NEUROPHYSIOLOGICAL EFFECTS OF SELECTIVE ATTENTION

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Dedicated to my mother,

who first inspired my interest

in the Arts and

Sciences

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ABSTRACT

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Electroencephalographic data were collected to investigate the effects of selective attention on visual evoked potential (VEP) responses to contrast-modulated flicker. VEP amplitude was determined by Fourier analysis (FFT) of steady-state flicker epochs. Attention was controlled by a psychophysical task in which the subject was required to detect a faint isoluminant chromatic change in the attended target. Two types of visual target sets were employed. First, while the subject foveated on a central fixation-point, attention was directed either to an eccentric flickering wedge or to the fixation-point itself. For every target set of this type, in the *Attend-Fixation-Point* condition, VEP amplitude was reduced to the level of noise in the spectral band surrounding the stimulus-driven frequency or was substantially attenuated. The second type of target set comprised a flickering wedge and an offset non-flickering wedge, both at an eccentric location in the visual field. For target sets of this type, comprising small flickering stimuli 0.36 x 0.36 degree of visual angle (v.a.) in size, separated by as little as 0.36 degree v.a. in the right visual hemifield, VEP amplitude was again reduced to the level of noise or substantially attenuated in the *Attend-Nonflickering-Target* condition. Small separated target sets in the

left visual hemifield and small adjacent target sets in both visual hemifields showed less consistent attentional effects. Contrast response functions obtained from small separated target sets in the right visual hemifield evidenced a nearly linear increase of VEP amplitude for contrasts up to 25%, with saturation at higher contrasts. A variety of temporal flicker frequencies were tested, and all VEP responses obtained were in the beta bandwidth, whether at the fundamental flicker frequency, the second, or third harmonic. Attentional effects were replicated in both the contrast and frequency response experiments, and high resolution eye-tracking data demonstrated no differences in visual fixation between attentional conditions. Results demonstrated an absence of spatial gradients of attention above the threshold of perception. The slope and half-saturation values of the contrast response curves indicate that magnocellular pathways in V1 and V2 were the primary cortical areas involved in the VEP responses silenced by selective attention.

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INTRODUCTION

At the dawn of the twenty-first century, researchers began to employ neurophysiological data to elucidate the architecture of mental processes. In such a manner, this dissertation informs the study of attention, which has long been an important area of inquiry for experimental psychology. "Selective attention" is the focal processing of perceptual information from the vast influx of sensory stimulation continuously being transduced into neural energy. How are irrelevant sensory inputs gated and those corresponding to attended, coherent percepts passed on for further processing?

The above question may be illustrated with everyday examples. When you are in a room, engrossed in reading or in some other task which strongly engages your attention, you may not hear the ticking of a clock. Later, when this is pointed out, it is hard to imagine not hearing the clock. In both instances, pressure waves from the clock's ticking cause your tympanic membrane to vibrate. How is that sensory input gated when the ticking is not perceived? Likewise, when you are viewing a traffic light that turns red, you may be aware of the colored light but not the texture of the glass through which the light emanates. If the light remains red for long enough, your attention may or may not peruse these features while your visual fixation remains foveated on the signal. In either case, retinal stimulation is identical, so how does perceptual processing of some features and not others proceed from the wealth of neural activation instigated by the visual field?

The research presented in this dissertation addresses these issues through the measurement of electroencephalograhic (EEG) responses to steady-state contrast-modulated flickering stimuli. An averaged EEG response to such periodic visual

stimulation is known as a visual evoked potential (VEP). In recent years, geometric increases in inexpensive digital storage and processing capacity have allowed VEPs to be recorded and analyzed in unprecedented ways (Baseler & Sutter, 1997; Muller et al., 1998), and this thesis will describe new findings which have been made possible by such advances in computer technology. Before now, however, the bulk of electrophysiological research concerning visual selective attention has relied upon transient responses to the onset of visual stimulation known as event related potentials (ERPs).

When a visual stimulus first appears to a subject, the potentials measured at various sites on the scalp relative to a reference electrode undergo a transient response. When the same visual stimulus is presented in repeated trials with experimental parameters controlled, the potentials sampled at each point in time relative to the time of stimulus-onset may be averaged across trials. For convenience, this will be called "time averaging." ERPs are the waveforms which arise from time averaging the transient shifts in potentials following stimulus-onset. The negative and positive deflections in time averaged potentials which occur roughly between 100 and 200 ms post stimulus-onset are known as "N1/P1," and these particular ERP waveforms have been extensively used for inferences about visual selective attention.

For a number of reasons, traditional ERP research paradigms have proved unsuitable for our enterprise of investigating the neural substrates of visual selective attention. A primary deficiency of ERPs as a dependent measure for our purposes is their relative insensitivity to changes in physical parameters of the stimulus. Another deficiency is the interaction of the N1 and earlier waveforms with endogenous oscillatory

activity in the alpha bandwidth (8-12.5 Hz). To illustrate these points, Fig. 1 presents analyses of a data set comprising a subject's EEG responses over ~1000 experimental trials similar to those which will be described in detail later in this dissertation.

Fig. 1 (A) is an example of one and a half seconds of raw data recorded during a single trial from an electrode on the scalp of one of our subjects. The blue line traces the rise and fall of the potentials at that electrode 300 times per second. The first half of the trace (-750 to 0 ms on the abscissa) occurred during the baseline period of the trial, when the subject was staring at a central fixation point on a neutral gray monitor. During the second half of the trial (0 to 750 ms on the abscissa), an eccentrically positioned flickering stimulus appeared on the monitor while the subject continued to stare at the central fixation point. The raw data trace of this trial is typical of those which exhibited relatively low amplitude alpha activity during the baseline epoch.

Fig. 1 (B), on the other hand, is typical of trials with high baseline alpha activity. In that trial, the potentials are clearly seen to rise and fall with a periodicity in the alpha bandwidth, and this high amplitude endogenous alpha activity occurring during the baseline epoch is suppressed after the onset of the flickering stimulus.

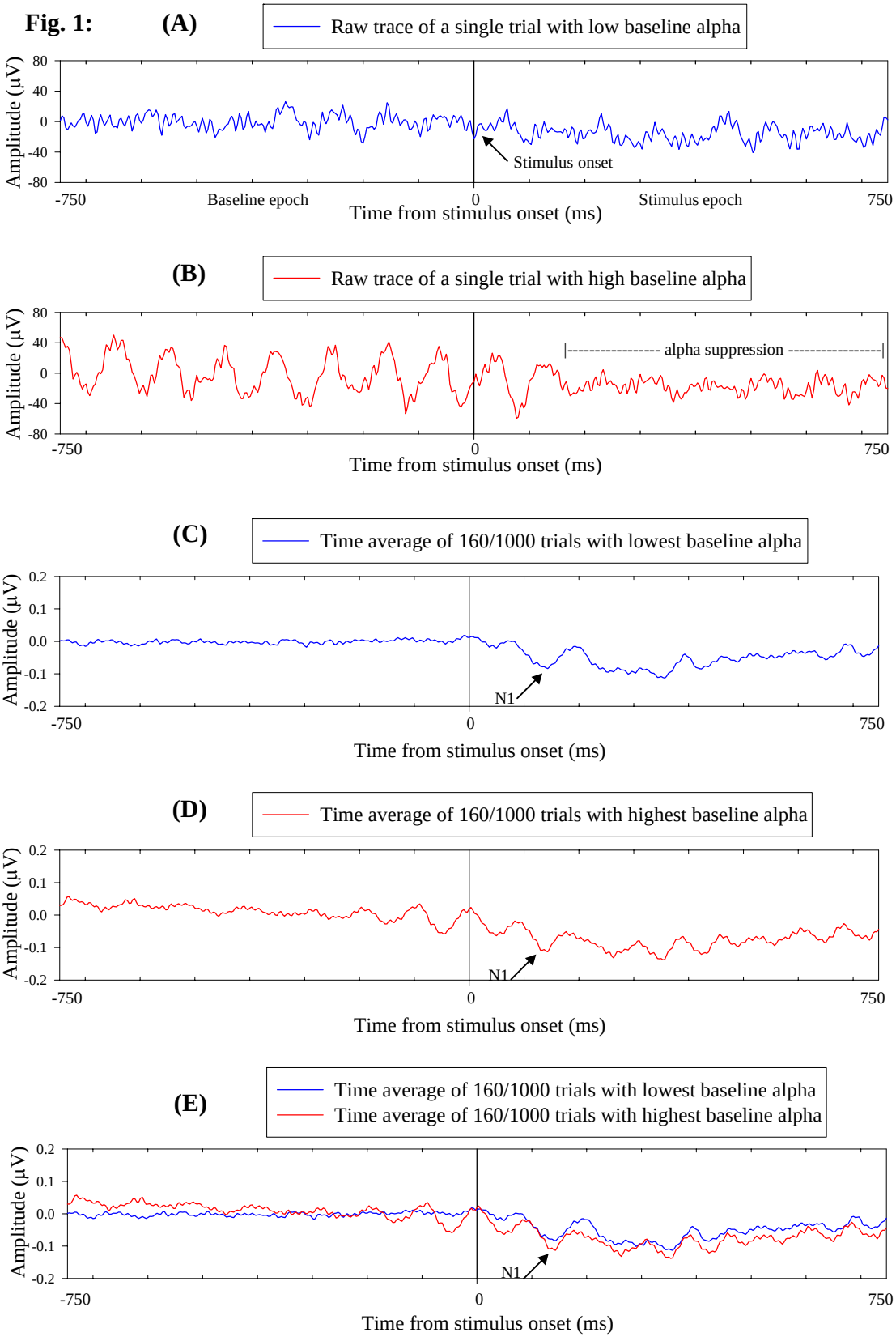
Fig. 1 (C) shows a time average of the 160 trials with lowest baseline alpha from the 1000-trial data set we're considering. Spontaneous fluctuations in EEG amplitude during the baseline epoch have been reduced through averaging. Between 100 and 200 ms post stimulus onset, the N1 waveform emerges from the averaging, and then the subsequent waveforms of the stimulus epoch become more complex as the stimulus cycle of the flicker repeats in a steady-state rhythm.

Fig. 1 (D) shows a time average of the 160 trials with highest baseline alpha activity. During the baseline epoch, the endogenous alpha rhythm is still discernable despite averaging and shows increased amplitude as the trial progresses through the baseline period. During the stimulus epoch, the N1 waveform can be identified by the time-frame in which it occurs, but in this case cannot be clearly discerned, visually, from the endogenous, background oscillatory activity.

Fig. 1 (E) superimposes the time averages of 1(C) and 1 (D) in the same plot. Here it can clearly be seen that spontaneous variations in alpha amplitude indeed affect the amplitude of the N1 ERP response. Extensive research into the relationship of early ERP waveforms with endogenous oscillatory activity has demonstrated that not only the amplitude of N1 is affected by the magnitude of background alpha, but that the latency of the N1 waveform is also systematically affected by the average phase of the preceding alpha activity (Brandt, 1989; Brandt & Jansen, 1991; Brandt, Jansen, & Carbonari, 1991; Dustman & Beck, 1965; Jansen & Brandt, 1991; Rodin, Grisell, Gudobba, & Zachary, 1965).

The importance of such contamination becomes apparent in Fig. 2 (A). In this figure, the time averaged responses to a stimulus flickering at three different contrast levels are compared. It is apparent how the small relative differences in N1 responses can easily be confounded by variations in the endogenous alpha activity. Moreover, contamination of the N1 response by background noise makes this waveform unsuitable for the sensitive measurement of contrast response curves. Finally, since ERPs are a

Fig. 1:


(A)
Raw trace of a single trial with low baseline alpha
Amplitude (μV)
80
40
0
-40
-80
Stimulus onset
-750
Baseline epoch
0
Stimulus epoch
750
Time from stimulus onset (ms)
(B)
Raw trace of a single trial with high baseline alpha
Amplitude (μV)
|---------- alpha suppression ----------|
-750
0
750
Time from stimulus onset (ms)
(C)
Time average of 160/1000 trials with lowest baseline alpha
Amplitude (μV)
0.2
0.1
0.0
-0.1
-0.2
N1
-750
0
750
Time from stimulus onset (ms)
(D)
Time average of 160/1000 trials with highest baseline alpha
Amplitude (μV)
N1
-750
0
750
Time from stimulus onset (ms)
(E)
Time average of 160/1000 trials with lowest baseline alpha
Time average of 160/1000 trials with highest baseline alpha
Amplitude (μV)
N1
-750
0
750
Time from stimulus onset (ms)

transient response to stimulus onset, they are completely incapable of measuring EEG responses to varying temporal characteristics of steady-state flicker.

Fig. 2 (B) is the time average of the 2 seconds of stimulus epoch following the first second of stimulus epoch at 30% contrast in Fig. 2 (A). Here, the transient response following stimulus onset is gone and a steady-state rhythm at 14 Hz is discernible.

Through fast Fourier transform (FFT) of the stimulus epochs of the same trials shown as time averages in Fig. 2 (A) and (B), FFT magnitude spectra of the EEG responses to the flickering stimuli are compared in Fig. 2 (C). The peaks of spectral activity at 14 Hz are stimulus-driven VEP responses, clearly differentiated from the endogenous alpha activity at 10 Hz, and these VEPs are seen to be sensitively dependent on stimulus contrast level.

Fig. 3 compares the FFT magnitude spectra of two stimuli flickering at different temporal frequencies. Dependence on temporal properties of the steady-state flicker is apparent in the VEP responses, which rise above background spectral noise at 14 and 16 Hz. Again, these stimulus-driven VEP responses are clearly differentiated from the endogenous alpha activity, which invariably occurred in this subject at 10 Hz and was also present during the baseline epoch when no flickering stimulus was present.

Detailed methodological descriptions of our stimulus presentations and extensive analyses of VEP responses to variations in contrast, temporal frequency, size and location of the flickering stimuli will be provided later in this dissertation, along with analyses of co-occurring spontaneous spectral activity. The brief introduction above simply explains

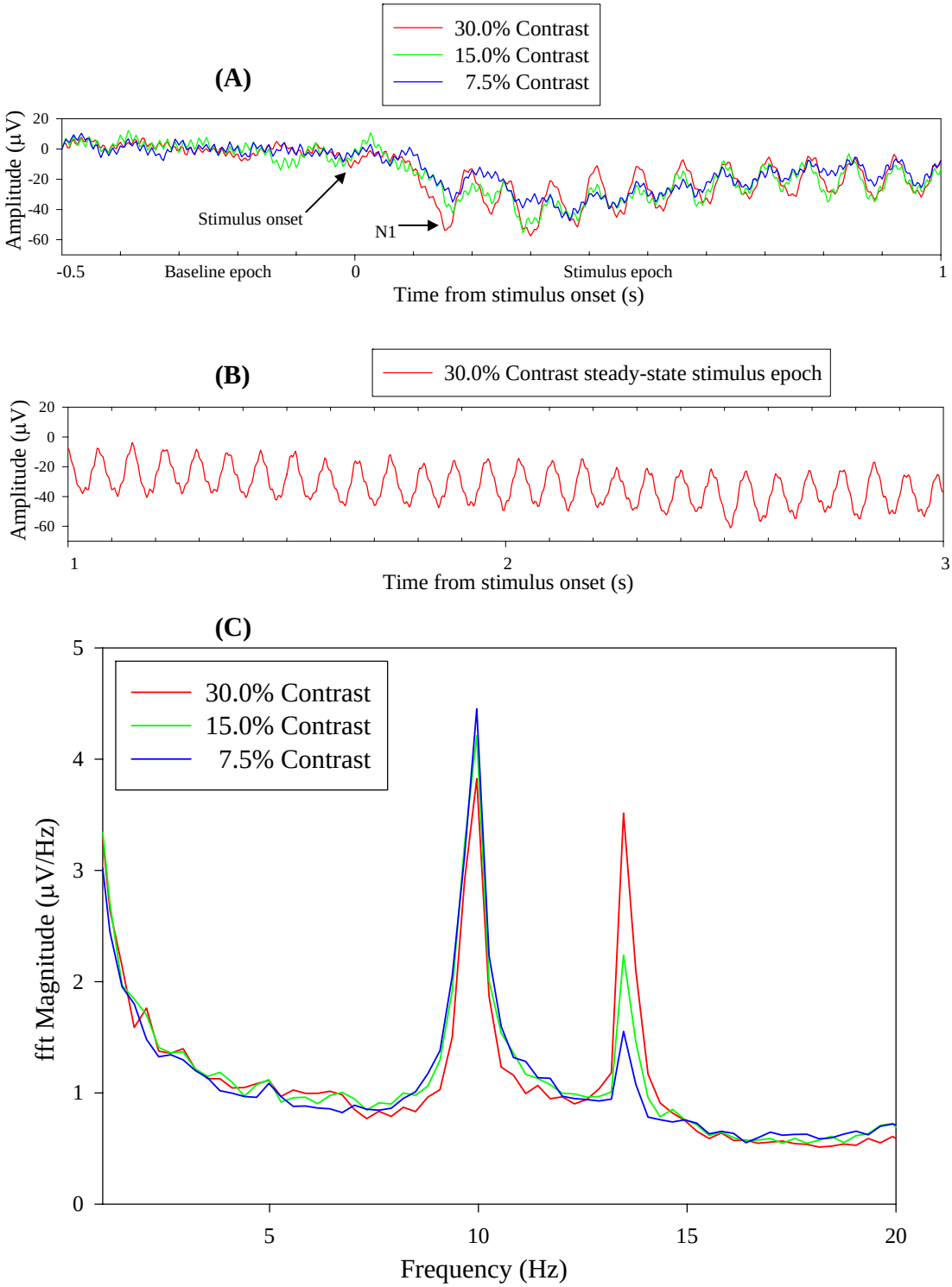


Fig. 2: *Contrast response to flickering stimuli at electrode Oz.*
(A) Time average across 160 trials of 1/2 s baseline and 1 s transient stimulus epoch.
(B) Time average across 160 trials of 2 s steady-state stimulus epoch.
(C) Fft magnitude spectra of steady-state stimulus epoch averaged across 160 trials.

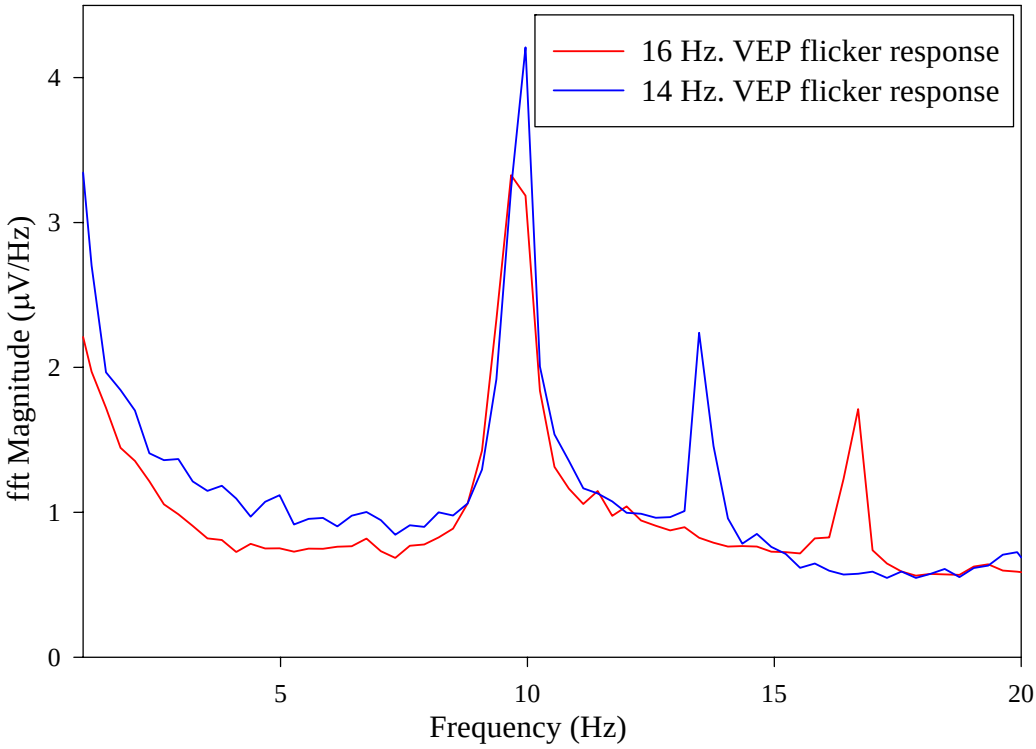


Fig. 3: *Fft magnitude spectra showing VEP responses to visual stimuli flickering at different temporal frequencies.*

the context for our choice of steady-state VEPs rather than ERPs as a dependent measure in our investigations of the neural substrates of attention.

As alluded to earlier, a further reason we did not employ ERPs in our research paradigm is that ERPs only measure the average transient EEG response to stimulus onset and, therefore, do not examine attentional processes beyond their initiation. Traditional ERP research into selective attention has, thus, often been concerned with the process of selection rather than attention, per se. ERPs and, for that matter, VEPs employed as dependent measures of attention have most often been used to compare different selection criteria. Higher order categories; e.g., digits, letters, relative

orientation and feature conjunctions, have been compared with simple physical features such as location, size, color, and brightness. Similarly, effectiveness of selection has been compared among these simple physical features themselves to probe for possible processing hierarchies. Moreover, these experimental probes of selection criteria have commonly involved other mental processes in addition to attention. Such paradigms have relied upon memory, identification, and orientation to the empty space where objects to be attended will later appear (Annlo-Vento & Hillyard, 1996; Belmonte, 1998; Girelli & Luck, 1997; Hillyard & Munte, 1984; Luck, Fan, & Hillyard, 1993; Morgan, Hansen, & Hillyard, 1996; Muller, Teder-Salejarvi, & Hillyard, 1998; Silberstein, et al., 1990; Tsal & Lavie, 1988; Tsal & Lavie, 1993; Wijers et al., 1989a; Wijers et al., 1989b).

ERPs have been used as a physiological measure together with choice reaction times and accuracy as a behavioral measure to investigate how early or late in the stream of perceptual processing identification of objects occurs, and how the onset of irrelevant sensory information may be filtered, or the onset of relevant information spotlighted. Likewise, these dependent measures have been employed to investigate whether spatial gradients of attentional allocation or attention to objects independent of locus are fundamental grounds of perceptual processing. Once again, such investigations typically concern only the initial identification and response to the onset of stimulation, and they commonly involve higher-order perceptual processes as well. (Belmonte, 1998; Clark & Hillyard, 1996; Duncan, 1984; Heinze et al., 1994; Johannes et al., 1995; Lauwereyns, 1998; Lavie & Driver, 1996; Mangun & Hillyard, 1987; Mangun & Hillyard, 1988;

Mangun & Hillyard, 1990; Morgan, Hansen, & Hillyard, 1996; Mounts & Melara, 1999; Valdes-Sosa et al., 1998; Vecera & Farah, 1994).

Findings from the experiments cited above have been taken to support or challenge a variety of theoretical formulations such as "filter" (Broadbent, 1958; Deutsch & Deutsch, 1963; Kahneman, 1973; Moray, 1959; Treisman, 1969; Yantis, 1990) and "spotlight" (Eriksen & Yeh, 1985; LaBerge, 1995; Posner, 1980) models of selective attention. Understanding such theories as metaphors, Fernandez-Duque & Johnson (1999) point out that each is suited to elucidate only an aspect of the phenomenon of attention. Yet a different class of attentional studies have cut across theoretical formulations underlying the above paradigms to explore where and how attention affects neural activity itself. Primate extracellular recordings have examined the effects of attention on competitive interactions in the cortex. Neuroimaging studies in humans, as well as primate extracellular recordings, have demonstrated robust effects of attention not only in extastriate areas, but in the primary visual cortex as well (Desimone & Duncan, 1995; Duncan, Humphreys, & Ward, 1997;Gandhi, Heeger, & Boynton, 1999; Gilbert & Posner, 1999; Motter, 1993; Somers, Anders, Seiffert, & Tootell, 1999). Such experimental paradigms investigating neurophysiology have introduced to the study of attention the types of lower-order visual stimuli that have long been employed in the area of psychophysics. Thus, moving gratings, reversing patterns, and contrast-modulated flicker have now been used to expand our knowledge of where in the brain different levels of perceptual processing and attentional dampening or gain occur. Such stimulus presentations allow attention to be sustained and examined without recourse to higher-

order mental processes and it is these types of basic stimuli that we have adapted for our own experimental purposes in the hope of adding to the corpus of neurophysiological knowledge concerning the phenomenon of attention.

In the pages that follow, our investigations into the effect of selective attention on visually evoked cortical responses will be set forth. The experiments have been grouped into four sets. In the first set, we probed the magnitude of attentional effects on VEP responses to flickering stimuli positioned at loci throughout the visual field. In the second set, we examined various spatial properties of attention. In the third set, we employed high resolution eye-tracking with our experimental paradigms in order to establish that the observed effects were, indeed, due to attention. Finally, in the fourth set of experiments, we determined contrast and frequency response characteristics of VEP responses to our stimuli in order to help elucidate the neural substrate of the attentional effects we observed.

EXPERIMENT 1

PURPOSE

EEG data were collected in order to determine the extent to which selective attention may affect the amplitude and phase of VEP responses to steady-state contrast-modulated flicker.

METHODS

EXPERIMENTAL PARADIGM:

While the subject maintained visual fixation on the center point of a CRT monitor, a wedge flickering sinusoidally about the mean luminance ("mean gray") at 7.5 Hz and 25% contrast was displayed at an eccentric location on the monitor for 5.6 seconds.

In the *Attend-Flickering-Wedge* condition, 1 to 5 seconds after stimulus onset, the flickering wedge became colored red or green (at any of three tint levels). Upon perceiving a shift to color, the subject indicated with a button-push whether she believed the color was red or green. In the *Attend-Fixation-Point* condition, the subject responded to a shift to color in the central fixation-point instead (Fig. 1-1).

Blocks of 32 trials in each condition were alternated. The subject was instructed before each block whether to train her attention on the flickering wedge or the fixation-point (i.e., on the target where a shift to color would occur). Fourier analysis (FFT) was performed on the stimulus epoch preceding the shift to color in each trial, excluding the first second following stimulus onset so as to minimize transient effects. Then, within each experimental condition, the complex FFT coefficients were averaged across trials at

every resolved spectral frequency for each electrode. The percentage of correct responses in the psychophysical task was also tabulated. Two subjects were tested in Experiment 1. They were twenty-three year old fraternal twin sisters with normal eyesight, well trained in psychophysical tasks requiring sustained attention.

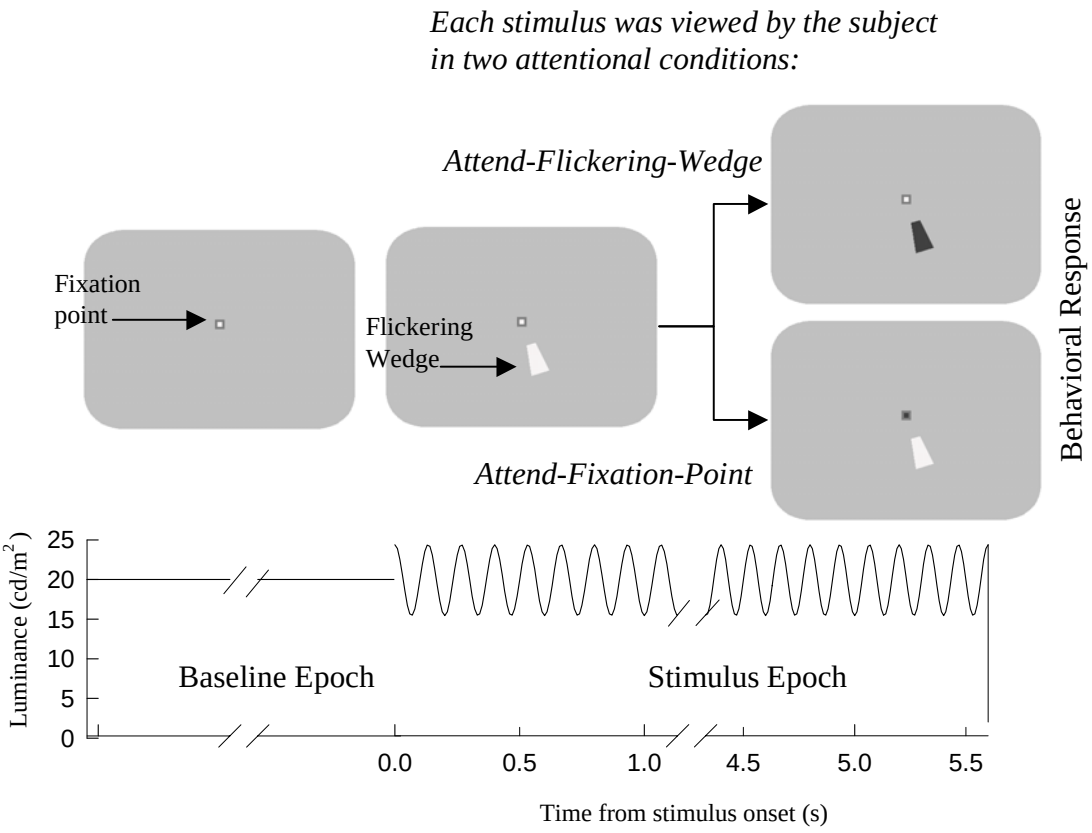


Fig. 1-1: *Description of a single trial in Experiment 1.*

METHODOLOGICAL DETAILS AND TECHNICAL SPECIFICATIONS:

Spatial parameters of the flickering wedges employed as stimuli in Experiment 1 were chosen to activate equivalent areas of cortex, according to the cortical magnification function represented in Fig. 1-2. The different size wedges positioned at the different

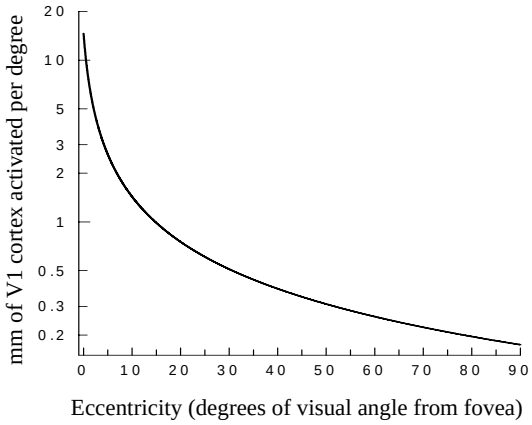


Fig. 1-2: *Cortical Magnification Function.* As eccentricity in the visual field decreases, the V1 cortical area responsive to visual stimulation (i.e., the corresponding "cortical activity field") increases exponentially (Engel et al., 1997).

