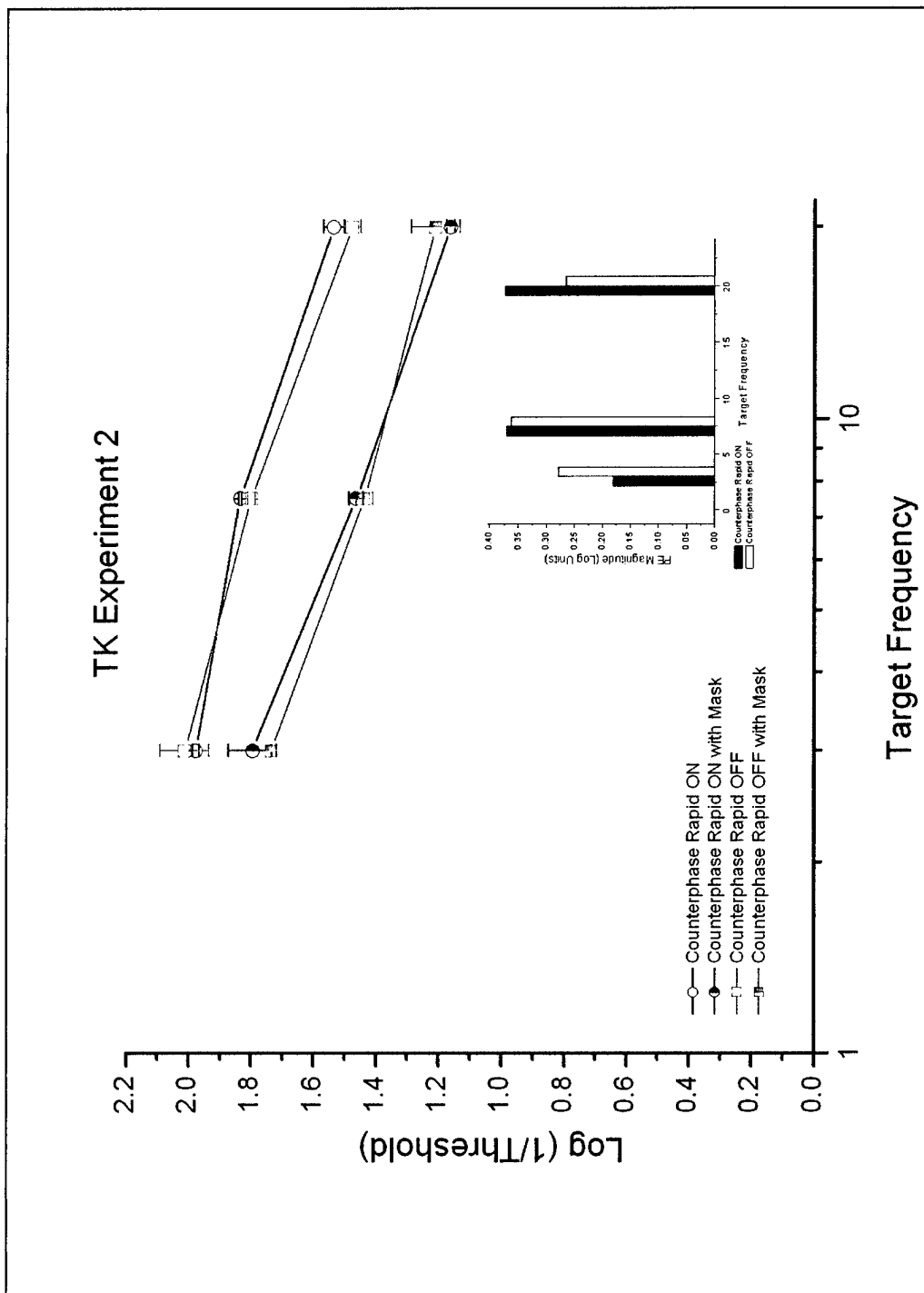


Figure B-8, TK Experiment 2.

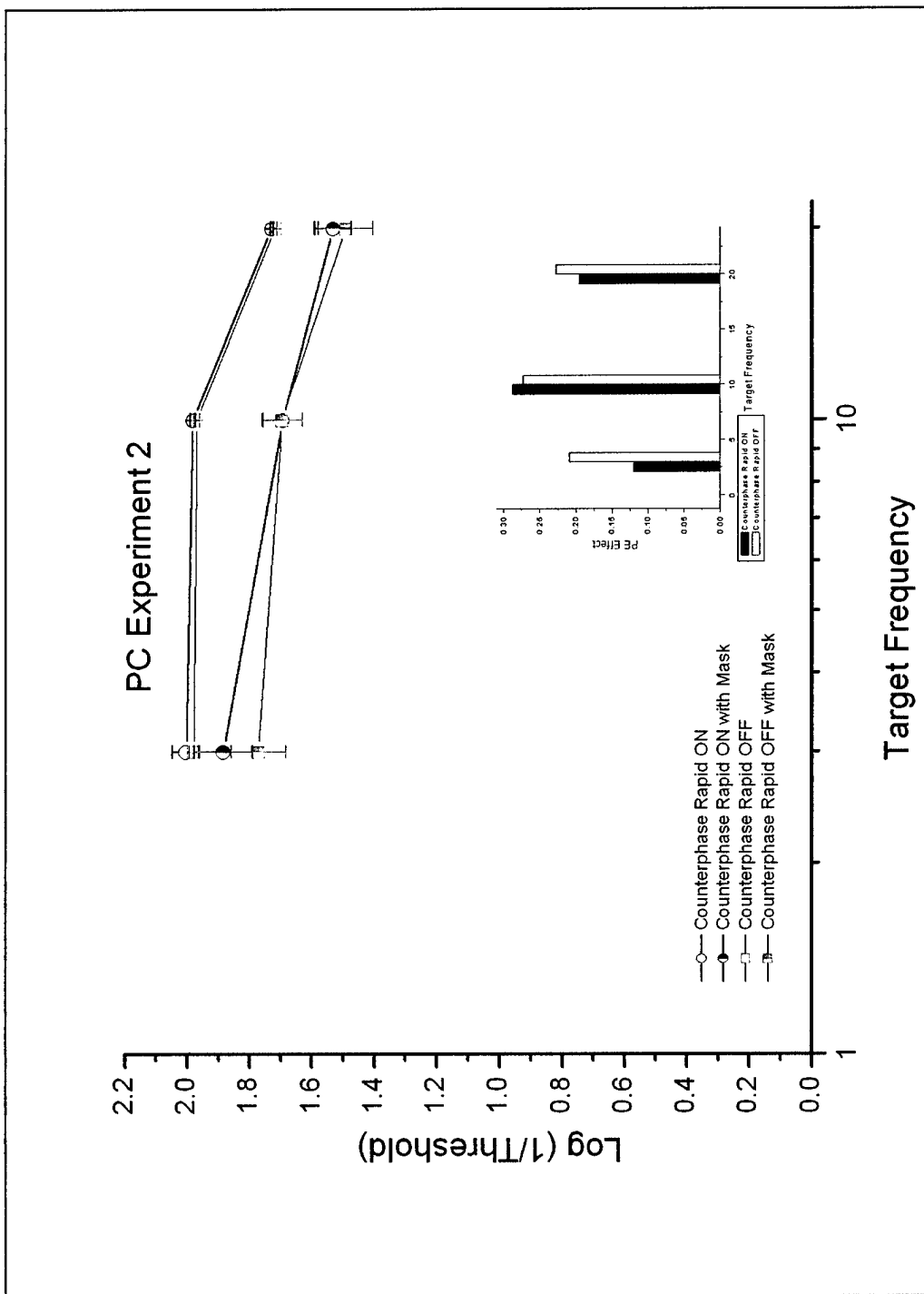


Figure B-9, PC Experiment 2.

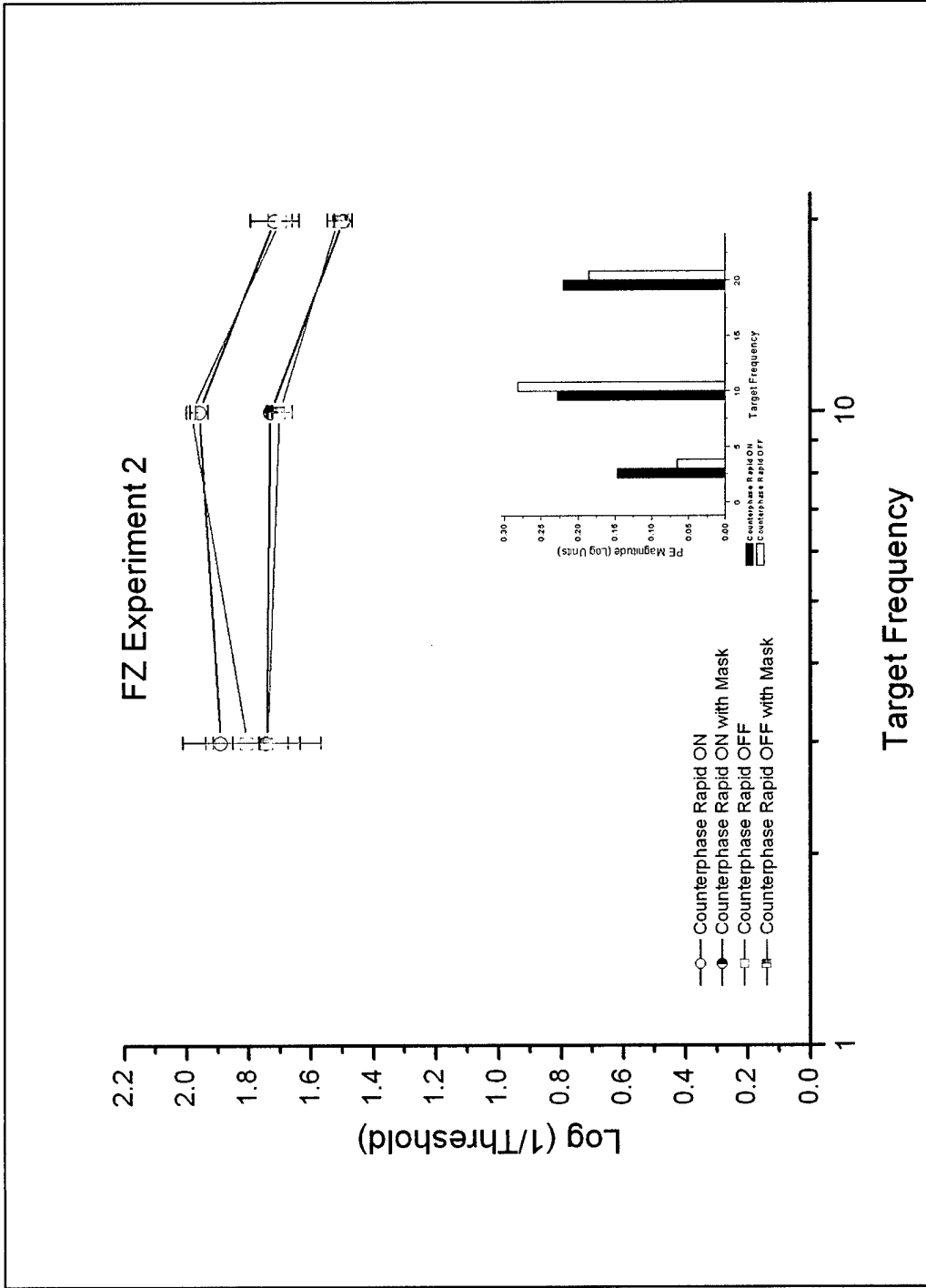


Figure B-10, FZ Experiment 2.

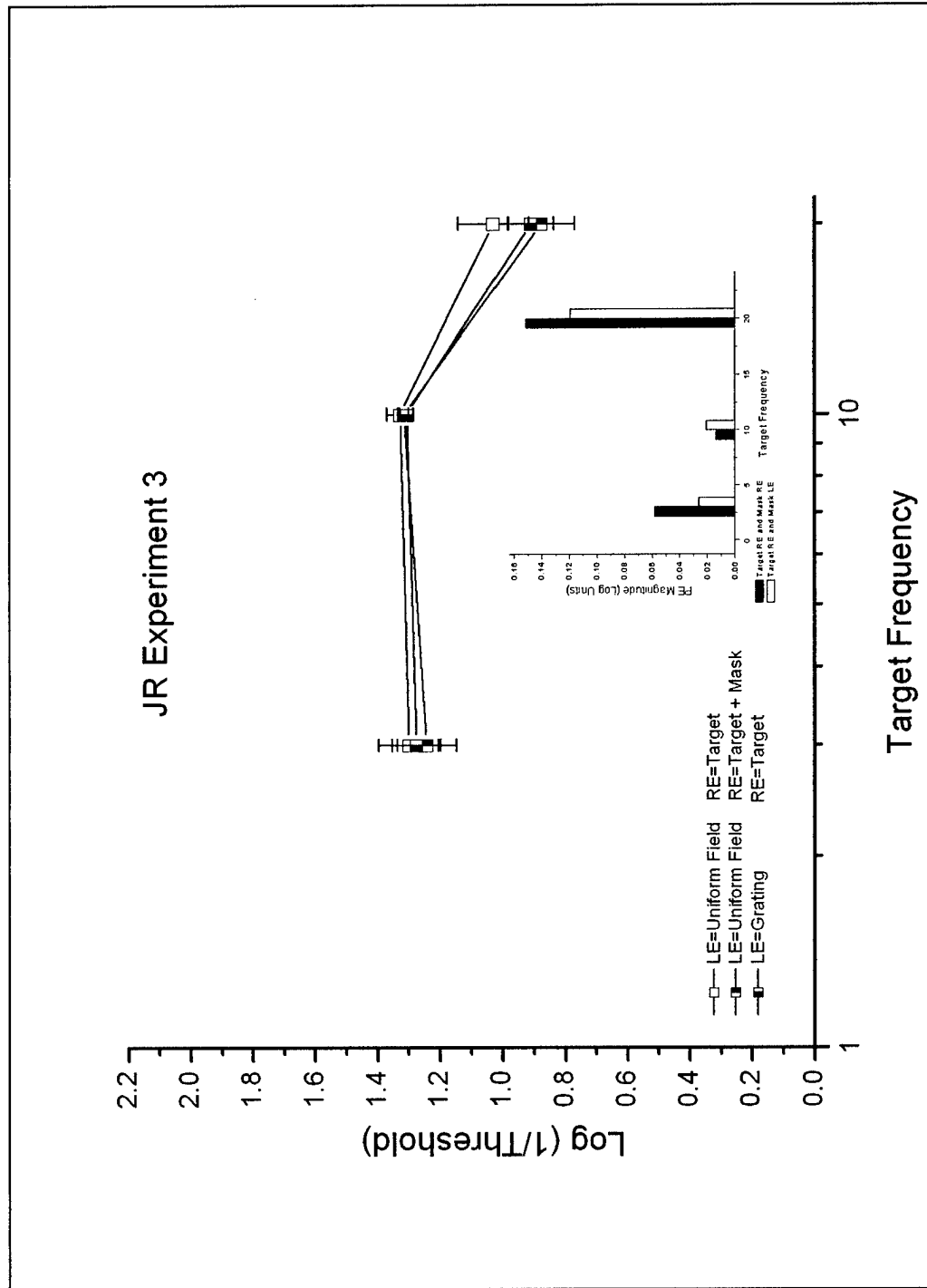


Figure B-11, JR Experiment 3.

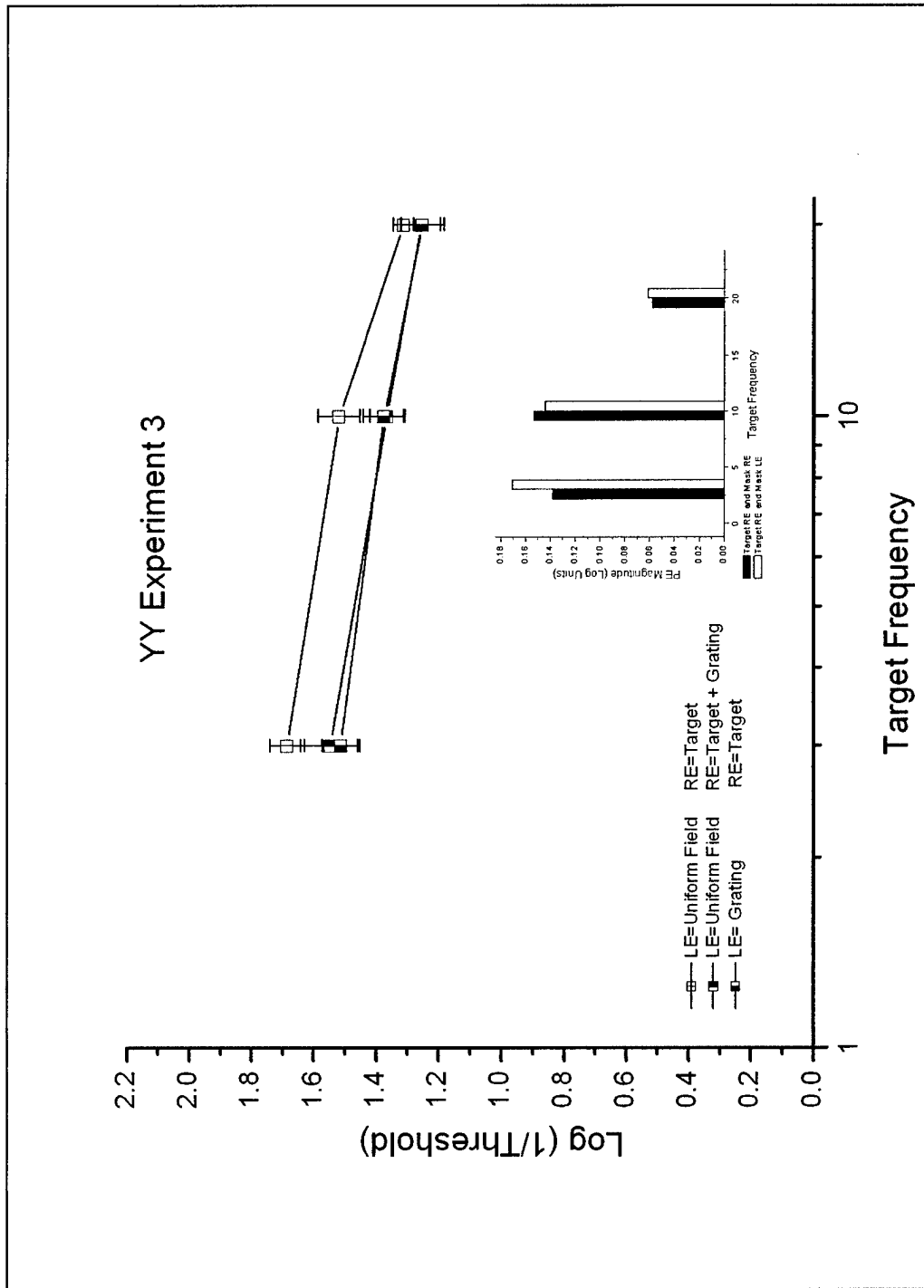


Figure B-12, YY Experiment 3.