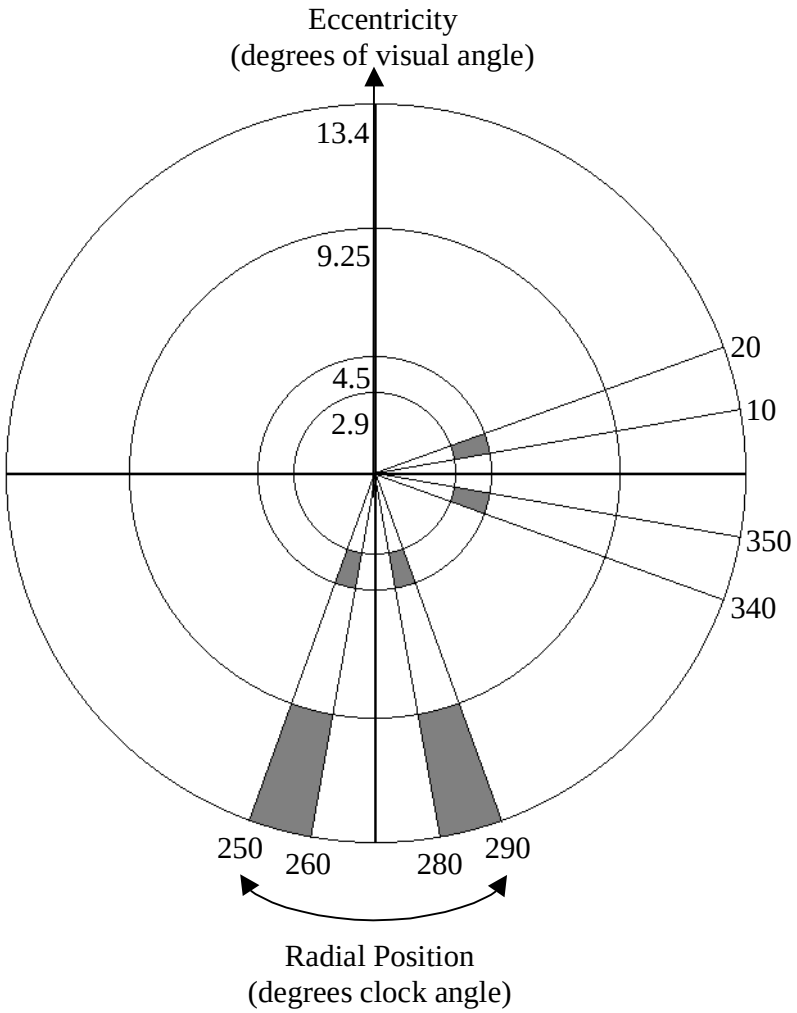


Fig. 1-3: *Relative size and position of flickering wedges in Experiment 1.* Flickering wedges occupying the above locations in the visual field were the primary stimuli employed in Experiment 1. According to the cortical magnification function, all stimuli depicted here would have corresponding fields of activity in the primary visual cortex subtending an area of ~11 mm^2.

eccentricities shown in Fig. 1-3, correspond to neuronal activity fields in the primary visual cortex of the same size–nominally 11 mm^2. The term "activity field" refers here to the cortical area to which the stimuli project in retinotopy according to various investigations (see Engel et al., 1997).

A flicker frequency of 7.5 Hz was chosen to best accommodate the 75 Hz refresh rate of the monitor and 300 Hz sampling rate of the electroencephalograph with minimal phase distortion in subsequent statistical analyses. Equally important to the choice of 7.5 Hz, both the fundamental frequency and second harmonic of this flicker frequency are outside the alpha bandwidth (8-12.5 Hz) where endogenous, high amplitude spectral activity is typically present and might well mask stimulus-driven activity. A contrast of 25% was chosen based on experiments in which it was determined that the contrast response function begins to saturate.

Stimuli were generated with software written in Matlab 5.1 on a PowerMac 6500/300, OS 7.6. They were displayed with a Radius PrecisionColor 24/1600 PCI Video Card on a MAG-DX1795 17" INVAR shadow mask picture tube with 0.26 mm fine dot pitch and 1024 X 768 pixel resolution refreshed at 75 Hz. The mean luminance was set at 20 cd/m^2 with linear calibration of R-G-B phosphors. A photo-diode in a corner of the screen provided output directly from the CRT display to precisely mark the stimulus onset with a TTL pulse. The TTL signal was simultaneously transmitted to: (a) a computer which contained the A/D converter circuitry for recording and storing the EEG data, (b) a computer for collecting behavioral responses to the psychophysical task, and, in a later experiment, (c) an ISCAN ETL-500 eye-tracking system.

Electrode impedances were maintained below 5 kΩ. Scalp potentials were amplified 10,000x, filtered at 0.01-100 Hz and sampled at 300 Hz with an SA Instrumentation Model UP-16/32BA 32-channel isolated bioelectric amplifier. Data were continuously recorded with InstEP software and stored on the master EEG data collection computer hard disk. Trial epochs, marked with the TTL pulse signaling stimulus-onset, were extracted as ASCII files and stored on optical disks for subsequent statistical analysis performed with Matlab 5.2 software.

EEG data were collected from tin electrodes mounted in an elastic cap. A 32 lead bunched occipital montage was employed with reference to the left mastoid; vertical EOG was collected from beneath the lower left eyelid and horizontal EOG from the right canthus (Fig. 1-4).

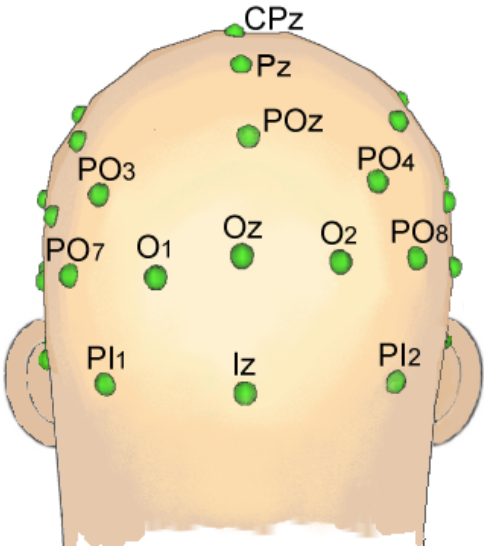


Fig. 1-4: *Bunched occipital montage with selected electrodes labeled.* Peak electrodes in Experiment 1; i.e., electrodes with maximal VEP response to flickering stimuli at various positions in the visual field were Oz, POz, PO3, PO4, and PO8. Maximal VEP response as measured at the scalp may be dependent not only on the location of the flickering stimulus within the visual field; i.e., on the position of maximal cortical activation, but also on the position of the activated cortex within the inhomogeneous volume conductance beneath the skull as determined by the structure of gray matter, white matter, and CSF.

After every placement of the elastic electrode cap on the subject, Cartesian coordinates for each electrode in the montage were obtained. These coordinates were

referenced to three fiducial points on the subject's head–left preauricular notch, right preauricular notch, and nasion. A Polhemus Isotrack II electromagnetic locating system with EMSE software was employed for this purpose.

After preliminary experimentation, three tint levels of color-shift for the psychophysical task were chosen to yield a task of sufficient difficulty that attention would be required, yet sufficient ease that the subject's fatigue would be minimized. Dependence of the subjects' performance on tint level is evident in the pooled behavioral data (Fig. 1-5) and demonstrates that attention directed to the intended stimulus (flickering wedge or fixation-point) was elicited by the psychophysical task. In other words, successful performance required attention.

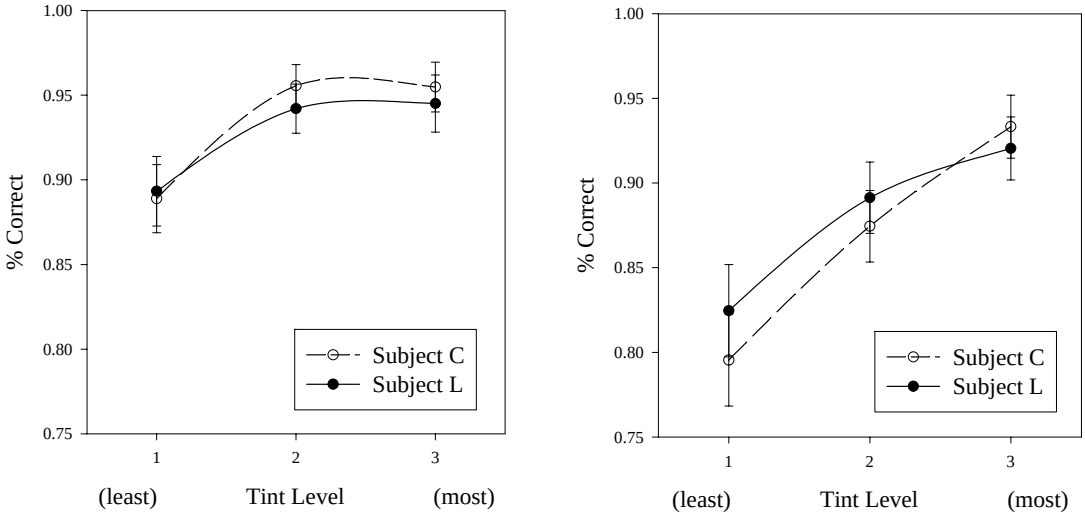


Fig. 1-5: *Pooled behavioral data for subjects' C and L psychophysical performance in Experiement 1.*

RESULTS

Table 1-1 lists pertinent information for "*attentional-pairs*"; i.e., data collected from a single subject successively viewing identical stimulus presentations in the two opposing attentional conditions (*Attend-Flickering-Wedge* vs. *Attend-Fixation-Point).* For every *attentional-pair* recorded, the "response ratio" was >1; i.e., the VEP response was greater when the subject was mentally attending to the flickering wedge than when her attention was on the fixation-point.

Pair #	Sub	Radial Position (degrees c.a.)	Eccentricity (vis angle)	N	Attend Flicker Amp (μV)	Attend Fix. Pt. Amp (μV)	Attend Flicker S.D.(μV)	Attend Fix. Pt. S.D.(μV)	Resp Ratio
1A	L	LRV(280-290)	2.9-4.5	88	1.60	0.34	1.45	1.15	4.7
1B	L	LLV (250-260)	2.9-4.5	88	1.06	0.45	0.90	1.02	2.3
1C	C	LRV (280-290)	2.9-4.5	88	1.67	0.52	1.12	0.95	3.2
1D	C	LLV (250-260)	2.9-4.5	88	1.41	0.65	1.06	1.42	2.2
1E	L	LRV (280-290)	2.9-4.5	88	2.46	0.35	1.76	1.37	7.1
1F	L	LLV (250-260)	2.9-4.5	88	1.87	0.60	1.56	1.27	3.1
1G	C	LRV (280-290)	2.9-4.5	88	1.85	0.53	1.19	1.11	3.5
1H	C	LLV (250-260)	2.9-4.5	88	1.74	0.41	1.19	1.38	4.2
1I	L	URH (10-20)	2.9-4.5	88	0.86	0.32	1.30	1.01	2.7
1J	L	LRH (340-350)	2.9-4.5	88	0.62	0.26	1.48	0.63	2.4
1K	C	URH (10-20)	2.9-4.5	88	0.62	0.25	0.92	0.87	2.5
1L	C	LRH (340-350)	2.9-4.5	88	0.63	0.27	0.69	0.75	2.4
1M	C	LRV (280-290)	9.25-13.4	88	0.79	0.42	1.02	1.08	1.9
1N	C	LLV (250-260)	9.25-13.4	88	1.24	0.50	1.21	1.32	2.5
1O	L	LRV (280-290)	11.0-13.4	112	1.31	0.35	1.49	1.14	3.8
1P	L	LLV (250-260)	8.16-10	112	1.66	0.41	1.41	1.07	4.0
1Q	C	LRV (275-285)	11.0-13.4	84	1.86	0.53	1.29	0.96	3.5
1R	C	LLV (250-260)	9.0-11.0	84	1.46	0.72	1.17	0.99	2.0
1S	C	URV (75-85)	5.0-6.2	84	0.73	0.18	0.82	0.72	4.0

Table 1-1: *Summary information for foveal vs. eccentric attentional-pairs.*
The first column lists an index number for each *attentional-pair* in Experiment 1. "Radial Position" refers to the location of the flickering wedge given in degrees of clock angle (c.a.): LRV indicates a location to the right of the lower vertical meridian, LLV to the left of the lower vertical meridian, URH above the right horizontal meridan, LRH below the right horizontal meridian, and URV to the right of the upper vertical meridian. "Attend Flicker" refers to the *Attend-Flickering-Wedge* condition; "Attend Fix. Pt" to the *Attend-Fixation-Point* condition. "Amp" and "S. D." refer to the amplitude and standard deviation of the 15 Hz VEP response at peak electrodes; i.e., the sites of maximal response, averaged across epochs with color-shift at 4 and 5 seconds post stimulus-onset. "N' refers to the number of trials averaged. "Resp Ratio" compares VEP amplitude in the *Attend-Flickering-Wedge* condition (the numerator) vs. the *Attend-Fixation-Point* condition (the denominator). The response ratio of all attentional-pairs recorded in Experiment 1was statistically reliable at $p < .001$.

Fig. 1-6 plots the VEP response averaged across stimulus epochs with the color shift occurring at 4 and 5 seconds post-stimulus onset at peak electrodes (the electrodes with maximal FFT amplitude at the response frequency). The stimulus-driven VEP response, which occurs at 15 Hz, is twice the temporal frequency of the 7.5 Hz flicker. The temporal properties of this stimulus-driven steady-state VEP response are further investigated in Experiment 4c.

As seen in Fig. 1-7, the response ratio increased with increasing stimulus-driven activity. This was due to the substantial attenuation of VEP amplitude in the *Attend-Fixation-Point* condition, even when VEP amplitude was high in the *Attend-Flickering-Wedge* condition of an *attentional-pair*. In fact, VEP amplitude in the *Attend-Fixation-Point* condition was typically reduced to a level close to the noise of the surrounding spectral bandwidth. This is evident in the amplitude spectra of many of the *attentional-pairs*, especially those with high response ratios (Figs. 1-8 Top and 1-9 Top). Even in cases where the response ratio was at its lowest, VEP amplitude in the *Attend-Fixation-Point* condition was substantially attenuated (Figs. 1-8 Bottom and 1-9 Bottom).

The other salient peaks evident in the amplitude spectra of Figs. 1-8 and 1-9 are in the alpha bandwidth (8-12.5 Hz).These do not signify stimulus-driven activity, but rather, spontaneous rhythmic neural activity commonly seen in occipital EEG recordings. Fig. 1-10 shows amplitude spectra of baseline and stimulus epochs for the *attentional-pairs* where subjects C and L evidenced their highest response ratios. During the baseline epochs, when no flickering stimulus was presented, the stimulus-driven response at 15 Hz is entirely absent, while high amplitude alpha activity is present. The high

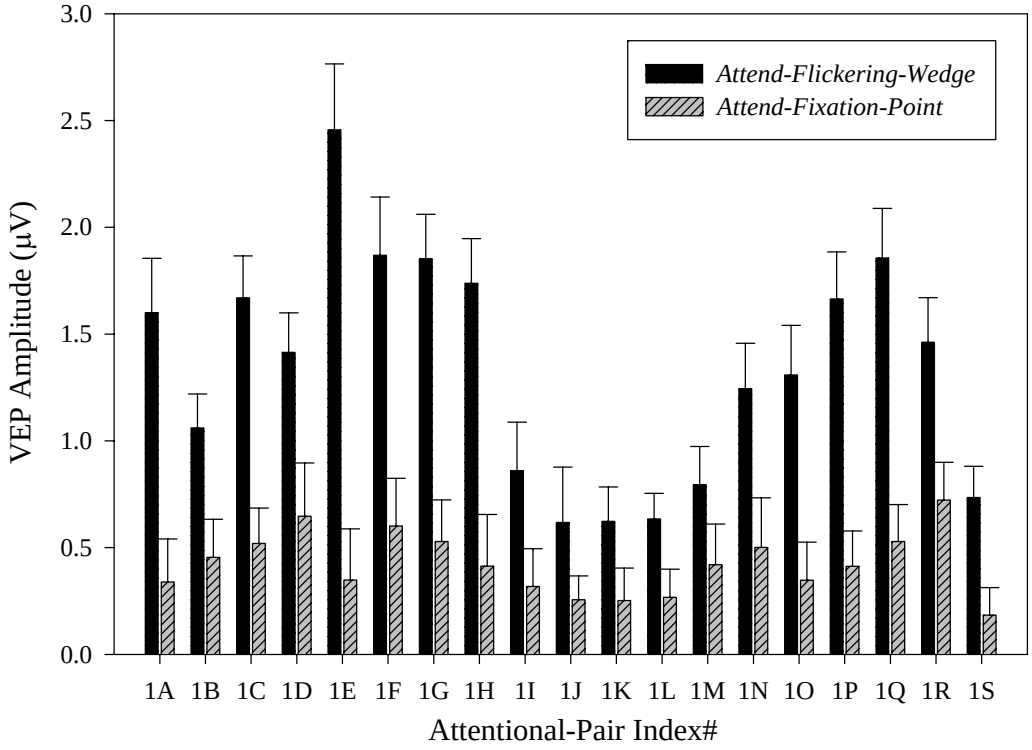
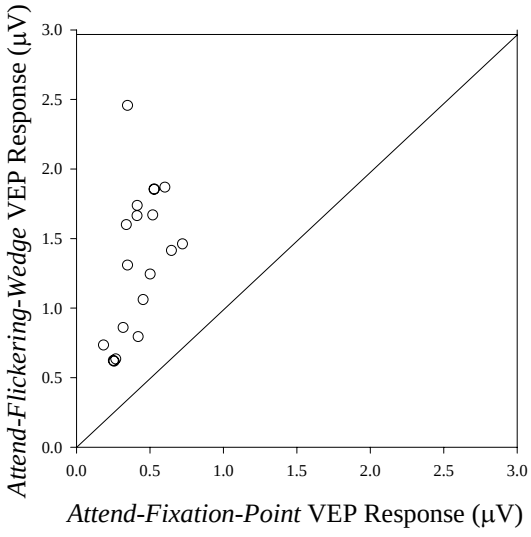


Fig. 1-6: *VEP response with 95% confidence intervals at peak electrodes for each attentional-pair in Experiment 1.* The difference in mean amplitudes for every *attentional-pair* was statistically reliable at $p < .001$.

Fig. 1-7: *Peak VEP response of each attentional-pair in the opposing attentional conditions.* Points above the diagonal show a response with greater VEP amplitude in the *Attend-Flickering-Wedge* condition than in the *Attend-Fixation-Point* condition. Note that with increased amplitude, distance from the diagonal tended to increase as well. This is due to the fact that amplitude in the *Attend-Fixation-Point* condition was always substantially attenuated in every *attentional-pair*, even when amplitude in the *Attend-Flickering-Wedge* condition was high.



amplitude alpha activity of the baseline epochs is seen to be diminished after stimulus onset in Fig. 1-10. This is a typical phenomenon know as "alpha suppression". (Note: because only one second preceding stimulus-onset was analyzed, the baseline spectra in these figures have a resolution of 1 Hz and are, thus, less articulated than the corresponding stimulus epoch amplitude spectra at 0.25 Hz resolution.) The function of such endogenous alpha-band activity (as well as alpha suppression) is, at present, not thoroughly understood, nor is its relationship to stimulus-driven VEP responses perfectly straightforward.

The alpha peaks seen in the averaged spectra do not completely average-out through the law of large numbers because spontaneous neural activity in the alpha band is in many cases so naturally high, that it would take a great many more trials than were recorded to eliminate it through averaging. In one of our typical experiments with four experimental conditions, less than 100 trials per condition could be conducted before subject performance deteriorated due to fatigue. The magnitude of baseline alpha activity for a given subject on a given day varied considerably, and, as is demonstrated in Fig. 1 (D), when baseline alpha is high, it does not average-out even across 160 trials. In Fig. 1-11, the great magnitude of this endogenous alpha rhythm can be seen without its being reduced in the average because of its random phase.

When the amplitude and phase of 10 Hz activity in each trial are simultaneously represented in a polar plot, the random distribution of alpha phases among individual trials is apparent as well as the great FFT alpha magnitude of individual trials (Fig. 1-12). In single trial polar plots of the 15 Hz VEP response, a similar random phase distribution

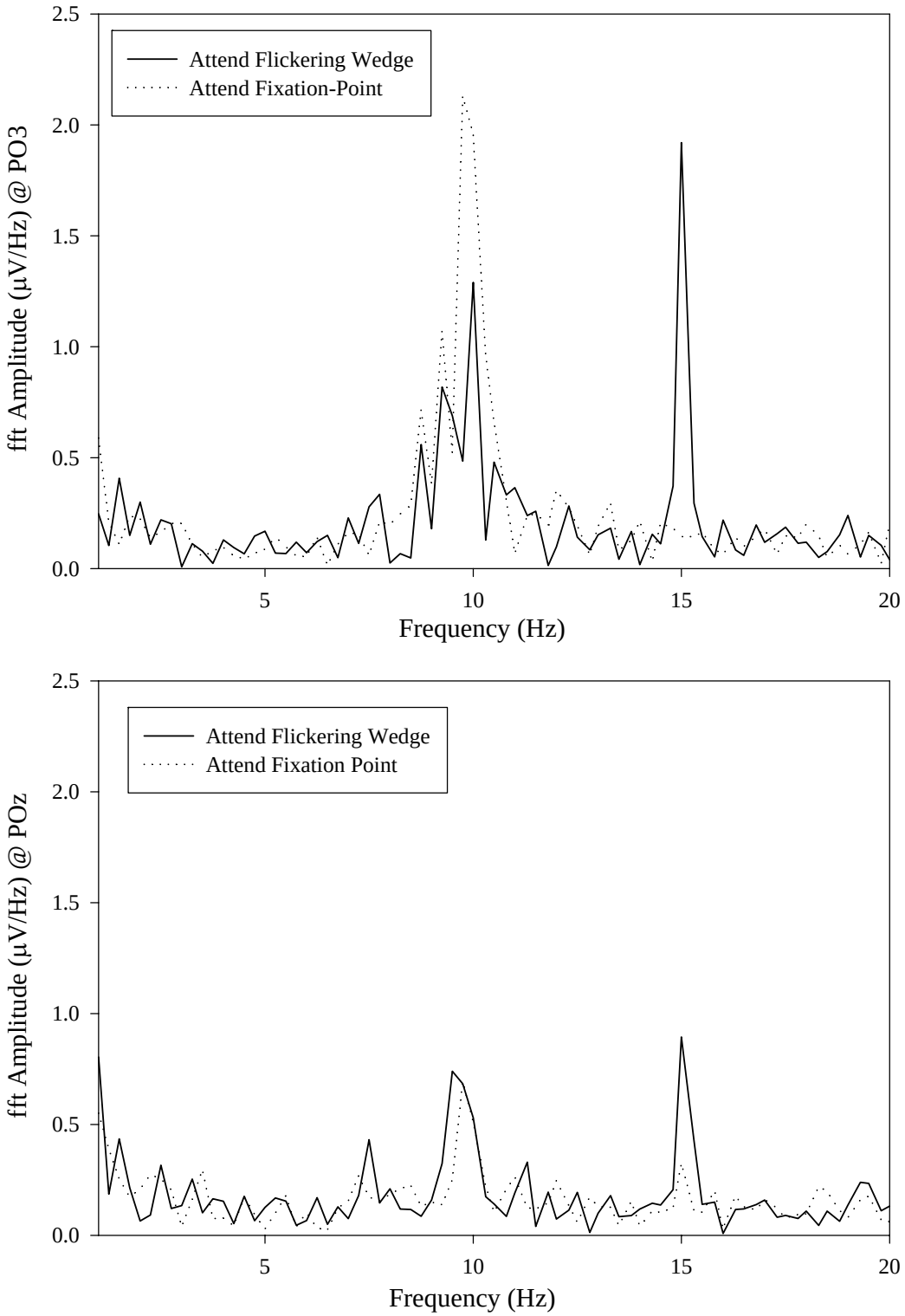


Fig. 1-8: *Amplitude spectra averaged across 5 s epochs at peak electrodes (N=48).* (Top) *Attentional-pair* #1H, where subject C evidenced the highest response ratio. (Bottom) *Attentional-pair* #1M, where subject C evidenced the lowest response ratio.

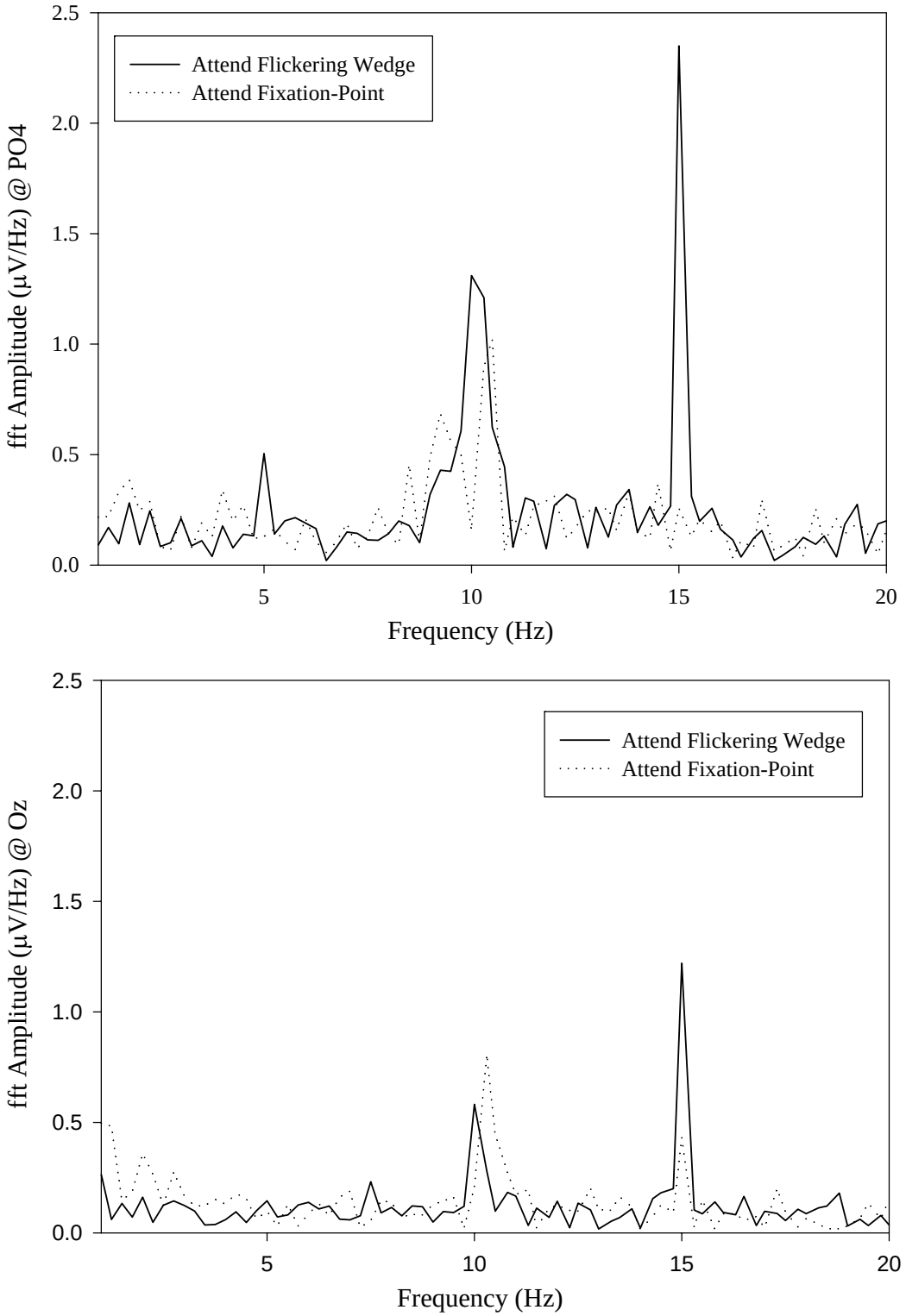


Fig. 1-9: *Amplitude spectra averaged across 5 s epochs at peak electrodes (N=48).* (Top) A*ttentional-pair* #1E, where subject L evidenced the highest response ratio. (Bottom) *Attentional-pair* #1B, where subject L evidenced the lowest response ratio.