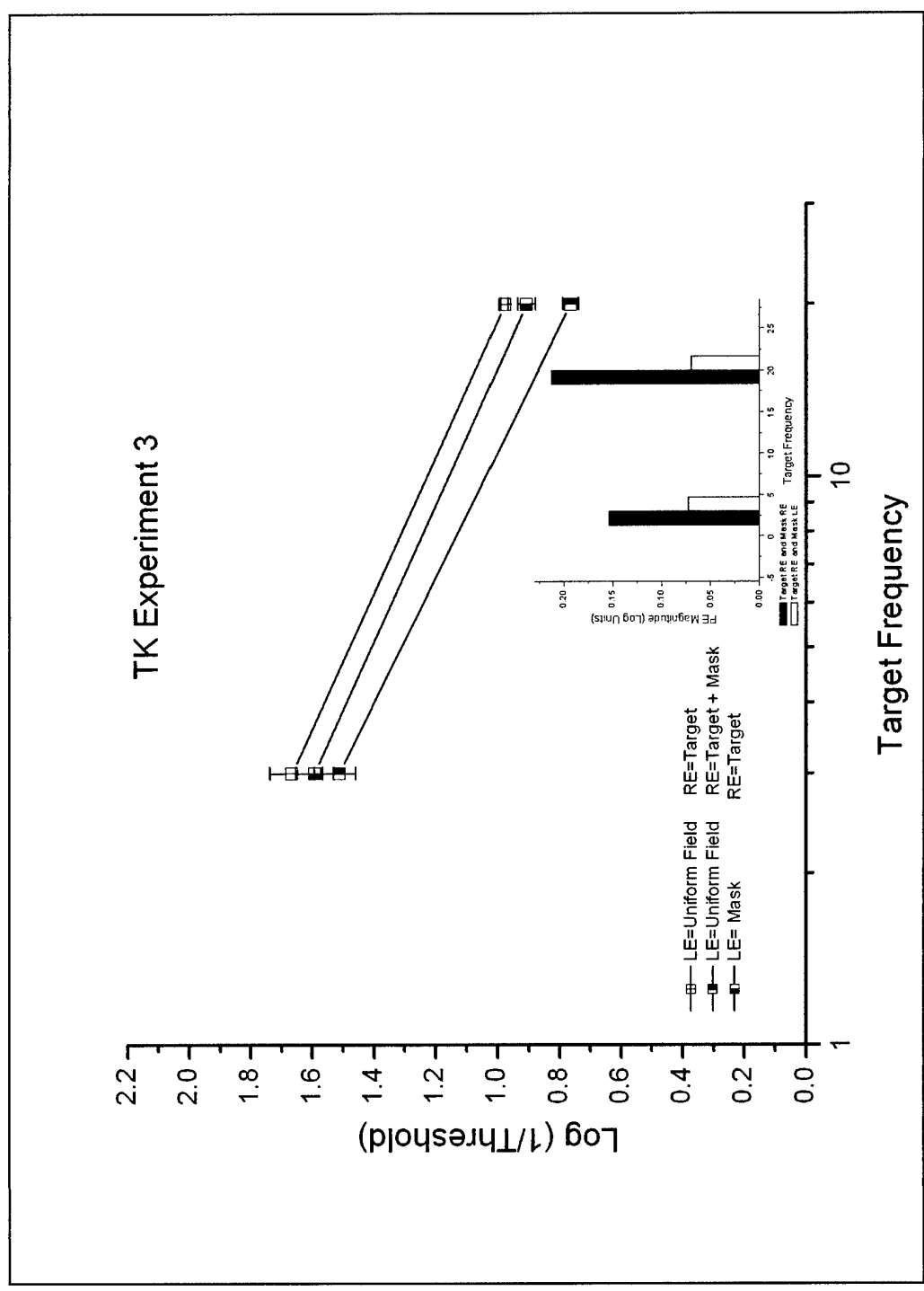


Figure B-13, TK Experiment 3.

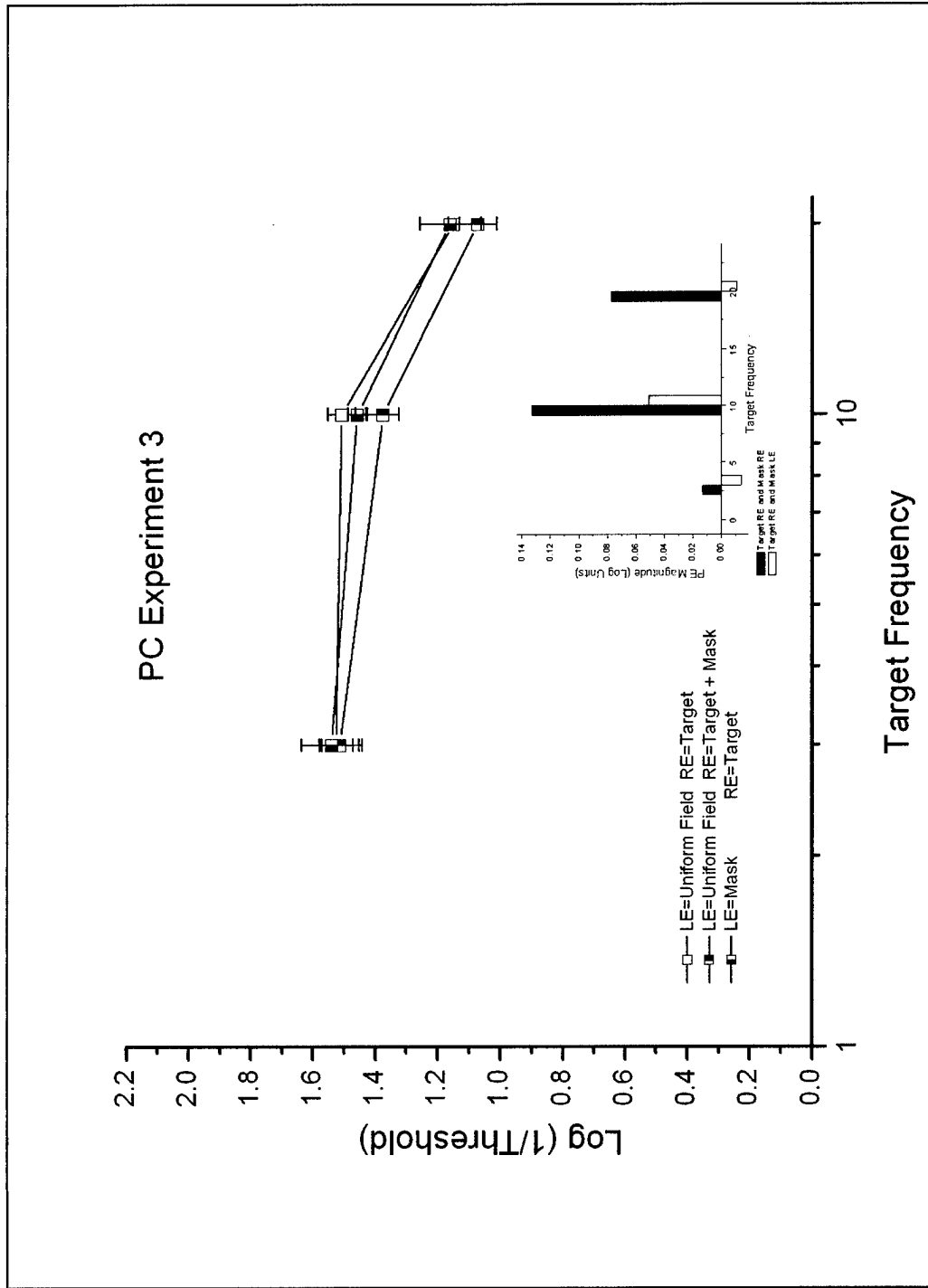


Figure B-14, PC Experiment 3.

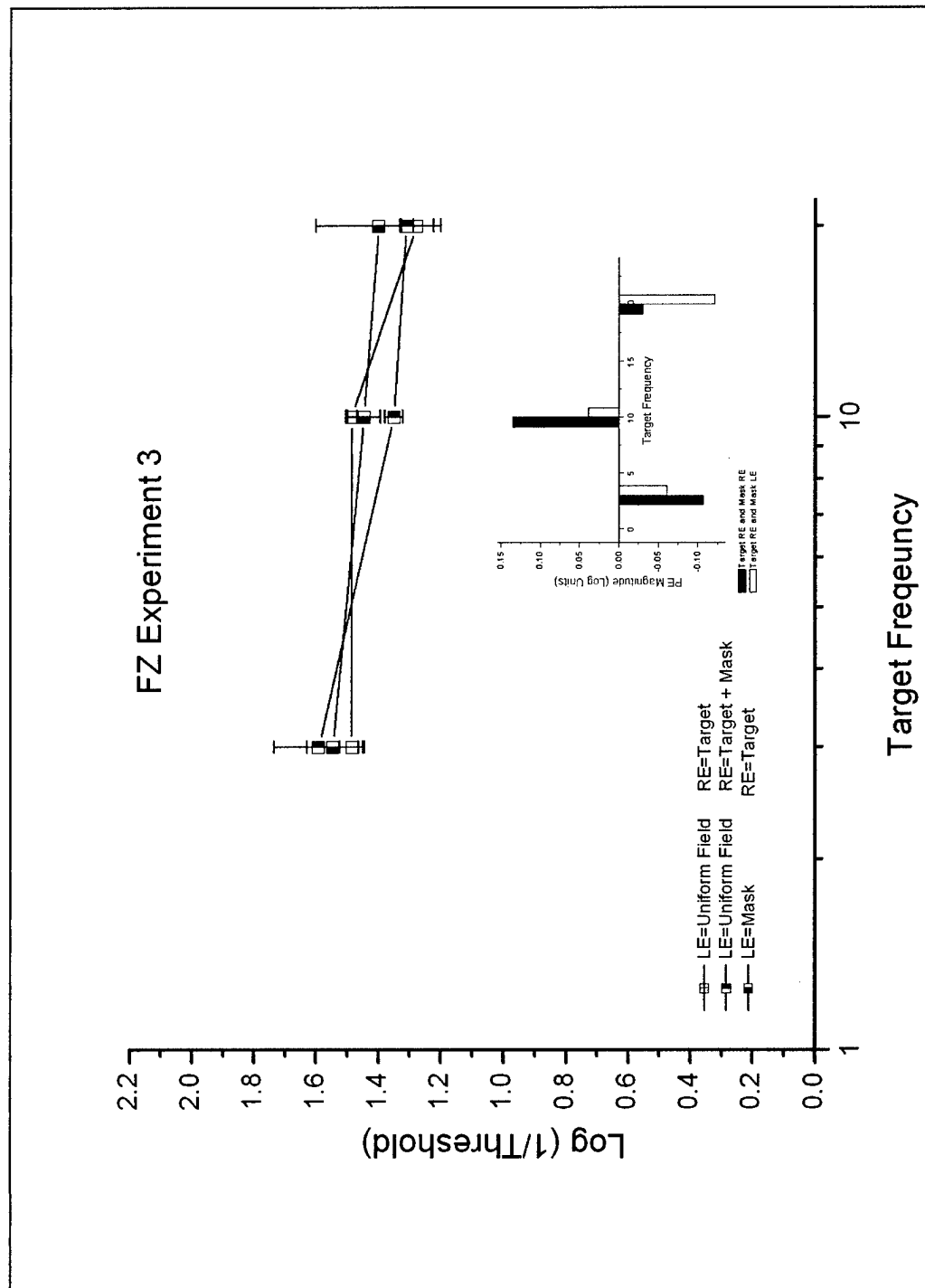


Figure B-15, FZ Experiment 3.