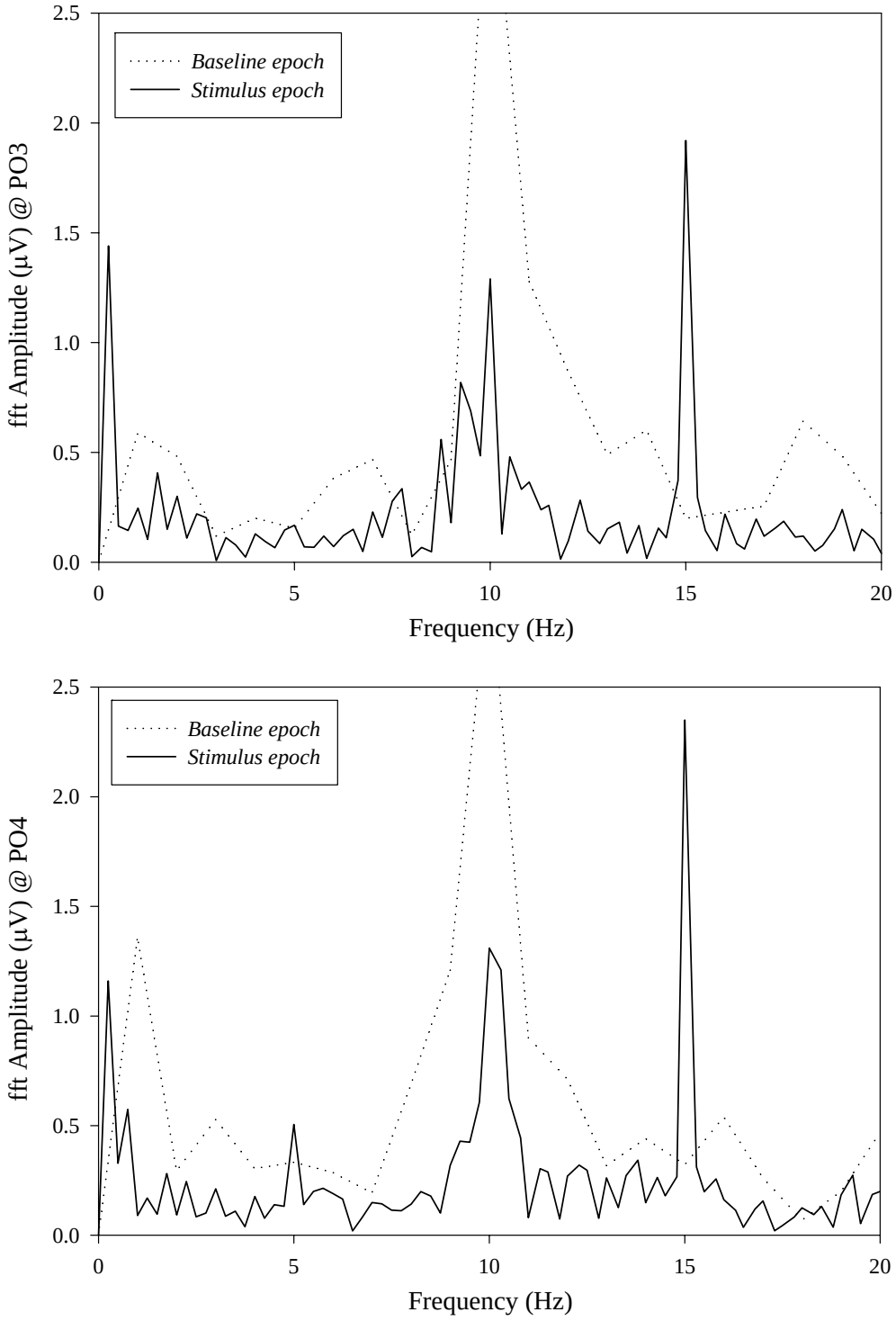


Fig. 1-10: *Amplitude spectra of 1 second baseline and 5 s stimulus epochs (N=48)* in the *Attend-Flickering-Wedge* condition for *attenitonal-pairs* with the highest response ratios. (Top) *Attentional-pair* #1H, Subject C. (Bottom) *Attentional-pair* #1E, Subject L .

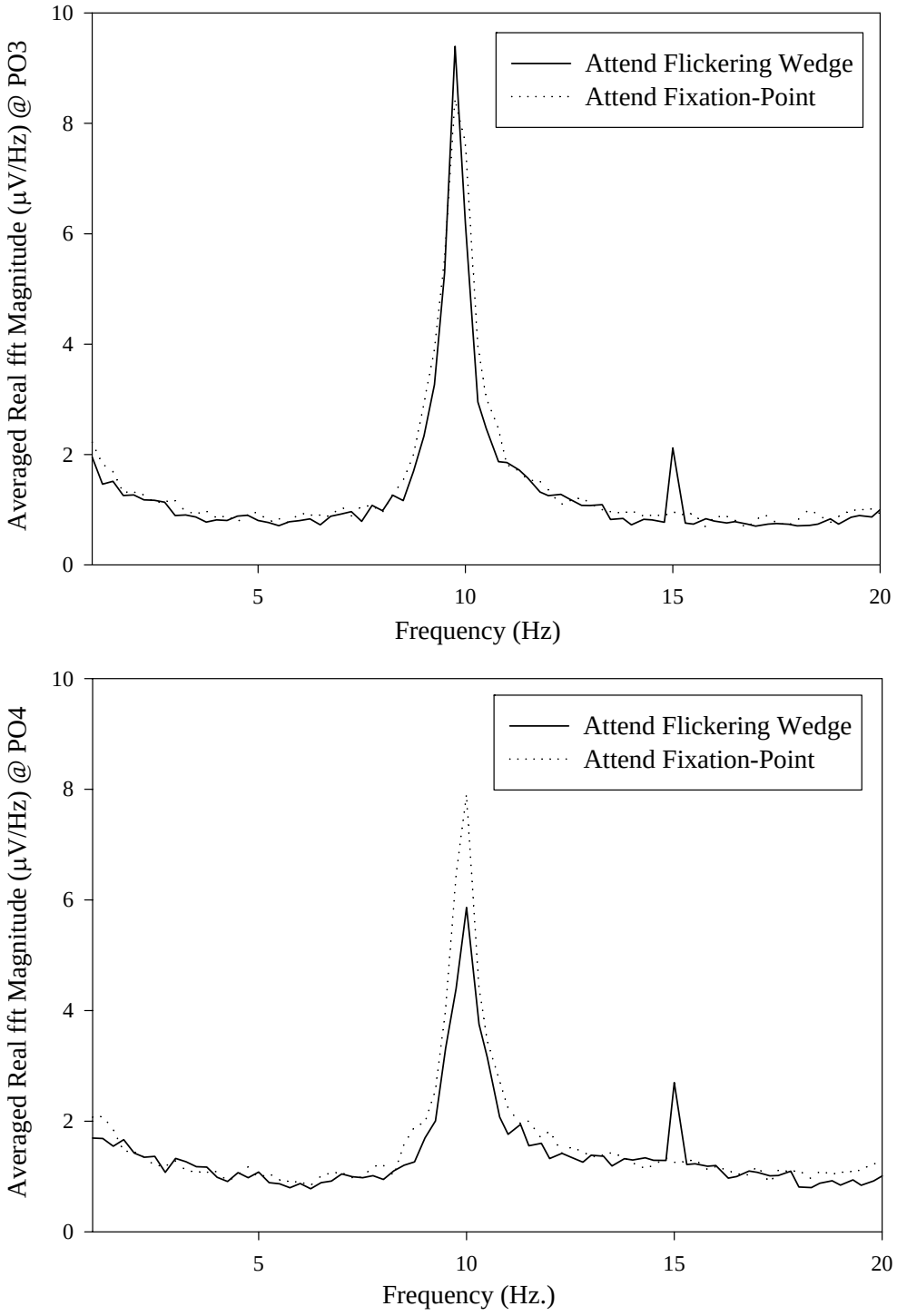


Fig. 1-11: *Spectra derived from real fft magnitude averaged across 5 s epochs (N=48).* (Top) *Attentional-pair* #1H; (Bottom) *Attentional-pair* #1E. Note the ordinate scale here as compared to the complex averages of Figs. 1-8 and 1-9. Also note that the real fft magnitude at 15 Hz in the *Attend-Fixation-Point* condition is clearly equivalent to the high basal level of noise.

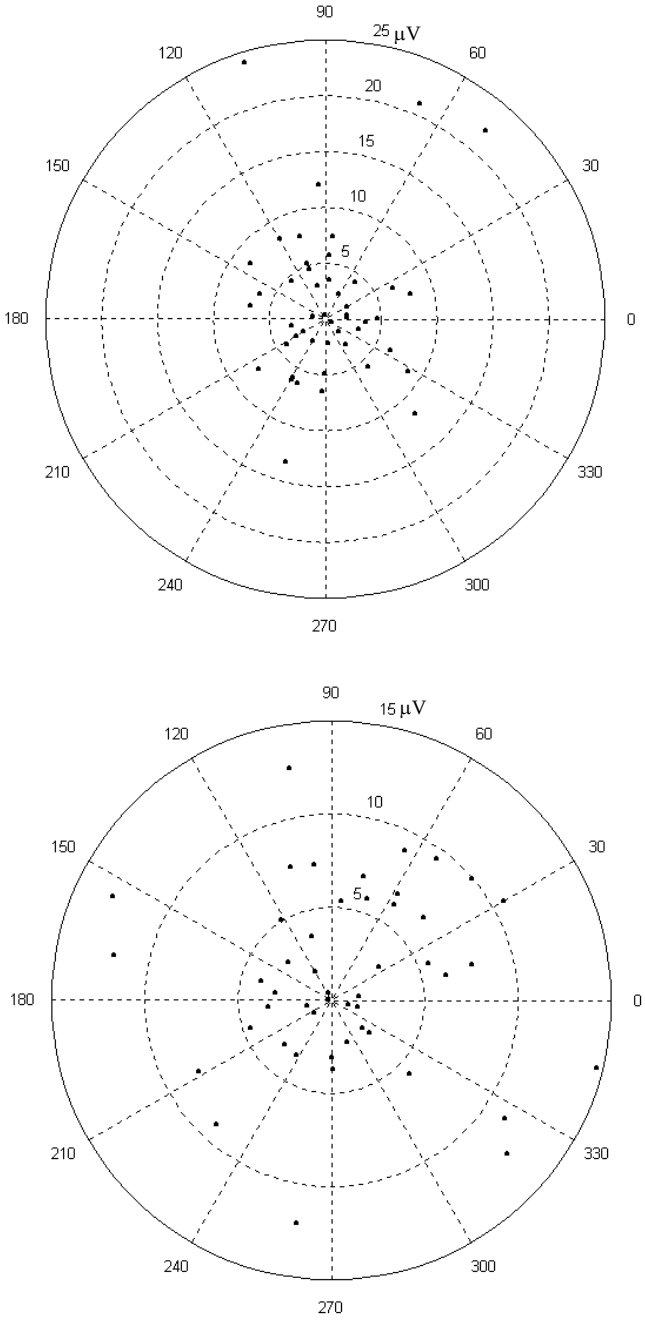


Fig. 1-12: *Amplitude and phase of 10 Hz alpha activity* for each trial is represented by a dot for which amplitude (μV) corresponds to eccentricity and phase corresponds to radial position. (Top) *Attend-Flickering-Wedge* condition of *attentional-pair* #1H at VEP peak electrode PO3; (Bottom) *Attend-Flickering-Wedge* condition of *attentional-pair* #1E at VEP peak electrode PO4. Note: the phase of alpha activity in both plots is randomly distributed and the amplitude is far higher for the 10 Hz. activity plotted here than for the 15 Hz. stimulus-driven VEP activity plotted in Fig. 1-13.

is seen in the *Attend-Fixation-Point* condition (Fig. 1-13 Left), which contrasts with the clearly non-random phases of the *Attend-Flickering-Wedge* conditions (Fig. 1-13 Right). Thus, it is apparent that greater phase coherence tied to stimulus flicker in the *Attend-Flickering-Wedge* condition is responsible, in part, for the greater amplitude evident in the average of the complex FFT components for that condition. Greater VEP amplitude in the individual trials, however, is also a factor in the average amplitude differential between attentional conditions. This is evident in the single trial polar plots (Fig. 1-13) and can be seen even more clearly in plots of the individual trial VEP amplitude distributions in opposing attentional conditions (Fig. 1-14).

All electrode amplitude and phase polar plots of the VEP response (Fig. 1-15) show phase relationships among the individual electrodes. In other experiments we have conducted, these relationships have been investigated to provide insights into VEP source localization. In the context of Experiment 1, suffice it to say that invariably, most electrodes in the *Attend-Flickering-Wedge* condition displayed greater amplitude than the peak electrode in the *Attend-Fixation-Point* condition; this was true even for *attentional-pairs* with the lowest response ratios. Also, one sees further evidence that the electrode phases were definitely non-random in the *Attend-Flickering-Wedge* condition. The close alignment in phase among electrodes is thought to indicate a compact cortical source for these VEP signals (Pugh et al., 1999). To provide a qualitative sense of the VEP response distribution among electrodes, in the bottom left polar plot of Fig. 1-15, the peak electrode (PO4) is labeled, as well as the electrode closest to it in both VEP

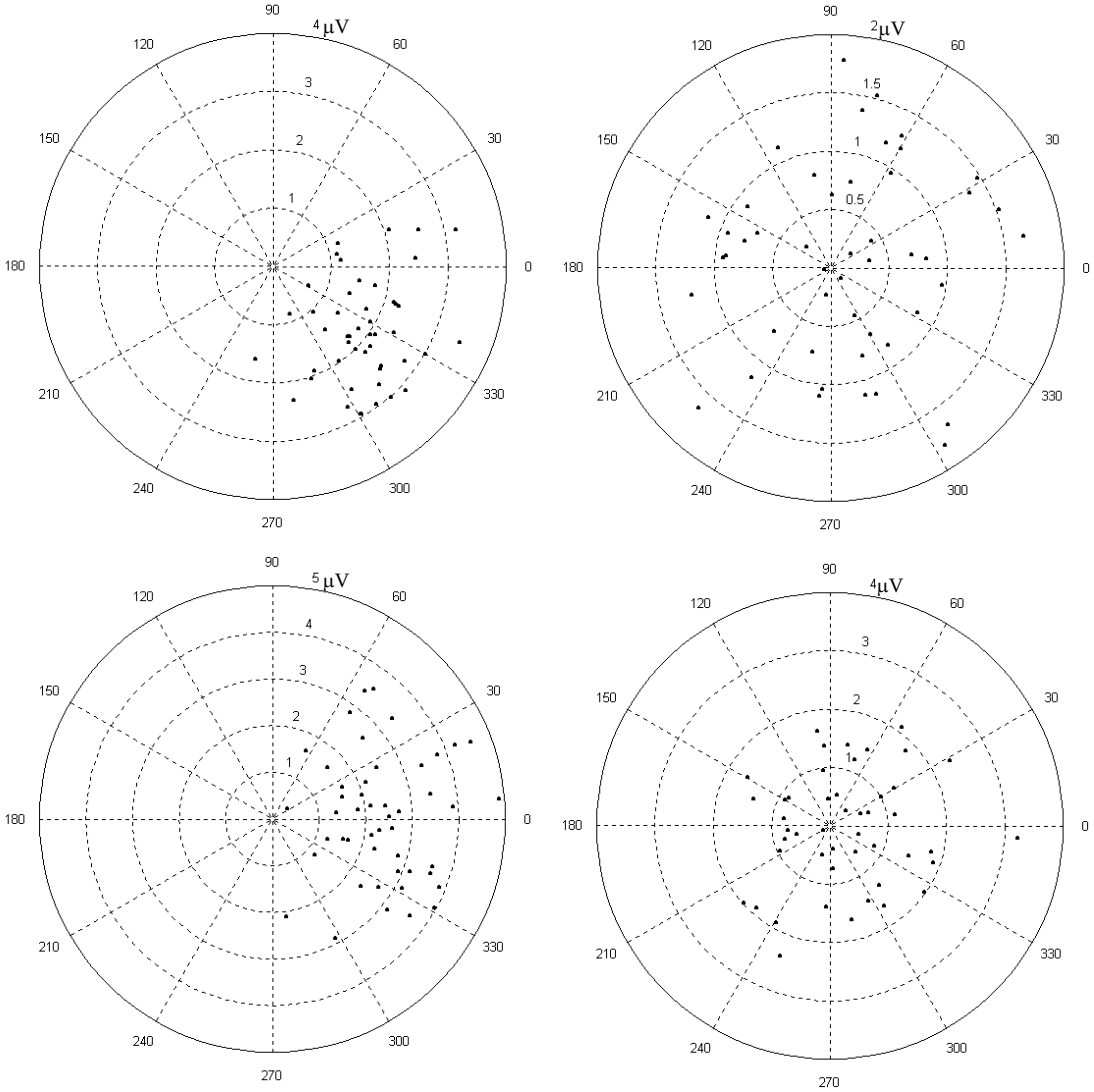


Fig. 1-13: *Single-trial amplitude and phase polar plots of 15 Hz. VEP response at peak electrodes.* (Top) *Attentional-pair* #1H, subject C. (Bottom) *Attentional-pair* #1E, subject L. (Left) A*ttend-Flickering-Wedge* condition; (Right) *Attend-Fixation-Point* condition. Note the qualitative difference in phase distribution between conditions (left Vs. right side plots).

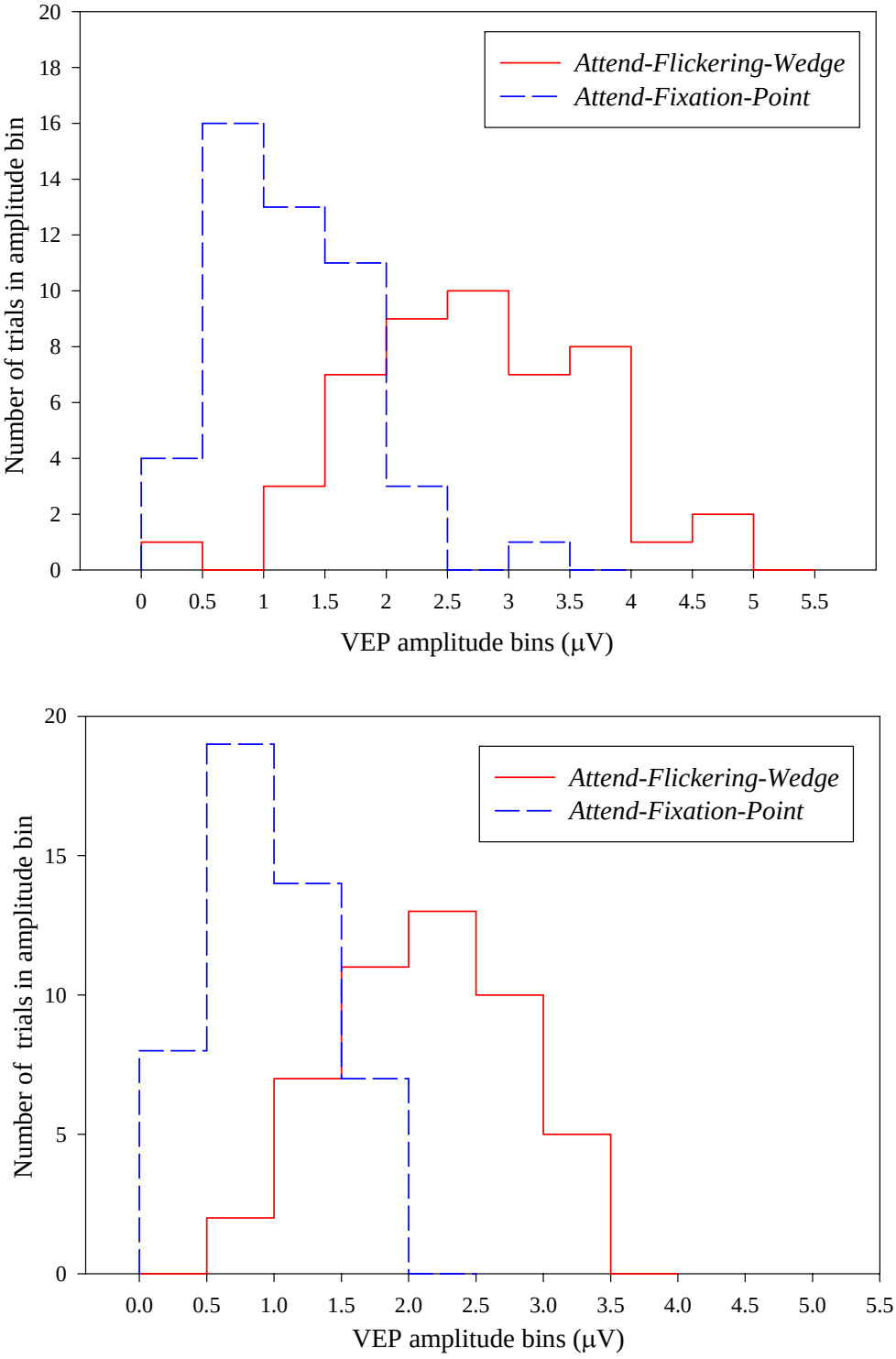


Fig. 1-14: *Single trial peak VEP amplitude distribution curves of attentional-pairs with the highest response ratios:* (Top) #1E, subject L; (Bottom) #1H, subject C.

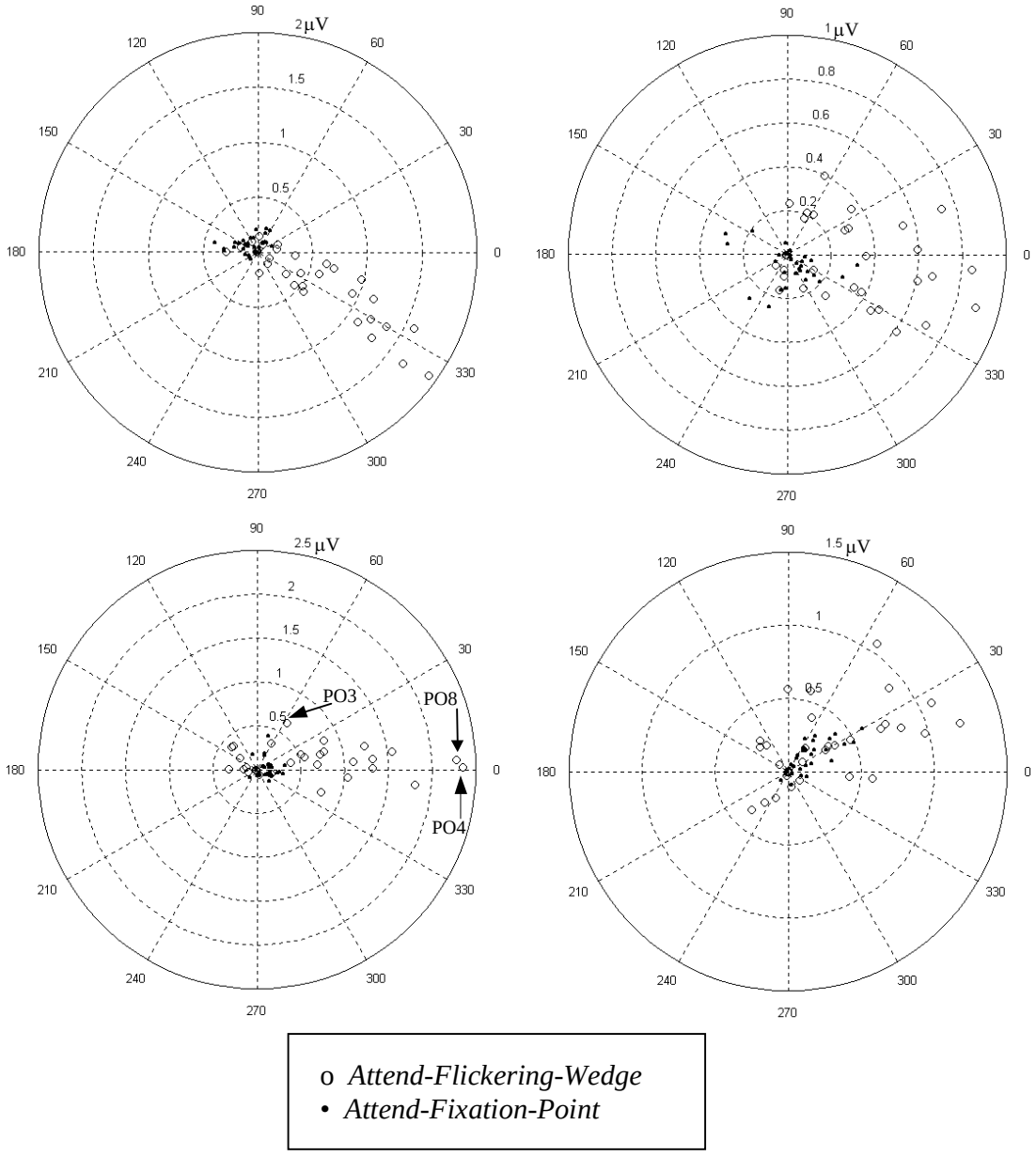


Fig. 1-15: *All electrode amplitude and phase polar plots of VEP response (N=48).*
(Top Left) *Attentional-Pair* #1H – Subject C's highest response ratio;
(Top Right) *Attentional-Pair* #1M – Subject C's lowest response ratio.
(Bottom Left) *Attentional-Pair* #1E – Subject L's highest response ratio.
(BottomRight) *Attentional-Pair* #1B – Subject L's lowest response ratio.
Amplitude and phase of VEP response for each electrode is represented by a circle (*Attend-Flickering-Wedge* condition) or a dot (*Attend-Fixation-Point* condition). Amplitude (μV) corresponds to eccentricity and phase (radians) corresponds to radial position. Note that most electrodes in the *Attend-Flickering-Wedge* condition have greater amplitude than the peak electrode in the *Attend-Fixation-Point* condition.

amplitude and physical proximity on the scalp (PO8). The other electrode that is labeled (PO3) is located on the opposite side of the head from the peak electrode, and is far removed from it in VEP amplitude as well.

CONCLUSIONS

Selective attention can produce substantial, robust modulation of cortical responses to steady-state contrast-modulated flicker from stimuli in a variety of positions across the visual field. In many cases, VEP amplitude elicited by such stimuli can be attenuated to the level of noise solely through the manipulation of selective attention. The attentional effects observed are manifestations, in part, of stimulus-tied phase coherence on the averages, and, in part, of greater VEP amplitude on individual trials.

EXPERIMENT 2a

PURPOSE

EEG data were collected in order to determine whether the effects of visual selective attention evident in Experiment 1 with foveal (*Attend-Fixation-Point*) vs. eccentric (*Attend-Flickering-Wedge*) attentional targets could be obtained with eccentric targets only (*Attend-Flickering-Wedge* vs. *Attend-Nonflickering-Wedge*). Also, the spatial properties of non-foveal attentional effects were preliminarily investigated.

METHODS

As in Experiment 1, while the subject maintained visual fixation on the center point of a CRT monitor, a wedge flickering sinusoidally around mean gray at 7.5 Hz and 25% contrast was displayed at an eccentric location on the monitor for 5.6 seconds. In the *Attend-Flickering-Wedge* condition, 1 to 5 seconds after stimulus onset, the flickering wedge became colored red or green (at any of three tint levels). After a shift to color, the subject indicated with a button-push whether she believed the color was red or green. In a departure from Experiment 1, instead of the *Attend-Fixation-Point* condition, the alternative attentional condition was *Attend-Nonflickering-Wedge,* where the subject responded to a shift to color in a nonflickering wedge of the same size and eccentricity as the flickering wedge, but at a different radial location (Fig. 2-1). Experiment 2a comprised four *attentional-pairs,* in all of which the flickering wedge remained at the same location; viz., 10 degrees clock angle (c.a.) right of the lower vertical meridian at an eccentricity of 2.9 to 4.5 degrees visual angle (v.a.) In each of the four *attentional-pairs*, the nonflickering wedge was located at the same eccentricity as the flickering wedge

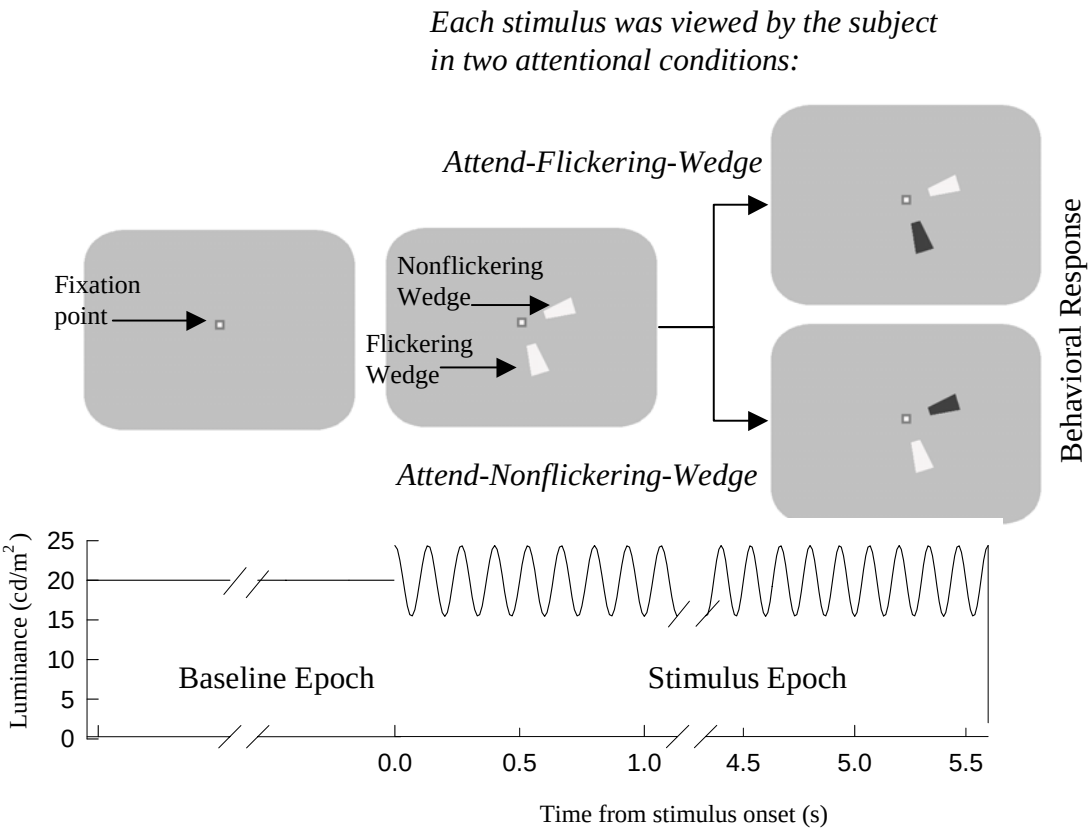


Fig. 2-1: *Description of a single trial in Experiment 2.*

(2.9-4.5 degrees v.a.), but at a different radial position. Separation between the flickering and nonflickering wedges was 180 degrees c.a. in *attentional-pair* 2A, 90 degrees c.a. in 2B, 10 degrees c.a. in 2C, and the two wedges were adjacent in 2D. The exact position of the wedges and other specifics are listed for *attentional-pairs* 2A through 2D in the first four rows of Table 2-1.

As in Experiment 1, blocks of 32 trials in each condition were alternated and the subject was instructed before each block whether to train her attention on the flickering wedge or the nonflickering wedge (i.e., on the target where a shift to color would occur).

Index #	S	Flickering Wedge Visual Field (Eccentricity))	Nonflickering Wedge Position	RR	Attend Flicker Amp (μV)	Attend Non-flick Amp (μV)	Attend Flicker S.D.(μV)	Attend Non-flick S.D.(μV)	N	p<
2A	L	RIGHT(2.9-4.5)	Sep 180 deg	3.5	1.32	0.38	1.19	1.18	88	.001
2B	L	RIGHT(2.9-4.5)	Sep 90 deg R	5.8	1.61	0.28	1.08	0.90	88	.001
2C	C	RIGHT(2.9-4.5)	Sep 10 deg R	6.8	1.74	0.26	0.98	1.17	88	.001
2D	C	RIGHT(2.9-4.5)	Adj Right	5.4	1.75	0.33	0.95	0.89	88	.001
2E	L	RIGHT(4.14-4.5)	Adj Right	0.7	0.21	0.30	0.77	1.22	44	ns
2F	L	RIGHT(4.14-4.5)	Sep 1unit R	2.4	0.75	0.31	1.11	1.26	44	.001
2G	L	RIGHT(4.14-4.5)	Adj Center	1.1	0.47	0.41	1.14	1.37	44	ns
2H	L	RIGHT(4.14-4.5)	Sep 1 unit C	1.5	0.82	0.54	1.30	1.49	44	.05
2I	C	RIGHT(4.14-4.5)	Adj Right	1.6	0.83	0.53	0.77	0.94	44	.001
2J	C	RIGHT(4.14-4.5)	Sep 1 unit R	2.2	0.80	0.36	0.69	0.88	44	.001
2K	C	RIGHT(4.14-4.5)	Adj Center	1.2	0.47	0.39	0.96	0.90	44	ns
2L	C	RIGHT(4.14-4.5)	Sep 1 unit C	2.2	0.77	0.35	0.92	0.95	44	.001
2M	C	RIGHT(4.14-4.5)	Not present	na	1.42	na	1.02	na	44	-
2N	L	LEFT(4.14-4.5)	Adj Left	0.7	0.34	0.47	1.12	1.15	44	ns
2O	L	LEFT(4.14-4.5)	Sep 1 unit L	1.1	0.56	0.52	1.11	0.99	44	ns
2P	L	LEFT(4.14-4.5)	Adj Center	1.4	0.48	0.35	1.08	1.04	44	ns
2Q	L	LEFT(4.14-4.5)	Sep 1 unit C	1.8	0.60	0.32	0.92	0.95	44	.001
2R	L	LEFT(4.14-4.5)	Not present	na	0.59	na	1.05	na	44	-
2S	C	LEFT(4.14-4.5)	Adj Left	0.8	0.37	0.43	0.93	0.71	44	ns
2T	C	LEFT(4.14-4.5)	Sep 1 unit L	2.1	0.52	0.25	1.04	0.72	44	.001
2U	C	LEFT(4.14-4.5)	Adj Center	1.1	0.37	0.33	0.75	0.88	44	ns
2V	C	LEFT(4.14-4.5)	Sep 1 unit C	1.1	0.39	0.35	0.91	1.07	44	ns
2W	C	LEFT(4.14-4.5)	Not present	na	0.76	na	0.75	na	44	-

Table 2-1: *Summary information for eccentric vs. eccentric attentional-pairs and controls (Experiments 2a & 2b).*

The first column lists an index number for each *attentional-pair* or control in Experiment 2. The "Flickering Wedge Visual Field" location begins either 10 degrees c.a. right or left of the lower vertical meridian and extends the width of the flickering wedge; eccentricity is given in degrees v.a. In the four attentional-pairs of Experiment 2a (four rows above the double line) the size of the flickering and nonflickering wedges is 0.75 x 1.5 degrees v.a. The size of the flickering and nonflickering wedges in Experiment 2b (rows below the double line) is 0.36 x 0.36 degree v.a. The nonflickering wedge was positioned either right or left of the flickering wedge, adjacent to it or separated by "1 unit"–an area nominally corresponding to a $1mm^2$ field of activation in the primary visual cortex. "Attend Flicker" refers to the *Attend-Flickering-Wedge* condition; "Attend Non-flick" to the *Attend-Nonflickering-Wedge* condition. "Amp" and "S. D." refer to the amplitude and standard deviation of the 15 Hz VEP response at the peak electrodes, averaged across 4 and 5 s stimulus epochs. "N' refers to the number of trials averaged. "RR" gives the response ratio of VEP amplitude in the *Attend-Flickering-Wedge* condition (the numerator) vs. the *Attend-Nonflickering-Wedge* condition (the denominator). "p<" gives the statistical reliability of the response ratios.

The same two subjects as in Experiment 1 were tested. Again, stimulus epochs preceding the shift to color in each trial were analyzed, excluding the first second following stimulus onset, and the complex FFT coefficients were averaged across all trials within each condition. Percent correct of behavioral responses to the psychophysical task were tabulated and performance dependence on tint level was again evident, signifying that attention was required by the psychophysical task as intended. Other methodological details and technical specifications were the same as in Experiment 1.

RESULTS

In all four *attentional-pairs* of Experiment 2a, the VEP response in the *Attend-Flickering-Wedge* condition was substantially greater than in the *Attend-Nonflickering-Wedge* condition. Fig. 2-2 shows a schematic of the stimulus presentation for each *attentional-pair* together with a bar graph of the 15 Hz VEP response at peak electrodes averaged across the epochs with color-shift at 4 and 5 seconds post stimulus-onset. Fig. 2-3 shows all-electrode polar plots of amplitude and phase at the response frequency averaged across the 5 s epochs. Note that in every polar plot, not only is the peak electrode of the *Attend-Flickering-Wedge* condition greater than that of the *Attend-Nonflickering-Wedge* condition, but most electrodes in the *Attend-Flickering-Wedge* condition are much greater in amplitude than the peak electrode in the *Attend-Nonflickering-Wedge* condition. Phase coherence between electrodes in the *Attend-Flickering-Wedge* condition is also clearly evident. Figs. 2-4 and 2-5 show the FFT amplitude spectra of each *attentional-pair* averaged across the 5 s epochs at peak electrodes. In these spectra, a sharp spike of stimulus-driven VEP activity is evident at

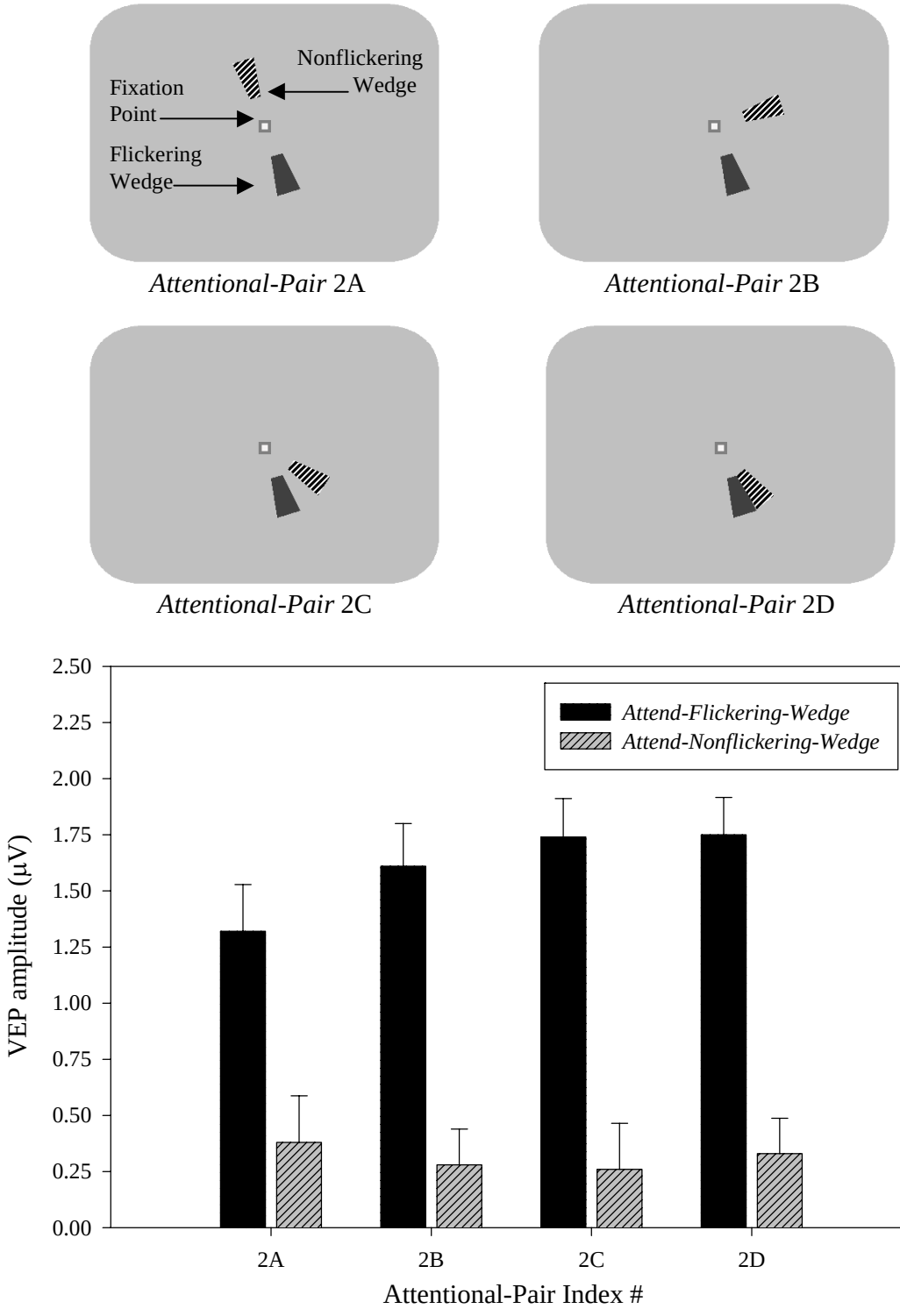


Fig. 2-2: *VEP response with 95% confidence intervals* averaged across 4 and 5 s epochs (N = 88) at peak electrodes for the *attentional-pairs* in Experiment 2a. The difference in mean amplitudes for every *attentional-pair* was statistically reliable at $p < .001$.

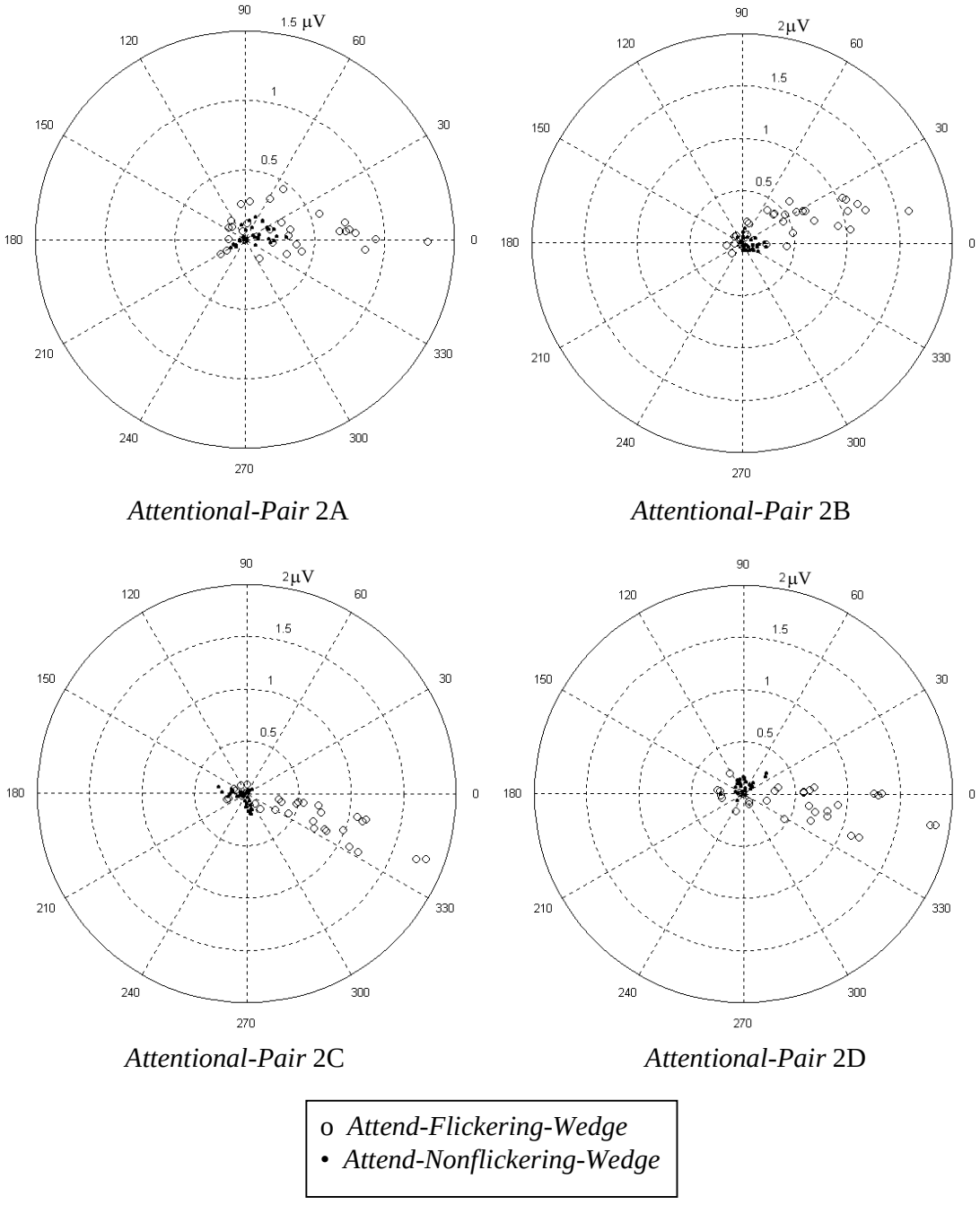


Fig. 2-3: *All electrode amplitude and phase polar plots of VEP response averaged across the 5 s epochs of each attentional-pair in Experiment 2a (N=48).*
Amplitude and phase of the VEP response for each electrode is represented by a circle (*Attend-Flickering-Wedge* condition) or a dot (*Attend-Nonflickering-Wedge* condition). Amplitude (μV) corresponds to eccentricity and phase (radians) corresponds to radial position.

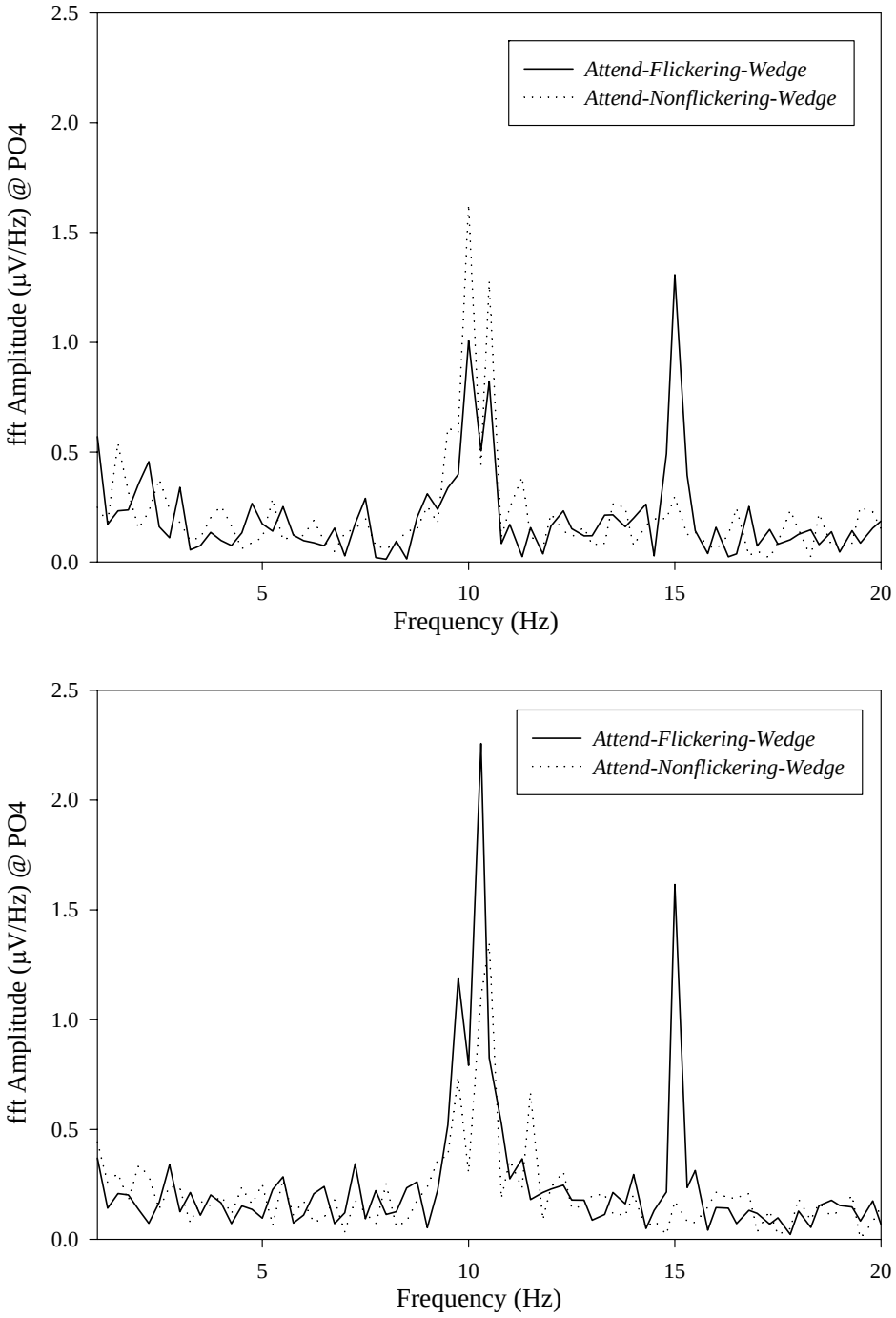


Fig. 2-4: *Amplitude spectra averaged across 5 s epochs at peak electrodes (N=48).* (Top) *Attentional-pair* #2A - 180 degree separation between flickering wedge and nonflickering wedge. (Bottom) *Attentional-pair* #2B - 90 degree separation between flickering wedge and nonflickering wedge.

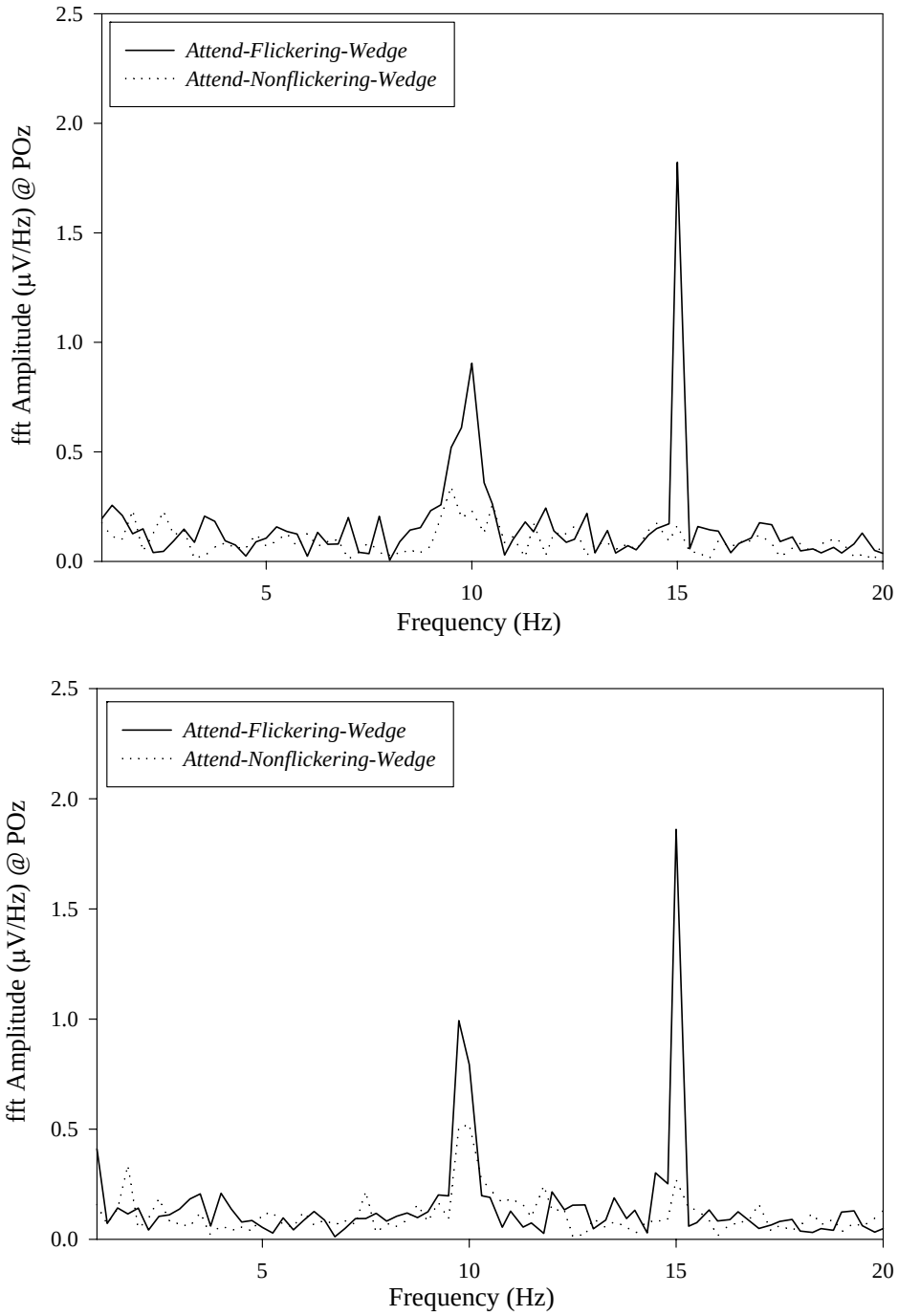


Fig. 2-5: *Amplitude spectra averaged across 5 s epochs at peak electrodes (N=48).* (Top) *Attentional-pair* #2C - 10 degree separation between flickering wedge and nonflickering wedge. (Bottom) *Attentional-pair* #2D - adjacent flickering and nonflickering wedges.

15 Hz in the *Attend-Flickering-Wedge* condition, whereas in the *Attend-Nonflickering-Wedge* condition, little, if any, stimulus-driven VEP response is evident above the noise level in neighboring bandwidths of the frequency spectrum. Regarding spatial properties of the attentional effects seen in Experiment 2a, it should be noted that the magnitude of attentional gain was not diminished by proximity of the nonflickering wedge to the flickering wedge, even when the two attentional targets were adjacent; i.e., in *attentional-pair* #2D.

CONCLUSIONS

Substantial effects of visual selective attention were evident for attentional targets positioned peripherally, at a common eccentricity in the visual field. Thus, the attentional effects observed in Experiment 2a were not due to variation in attention directed to the fovea vs. the periphery, as might have been the case in Experiment 1. Furthermore, attentional gain was unaffected by the degree of separation between the attentional targets employed in Experiment 2a, indicating the need for smaller visual targets to further investigate the spatial properties and neural substrate of these attentional effects.

EXPERIMENT 2b

PURPOSE

EEG data were collected from very small eccentric visual targets in Experiment 2b to further investigate the spatial properties and neural substrate of the attentional effects observed in Experiment 2a.

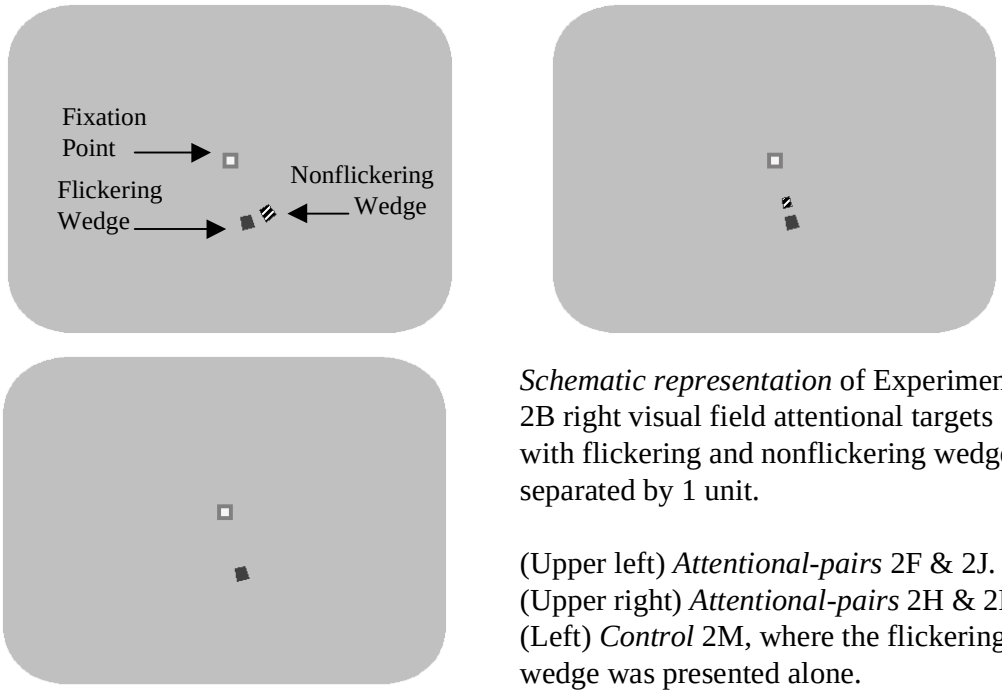
METHODS

In Experiment 2b, as in Experiment 2a, the subjects were tested in two attentional conditions: *Attend-Flickering-Wedge* vs. *Attend-Nonflickering-Wedge* (see Fig. 2-1 for a review of the experimental paradigm employed here). In Experiment 2b, however, the wedges were much smaller (0.36 x 0.36 degree v.a.) than in previous experiments. The V1 neuronal activity field of flickering wedges with spatial characteristics such as those in Experiments 1 and 2a was ~11 mm^2, whereas the area of primary visual cortex corresponding to the neuronal activity field of wedges in Experiment 2b was ~1 mm^2, an area that will hereafter be referred to as "1 unit". This is roughly the area subtended by a single cortical hypercolumn in V1. Preliminary experiments had demonstrated that these were the smallest visual targets upon which our subjects were able to sustain their attention with adequate psychophysical performance. Furthermore, in preliminary experiments with these small stimuli, our subjects found that the nonflickering wedge would often fade from perceptual view by the end of the 5.6 second stimulus epoch. In order to eliminate such perceptual fading, the nonflickering wedges were made to slowly oscillate at 0.5 Hz around mean gray at 25% contrast.

The flickering wedge was located at 4.14 to 4.5 degrees eccentricity in two different radial positions for Experiment 2b: 10 degrees c.a. right of the lower vertical meridian (*attentional-pairs* 2E through 2M) or 10 degrees c.a. left of the lower vertical meridian (*attentional-pairs* 2N through 2W). The nonflickering wedges in Experiment 2b were either adjacent to the flickering wedges or separated by "1 unit" to the left or to the right at the same eccentricity, or toward the center (see Table 2-1 for specifics). Apart from the differences delineated above, all other experimental details of Experiment 2b were the same as in Experiment 2a.

RESULTS

For all *attentional-pairs* with wedges separated by 1 unit, VEP response in the *Attend-Flickering-Wedge* condition was greater than in the *Attend-Nonflickering-Wedge* condition (Table 2-1). For wedges in the right visual hemifield, where the highest amplitude VEP responses were routinely obtained, the response ratio was substantial for all the *attentional-pairs* with separated wedges. Fig. 2-6 shows a schematic of the stimulus presentation for each *attentional-pair* with separated attentional targets in the right visual hemifield together with a bar graph of the 15 Hz VEP response at peak electrodes averaged across the epochs with color-shift at 4 and 5 seconds post stimulus-onset. Fig. 2-7 shows all-electrode polar plots of amplitude and phase at the VEP response frequency averaged across 5 s epochs and, again, most electrodes in the *Attend-Flickering-Wedge* condition have much greater amplitude than the peak electrode of the *Attend-Nonflickering-Wedge* condition. Figs. 2-8 and 2-9 show FFT amplitude spectra averaged across the same 5 s epochs at the peak electrodes for subjects C and L. Again,



Schematic representation of Experiment 2B right visual field attentional targets with flickering and nonflickering wedges separated by 1 unit.

(Upper left) *Attentional-pairs* 2F & 2J. (Upper right) *Attentional-pairs* 2H & 2L. (Left) *Control* 2M, where the flickering wedge was presented alone.