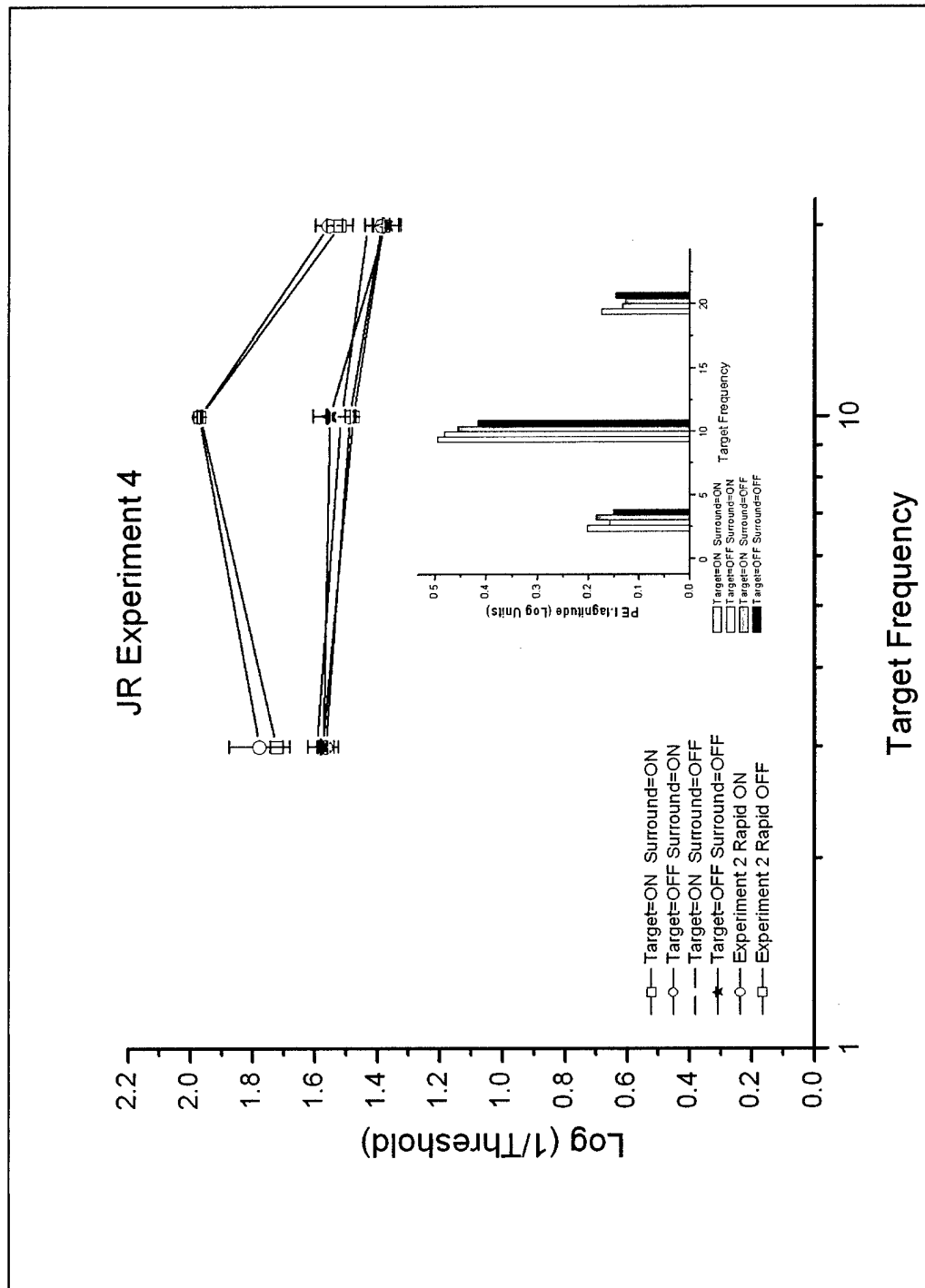


Figure B-16, JR Experiment 4.

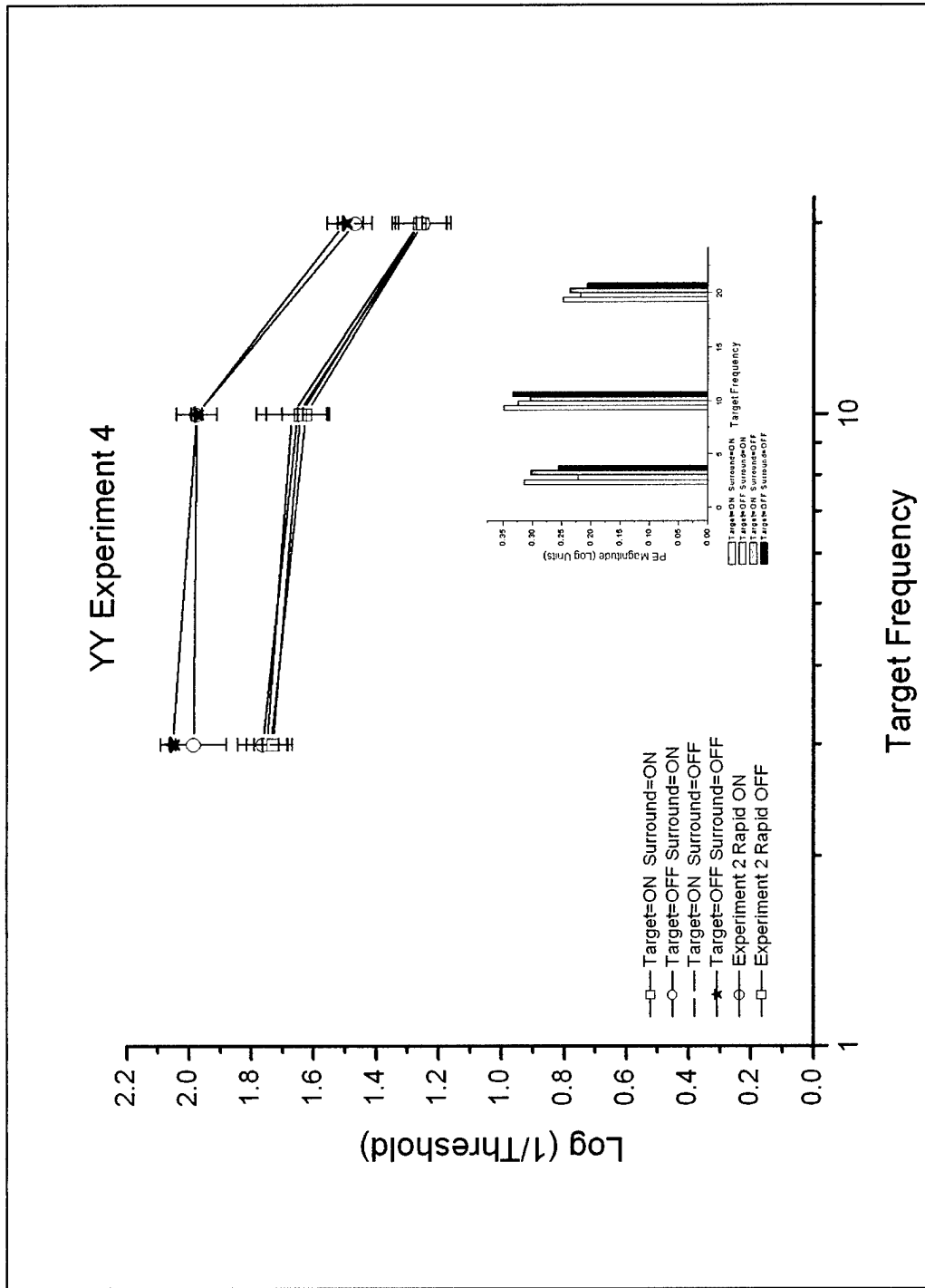


Figure B-17, YY Experiment 4.

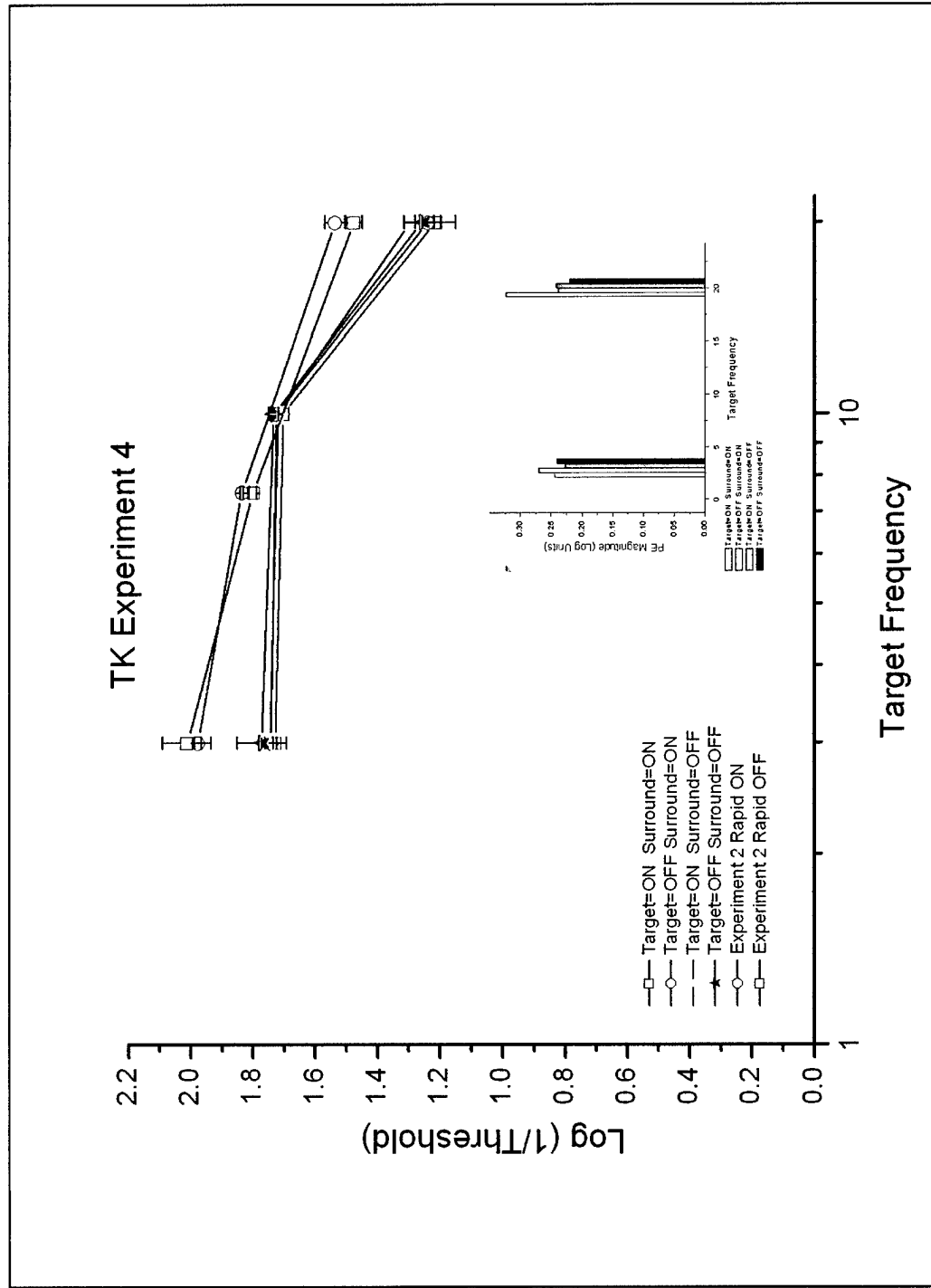


Figure B-18, TK Experiment 4.

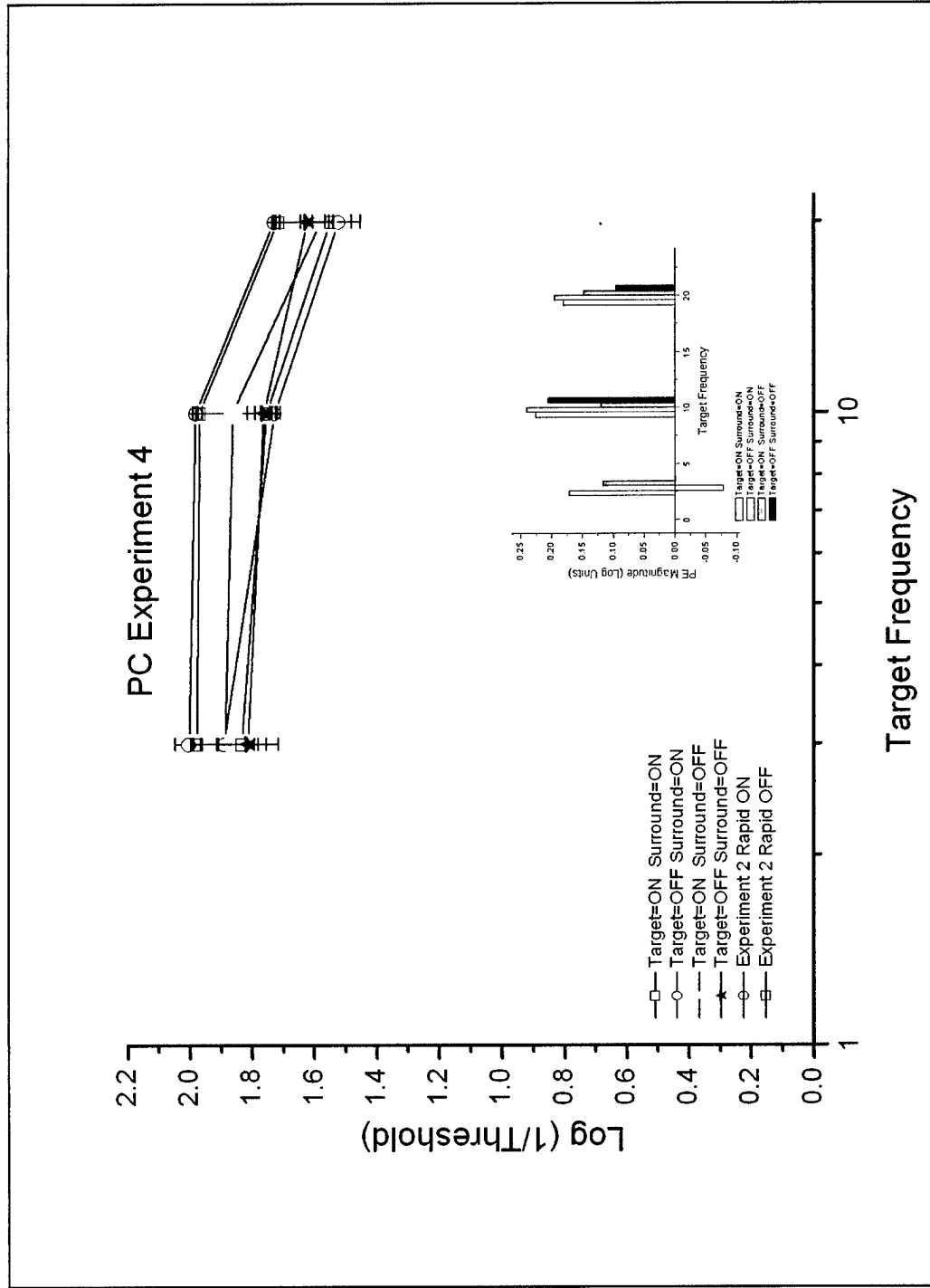


Figure B-19, PC Experiment 4.

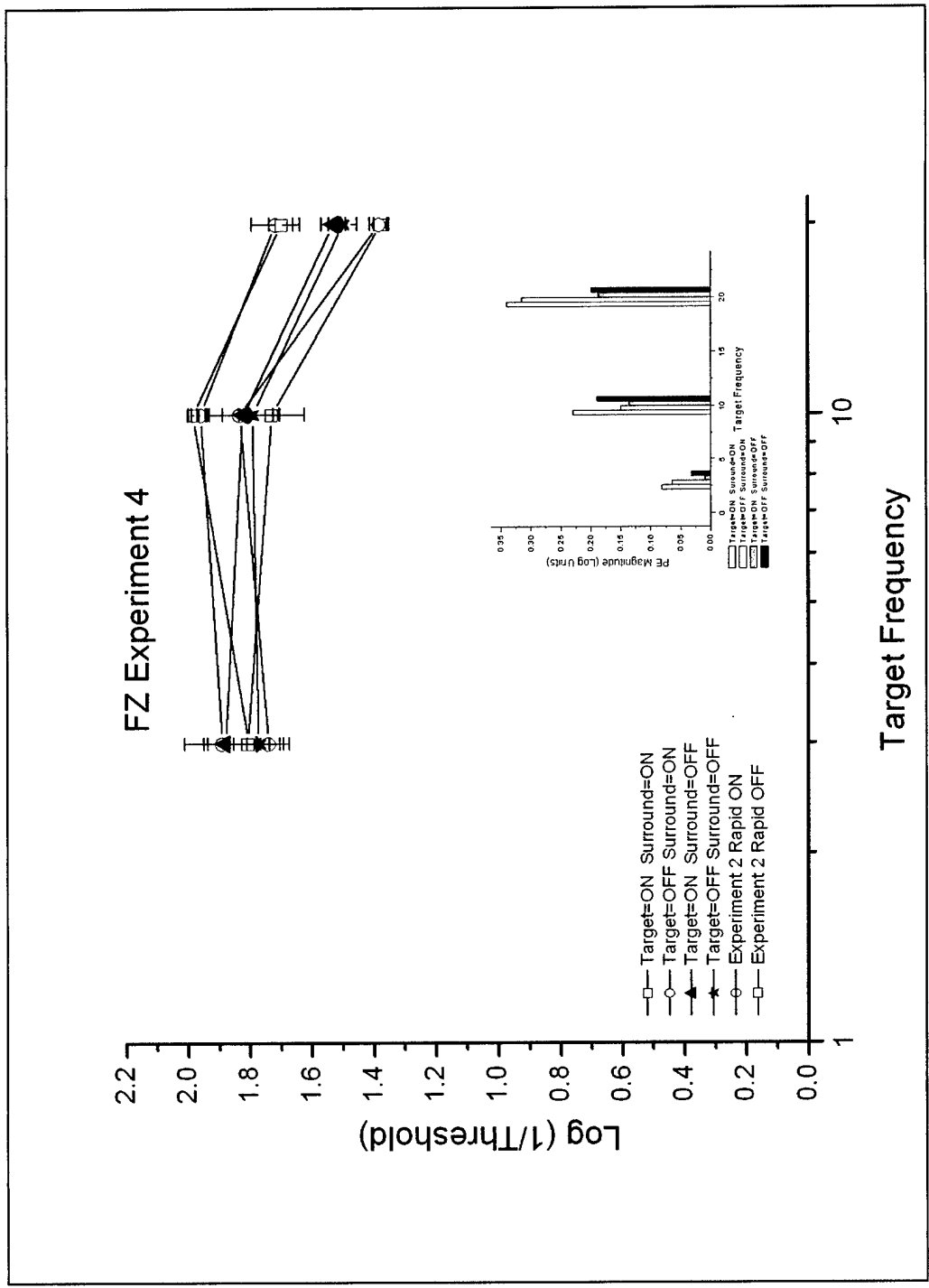


Figure B-20, FZ Experiment 4.