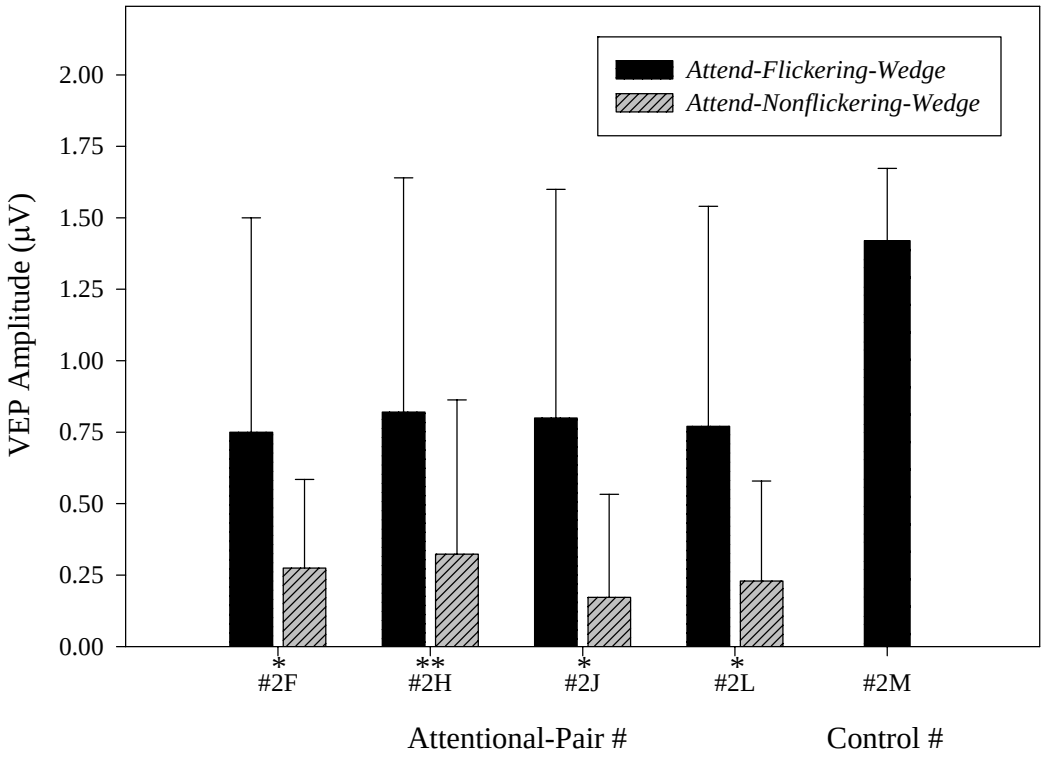


Fig. 2-6: *VEP response with 95% confidence intervals* averaged across 4 and 5 s epochs (N = 44) at peak electrodes for *attentional-pairs* with right visual field flickering and nonflickering wedges separated by 1 unit. * p<.001 ** p<.05

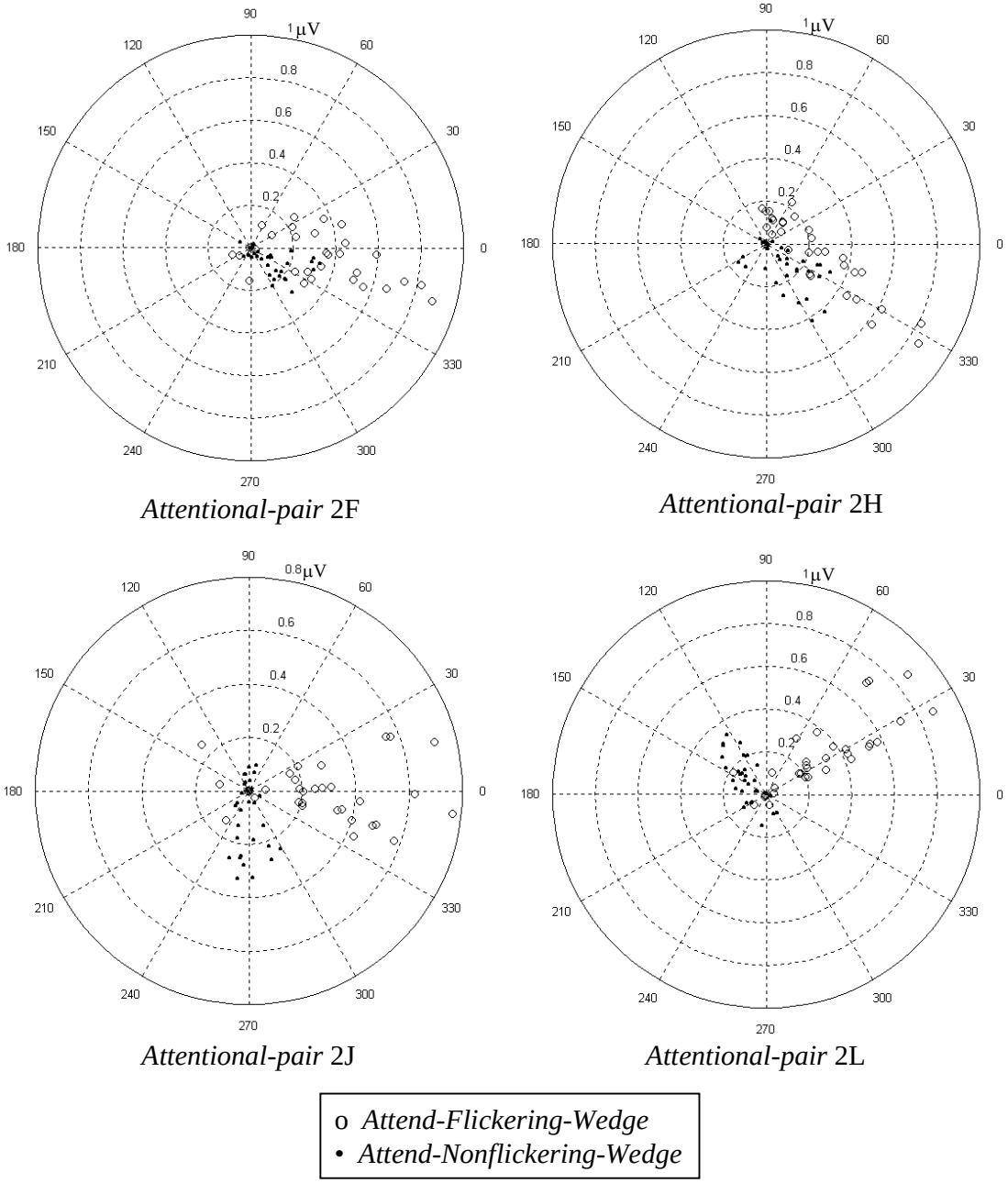


Fig. 2-7: *All electrode amplitude and phase polar plots of VEP response averaged across 5 s epochs (N=24) for Experiment 2b attentional-pairs with right visual field flickering and nonflickering targets separated by 1 unit.* Amplitude and phase of VEP response for each electrode is represented by a circle (*Attend-Flickering-Wedge* condition) or a dot (*Attend-Nonflickering-Wedge* condition). Amplitude (μV) corresponds to eccentricity and phase (radians) corresponds to radial position.

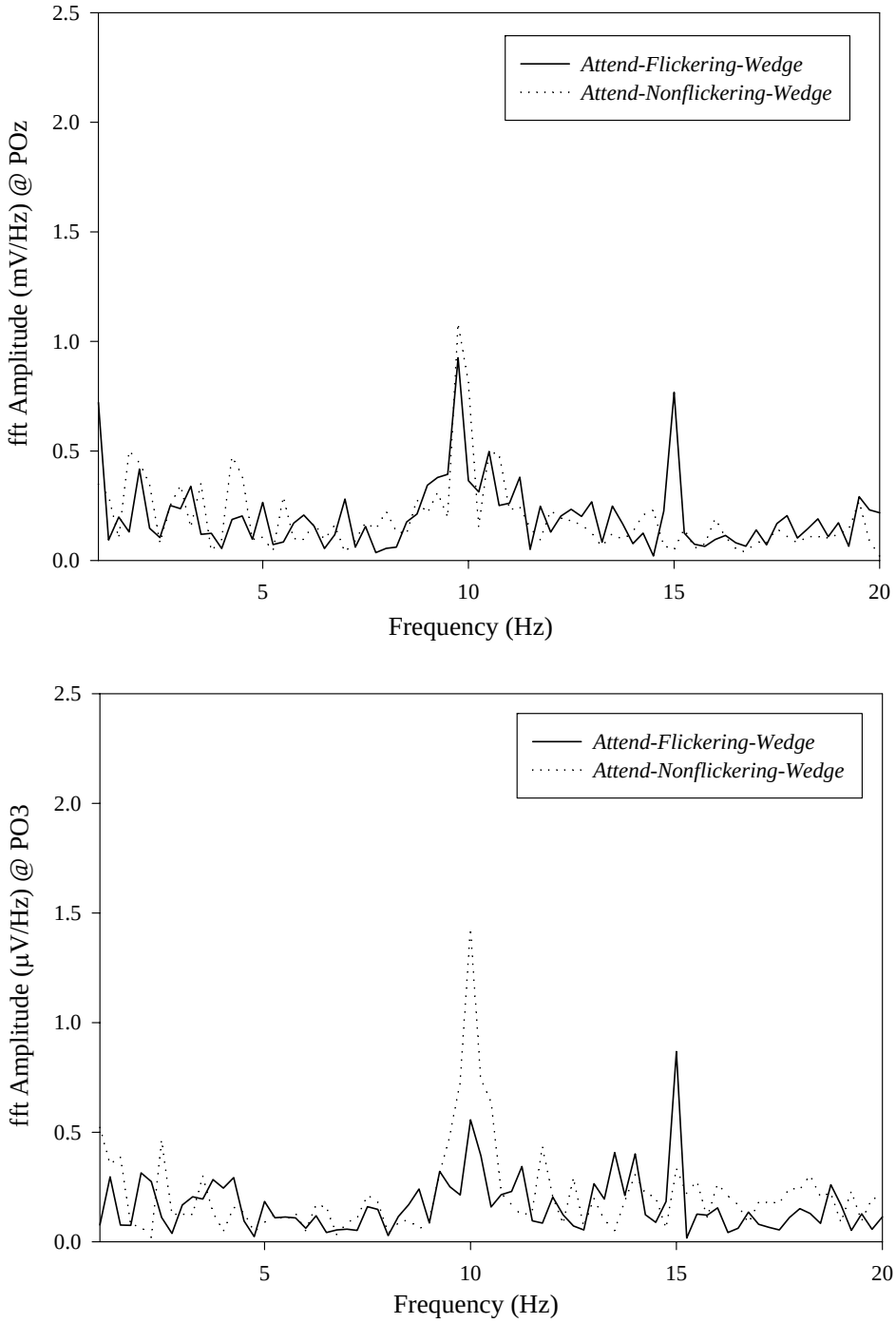


Fig. 2-8: *Amplitude spectra averaged across 5 s epochs at peak electrodes for subject C (N=24).* (Top) *Attentional-pair* #2J - flickering wedge in right visual field with nonflickering wedge separated 1 unit to the right. (Bottom) *Attentional-pair* #2L - flickering wedge in right visual field with nonflickering wedge separated 1 unit toward the center.

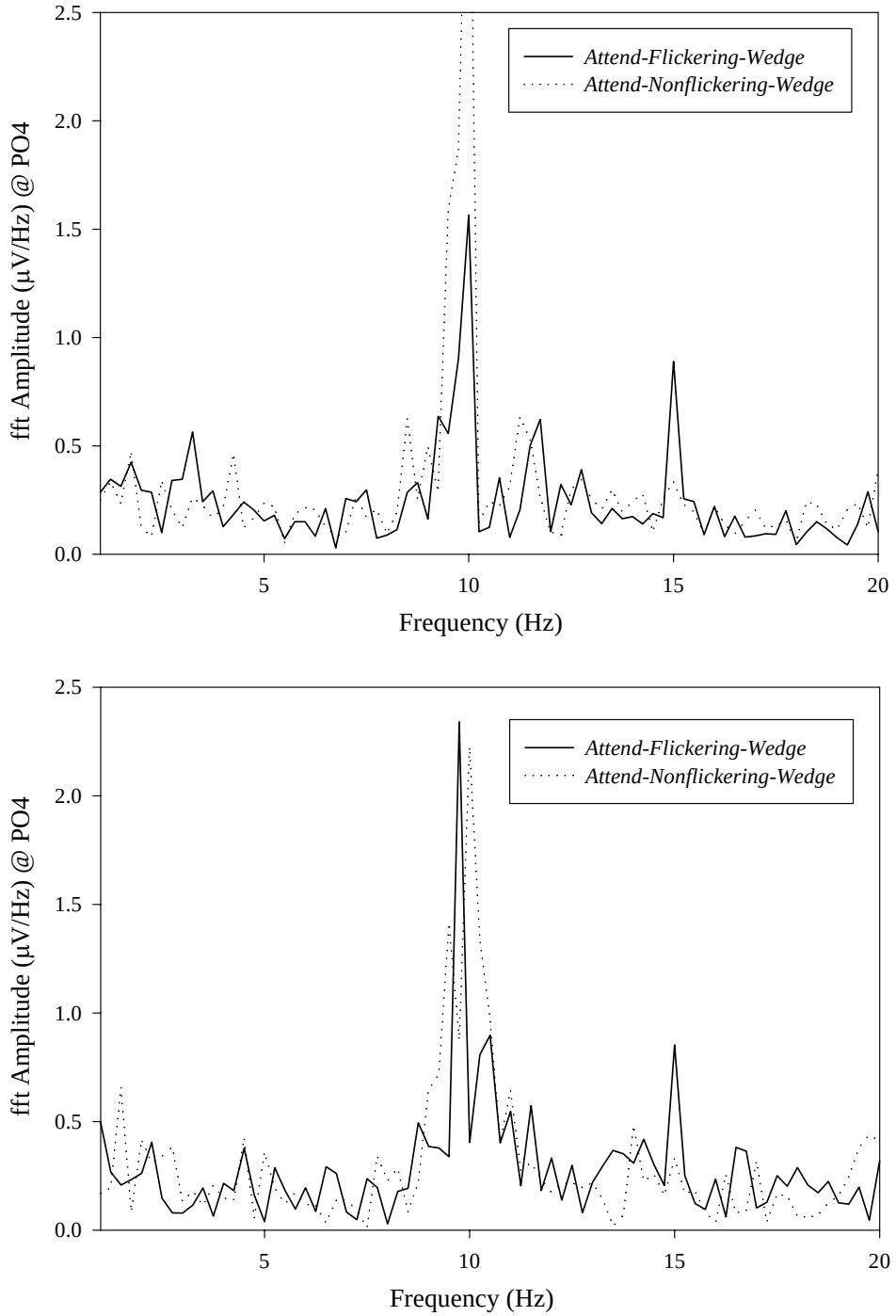


Fig. 2-9: *Amplitude spectra averaged across 5 s epochs at peak electrodes for subject L (N=24).* (Top) *Attentional-pair* #2F - flickering wedge in right visual field with nonflickering wedge separated 1 unit to the right. (Bottom) *Attentional-pair* #2H - flickering wedge in right visual field with nonflickering wedge separated 1 unit toward the center.

little, if any, 15 Hz activity above spectral noise is evident in the *Attend-Nonflickering-Wedge* condition, while a 15 Hz VEP response is clearly evident in the *Attend-Flickering-Wedge* condition.

In the left visual hemifield, where stimulus-driven signals were approximately half the amplitude of those generated in the right visual field and, thus, where the signal-to-noise ratio was much lower (Fig. 2-10), the attentional gain for separated targets was not always significant (Fig. 2-11). When the attentional targets were adjacent, there was no consistent attentional gain (Fig. 2-12). Both subjects reported that in that situation, when the small attentional targets were adjacent, the two visual stimuli would sometimes perceptually merge, such that the flickering wedge could not be distinguished from the nonflickering wedge or vica versa. It should be noted that the amplitude of the VEP response from flickering wedges presented alone, without alternative attentional targets, was consistently higher than the VEP response in the *Attend-Flickering-Wedge* condition,

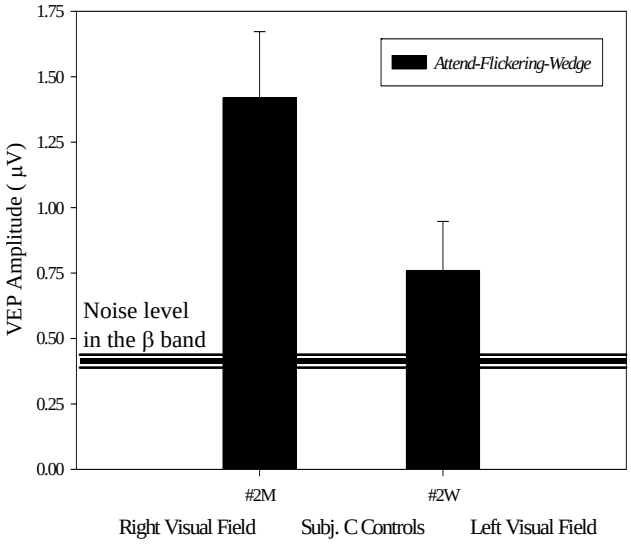
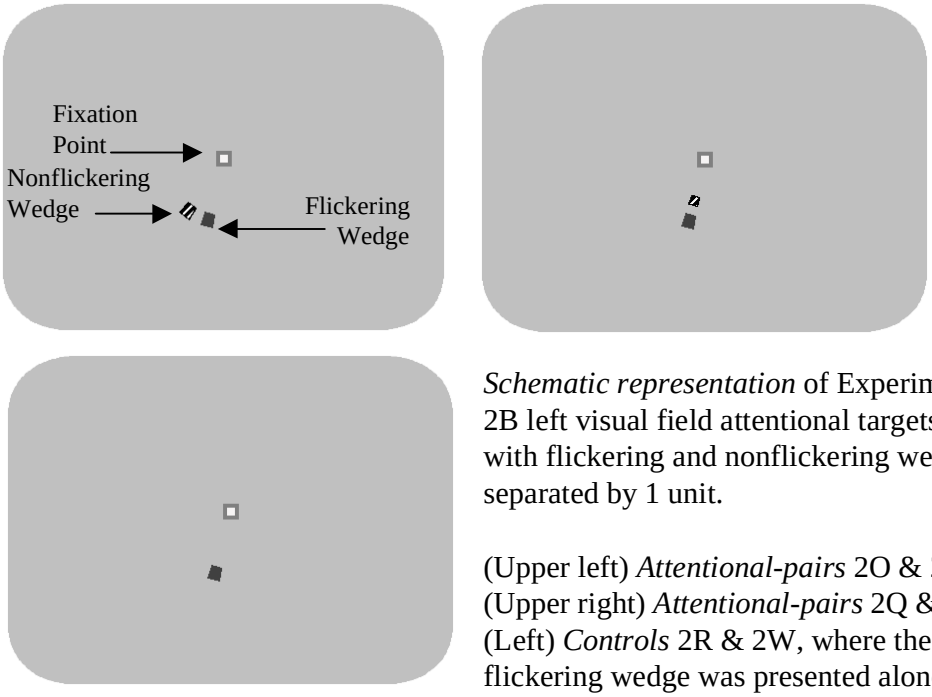


Fig. 2-10: *VEP responses with 95% confidence intervals* averaged across the 4 and 5 s epochs (N=44) at peak electrodes for the flickering wedges presented alone, as controls, in the right and left visual fields. Noise level in the β bandwidth (12.5-25 Hz) was ~0.3 μV. Note that while the noise level, which is a function of N, was the same in the right vs. left visual fields, the right visual field had a much higher signal-to-noise ratio than the left visual field.



Schematic representation of Experiment 2B left visual field attentional targets with flickering and nonflickering wedges separated by 1 unit.

(Upper left) *Attentional-pairs* 2O & 2T. (Upper right) *Attentional-pairs* 2Q & 2V. (Left) *Controls* 2R & 2W, where the flickering wedge was presented alone.

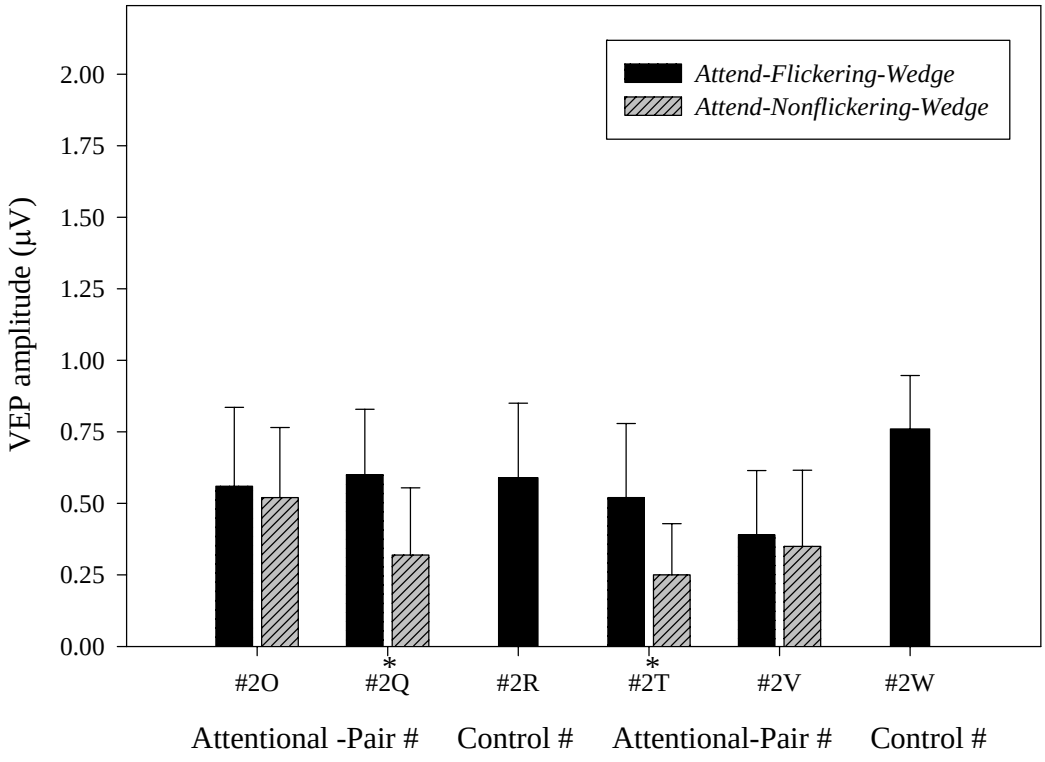


Fig. 2-11: *VEP response with 95% confidence intervals averaged across 4 and 5 s epochs (N = 44) at peak electrodes for attentional-pairs with left visual field flickering and nonflickering wedges separated by 1 unit.* * p<.001

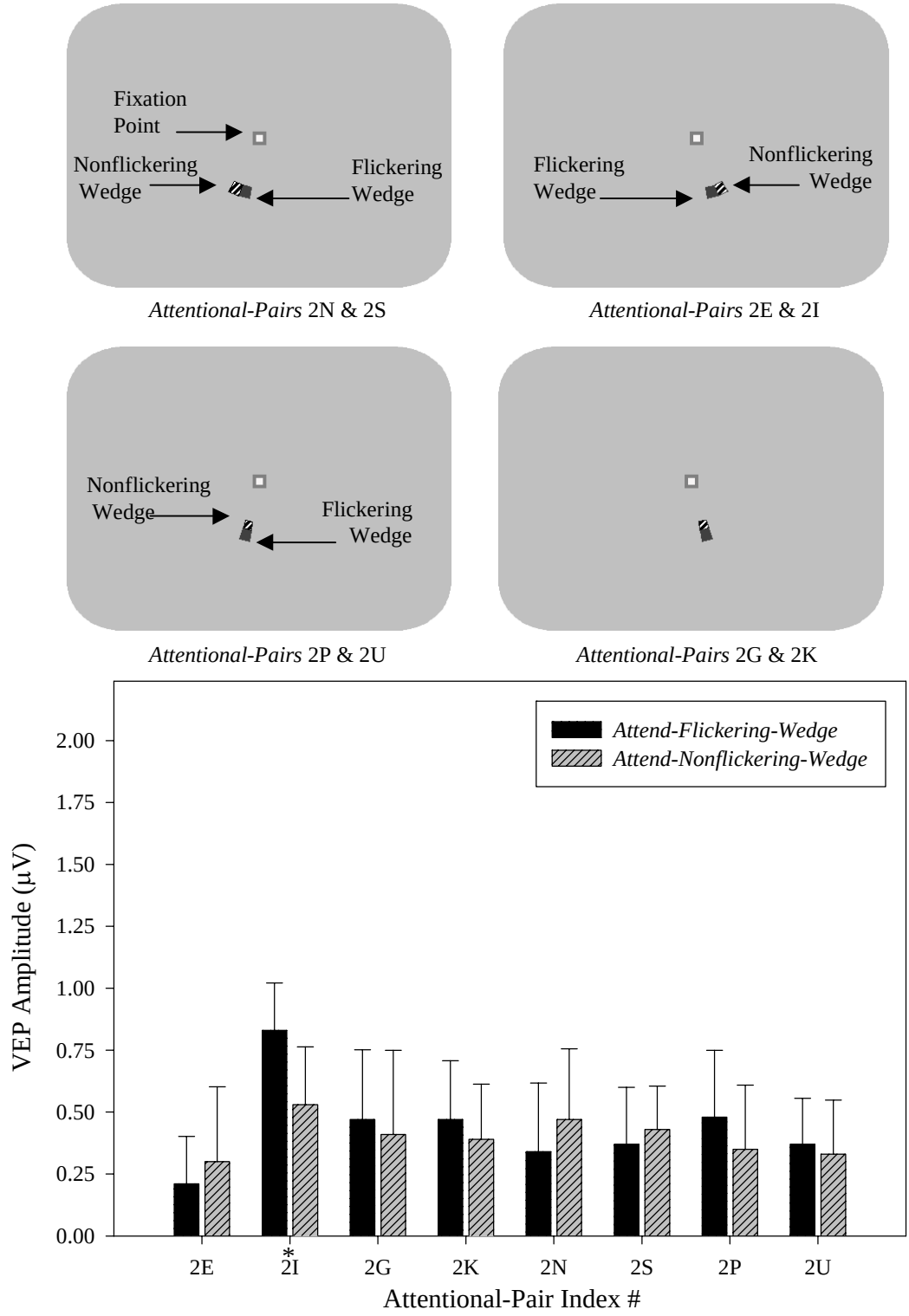


Fig. 2-12: *VEP response with 95% confidence intervals averaged across 4 and 5 s epochs (N = 44) at peak electrodes for attentional-pairs with adjacent flickering and nonflickering wedges in both right and left visual fields.* * p<.001

even though the alternative visual target was supposed to be ignored in that condition. It should also be noted that no systematic differences were observed between eccentrically vs. laterally offset attentional targets.

CONCLUSIONS

Consistent, substantial attentional gain was obtained with very small visual stimuli, 0.36 x 0.36 degree v.a. in size, separated from each other by 0.36 degree v.a., when these stimuli were presented in the right visual field, where the signal-to-noise ratio was highest. Some attentional effects were also seen in the left visual field for small separated stimuli. When the small attentional targets were adjacent, subjects reported difficulty maintaining them as perceptually distinct and no consistent attentional effects were observed.

EXPERIMENT 3

PURPOSE

EEG and eye-tracking data were simultaneously collected from attentional target sets employed in Experiments 1 and 2 to insure that the effects seen previously were due to attentional gain rather than to inadvertent, systematic variations in visual fixation between attentional conditions.

METHODS

In Experiment 3, an ISCAN ETL-500 High Resolution Pupil/Corneal Reflection Eye-Tracking System was linked with the stimulus presentation and EEG data collection systems previously described in Experiments 1 and 2. The eye-tracking system employs a CPU containing an on-line digital image processor that automatically measures and tracks the center of a subject's dark pupil through a visor-mounted camera focused on the subject's eye. The processor simultaneously tracks a reflection from the subject's corneal surface generated by an infrared (IR) light source also located in the visor worn on the subject's head, over the electrode cap. The relative positions of pupil and IR corneal reflection, obtained in real-time with 12 bit resolution, are used to determine the subject's eye position. A second visor-mounted camera points at a dichroic mirror angled away from the subject's eye, toward the scene which the subject is viewing. By integrating scene-camera data with the subject's eye position, the subject's point-of-regard is determined with an accuracy of better than 0.3 degree v.a. Such point-of-regard data, expressed in scene-camera pixel coordinates, was recorded 60 times per second

beginning with the TTL trigger at the start of every trial, and stored on the CPU hard disk for later analysis.

Attentional target sets from Experiments 1 and 2b were again employed in Experiment 3 (Fig. 3-1) with the same two subjects. The experimental paradigm, however, was slightly altered in order to accommodate the eye-tracking system. Each trial, as before, began with a brief, baseline rest period during which the CRT monitor was uniformly mean gray, except for the central fixation-point. An alerting tone then sounded and the subject began visually fixating on the center point of the screen. After one second, while the subject maintained visual fixation on the center point, a flickering wedge was presented for four seconds (along with a nonflickering wedge in some conditions). Following this stimulus epoch, as in Experiments 1 and 2, either the flickering wedge or the alternative attentional target (i.e., fixation-point or nonflickering wedge) became tinted and the subject responded with a button-push to indicate whether the shift to color was red or green. EEG data was analyzed from the 4 second stimulus epoch, excluding the first second post stimulus-onset (Fig. 3-2).

Eye-tracking data were collected and analyzed as follows. Every time the eye-tracking visor was placed on the subject's head (either at the beginning of a session, or after extended rest periods between blocks of trials), computerized calibration was performed to insure that the eye-position and scene-camera data were correctly integrated. Point-of-regard accuracy was then verified by having the subject individually fixate a grid of nine registration points displayed on the monitor. Whenever the point-of-regard data failed to match a registration point, the system was recalibrated. Before the

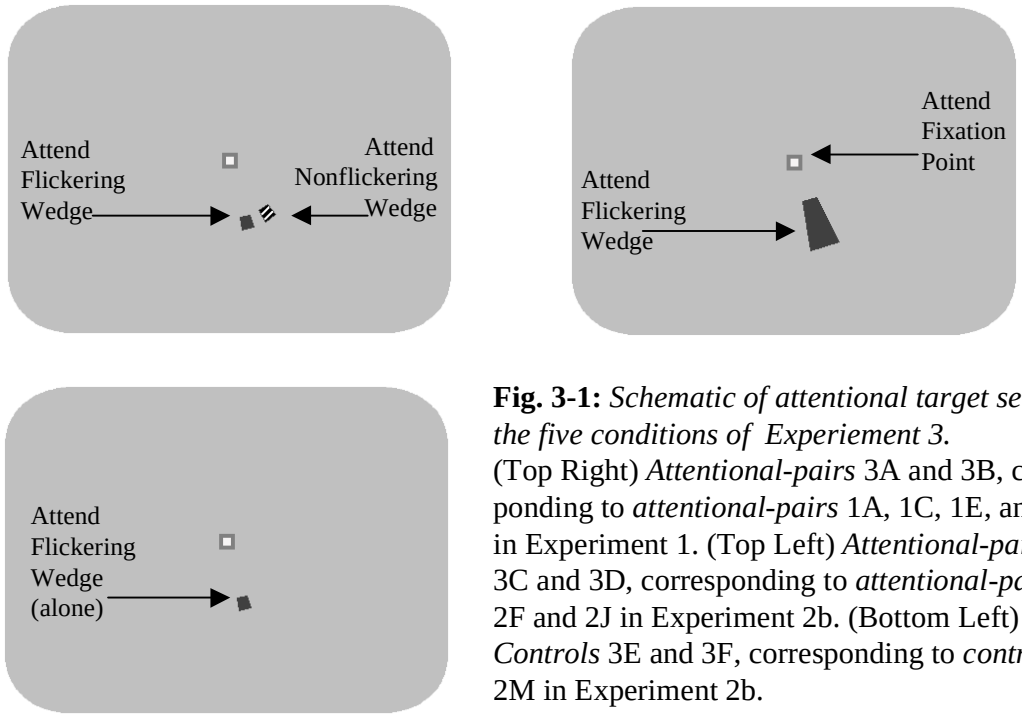


Fig. 3-1: *Schematic of attentional target sets for the five conditions of Experiement 3.*
(Top Right) *Attentional-pairs* 3A and 3B, corresponding to *attentional-pairs* 1A, 1C, 1E, and 1G in Experiment 1. (Top Left) *Attentional-pairs* 3C and 3D, corresponding to *attentional-pairs* 2F and 2J in Experiment 2b. (Bottom Left) *Controls* 3E and 3F, corresponding to *control* 2M in Experiment 2b.