APPENDIX C
DATA TABLES

Table C-1.

Frequency	A	B	C	D
1.5 Hz	1.7747398	1.6626968	1.6647602	1.5859898
3.0 Hz	1.8003063	1.5968150	1.7235279	1.5580821
7.5 Hz	1.7494747	1.4927397	1.7293860	1.5164456
10.0 Hz	1.7034089	1.4983355	1.6381965	1.4974561
20.0 Hz	1.4057095	1.2382391	1.3474837	1.2167267
24.0 Hz	1.2466273	1.0344586	1.2380214	1.0765379

Experiment 1, average log (1/Threshold) values for all subjects. Column A represents the testing condition of a rapid-ON target with a uniform surround. Column B represents the testing condition of a rapid-ON target with a grating mask surround. Column C represents a rapid-OFF target with a uniform surround. Column D represents a rapid a rapid-OFF target with a grating mask surround. Each data point is the average of the subjects average yes/no QEUST repeated measures thresholds.

Table C-2.

Frequency	A	B	C	D
1.5 Hz	0.1017565	0.1012774	0.0705194	0.0828727
3.0 Hz	0.1129153	0.1327390	0.1093044	0.1516585
7.5 Hz	0.1325145	0.1922438	0.1281859	0.2001677
10.0 Hz	0.0800262	0.1425647	0.0847072	0.1732148
20.0 Hz	0.1595301	0.3126201	0.1187879	0.3023499
24.0 Hz	0.2965092	0.3687434	0.2187623	0.3971900

Experiment 1, all subjects, standard deviation of average log (1/Theshold) values.

Table C-3.

Frequency	A	B	C	D
1.5 Hz	1.7005300	1.5109343	1.6049785	1.4867532
3.0 Hz	1.6181125	1.3962116	1.5517611	1.3600104
7.5 Hz	1.5588766	1.2824621	1.5627844	1.2979935
10.0 Hz	1.6454357	1.3028511	1.5806454	1.2710942
20.0 Hz	1.3510064	1.0278264	1.2959741	1.0373706
24.0 Hz	1.1122902	0.8268597	1.0620767	0.7329954

Experiment 1, JR average $\log(1/\text{Threshold})$ values. Column A represents the testing condition of a rapid-ON target with a uniform surround. Column B represents the testing condition of a rapid-ON target with a grating mask surround. Column C represents a rapid-OFF target with a uniform surround. Column D represents a rapid a rapid-OFF target with a grating mask surround. Each data point is the average of approximately eight yes/no QEUST repeated measures.

Table C-4.

Frequency	A	B	C	D
1.5 Hz	0.0352530	0.0402870	0.0765572	0.0346859
3.0 Hz	0.0624486	0.0537058	0.0563777	0.0320261
7.5 Hz	0.0366653	0.0451381	0.0134943	0.0378018
10.0 Hz	0.0759886	0.0215163	0.0664319	0.0633264
20.0 Hz	0.0471578	0.0859568	0.0925531	0.1122689
24.0 Hz	0.1298925	0.1206370	0.1091470	0.0860573

Experiment 1, subject JR, standard deviation of average $\log(1/\text{Theshold})$ values.

Table C-5.

Frequency	A	B	C	D
1.5 Hz	1.7287453	1.6940829	1.6063819	1.5273234
3.0 Hz	1.8438954	1.5889043	1.6836864	1.5167505
10.0 Hz	1.6572210	1.5121702	1.5754909	1.5159606
20.0 Hz	1.4209601	1.3470979	1.3774306	1.3379676
24.0 Hz	1.4324627	1.4033249	1.4093870	1.3777083

Experiment 1, YY average log (1/Threshold) values. Column A represents the testing condition of a rapid-ON target with a uniform surround. Column B represents the testing condition of a rapid-ON target with a grating mask surround. Column C represents a rapid-OFF target with a uniform surround. Column D represents a rapid a rapid-OFF target with a grating mask surround. Each data point is the average of approximately eight yes/no QEUST repeated measures.

Table C-6.

Frequency	A	B	C	D
1.5 Hz	0.0190622	0.0509006	0.0652401	0.0379766
3.0 Hz	0.1450986	0.0754555	0.0591262	0.0558989
10.0 Hz	0.0640891	0.0748157	0.0090654	0.0337251
20.0 Hz	0.0715032	0.0321289	0.0470858	0.0425290
24.0 Hz	0.0617378	0.0369981	0.0560563	0.0485190

Experiment 1, subject YY, standard deviation of average log (1/Theshold) values.

Table C-7.

Frequency	A	B	C	D
1.5 Hz	1.8028850	1.6375052	1.7562283	1.6720039
3.0 Hz	1.7855097	1.5657189	1.7604318	1.5352312
7.5 Hz	1.8661670	1.4387269	1.8319054	1.4735034
10.0 Hz	1.6802807	1.4704118	1.7818769	1.5000587
20.0 Hz	1.1813283	0.8581504	1.1843161	0.8533325
24.0 Hz	0.8359527	0.5122626	0.9803774	0.6462738

Experiment 1, TK average log (1/Threshold) values. Column A represents the testing condition of a rapid-ON target with a uniform surround. Column B represents the testing condition of a rapid-ON target with a grating mask surround. Column C represents a rapid-OFF target with a uniform surround. Column D represents a rapid a rapid-OFF target with a grating mask surround. Each data point is the average of approximately four yes/no QEUST repeated measures.

Table C-8.

Frequency	A	B	C	D
1.5 Hz	0.1243919	0.0696354	0.0455155	0.0705261
3.0 Hz	0.1142156	0.0982514	0.0560387	0.0375766
7.5 Hz	0.1267073	0.0407369	0.0794727	0.0131992
10.0 Hz	0.0658793	0.0296630	0.0627941	0.0509095
20.0 Hz	0.0560180	0.0545153	0.0388038	0.0294697
24.0 Hz	0.0673145	0.0430125	0.0096113	0.0765037

Experiment 1, subject TK, standard deviation of average log (1/Theshold) values.

Table C-9.

Frequency	A	B	C	D
1.5 Hz	1.8951356	1.7892482	1.7238632	1.6677570
3.0 Hz	1.9212783	1.7007963	1.8170406	1.5993492
7.5 Hz	1.7849264	1.5048552	1.6944370	1.5121011
10.0 Hz	1.6912700	1.5027403	1.6100719	1.4462009
20.0 Hz	1.4557018	1.2862595	1.3720036	1.2062311
24.0 Hz	1.2446499	1.0989408	1.2459579	1.0623618

Experiment 1, PC average log (1/Threshold) values. Column A represents the testing condition of a rapid-ON target with a uniform surround. Column B represents the testing condition of a rapid-ON target with a grating mask surround. Column C represents a rapid-OFF target with a uniform surround. Column D represents a rapid a rapid-OFF target with a grating mask surround. Each data point is the average of approximately six yes/no QEUST repeated measures.

Table C-10.

Frequency	A	B	C	D
1.5 Hz	0.0939599	0.0883986	0.0252678	0.0633750
3.0 Hz	0.1480946	0.0870421	0.1490883	0.0482993
7.5 Hz	0.1858514	0.0382998	0.0614707	0.0456538
10.0 Hz	0.0649701	0.0553279	0.0606282	0.1145419
20.0 Hz	0.0309587	0.0682033	0.0173168	0.0379520
24.0 Hz	0.0636759	0.0348370	0.0327645	0.0730329

Experiment 1, subject PC, standard deviation of average log (1/Theshold) values.

Table C-11.

Frequency	A	B	C	D
1.5 Hz	1.7008414	1.6817135	1.6323491	1.5761115
3.0 Hz	1.8327355	1.7324441	1.8047197	1.7790693
7.5 Hz	1.7879287	1.7449146	1.8284170	1.7821844
10.0 Hz	1.8428373	1.7035039	1.6428976	1.7539663
20.0 Hz	1.6195512	1.6718613	1.5076939	1.6487317
24.0 Hz	1.5196634	1.2669770	1.4815736	1.5093668

Experiment 1, FZ average log (1/Threshold) values. Column A represents the testing condition of a rapid-ON target with a uniform surround. Column B represents the testing condition of a rapid-ON target with a grating mask surround. Column C represents a rapid-OFF target with a uniform surround. Column D represents a rapid a rapid-OFF target with a grating mask surround. Each data point is the average of approximately six yes/no QEUST repeated measures.

Table C-12.

Frequency	A	B	C	D
1.5 Hz	0.0795046	0.0406872	0.0588623	0.0540273
3.0 Hz	0.1483362	0.0206229	0.1348394	0.0712668
7.5 Hz	0.1202185	0.1165467	0.1447762	0.1111994
10.0 Hz	0.1721495	0.1696212	0.0724358	0.2163281
20.0 Hz	0.1578727	0.0990535	0.0411095	0.0708313
24.0 Hz	0.0744535	0.2558194	0.0098983	0.0423599

Experiment 1, subject FZ, standard deviation of average log (1/Theshold) values.

Table C-13.

Frequency	A	B	C	D
3 Hz	1.9403282	1.7453210	1.9008972	1.6917338
10 Hz	1.9729530	1.6067056	1.9755893	1.5737257
20 Hz	1.5703578	1.3246588	1.5316035	1.3078513

Experiment 2, average log (1/Threshold) values for all subjects. Column A represents the testing condition of a rapid-ON counterphased target with a uniform surround. Column B represents the testing condition of a rapid-ON counterphased target with a grating mask surround. Column C represents a rapid-OFF counterphased target with a uniform surround. Column D represents a rapid a rapid-OFF counterphased target with a grating mask surround. Each data point is the average of the subjects average yes/no QEUST repeated measures thresholds.

Table C-14.