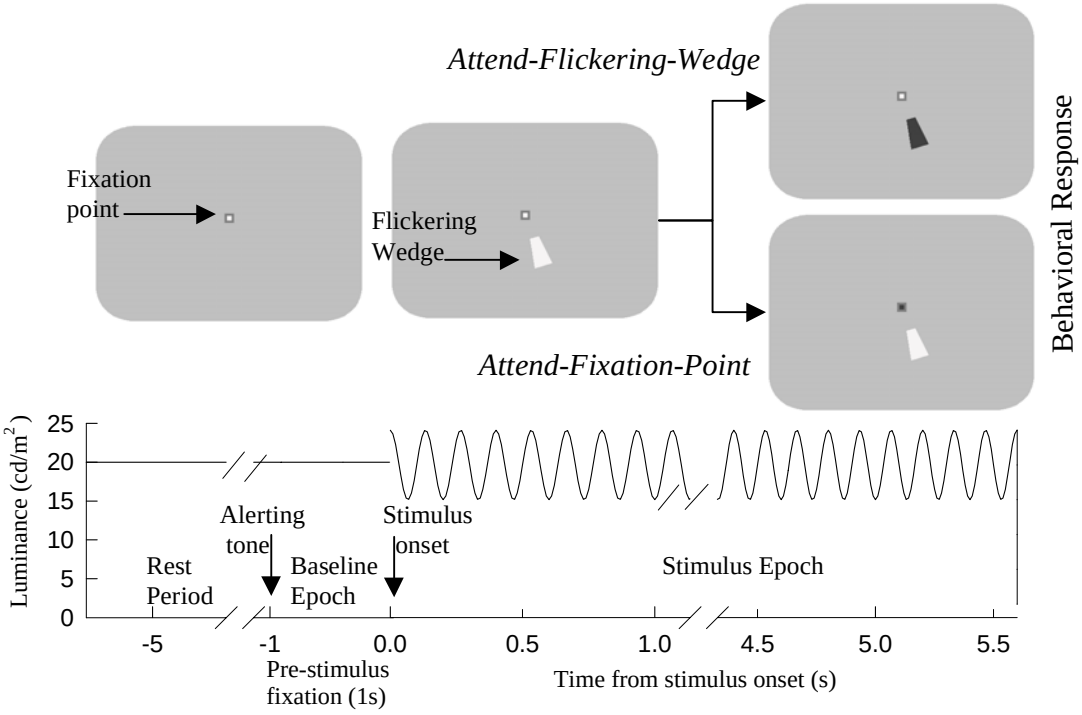


Fig. 3-2: *Description of a single trial in Experiment 3.*
Each stimulus was viewed by the subject in two attentional conditions. The attentional target set shown above (large flickering wedge Vs. fixation-point) is from Experiment 1; the other set (small flickering wedge Vs. small nonflickering wedge) as well as a control (small flickering wedge alone) were from Experiment 2b.

start of each block of 32 trials, point-of-regard accuracy was again verified and recalibration performed if necessary.

Because point-of-regard data were generated in scene-camera pixel coordinates, the raw point-of-regard x/y coordinates corresponding to fixation on the central point of the monitor changed slightly from trial to trial, depending upon the visor position on the subject's head as well as the precise orientation of the subject's head in the chin-rest. So, for each separate trial, point-of-regard coordinates were averaged for the half-second before stimulus-onset, after the subject had been alerted to fixate on the central-point which was being presented alone. These average x/y fixation coordinates at baseline for each individual trial were later subtracted from each of the 275 point-of-regard x/y coordinates sampled during the corresponding four-second stimulus epoch to produce "deviation from central fixation" values. These deviation values could thus be averaged and plotted across trials without regard to variations between trials in visor and head position. This was both the most accurate and conservative procedure for analyzing the eye-tracking data, since fixation coordinates could thus be independently determined for each trial, and any random distortion that might occur in the baseline fixation average for a given trial would introduce noise into that trial alone; i.e., would translate into higher deviation values for the corresponding stimulus epoch only. Analysis of the absolute baseline fixation coordinates showed no systematic differences between attentional conditions. Noise was further reduced from the deviation values by excising the position coordinates sampled during eye-blinks, when pixel values precipitously drop to and then rise again from 0.

RESULTS

For all *attentional-pairs* in Experiment 3, the amplitude of the VEP response in the *Attend-Flickering-Wedge* condition was substantially greater than in the *Attend-Nonflickering-Target* condition; in fact, response ratios were all greater than 2:1 (see Table 3-1 below).

Index #	Sub	Attentional Conditions	Resp Ratio	Attend Flicker Amp (μV)	Attend Non-flick Amp (μV)	Attend Flicker S.D. (μV)	Attend Non-flick S.D. (μV)	N
3A	L	LgFW/FxPt	3.9	1.10	0.28	1.11	1.04	56
3B	C	LgFW/FxPt	2.8	2.43	0.86	1.61	1.08	56
3C	L	SmFW/NW	2.4	0.46	0.19	1.12	0.94	56
3D	C	SmFW/NW	3.0	1.26	0.42	1.21	0.96	56
3E	L	SmFW(cont)	n.a.	0.65	n.a.	1.28	n.a.	56
3F	C	SmFW(cont)	n.a.	1.96	n.a.	1.55	n.a.	56

Table 3-1: *EEG summary information for eye-tracking (Experiment 3).*

The opposing attentional conditions were "LgFW/FxPt"–large flickering wedge vs. fixation-point; "SmFW/NW"–1 unit flickering wedge vs. 1 unit nonflickering wedge separated by 1 unit; and "SmFW(cont)"–small flickering wedge presented alone. "Attend Flicker" refers to the *Attend-Flickering-Wedge* condition; "Attend Non-flick" to the *Attend-Nonflickering-Target* condition. "Amp" and "S.D." refer to the averaged amplitude and standard deviation of the 15 Hz VEP response at peak electrodes. "N' refers to the number of trials averaged. "Resp Ratio" compares VEP amplitude in the *Attend-Flickering-Wedge* condition (the numerator) with the *Attend-Nonflickering-Target* condition (the denominator).

The attentional effects observed in Experiment 3 were comparable in every way to the EEG gain observed in Experiments 1 and 2b. This is evidenced by the pattern of response to different target sets seen in the VEP amplitudes plotted in the bar graph of Fig. 3-3 as well as by the replication of attentional effects seen in the amplitude spectra for Subjects C and L (Figs. 3-4 and 3-5) and the all electrode amplitude and phase polar plots (Fig. 3-6). These graphs match their counterparts from Experiments 1 and 2b well.

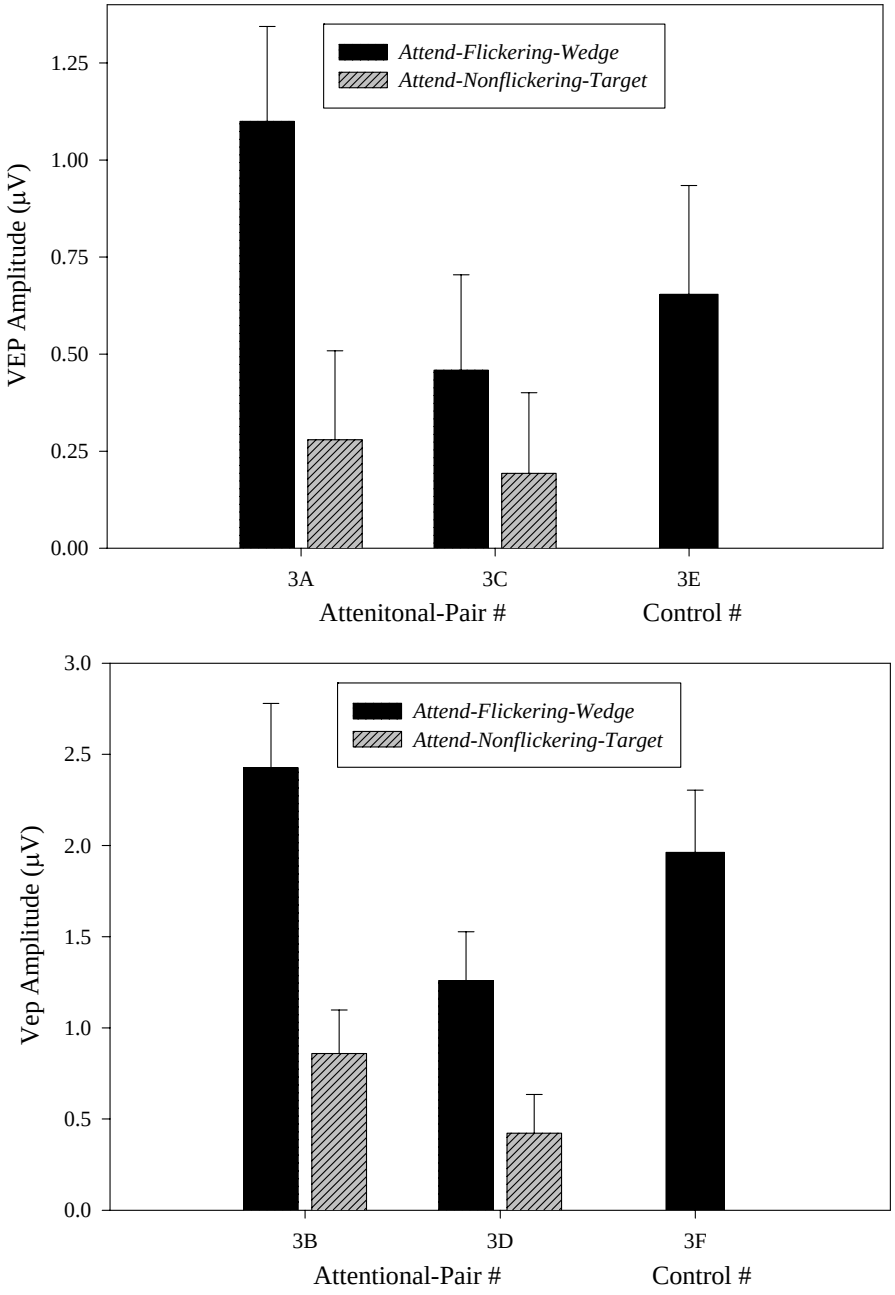


Fig. 3-3: *VEP response with 95% confidence intervals averaged across trials (N = 56) at peak electrodes for each attentional-pair in Experiment 3.*
(Top) Subect L. (Bottom) Subject C. The opposing attentional conditions represented by the group of bars on the left side of each graph (*attentional-pairs* 3A & 3B) consist of attending the large flickering wedge Vs. attending the fixation-point. The attentional conditions represented in the center (*attentional-pairs* 3C & 3D) consist of attending the small (1 unit) flickering wedge Vs. attending the small nonflickering wedge. The *control* condition at right consists of attending the small flickering wedge presented alone.

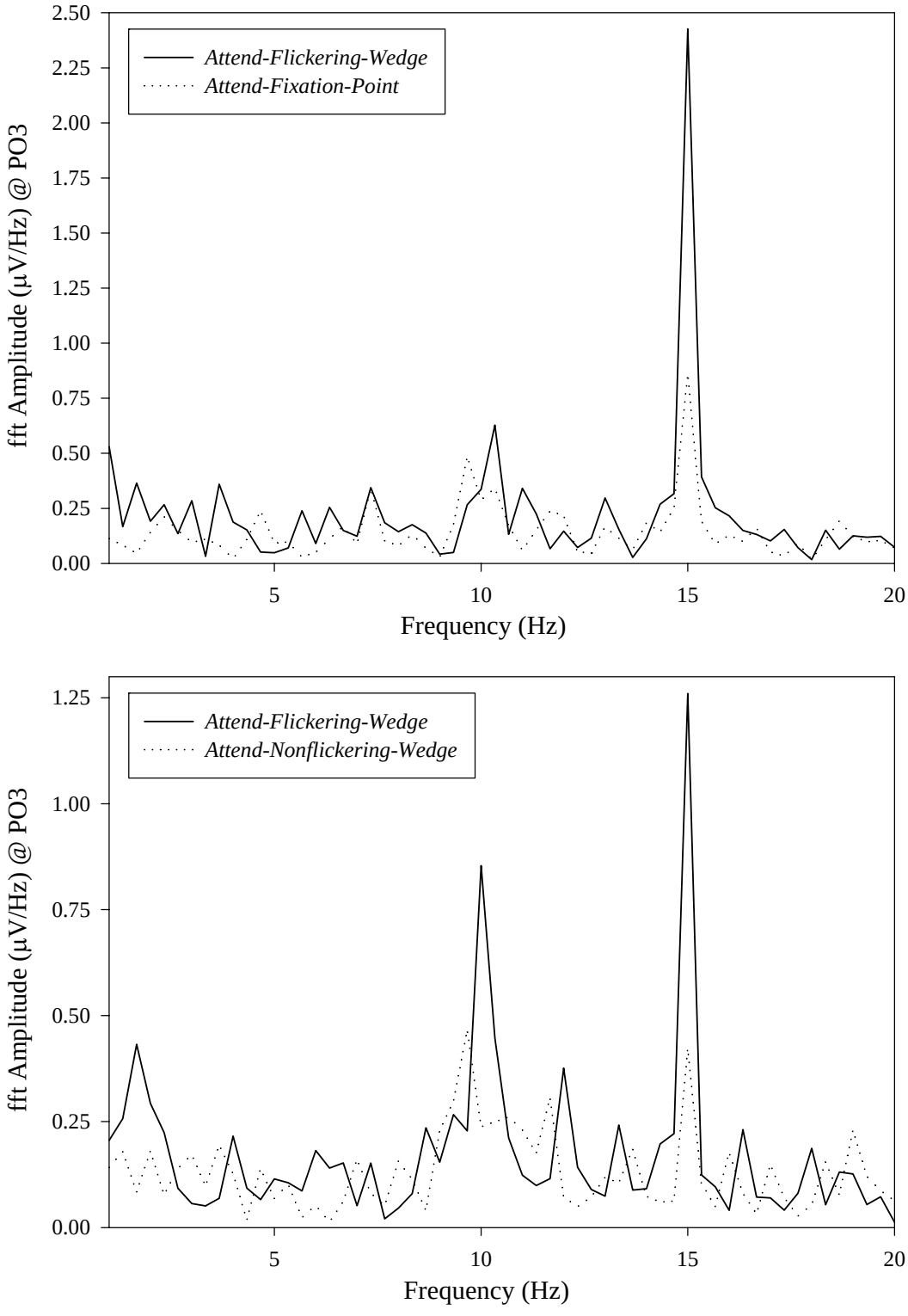


Fig. 3-4: *Amplitude spectra averaged across trials at peak electrode for subject C (N=56).* (Top) *Attentional-pair* 3B. (Bottom) *Attentional-pair* 3D.

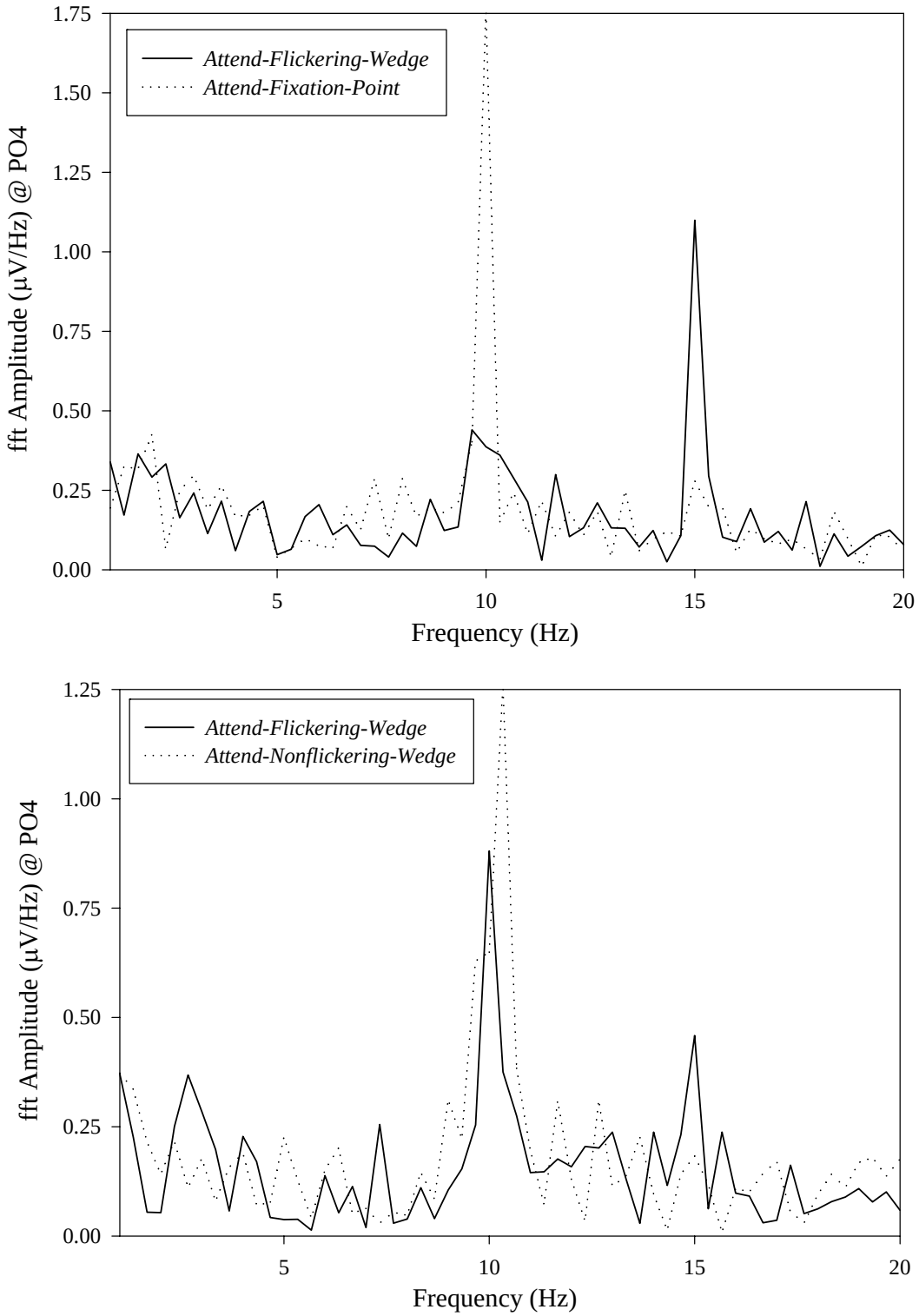


Fig. 3-5: *Amplitude spectra averaged across trials at peak electrode for subject L (N=56).* (Top) *Attentional-pair* 3A. (Bottom) *Attentional-pair* 3C.

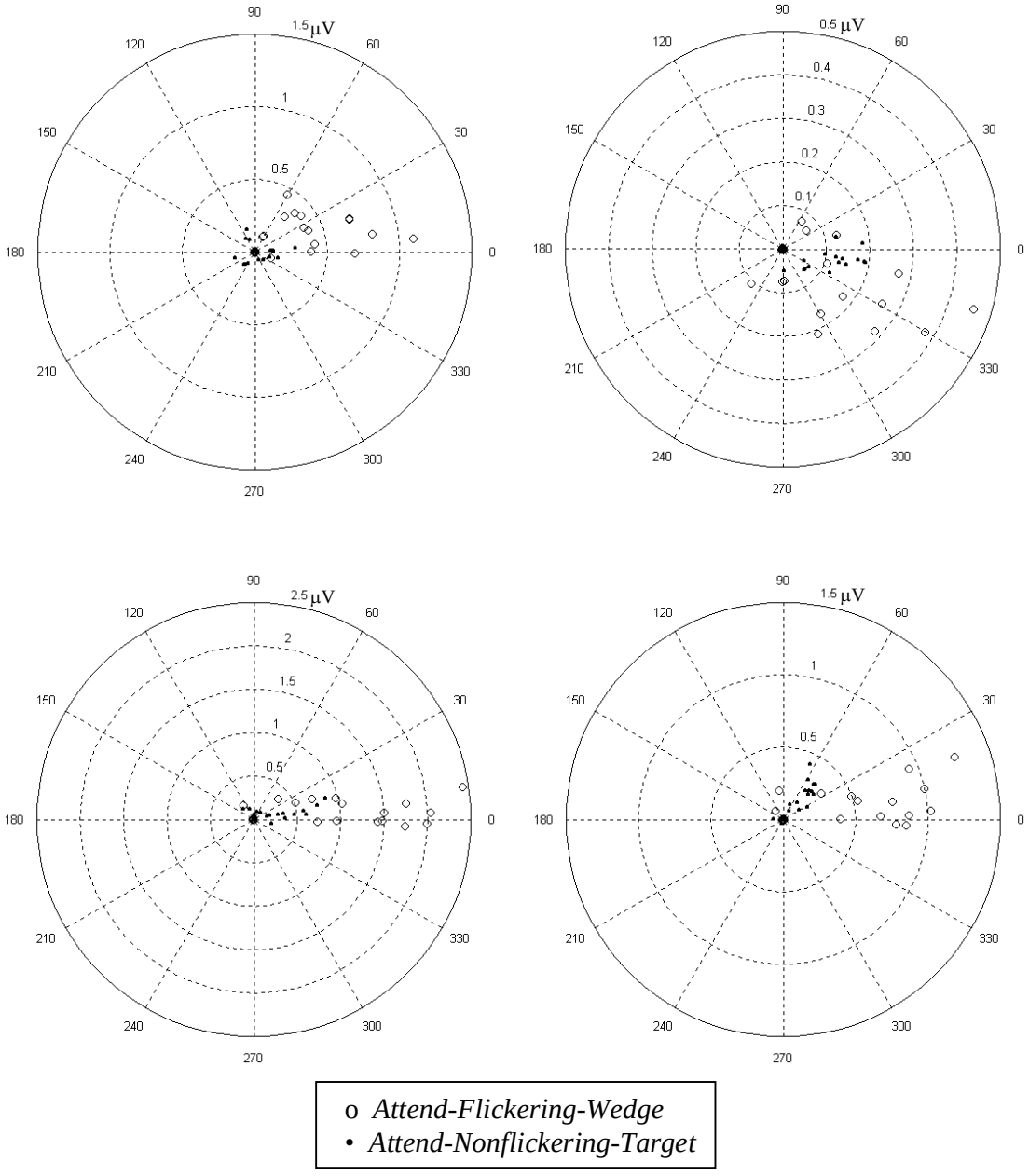


Fig. 3-6: *All-electrode amplitude and phase polar plots of VEP response averaged across trials (N=56).* (Top Left) *Attentional-pair* 3A. (Top Right) *Attentional-pair* 3C. (Bottom Left) *Attentional-pair* 3B. (Bottom Right) *Attentional-pair* 3D.

Note: These polar plots show fewer than the usual number of 32 electrodes in each attentional condition because in Experiment 3, some of the temporal electrodes (far from the occipital area of peak VEP response) were eliminated in order to accommodate the eye-tracking visor.

Regarding visual fixation, no significant differences whatever were observed between conditions. Table 3-2 shows the average vertical and horizontal deviation from central fixation for each attentional condition, given in fractions of a degree v.a. Note that even the highest of these deviation values (0.21 degree v.a.) is less than the resolution of the eye-tracking system itself (~0.3 degree v.a.). Furthermore, there was no systematic bias toward or away from the fixation-point across opposing attentional conditions and, in any case, the average deviations were so miniscule as to be entirely irrelevant to the VEP responses (Experiment 4a provides data demonstrating that a large degree of deviation from central fixation would be necessary to account for the observed differences in VEP amplitude between conditions).

Index #	Sub	Condition	FW V-mu (deg)	NT V-mu (deg)	FW H-mu (deg)	NT H-mu (deg)	FW V-s.d. (deg)	NT V-s.d. (deg)	FW H-s.d (deg)	NT H-s.d (deg)
3A	L	LgFW/FxPt	0.06	0.03	0.01	0.00	0.34	0.46	0.29	0.45
3B	C	LgFW/FxPt	0.05	0.06	0.08	0.14	0.45	0.46	0.29	0.33
3C	L	SmFW/NW	0.06	0.05	0.15	0.07	0.36	0.41	0.30	0.25
3D	C	SmFW/NW	0.21	0.10	0.05	0.12	0.48	0.43	0.36	0.37
3E	L	SmFW(cont)	0.07	n.a.	0.09	n.a.	0.44	n.a.	0.36	n.a.
3F	C	SmFW(cont)	0.15	n.a.	0.08	n.a.	0.50	n.a.	0.38	n.a.

Table 3-2: *Deviation from fixation summary information for eye-tracking experiment*

The first column lists the index number of each *attentional-pair* or control in Experiment 3. The opposing attentional conditions are "LgFW/FxPt"–large flickering wedge in the right visual field vs. fixation-point (as in Experiment 1), "SmFW/NW"–small (1 unit) flickering wedge vs. small (1 unit) non-flickering wedge separated by 1 unit in the right visual field (as in Experiment 2b), and "SmFW(cont)"–small (1 unit) flickering wedge presented alone as a control (as in Experiment 2b). "FW" refers to the *Attend-Flickering-Wedge* condition; "NT" to the *Attend-Nonflickering-Target* condition (i.e., either *Attend-Fixation-Point* or *Attend-Nonflickering-Wedge).* "V-mu" and "V-s.d." refer to the average vertical deviation from central fixation and standard deviation in fractions of a degree v.a.; H refers to the horizontal deviation. N is 17,600 x/y position coordinates sampled during the stimulus epochs of each experimental condition (minus excised points corresponding to eye-blinks).

The four scatter plots on the left side of Fig. 3-7 provide a graphic sense of the average trial by trial deviation values (given in pixel coordinates--14 pixels per degree v.a.) relative to the position and size of the atttentional targets. The four scatter plots on the right zoom in to give a clear view of the random distribution of these deviation values, closely ranged, within several pixels, around the central fixation-point, which subtended an area just inside the rectangle at the center of the graphs. The single trial deviation values plotted with dots (*Attend-Nonflickering-Target* condition trials) and circles (*Attend-Flickering-Wedge* condition trials) were averaged from 275 position coordinates sampled during the 4 second stimulus epoch of each trial, minus the points recorded during eye-blinks. Note the random, overlapping distributions between attentional conditions (i.e., dots vs. circles).

In all data sets that were recorded, the eye-position coordinates fall-off in a radially symmetric distribution around their peak. This can be seen in a 3D histogram of the 8,800 eye-position deviation values sampled during one block of 32 trials (Fig. 3-8). The block that has been plotted in Fig. 3-8 is from the *Attend-Flickering-Wedge* condition of *attentional-pair* 3A, which had both the highest response ratio (3.9 to 1) as well as the lowest deviation values (only hundredths of a degree of visual angle) for both of the opposing attentional conditions (Table 3-2). 3D histograms of the other data sets in Experiment 3 are all strikingly similar to the one shown here.

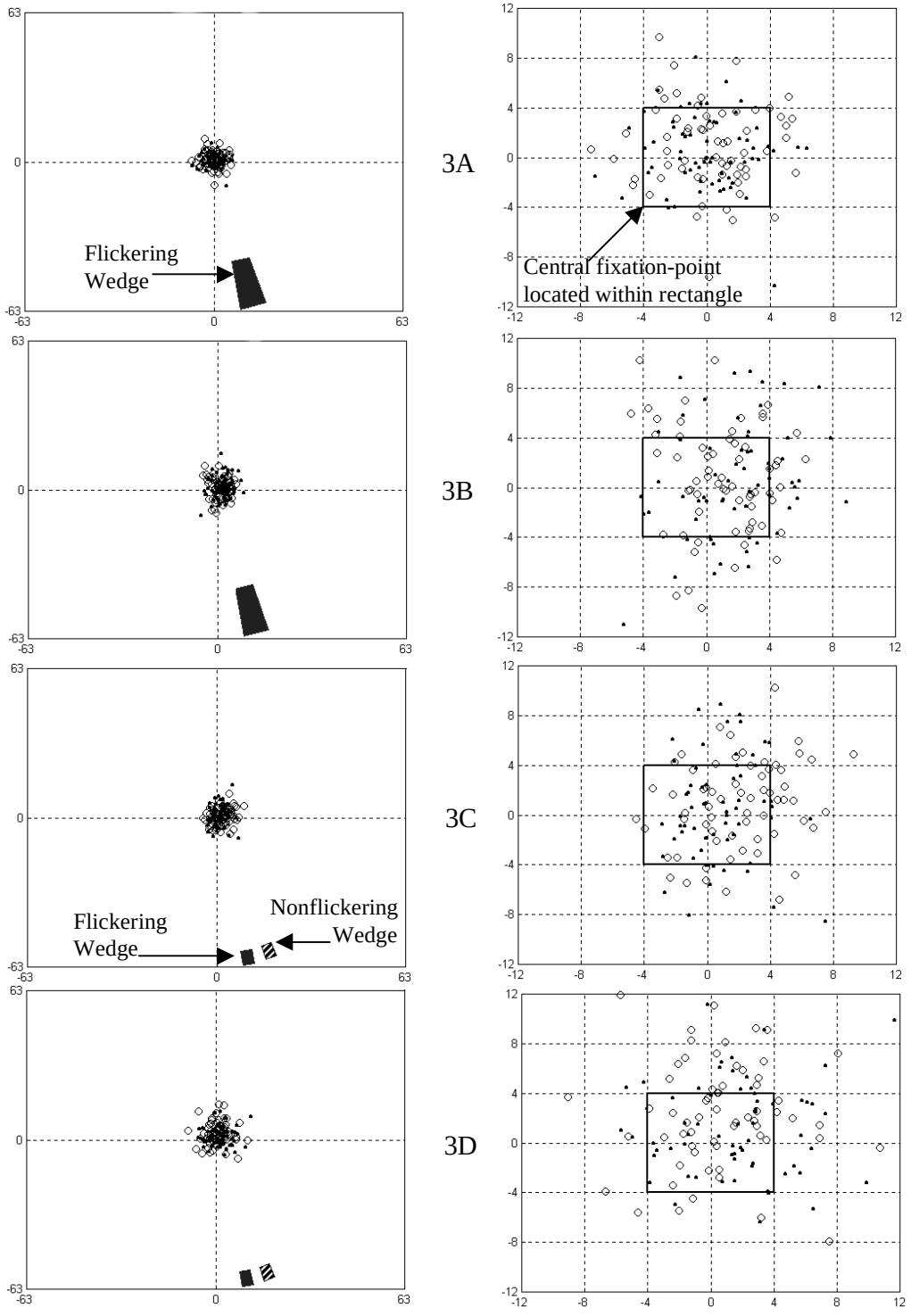


Fig. 3-7: *Trial by trial average deviation from central fixation values (N~275 per trial)* for *attentional-pairs* 3A, 3B, 3C, and 3D *(~14 pixels per degree visual angle).*

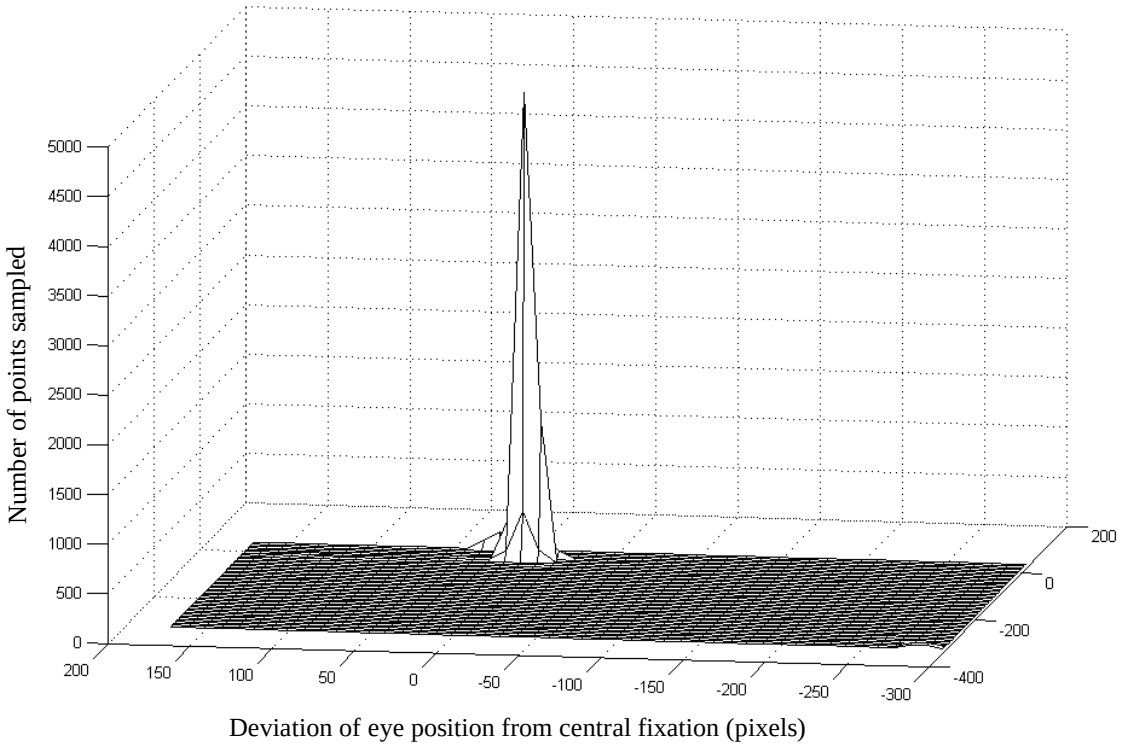


Fig. 3-8: *3D histogram of eye position deviations sampled during one block of 32 trials (N=8,800).* The central fixation point of the monitor is represented by the horizontal (x) and vertical (y) coordinates 0/0. The tall spike centered at 0/0 comprises the 8,800 eye position deviation values sampled during one block of the *Attend-Flickering-Wedge* condition of *attentional pair* 3A. The flared base of the spike comprises the deviation values recorded during eye blinks. The distribution of deviation values for all other trial blocks in all the conditions of Experiment 3 were strikingly similar to the one plotted here.

CONCLUSIONS

In Experiment 3, virtually identical visual fixation between opposing attentional conditions was observed with high resolution eye-tracking equipment during the collection of EEG data that replicated the attentional effects obtained in Experiments 1 and 2. Thus, high levels of gain in VEP amplitude can be confidently attributed solely to the effect of selective attention.

EXPERIMENT 4a

PURPOSE

The robust attentional effects observed in Experiments 1 and 2b were obtained from flickering stimuli whose size and location in the visual field corresponded, respectively, to neuronal activity fields in the primary visual cortex of ~11 vs 1 mm^2, a range in area of >100:1. To whatever extent extrastriate cortical areas were activated by those stimuli, they would have ranged widely in the nominal area of activation as well, though to a somewhat lesser extent (Lennie, 1998). The VEP amplitudes generated in Experiment 2b, however, were in many cases almost as great as they were in Experiment1. Therefore, in Experiment 4a, EEG data was collected from flickering stimuli with differently sized neuronal activity fields occupying areas as nearly contiguous on subject L's cortex as possible while all other parameters, including attention, were held constant. This was done so as to accurately measure any effects of superposition with minimal distortion from uncontrolled attentional states or differential volume conductance beneath the skull.

METHODS

The four experimental conditions of Experiment 4a consisted of subject L attending, in blocks of 32 trials, to each of four flickering wedges with differently sized neuronal activity fields. Only the spatial parameters of the stimuli were varied, while attention was held constant with the psychophysical task corresponding to "*Attend-Flickering-Wedge*" in previous experiments. All stimuli subtended the same "clock angle" location; viz., from 10 to 19 degrees c.a. right of the lower vertical meridian. The

outer eccentricity for all stimuli was 4.5 degrees v.a. while the inner eccentricity ranged from 2.9 degrees for the largest stimulus to 4.14 degrees for the smallest stimulus; the inner eccentricities of the other two stimuli were set at intermediate positions (Fig. 4-1). The spatial parameters of these stimuli were such that any areas of V1 or V2 activated would lie in close proximity to one another within the sagittal fissure, well outside the calcarine sulcus. This was determined through detailed fMRI mapping of Subject L's visual cortical areas. The mapping was performed at Stanford University with the methods of Engel, Glover & Wandell (1997), using software available at http://white.stanford.edu:80/~brian/. All other details of the experimental paradigm for Experiment 4a were the same as in Experiments 1, 2, and 3.

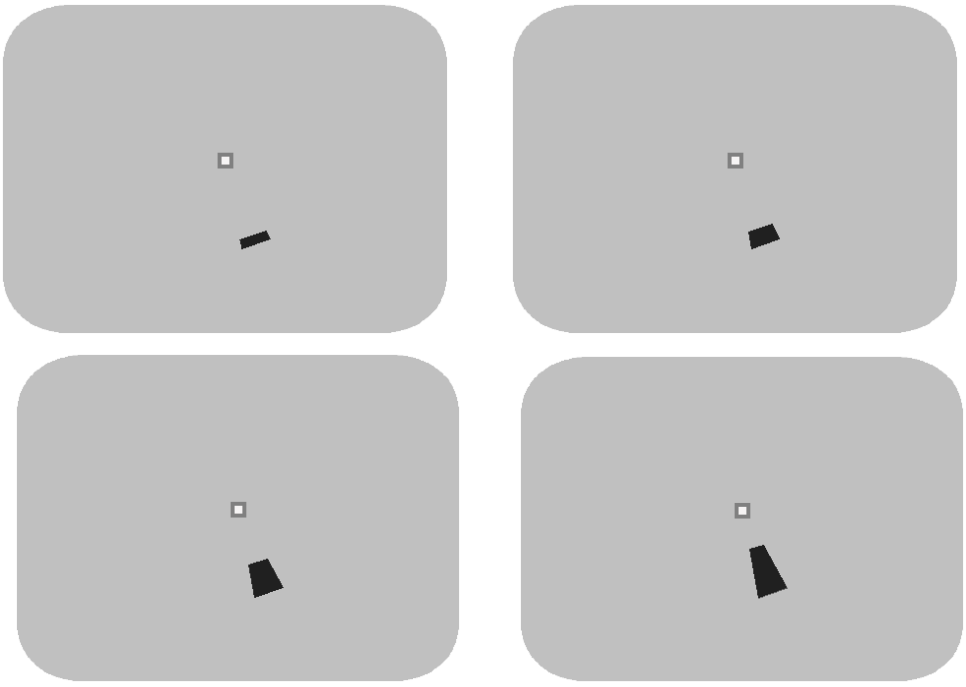


Fig. 4-1: *Graphic representation of flickering stimulus wedges in Experiment 4a.* (Top Left) Stimulus 4a1. (Top Right) Stimulus 4a2. (Bottom Left) Stimulus 4a3. (Bottom Right) Stimulus 4a4.

RESULTS

Although the V1 neuronal activity fields corresponding to the four stimuli of Experiment 4a ranged in area from smallest to largest by a factor of 25, there were no significant differences in the VEP amplitude generated by these stimuli (Table 4-1). Fig. 4-2 shows the broadly overlapping confidence intervals of the tightly ranged VEP mean amplitudes for these four stimuli, while Fig. 4-3 plots these observed amplitudes in the context of a projection highlighting the spectacular failure of VEP superposition relative to the areas of primary visual cortex nominally subject to activation by these stimuli.

Index #	Eccentricity (deg.rees v.a.)	V1 Area (mm^2)	VEP Amplitude (μV)	VEP Std. Dev. (μV)
4a1	4.14–4.5	2.00	1.12	1.25
4a2	3.9–4.5	3.4	1.45	1.37
4a3	3.52–4.5	5.8	1.33	1.33
4a4	2.9–4.5	10.1	1.59	1.27

Table 4-1: *Summary information for superposition experiment*

At left are the index numbers for each stimulus followed by the eccentricity subtended by that stimulus. The position and width of all the stimuli were constant, beginning 10 degrees c.a. right of the lower vertical meridian and extending 9 degrees c.a. further to the right. The area of primary visual cortex nominally corresponding to the activity field of each stimulus is given in square millimeters, while VEP amplitude and standard deviation, averaged across trials (N=56) at the peak electrodes, is given in microvolts. The *Attend-Flickering-Wedge* psychophysical task was employed for all stimuli without an alternative attentional condition in order to control for possible differences that might occur from random attentional effects across stimulus conditions.

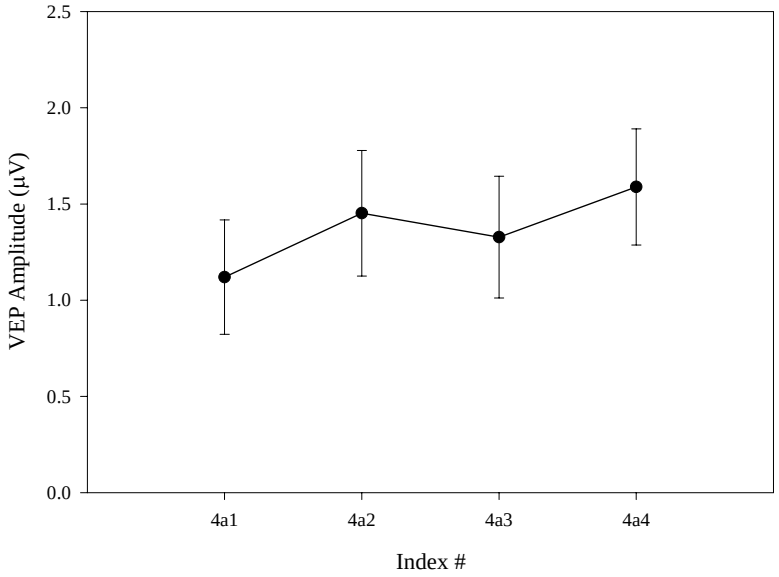


Fig. 4-2: *VEP amplitude with 95% confidence intervals averaged across trials (N=56)* for each of the stimuli in Experiment 4a. Note that there is no significant increase in VEP amplitude for stimulus 4a4, which has a V1 activity field ~25x the cortical area of 4a1. The other two stimuli (4a2 and 4a3) have activity fields of intermediate area.

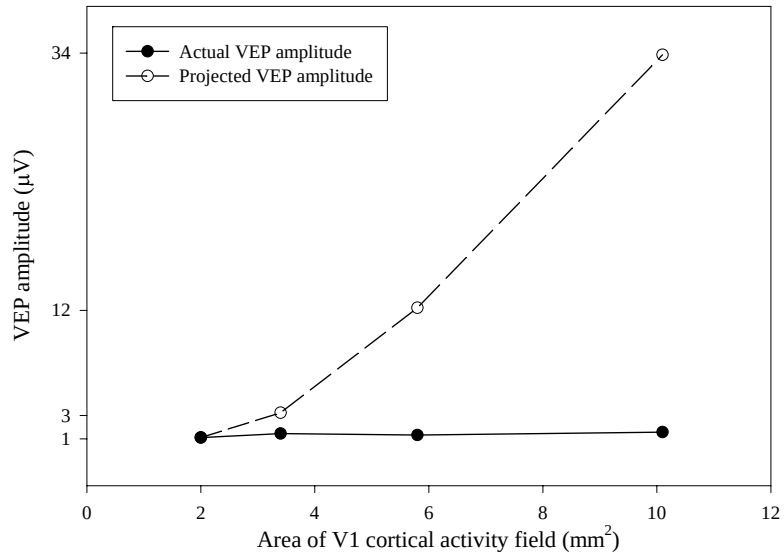


Fig. 4-3: *VEP amplitude (observed and projected) Vs. nominal area of V1 activity field.* The solid line and black dots plot the actual VEP amplitudes recorded in Experiment 4a for the four flickering wedges with different size cortical activity fields. The dashed line and open circles plot projected VEP amplitude based on actual VEP response to the smallest stimulus multiplied by factors corresponding to the increased V1 activity field area of larger stimuli. Note the spectacular failure of superposition; i.e., the amplitude of the observed VEP response does not increase for stimuli corresponding to larger areas of V1, as would be projected if current densities were subject to linear superposition.

CONCLUSIONS

VEP amplitude was not affected by the size of the mapped cortical areas corresponding to flickering stimuli for which all other factors were held constant. Since this result obtained for stimuli with cortical activity fields in close physical proximity, it is possible that, within the limits of this experiment, lateral inhibition may have been a contributory factor to the complete failure of superposition. However, in other superposition experiments that we have conducted, visual stimuli subtending activity fields in opposite hemispheres were employed, and in those experiments as well, a failure of linear superposition was observed. Since lateral inhibition would not have been a factor in those results, we suspect that those failures of superposition may owe, at least in part, to limitations imposed by attention. In any case, these findings certainly bear further investigation.

EXPERIMENT 4b

PURPOSE

In Experiment 4b, the contrast of a flickering wedge was systematically varied between conditions in order to determine how attentional effects observed in earlier experiments might be altered in response to such modifications of physical properties of the stimulus. Contrast response functions were obtained in order to further elucidate the neurophysiological substrates of the VEP response to steady-state flicker.

METHODS

Subjects C and L were each tested across seven conditions in which flickering wedges were presented with identical physical properties, except for varying contrast as given by the formula Lmax - Lmin / Lmax + Lmin where "L" is luminance. The flicker contrasts were 6.25%, 12.5%, 25% (the standard contrast of previous experiments), 50%, and 90%. The 25% and 90% contrast stimuli were each presented in two attentional conditions, *Attend-Flickering-Wedge* and *Attend-Nonflickering-Wedge*, while all other stimuli were presented in only the *Attend-Flickering-Wedge* attentional condition. In all five *Attend-Flickering-Wedge* conditions, the small (1 unit) flickering wedge was presented alone, 10 degrees c.a. right of the lower vertical meridian at an eccentricity of 4.15 to 4.5 degrees v.a. In the two *Attend-Nonflickering-Wedge* conditions, a small (1 unit) nonflickering wedge was also presented 18 degrees c.a. (4 units) right of the flickering wedge at the same eccentricity (Fig. 4-4). All other experimental parameters were the same as in Experiment 2b.

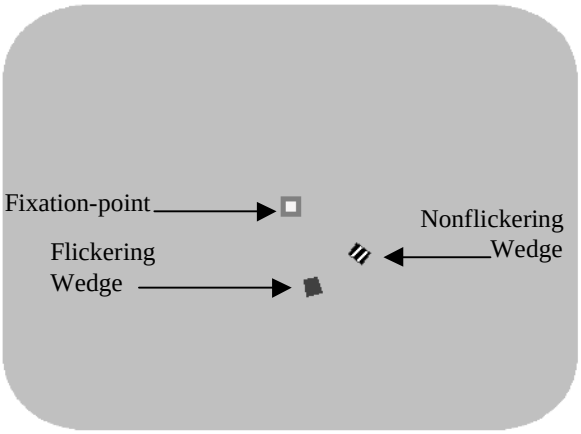


Fig. 4-4: *Schematic of stimuli* presented in Experiment 4b (contrast response) and Experiment 4c (frequency response). Note that the nonflickering wedge was present only in the *Attend-Nonflickering-Wedge* conditions.

RESULTS

The main findings of Experiment 4b were the same for both subjects (Table 4-2). For both subjects, in the *Attend-Flickering-Wedge* condition, systematic variation in the contrast of a flickering wedge presented alone produced a nearly linear increase in VEP amplitude from 6.25% to 25% contrast, and saturation at contrasts higher than 25%.

Table 4-2: *Summary information for contrast response.*
The first column lists index numbers for data collected in the seven conditions experienced by each subject. In the third column, "F" stands for the *Attend-Flickering-Wedge* condition, while "N" refers to the *Attend-Nonflickering-Wedge* condition. Peak VEP amplitude is averaged across trials (N=56).

Index #	Subject	Attend	Contrast (%)	Amplitude (μV)
4b1	C	F	6.25	0.17
4b2	C	F	12.5	0.56
4b3	C	F	25	1.74
4b4	C	F	50	1.81
4b5	C	F	90	1.85
4b6	C	N	25	0.09
4b7	C	N	90	0.44
4b8	L	F	6.25	0.30
4b9	L	F	12.5	0.38
4b10	L	F	25	1.27
4b11	L	F	50	1.68
4b12	L	F	90	1.33
4b13	L	N	25	0.10
4b14	L	N	90	0.44

This result replicated several contrast response experiments which had been previously conducted with much larger flickering wedges and no attentional control; i.e., no psychophysical task, as in the present experiment, to focus the subject's mental attention on the flickering wedge and, thus, control for attentional factors between stimulus conditions. In the *Attend-Nonflickering-Wedge* condition (when the flickering wedge was presented together with a nonflickering wedge separated by 18 degrees c.a. and attention was directed toward the nonflickering wedge), FFT amplitude at the response frequency did not rise above noise when the flickering wedge was at 25% contrast. This replicated the findings of previous experiments. When attention was directed to the nonflickering wedge with the flickering wedge at 90% contrast, VEP amplitude was substantially attenuated, but not reduced to the level of noise. Subjects reported that in the *Attend-Nonflickering-Wedge* condition, the flickering wedge was difficult to ignore at 90% contrast. The findings of Experiment 4b are plotted on a log/log scale in Fig. 4-5.

CONCLUSIONS

VEP amplitude generated by small flickering stimuli, such as those employed in previous experiments, was subject to systematic modulation through variation of flicker contrast. The contrast response curve manifested a nearly linear increase at lower contrasts with saturation at higher contrasts. This corresponds to the contrast response function of the magnocellular pathway (Kaplan and Shaply, 1986). The exponent value of the contrast response slope in Experiment 4b was ~2.2, corresponding to the contrast gain of V1/V2 neurons (Lennie, 1988). At 25% contrast, attentional effects were

replicated. At 90% contrast, attentional effects were present but attenuated while subjects reported difficulty ignoring the flickering stimulus in the *Attend-Nonflickering-Wedge* condition.

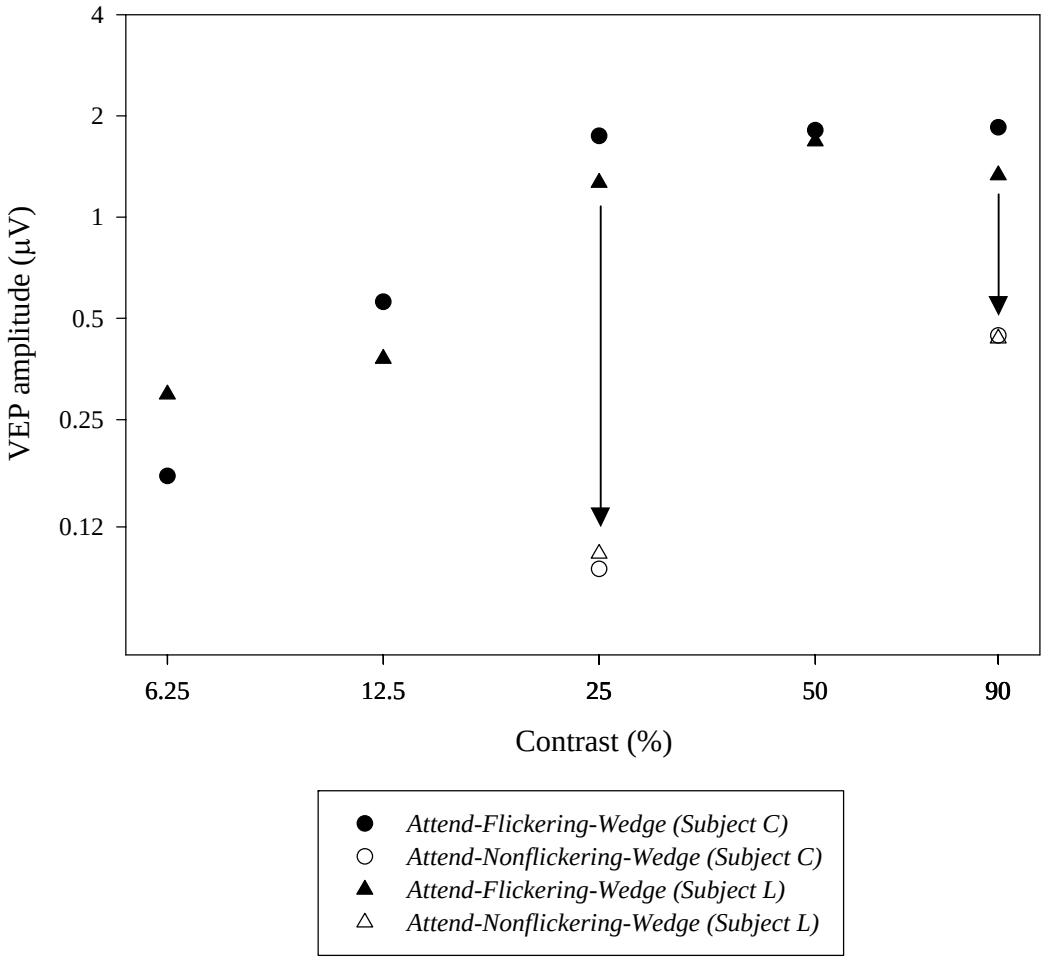


Fig. 4-5: *Contrast response of subjects C and L* . VEP amplitude at peak electrodes was averaged across trials (N=56) in the five stimulus-only conditions of varying contrasts (filled symbols) and the two conditions with attention directed to an alternative visual target (open symbols). Note the classic magnocellular contrast response function of the stimuli presented alone (filled symbols), as well as the replication of previous attentional effects at 25% contrast (long arrow) and the partial VEP attenuation at 90% contrast (short arrow).

EXPERIMENT 4c

PURPOSE

In Experiment 4c, the temporal frequency of a flickering wedge was systematically varied between conditions in order to acquire further information concerning neurophysiological characteristics of VEP response to steady-state flicker. Two attentional conditions and two contrasts were employed at each temporal frequency tested in order to investigate possible interactions between physical and psychological parameters.

METHODS

Spatial parameters of the flickering wedge in Experiment 4c were constant; viz., the flickering stimulus was a 1 unit wedge, such as those employed in Experiment 4b, positioned at 4.14 to 4.5 degrees v.a. eccentricity, 10 degrees c.a. right of the lower vertical meridian. In the *Attend-Nonflickering-Wedge* condition, the flickering wedge was displayed simultaneously with a nonflickering wedge of the same size and eccentricity, separated 18 degrees c.a. (4 units) to the right of the flickering wedge (Fig. 4-4); in the *Attend-Flickering-Wedge* condition, it was displayed alone. The flickering wedge was presented at six temporal frequencies: 3.0, 4.2, 4.7, 9.38, 12.5, and 18.75 Hz. At 3, 4.2 and 4.7 Hz, the flicker was modulated sinusoidally, while at 9.38, 12.5, and 18.75 Hz it was modulated in a square wave. There were three experimental conditions at each temporal frequency: (1) *Attend-Flickering-Wedge* at 25% contrast, (2) *Attend-Nonflickering-Wedge* at 25% contrast, and (3) *Attend-Flickering-Wedge* at 90% contrast. Other methodological specifics in Experiment 4c were the same as in Experiment 2b.

RESULTS

At all flicker frequencies for which a VEP response was apparent in Experiment 4c, the VEP response occurred within the beta bandwidth (12.5 to 25 Hz). The 4.2 Hz flicker, at 25% and 90% contrast, generated a VEP response at its third harmonic--12.5 Hz (Fig. 4-6), while the 12.5 Hz flicker, at 25% and 90% contrast, generated a VEP response at its own fundamental frequency--12.5 Hz (Fig. 4-7). Similarly, the 9.38 Hz flicker, at 25% and 90% contrast, generated a VEP response at its second harmonic--18.75 Hz (Fig. 4-8), while the 18.75 Hz flicker, at 90% contrast only, generated a VEP response at its own fundamental frequency--18.75 Hz (Fig. 4-9). In the *Attend-Nonflickering-Wedge* condition of all flicker frequencies evidencing a VEP response, FFT amplitude at the response frequency was at or close to the level of noise. The 3 and 4.7 Hz flicker frequencies did not generate any observable VEP response. These results are summarized in Table 4-3.

Because of the high level of spontaneous neural activity in the alpha bandwidth (8 to 12.5 Hz), some stimulus driven activity might well have been masked, whether occurring in the harmonic response to a lower flicker frequency, or in the fundamental frequency of the 9.38 Hz flicker. The usual 10 Hz peak of alpha activity may have been entrained to a slightly lower frequency in such cases, but this could not be definitively determined or ruled-out in the present circumstances.

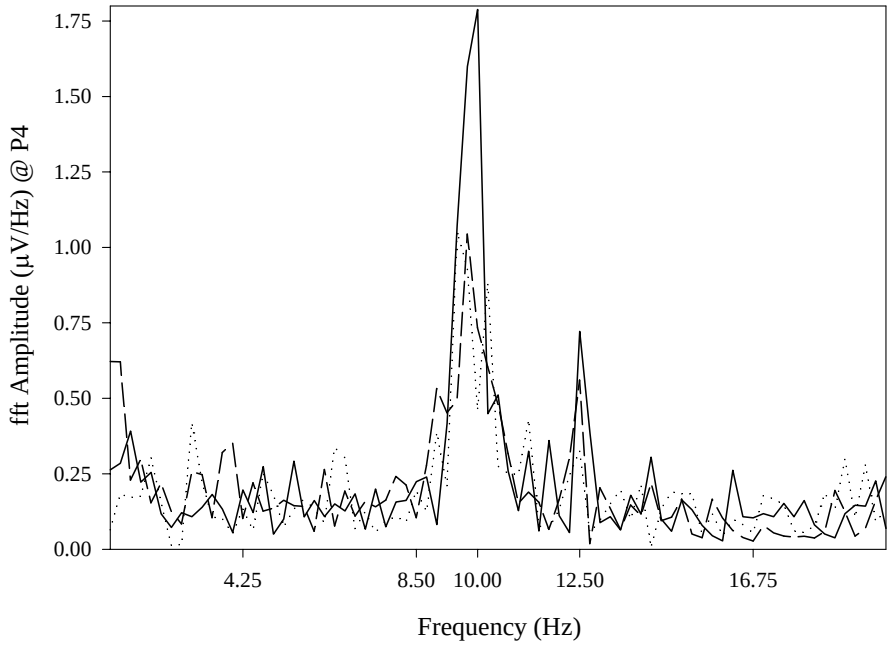


Fig. 4-6: *fft amplitude spectra for stimuli flickering at 4.2 Hz.* (index#s 4c4, 4c5, & 4c6). Note the VEP response at 12.5 Hz., which is the third harmonic of the flicker frequency.