Frequency	A	B	C	D
3 Hz	0.1084314	0.1271798	0.1291884	0.1059388
10 Hz	0.0043110	0.0628447	0.0034232	0.0731883
20 Hz	0.0907280	0.1328711	0.1069412	0.1080061

Experiment 2, all subjects, standard deviation of average log (1/Theshold) values.

Table C-15.

Frequency	A	B	C	D
3 Hz	1.7776313	1.5393773	1.7222286	1.5065467
10 Hz	1.9718821	1.5760087	1.9704911	1.5523926
20 Hz	1.5558555	1.3241275	1.5192857	1.3061662

Experiment 2, JR average log (1/Threshold) values. Column A represents the testing condition of a rapid-ON counterphased target with a uniform surround. Column B represents the testing condition of a rapid-ON counterphased target with a grating mask surround. Column C represents a rapid-OFF counterphased target with a uniform surround. Column D represents a rapid a rapid-OFF counterphased target with a grating mask surround. Each data point is the average of approximately seven yes/no QEUST repeated measures

Table C-16.

Frequency	A	B	C	D
3 Hz	0.0978990	0.0393162	0.0210918	0.0416337
10 Hz	0.0061026	0.0157191	0.0092759	0.0301844
20 Hz	0.0428191	0.0163328	0.0420290	0.0331881

Experiment 2, subject JR, standard deviation of average log (1/Theshold) values.

Table C-17.

Frequency	A	B	C	D
3 Hz	2.0523657	1.7635522	1.9851856	1.7074381
10 Hz	1.9757013	1.7006442	1.9769783	1.6716249
20 Hz	1.4995835	1.2913225	1.4685618	1.2625493

Experiment 2, subject YY average log (1/Threshold) values. Column A represents the testing condition of a rapid-ON counterphased target with a uniform surround. Column B represents the testing condition of a rapid-ON counterphased target with a grating mask surround. Column C represents a rapid-OFF counterphased target with a uniform surround. Column D represents a rapid a rapid-OFF counterphased target with a grating mask surround. Each data point is the average of approximately eight yes/no QEUST repeated measures

Table C-18.

Frequency	A	B	C	D
3 Hz	0.1049300	0.0713696	0.0615419	0.0705670
10 Hz	0.0167906	0.1048909	0.0083113	0.1037315
20 Hz	0.0549794	0.0675542	0.0091636	0.0661640

Experiment 2, subject YY, standard deviation of average log (1/Threshold) values.

Table C-19.

Frequency	A	B	C	D
3.0 Hz	1.9768839	1.7958220	2.0124869	1.7339300
7.5 Hz	1.8361046	1.4655798	1.8009881	1.4382632
20.0 Hz	1.5370995	1.1631612	1.4771636	1.2115577

Experiment 2, subject TK average log (1/Threshold) values. Column A represents the testing condition of a rapid-ON counterphased target with a uniform surround. Column B represents the testing condition of a rapid-ON counterphased target with a grating mask surround. Column C represents a rapid-OFF counterphased target with a uniform surround. Column D represents a rapid a rapid-OFF counterphased target with a grating mask surround. Each data point is the average of approximately four yes/no QEUST repeated measures

Table C-20.

Frequency	A	B	C	D
3.0 Hz	0.0101563	0.0766760	0.0780260	0.0032837
7.5 Hz	0.0051944	0.0225153	0.0124072	0.0252682
20.0 Hz	0.0338417	0.0135844	0.0272977	0.0788037

Experiment 2, subject TK, standard deviation of average log (1/Theshold) values.

Table C-21.

Frequency	A	B	C	D
1.5 Hz	2.0248472	1.9685648	1.9597070	1.7466464
3.0 Hz	2.0046992	1.8846013	1.9792732	1.7707031
7.5 Hz	2.1337905	1.8293927	1.9898398	1.7443887
10.0 Hz	1.9812451	1.6934525	1.9687051	1.6956620
20.0 Hz	1.7285586	1.5326637	1.7194505	1.4914492
24.0 Hz	1.8497129	1.6762914	1.6586847	1.5236839

Experiment 2, subject PC average log (1/Threshold) values. Column A represents the testing condition of a rapid-ON counterphased target with a uniform surround. Column B represents the testing condition of a rapid-ON counterphased target with a grating mask surround. Column C represents a rapid-OFF counterphased target with a uniform surround. Column D represents a rapid a rapid-OFF counterphased target with a grating mask surround. Each data point is the average of approximately six yes/no QEUST repeated measures

Table C-22.

Frequency	A	B	C	D
1.5 Hz	0.0221103	0.0093175	0.0182932	0.0015388
3.0 Hz	0.0439277	0.0938774	0.0132278	0.0887673
7.5 Hz	0.1763454	0.1034039	0.0321969	0.0228271
10.0 Hz	0.0082434	0.0641143	0.0101949	0.0644505
20.0 Hz	0.0050329	0.0590591	0.0085597	0.0883196
24.0 Hz	0.0046387	0.0618368	0.0760782	0.0508068

Experiment 2, subject PC, standard deviation of average log (1/Theshold) values.

Table C-23.

Frequency	A	B	C	D
3.0 Hz	1.8900609	1.7432522	1.8053117	1.7400511
7.5 Hz	1.9529026	1.7642549	1.9736585	1.8942923
10.0 Hz	1.9583935	1.7305518	1.9827630	1.7004929
20.0 Hz	1.7155381	1.4956459	1.6969895	1.5119143

Experiment 2, subject FZ average log (1/Threshold) values. Column A represents the testing condition of a rapid-ON counterphased target with a uniform surround. Column B represents the testing condition of a rapid-ON counterphased target with a grating mask surround. Column C represents a rapid-OFF counterphased target with a uniform surround. Column D represents a rapid a rapid-OFF counterphased target with a grating mask surround. Each data point is the average of approximately six yes/no QEUST repeated measures.

Table C-24.

Frequency	A	B	C	D
3.0 Hz	0.1223170	0.1072117	0.1322427	0.1734841
7.5 Hz	0.0358279	0.0816952	0.0192604	0.0307133
10.0 Hz	0.0288532	0.0071282	0.0141870	0.0417335
20.0 Hz	0.0787155	0.0297762	0.0384713	0.0345945

Experiment 2, subject FZ, standard deviation of average log (1/Theshold) values.

Table C-25.

Frequency	A	B	C
3 Hz	1.5330653	1.4818530	1.4941906
10 Hz	1.4612461	1.3524684	1.3974487
20 Hz	1.1497434	1.0560162	1.1547473

Experiment 3, average log (1/Threshold) for all subjects. Column A represents the sensitivity values obtained while the subject viewed a uniform field with his left eye and a superimposed rapid-ON target with his right eye. Column B represents the sensitivity values obtained when the subject viewed a uniform field with his left eye and a superimposed rapid-ON target surrounded by a grating mask with his left eye. Column C represents the sensitivity values obtained when the subject viewed a rapid-ON target with his left eye and a superimposed grating mask with his right eye.

Table C-26.

Frequency	A	B	C
3 Hz	0.1561516	0.1377772	0.1259344
10 Hz	0.0890696	0.0267518	0.0697563
20 Hz	0.1480581	0.2350412	0.2651246

Experiment 3, all subjects, standard deviation values for the average log (1/Thresholds) values.

Table C-27.

Frequency	A	B	C
3 Hz	1.3007648	1.2425083	1.2747914
10 Hz	1.3292833	1.3155064	1.3085643
20 Hz	1.0293367	0.8777911	0.9097852

Experiment 3, subject JR, average (1/Threshold) values. Column A represents the sensitivity values obtained while the subject viewed a uniform field with his left eye and a superimposed rapid-ON target with his right eye. Column B represents the sensitivity values obtained when the subject viewed a uniform field with his left eye and a superimposed rapid-ON target surrounded by a grating mask with his left eye. Column C represents the sensitivity values obtained when the subject viewed a rapid-ON target with his left eye, and a superimposed grating mask with his right eye. Each data point is the average of approximately eight yes/no QEUST repeated measures.

Table C-28.

Frequency	A	B	C
3 Hz	0.0967371	0.0947326	0.0784073
10 Hz	0.0428081	0.0147065	0.0246504
20 Hz	0.1126644	0.1064069	0.0729874

Experiment 3, subject JR, standard deviation values for the average log (1/Thresholds) values.

Table C-29.

Frequency	A	B	C
3 Hz	1.6858075	1.5474669	1.5149406
10 Hz	1.5197063	1.3667523	1.3754630
20 Hz	1.3145733	1.2568256	1.2532410

Experiment 3, subject YY, average (1/Threshold) values. Column A represents the sensitivity values obtained while the subject viewed a uniform field with his left eye and a superimposed rapid-ON target with his right eye. Column B represents the sensitivity values obtained when the subject viewed a uniform field with his left eye and a superimposed rapid-ON target surrounded by a grating mask with his left eye. Column C represents the sensitivity values obtained when the subject viewed a rapid-ON target with his left eye, and a superimposed grating mask with his right eye. Each data point is the average of approximately eight yes/no QEUST repeated measures.

Table C-30.

Frequency	A	B	C
3 Hz	0.0549947	0.0950475	0.0567441
10 Hz	0.0666761	0.0552187	0.0679271
20 Hz	0.0322773	0.0623485	0.0696074

Experiment 3, subject YY, standard deviation values for the average log (1/Thresholds) values.

Table C-31.

Frequency	A	B	C
3 Hz	1.6669489	1.5129875	1.5940585
20 Hz	0.9778216	0.7648852	0.9079915

Experiment 3, subject TK, average (1/Threshold) values. Column A represents the sensitivity values obtained while the subject viewed a uniform field with his left eye and a superimposed rapid-ON target with his right eye. Column B represents the sensitivity values obtained when the subject viewed a uniform field with his left eye and a superimposed rapid-ON target surrounded by a grating mask with his left eye. Column C represents the sensitivity values obtained when the subject viewed a rapid-ON target with his left eye, and a superimposed grating mask with his right eye. Each data point is the average of approximately eight yes/no QEUST repeated measures.

Table C-32.

Frequency	A	B	C
3 Hz	0.0728952	0.0541301	0.0615170
20 Hz	0.0119780	0.0254501	0.0291935

Experiment 3, subject TK, standard deviation values for the average log (1/Thresholds) values

Table C-33.

Frequency	A	B	C
1.5 Hz	1.5327102	1.5124150	1.5357926
3.0 Hz	1.5263866	1.5131328	1.5405124
10.0 Hz	1.5095532	1.3764488	1.4587129
20.0 Hz	1.1489439	1.0718138	1.1599752
24.0 Hz	0.9965151	0.8476495	0.8727840

Experiment 3, subject PC, average (1/Threshold) values. Column A represents the sensitivity values obtained while the subject viewed a uniform field with his left eye and a superimposed rapid-ON target with his right eye. Column B represents the sensitivity values obtained when the subject viewed a uniform field with his left eye and a superimposed rapid-ON target surrounded by a grating mask with his left eye. Column C represents the sensitivity values obtained when the subject viewed a rapid-ON target with his left eye, and a superimposed grating mask with his right eye. Each data point is the average of approximately six yes/no QEUST repeated measures.

Table C-34.

Frequency	A	B	C
1.5 Hz	0.0405382	0.0413025	0.0352935
3.0 Hz	0.0535280	0.0608794	0.0967665
10.0 Hz	0.0443486	0.0506165	0.0287172
20.0 Hz	0.0191867	0.0584120	0.0985924
24.0 Hz	0.0541909	0.0237445	0.0385699

Experiment 3, subject PC, standard deviation values for the average log (1/Thresholds) values.

Table C-35.

Frequency	A	B	C
3 Hz	1.4854187	1.5931694	1.5466499
10 Hz	1.4864418	1.3511660	1.4470545
20 Hz	1.2780414	1.3087653	1.4000435

Experiment 3, subject FZ, average (1/Threshold) values. Column A represents the sensitivity values obtained while the subject viewed a uniform field with his left eye and a superimposed rapid-ON target with his right eye. Column B represents the sensitivity values obtained when the subject viewed a uniform field with his left eye and a superimposed rapid-ON target surrounded by a grating mask with his left eye. Column C represents the sensitivity values obtained when the subject viewed a rapid-ON target with his left eye, and a superimposed grating mask with his right eye. Each data point is the average of approximately six yes/no QEUST repeated measures.

Table C-36.

Frequency	A	B	C
3 Hz	0.0390488	0.1427525	0.0824706
10 Hz	0.0175505	0.0276724	0.0537788
20 Hz	0.0548333	0.0196021	0.2005815

Appendix B, Table 1a, Experiment 3, subject FZ, standard deviation values for the average log (1/Thresholds) values.

Table C-37.

Frequency	A	B	C	D
3 Hz	1.7373198	1.7403469	1.7718134	1.7322579
10 Hz	1.6083183	1.6165351	1.6627822	1.6385331
20 Hz	1.3449201	1.3552238	1.3828970	1.3836522

Experiment 4 average log (1/Threshold) values for all subjects. Column A represents the sensitivity obtained when the subject viewed a rapid-ON target surrounded by a full-field, rapid-ON surround. Column B represents the sensitivity obtained when the subject viewed a rapid-OFF target surrounded by a full-field, rapid-ON surround. Column C represents the sensitivity obtained when the subject viewed a rapid-ON target surrounded by a full-field, rapid-OFF surround. Column D represents the sensitivity obtained when the subject viewed a rapid-OFF target surrounded by a full-field, rapid-OFF surround.

Table C-38.

Frequency	A	B	C	D
3 Hz	0.1007517	0.1165751	0.1204923	0.0937425
10 Hz	0.1270824	0.1218568	0.1394920	0.1132866
20 Hz	0.1309755	0.1166827	0.1269844	0.1487848

Experiment 4, standard deviation values for the average log (1/Thresholds) for all subjects.

Table C-39.

Frequency	A	B	C	D
3 Hz	1.5757304	1.5642015	1.5940570	1.5731252
10 Hz	1.4776702	1.4887008	1.5165599	1.5546334
20 Hz	1.3819846	1.3873630	1.4290998	1.3742344

Experiment 4, subject JR, average log (1/Threshold) values. Column A represents the sensitivity obtained when the subject viewed a rapid-ON target surrounded by a full-field, rapid-ON surround. Column B represents the sensitivity obtained when the subject viewed a rapid-OFF target surrounded by a full-field, rapid-ON surround. Column C represents the sensitivity obtained when the subject viewed a rapid-ON target surrounded by a full-field, rapid-OFF surround. Column D represents the sensitivity obtained when the subject viewed a rapid-OFF target surrounded by a full-field, rapid-OFF surround. Each data point is the average of approximately eight yes/no QEUST repeated measures

Table C-40.

Frequency	A	B	C	D
3 Hz	0.0163350	0.0254452	0.0380108	0.0492748
10 Hz	0.0091109	0.0148294	0.0324646	0.0520222
20 Hz	0.0570962	0.0269581	0.0493168	0.0422014

Experiment 4, subject JR, standard deviation values for the average log (1/Thresholds) values.

Table C-41.

Frequency	A	B	C	D
3 Hz	1.7378722	1.7635517	1.7496573	1.7299352
10 Hz	1.6256782	1.6529464	1.6705300	1.6431885
20 Hz	1.2522357	1.2502586	1.2636706	1.2627009

Experiment 4, subject YY, average log (1/Threshold) values. Column A represents the sensitivity obtained when the subject viewed a rapid-ON target surrounded by a full-field, rapid-ON surround. Column B represents the sensitivity obtained when the subject viewed a rapid-OFF target surrounded by a full-field, rapid-ON surround. Column C represents the sensitivity obtained when the subject viewed a rapid-ON target surrounded by a full-field, rapid-OFF surround. Column D represents the sensitivity obtained when the subject viewed a rapid-OFF target surrounded by a full-field, rapid-OFF surround. Each data point is the average of approximately eight yes/no QEUST repeated measures.

Table C-42.

Frequency	A	B	C	D
3 Hz	0.0269258	0.0798298	0.0653720	0.0093109
10 Hz	0.0756728	0.0986096	0.1127780	0.0657003
20 Hz	0.0779904	0.0886753	0.0868804	0.0575679

Experiment 4, subject YY, standard deviation values for the average log (1/Thresholds) values.

Table C-43.

Frequency	A	B	C	D
3 Hz	1.7302656	1.7424069	1.7466637	1.7719858
10 Hz	1.7036954	1.7261545	1.7193376	1.7340077
20 Hz	1.2136667	1.2388278	1.2953117	1.2570103

Experiment 4, subject TK, average log (1/Threshold) values. Column A represents the sensitivity obtained when the subject viewed a rapid-ON target surrounded by a full-field, rapid-ON surround. Column B represents the sensitivity obtained when the subject viewed a rapid-OFF target surrounded by a full-field, rapid-ON surround. Column C represents the sensitivity obtained when the subject viewed a rapid-ON target surrounded by a full-field, rapid-OFF surround. Column D represents the sensitivity obtained when the subject viewed a rapid-OFF target surrounded by a full-field, rapid-OFF surround. Each data point is the average of approximately four yes/no QEUST repeated measures.

Table C-44.

Frequency	A	B	C	D
3 Hz	0.0060331	0.0200628	0.0299414	0.0800248
10 Hz	0.0194310	0.0098069	0.0043289	0.0149298
20 Hz	0.0648314	0.0191783	0.0335042	0.0584910

Experiment 4, subject TK, standard deviation values for the average log (1/Thresholds) values.

Table C-45.

Frequency	A	B	C	D
3.0 Hz	1.8339167	1.8913074	1.8879734	1.8135539
7.5 Hz	1.7258431	1.7304967	1.7476535	1.7311524
10.0 Hz	1.7550641	1.7289832	1.8615981	1.7627576
20.0 Hz	1.5478233	1.5238560	1.5806360	1.6234328

Experiment 4, subject PC, average log (1/Threshold) values. Column A represents the sensitivity obtained when the subject viewed a rapid-ON target surrounded by a full-field, rapid-ON surround. Column B represents the sensitivity obtained when the subject viewed a rapid-OFF target surrounded by a full-field, rapid-ON surround. Column C represents the sensitivity obtained when the subject viewed a rapid-ON target surrounded by a full-field, rapid-OFF surround. Column D represents the sensitivity obtained when the subject viewed a rapid-OFF target surrounded by a full-field, rapid-OFF surround. Each data point is the average of approximately six yes/no QEUST repeated measures.

Table C-46.

Frequency	A	B	C	D
3.0 Hz	0.0796487	0.0967803	0.1067100	0.0959478
7.5 Hz	0.0056881	0.0010044	0.0316413	0.0029560
10.0 Hz	0.0365127	0.0065652	0.1196415	0.0523604
20.0 Hz	0.0956575	0.0425547	0.0266108	0.0851279

Experiment 4, subject PC, standard deviation values for the average log (1/Thresholds) values.

Table C-47.

Frequency	A	B	C	D
3 Hz	1.8088140	1.7402670	1.8807158	1.7726891
10 Hz	1.7286970	1.8329293	1.8214868	1.7933112
20 Hz	1.3756612	1.3812654	1.5286592	1.4978128

Experiment 4, subject PC, average log (1/Threshold) values. Column A represents the sensitivity obtained when the subject viewed a rapid-ON target surrounded by a full-field, rapid-ON surround. Column B represents the sensitivity obtained when the subject viewed a rapid-OFF target surrounded by a full-field, rapid-ON surround. Column C represents the sensitivity obtained when the subject viewed a rapid-ON target surrounded by a full-field, rapid-OFF surround. Column D represents the sensitivity obtained when the subject viewed a rapid-OFF target surrounded by a full-field, rapid-OFF surround. Each data point is the average of approximately six yes/no QEUST repeated measures

Table C-48.

Frequency	A	B	C	D
3 Hz	0.0700878	0.0355478	0.0697821	0.0798001
10 Hz	0.1064760	0.1105400	0.1167155	0.0925282
20 Hz	0.0210874	0.0308369	0.0402336	0.0453704

Experiment 4, subject PC, standard deviation values for the average log (1/Thresholds) values.