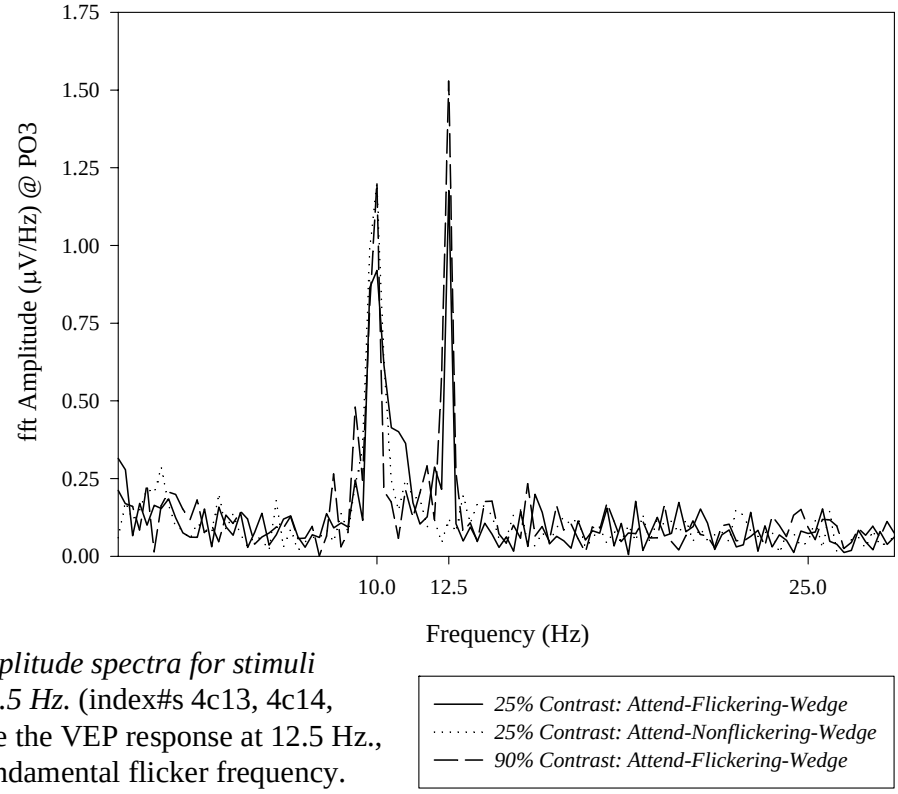


Fig. 4-7: *fft amplitude spectra for stimuli flickering at 12.5 Hz.* (index#s 4c13, 4c14, and 4c15). Note the VEP response at 12.5 Hz., which is the fundamental flicker frequency.

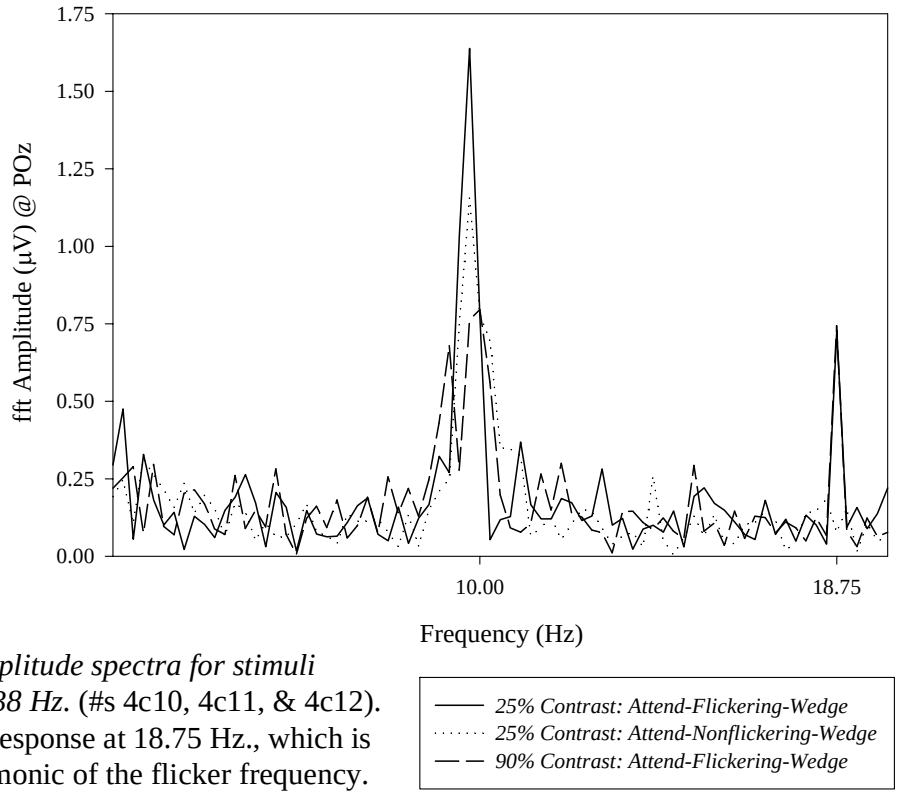


Fig. 4-8: *fft amplitude spectra for stimuli flickering at 9.38 Hz.* (#s 4c10, 4c11, & 4c12). Note the VEP response at 18.75 Hz., which is the second harmonic of the flicker frequency.

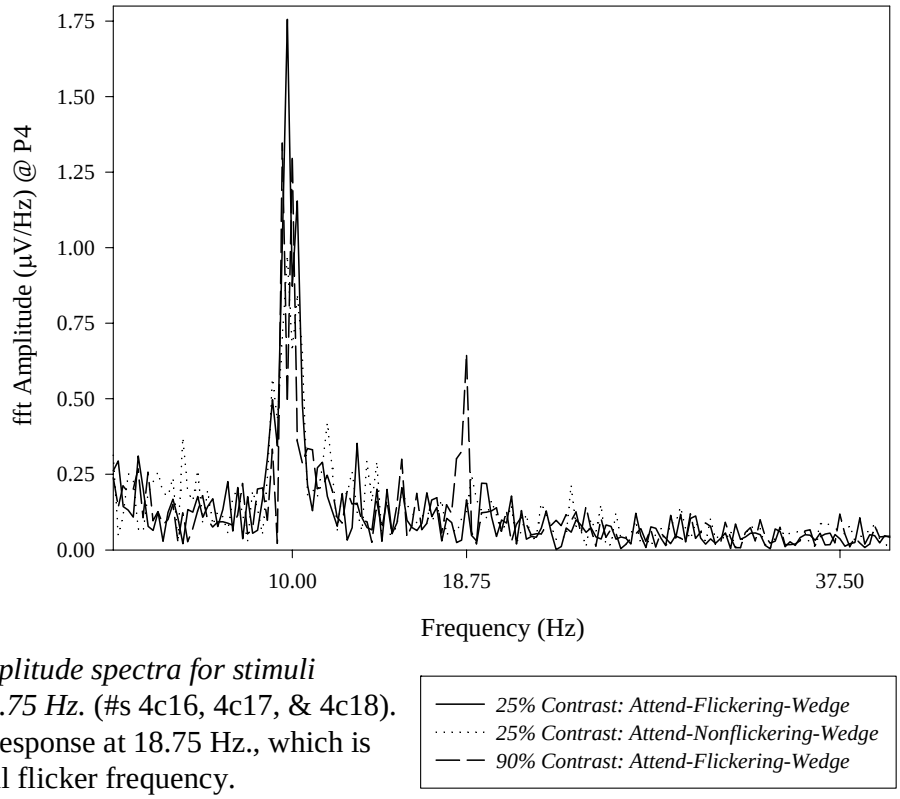


Fig. 4-9: *fft amplitude spectra for stimuli flickering at 18.75 Hz.* (#s 4c16, 4c17, & 4c18). Note the VEP response at 18.75 Hz., which is the fundamental flicker frequency.

Index #	Sub	Attend	Contrast (%)	Flicker Freq (Hz)	VEP Resp Freq (Hz) [Harmonic]	VEP Resp Ampl (μV)
4c1	C	F	25	3	n.a.	n.a.
4c2	C	N	25	3	n.a.	n.a.
4c3	C	F	90	3	n.a.	n.a.
4c4	L	F	25	4.2	12.5 [3F]	0.72
4c5	L	N	25	4.2	12.5 [3F]	0.36
4c6	L	F	90	4.2	12.5 [3F]	0.56
4c7	L	F	25	4.7	n.a.	n.a.
4c8	L	N	25	4.7	n.a.	n.a.
4c9	L	F	90	4.7	n.a.	n.a.
4c10	C	F	25	9.38	18.75 [2F]	0.73
4c11	C	N	25	9.38	n.a.	n.a.
4c12	C	F	90	9.38	18.75 [2F]	0.74
4c13	C	F	25	12.5	12.5 [F]	1.18
4c14	C	N	25	12.5	n.a.	n.a.
4c15	C	F	90	12.5	12.5 [F]	1.53
4c16	L	F	25	18.75	n.a.	n.a.
4c17	L	N	25	18.75	n.a.	n.a.
4c18	L	F	90	18.75	18.75 [F]	0.65

Table 4-3: *Summary information for frequency response (Experiment 4c).*
Information concerning the three conditions (*Attend-Flickering-Wedge* at 25% contrast, *Attend-Nonflickering-Wedge* at 25% contrast, and *Attend-Flickering-Wedge* at 90% contrast) employed at each of the six flicker frequencies tested in Experiment 4c is displayed between double lines in the above table. When no FFT amplitude spike clearly above the level of spectral noise was observed at the flicker frequency or at any harmonic of that frequency, this is indicated with "n.a.".

CONCLUSIONS

VEP responses were generated by a variety of flicker frequencies. These VEP responses all occurred in the beta bandwidth, whether at the fundamental flicker frequency, the second, or the third harmonic of that frequency. Saturation of the VEP response above 25% contrast was observed and attentional effects, such as those obtained in earlier experiments, were again evident for every frequency at which a VEP response occurred.

DISCUSSION

The evidence we have gathered is only as good as the fidelity with which we have been able to assure visual fixation. After all, if subjects were shifting their gaze in different attentional conditions, then any inferences concerning neural bases of these effects would be rendered meaningless. In fact, strong assurance of visual fixation was attained through simultaneous recording of EEG and high resolution eye-tracking in Experiment 3. Thus, we are able to confidently assert that the effect of volition on neuronal responses to physical stimuli can not only be significant, it can be overriding. In Experiments 1 and 2, selective attention was solely responsible for the complete elimination or substantial attenuation of robust VEP activity driven by steady-state contrast-modulated flicker. In many cases, VEP amplitude exceeding 2 μV was reduced to the level of noise in the neighboring spectral bandwidth, a more than ten-fold diminution (Tables 1-1 and 2-1). In recent years, electrophysiological and neuroimaging studies in humans as well as extracellular recordings in primates have shown that selective attention can alter the response of neurons to visual stimuli in the striate as well as the extrastriate cortex (Gandhi, Heeger, & Boynton, 1999; Gilbert & Posner, 1999; Somers, Anders, Seiffert, & Tootell, 1999), and such effects have never been more strongly demonstrated than in the present series of experiments. These findings argue, at the very least, for the necessity of attentional controls in all experiments where VEP amplitude and phase as well as signal-to-noise ratio might be of importance.

When the attention of subjects was directed to contrast-modulated flicker, the VEP signals that were generated were phase-locked with the temporal modulation of the stimulus. Conversely, when attention was directed to an alternative, non-flickering visual target, there was little or no phase-locked electrophysiological activity at the flicker response frequency (Figs. 1-13, 1-15, 2-3, 2-7, and 3-6; also see Figs. 2(B) and 3). Thus, stimulus driven coherence of neuronal activity was responsible for the generation of higher average VEP amplitudes when subjects selectively attended to the flickering stimulus. Additionally, the VEP responses on individual trials were themselves of greater magnitude when subjects selectively attended to the flickering stimulus (Fig. 1-14), and this trial-by-trial gain in amplitude, as well as increased coherence between trials, contributed to the large average VEP amplitude differential between attentional conditions. It appears, therefore, that selective attention promotes both greater synchrony and greater neural response to visual stimulation.

The "greater neural response" referred to above manifests as greater VEP amplitude at the response frequency when subjects attend to the flicker vs. when they attend to the alternative, non-flickering visual target. This corresponds to findings in primate extracellular studies which have shown differential firing rates due to selective attention for individual neurons in both striate and extrastriate cortex (Desimone & Duncan, 1995; Duncan, Humphreys, & Ward 1997; Motter, 1993). The attentional gain observed, however, might be due as much to dampening of neural activity when subjects are not attending to the visual stimulus as to enhanced neural activity when they are attending. This is a meaningful distinction for "filter" theories, where the function of

attention is thought to be the capacity to disregard, or gate, irrelevant information (Broadbent, 1958; Deutsch & Deutsch, 1963; Kahneman, 1973; Moray, 1959; Treisman, 1969; Yantis, 1990) and, likewise, for "spotlight" theories, where attention is thought to enhance relevant perceptual processing (Eriksen & Yeh, 1985; LaBerge, 1995; Posner, 1980). Our own data showed that inattention to the flickering stimulus often caused FFT amplitudes at the VEP response frequency to drop to the level of noise (Figs. 1-6, 2-2, 2-6, 2-10, 3-3, and 4-5) and this would seem to be consistent with filter theories of attention. On the other hand, in numerous pilot experiments we have conducted, VEP amplitude is consistently lower when psychophysical tasks are not employed to entrain the subject's attention than when they are so employed and this would seem to be consistent with spotlight theories of attention. Many of the studies referred in this thesis have found evidence of both enhancement and attenuation of neural activity due to attentional factors. From a perspective outside the mold of traditional filter and spotlight models, this is not surprising since there is no necessity for these two aspects of attentional gain to be mutually exclusive.

At what level do the volitional, top-down processes of attention affect automatic, bottom-up processes of visual perception? At what point(s) does attention interact with neural processing? This question, in one form or another, has long been of central interest to researchers. One traditional avenue of inquiry has been concerned with "spatial gradients" which might underlie visual processing. Our results demonstrated that for visual stimuli subtending an area of 0.75 x 1.5 degrees v.a., no spatial fall-off of attentional effects was evident whatever; i.e., with targets such as these adjacent to each

other, VEP activity was reduced to the level of spectral noise when attention was paid to the non-flickering rather than to the flickering stimulus (Fig. 2-2). This finding is consistent with object-oriented theories of visual attention, in which spatial gradients do not hold a privileged position in the processing of visual information. ERP studies reporting evidence ostensibly in direct support of spatial gradients of attention (Mangun and Hillyard, 1987; Mangun and Hillyard, 1988) have relied upon experimental paradigms which require the subject to focus attention on areas of space where a visual target will transiently appear. Our paradigm, on the other hand, requires the subject to attend to a visual target present in space. Perhaps this accounts for the discrepancy between Mangun and Hillyard's finding of differential attentional gain between 5 and 10 degrees v.a. and our findings of no fall-off of attentional gain down to 0.36 degree v.a. (Figs. 3-3 and 4-5).

The visual targets we employed to investigate whether an extremely fine spatial gradient might underlie visual attention were of very small size, 0.36 x 0.36 degree v.a. These stimuli were calculated to subtend an area of the visual field corresponding to a $1mm^2$ field of activity in the primary visual cortex. In order to appreciate how such stimuli help elucidate the neural substrate of observed attentional effects, certain features of functional neuroanatomy in the human visual system should be considered. Visual information processed in the human eye is transmitted through retinal ganglion cells primary to the lateral geniculate nucleus (LGN) of the thalamus, and hence to the primary visual cortex (V1), with the retinotopic organization of this information preserved throughout. Cells in V1 that receive, process, and relay this information have a columnar

organization. Each column comprises layers of cells, with each of the laminae in the column having specific afferent and efferent connections. Individual columns are specialized for processing visual stimuli with specific orientations in the visual field ("orientation columns") from one or the other eye ("occular dominance columns"). The entire visual field is systematically represented by "hypercolumns," each of which is made up of a full set of orientation x occular dominance columns (Kandel, Schwartz & Jessell, 1991; Martin, 1996; Nolte, 1993). The V1 hypercolumns have a cortical area of ~1mm^2, an area we have designated as "1 unit." As mentioned above, this is also the area of primary visual cortex nominally activated by our small visual stimuli.

Results of experiments performed with these small stimuli demonstrated that VEP activity could be consistently reduced to the level of noise when attention was paid to a 1 unit non-flickering visual target separated by 1 unit from a 1 unit flickering target (Fig. 2-6). When two such visual targets were adjacent, however, VEP activity was not consistently attenuated through selective attention (Fig. 2-12). Interestingly, subjects reported that they were often unable to perceptually distinguish the small visual targets when they were not separated. In sum, it seems that spatial gradients were a factor in our results only insofar as they affected perceptual acuity.

Whereas object oriented theories of attention have traditionally been concerned with objects displaying higher order visual properties (Rock & Gutman, 1981; Weber, Kramer, & Miller, 1997), our tiny achromatic stimuli presented in the parafoveal region were not visual "objects" in that sense. A different theoretical approach consistent with our null findings concerning spatial gradients of attention as well as the primitive nature

of our stimuli is represented by biased and integrated competition models (Desimone & Duncan, 1995; Duncan, Humphreys & Ward, 1997; Motter, 1993). In these theories, spatial and other types of featural information may be of more or less importance in discriminating a visual perception, depending upon the context. Attention is not seen as a spotlight that scans sensory information in a serial process of object recognition, but, rather, as an emergent property of parallel, competitive interactions in the construction of object features, biased by top-down as well as bottom-up processes.

Investigating the neural processes affected by visual attention can be informative in probing theories such as the competition models. Our experiments with variations in the contrast level of flickering stimuli evidenced non-linear contrast response functions such as those which have been associated with magnocellular pathways through primate extracellular and human VEP recordings (Baseler & Sutter, 1997; Derrington & Lennie, 1984; Kaplan & Shapley, 1986; Purpura, Kaplan & Shapley, 1988). The classic magnocellular contrast response curve begins in a linear manner at low contrasts and then saturates at higher contrasts (Fig. 4A), just as was the case with our results (Fig 4C). The parvocellular contrast response function, on the other hand, has been shown to be entirely linear throughout the mesopic range of mean illumination up to 4000 photopic trolands (td), and insensitive in the scotopic range <0.43 td in macaque monkeys (Purpura, Kaplan & Shapley, 1988). The half-saturation contrast (C1/2) has been calculated to be 0.13 for magnocellular-projecting retinal ganglion cells and 1.74 for parvocellular-projecting cells in macaque monkeys (Kaplan & Shapley, 1986). The gap in contrast response between these two pathways is qualitatively distinct, and the C1/2 of our two subjects, 0.17, was

clearly within the magnocellular range (Fig. 4C). The exponent value of our contrast response slope was 2.2, very close to the values reported by Lennie (1998) for the contrast response gain of V1/V2 neurons in Macaque monkeys (Fig. 4B). Although these findings do not rule out the possibility of some parvocellular and/or higher order extrastiate involvement in the VEP response to our flickering stimuli, they do indicate that primarily magnocellular V1 and V2 neurons are involved in generating the VEP responses we have recorded and modulated through selective attention.

What then can be said about the neural substrate of the VEP responses we have measured in our experiments? First, the cells primarily responsible for generating scalp potentials recorded with steady-state flickering stimuli such as we have employed are most likely cortical pyramidal neurons (Lennie, 1998; Regan, 1989). The wide range of stimulus loci and size–controlled for cortical magnification–from which we have obtained our results (Figs. 1-3 and 4-1, Tables 1-1 and 2-1) lend empirical support to this assertion in the context of EEG source localization (Alterman et al., 1999; Pugh et al., 1999). Second, in the case of our 1 unit flickering stimuli (which display contrast variance but no overall line segment orientation, chromaticity, or movement), areas V1 and V2 are primarily activated. Extrastriate areas involved in higher-order visual processing are only peripherally activated, if at all, by such lower-order visual stimulation. This assertion is consistent with what is known about the functional neuroanatomy of the various visual processing areas (Kandel, Schwartz & Jessell, 1991; Lennie, 1998; Martin, 1996; Nolte, 1993), and it is empirically supported by extensive mapping and source localization experiments (Alterman et al., 1999; Pugh et al., 1999).

Furthermore, the exponent value of our contrast response slope matches the contrast gain of V1 and V2 neurons (Lennie, 1998). Third, the neural pathway underlying the effects of visual selective attention we have observed with steady-state flicker is primarily magnocellular (Fig. 4A, B, and C).

The above insights are germane to the competition models in light of the following. We have obtained substantial attentional effects from visual target sets spanning areas of the visual field well outside the receptive fields of V1 and V2 neurons in the magnocellular pathway and, for that matter, outside the receptive fields of V3 and V4 neurons. These findings, therefore, support the hypothesis that competitive interactions in the emergence of object properties can occur far beyond the receptive field of individual cells. The way in which competition models are structured may, thus, be informed by this neurophysiological evidence.

The psychophysical task we employed to elicit attention involved perceptual judgements of color, and parvocellular pathways are chiefly involved in color perception. Why then might such an attentional paradigm so strongly have affected magnocellular processing? The answer to this question may lie in the level at which perceptual binding occurs. It may be that integral to the process of determining the color of a stimulus such as ours with the parvocellular system, the stimulus itself is resolved through figure/ground separation with the magnocellular system. In other words, attention was paid to the object itself in the process of attending to a property of the object.

This supposition gains empirical support from the striking fact that many of the attentional effects we observed evidenced amplitude at VEP response frequencies below

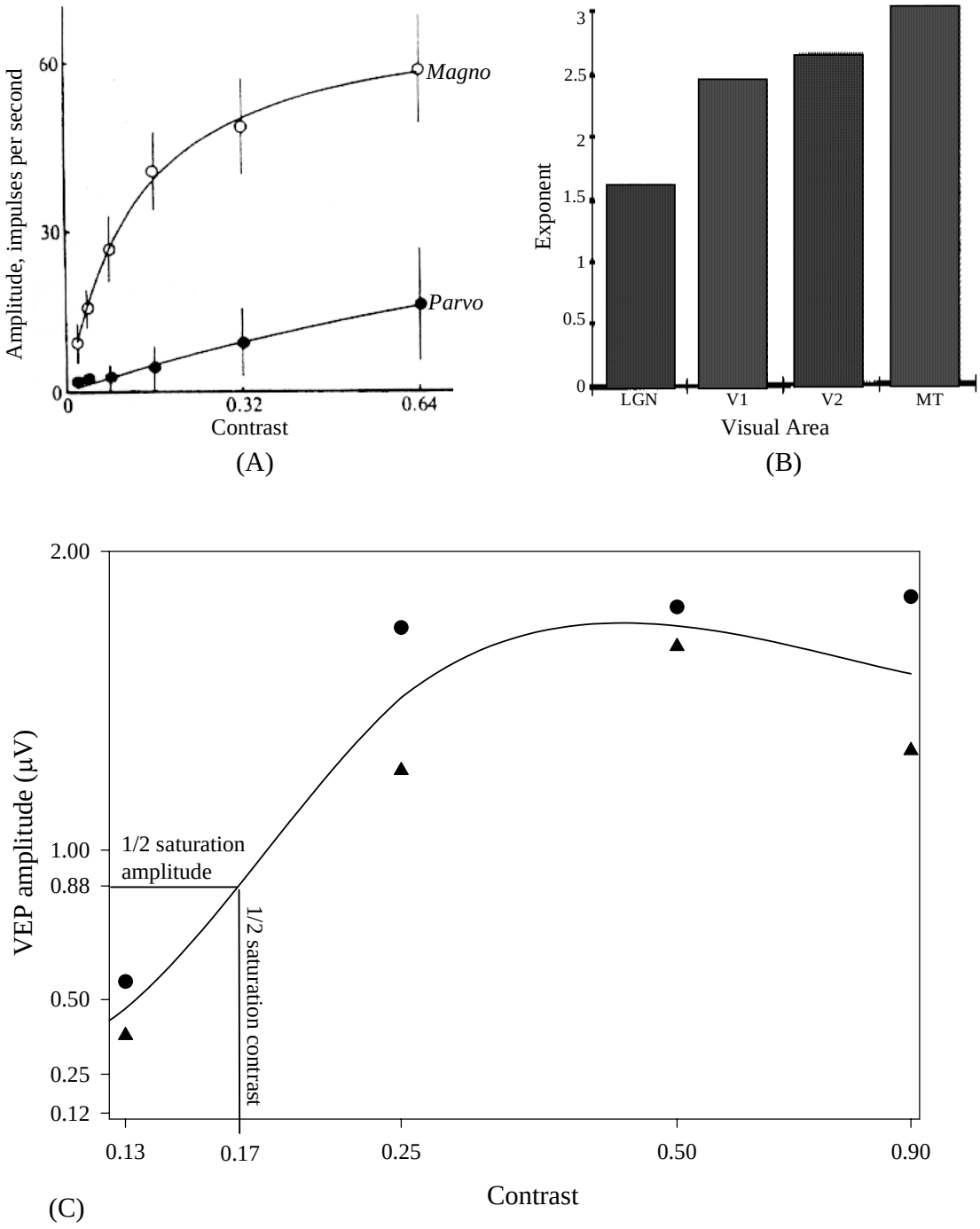


Fig. 4: (A) Contrast response functions for magnocellular and parvocellular projecting retinal ganglion cells in Macaque monkeys (Kaplan and Shapley, 1986).
(B) Relationship between stimulus contrast and response amplitude for neurons in different visual processing areas (Lennie, 1998). (C) Log/linear contrast response function from Experiment 4b with half-saturation values.

the baseline noise level; i.e., many of the results of our attentional experiments demonstrated *the complete elimination of VEP responses due solely to selective attention*. This finding suggests that gating of these VEP signals occurred at or before the primary visual cortex, since in these cases, contributions to the VEP response from the input laminae of V1 as well as downstream processing areas were silenced. While massive cortical inhibition of V1 and downstream processing areas may have been responsible for eliminating the VEP response, this seems less likely than thalamic gating, when one entertains considerations of functional neuroanatomy and parsimony. In other words, the processing of irrelevant visual stimuli may not have progressed beyond the LGN, in our experiments, for the reasons argued below.

Contrast variation across the visual field is processed first in the retina then further in the LGN, and this provides the visual system with information which contributes to the basic figure/ground separation needed to distinguish objects. The first point in the primary visual processing stream where there are radical changes in the character of receptive fields is at the imput laminae of V1. Receptive fields remain discrete and relatively constant from the retinal ganglion cells through the LGN. Then, in the case of the magnocellular pathways, individual LGN outputs synapse with scores of orientation specific and ocular dominance columns in V1 (Kandel, Schwartz & Jessell, 1991; Lennie, 1998; Martin, 1996; Nolte, 1993). Thus it would be far more efficient to gate irrelevant signals in the visual stream at the LGN, where they remain discrete, than after they diffuse, 200 to 400 times (Lennie, 1998), in the input laminae of V1.

Furthermore, the number of presynaptic connections from the retina to LGN relay cells is roughly one-tenth the number of presynaptic geniculate connections from V1 and the other downstream cortical and subcortical areas that feed information back to the LGN (Kandel, Schwartz & Jessell, 1991). Neither V1 nor any of the other cortical processing areas receive such extensive feedback from all areas of the visual processing stream and far fewer feedback connections go to the retina itself from downstream visual areas (Kandel, Schwartz & Jessell, 1991; Lennie, P., 1998; Martin, 1996; Nolte, 1993). Since cortical processing is highly specialized and distributed while the receptive field properties of LGN neurons are compact and close to those of their retinal inputs, parsimony prompts consideration of the thalamus as the most efficient and able site to gate "irrelevant" afferent signals in the visual stream by passing on for further processing mainly those afferent signals relevant to the perception of attended objects.

The thalamus, unlike any other processing area in the visual stream, is equidistant in terms of synaptic connectivity from the numerous areas of parallel processing in the visual system and it receives inputs from other sensory modalities in a similar manner to those it receives from visual areas. For instance, locations represented by tonotopic maps in the inferior colliculous have corresponding locations represented by retinotopic maps directly above in the superior colliculous. Moreover, spontaneous rhythmic activity originating in the thalamus is cortically entrained (Contreras et al., 1996; Contreras et al., 1997; Kirkland & Gerstein, 1998). This rhythmic activity and cortical entrainment could provide a mechanism for binding various discrete streams of processing that contribute to the unitary perception of an object. Perhaps the "alpha suppression" evident in our data

reflects the processing of discrete visual perceptions through the enlistment of cell populations stochastically oscillating at the alpha frequency (Arieli et al., 1996; Kamiya, Callaway & Yeager, 1969; Trimble & Potts, 1975). Some researchers have hypothesized that other endogenous, cortically entrained oscillatory rhythms (e.g., gamma) originating in the thalamus are instrumental in perceptual binding (Tiitinen et al., 1993). In any case, converging evidence suggests that the binding of parallel streams of sensory processing into emergent objects of perception may occur within networks of rhythmic cellular interactions, brought into coherence and, perhaps, gated or fed forward at the thalamus (Lennie, 1988; Mahoney, 1991). As discussed above, additional empirical support for this theory is contributed by our finding that robust VEP responses generated by V1/V2 magnocellular neurons can be sensitively modulated through manipulation of the physical properties of visual stimuli and that these stimulus-driven responses can be entirely quelled through the operation of selective attention.

Our experiments with variations in the temporal frequency of stimulus flicker evidenced first, second, and third harmonic VEP responses, all within the beta bandwidth (Table 4-3). Regan (1989) speculates that second-order harmonic responses to steady-state flicker may arise in the retina, while third-order VEP responses might arise in V2, at the level of binocular convergence. These harmonic responses may, therefore, further inform our understanding of the neural pathways involved with VEP response to steady-state contrast-modulated flicker.

Of greater importance than the harmonic distortions is our finding that the cellular substrate of this steady-state VEP activity is responsive only within the beta bandwidth

(Table 4-3 and Figs. 4-6, 4-7, 4-8, and 4-9). Consistent with our other findings, magnocellular neurons are said to show preferential response in the beta bandwidth (Derrington & Lennie, 1984; Kaplan & Shapley, 1986). Furthermore, photosensitive epileptic seizures are focally driven by cells in the visual cortex which respond to flicker frequencies primarily in the beta bandwidth (Harding & Jeavons, 1994). Thus, our finding that selective attention is capable of dampening and even eliminating stimulus-driven cortical responses of this type could have great clinical significance. This author has successfully employed attentional training in the treatment of a variety of clinical disorders and has begun to develop an attentional training program for the control of photo-epileptic seizures. In this regard, the documented effectiveness of behavioral treatments for the control of other types of refractory epileptic seizures is encouraging (Cataldo, Russo, and Freeman, 1979; Cott, Pavloski, and Black, 1979; Dahl et al., 1985; Dahl, Brorson and Melin, 1992; Dahl, Lennart, and Lars, 1987; Goldstein, 1990; Kaplan, 1975; Kuhlman, 1978; Lubar et al., 1981; Mostofsky and Balaschak, 1977; Mostofsky and Loyning, 1993; Pritchard, Holmstrom, and Giacinto, 1985; Sterman and Macdonald, 1978; Williams et al., 1979; Wyler, Robbins, and Dodrill, 1979).

Experimental paradigms such as we have employed make possible the measurement of effects which, in the future, may help us better meet the challenge of EEG source localization. Careful attentional controls may allow us to answer questions about the intriguing failures of superposition we have uncovered. Attentional training may well have profound clinical importance, not just for the treatment of photosensitive epilepsy, but for more pervasive pathologies such as chronic pain, anxiety, mood, and

developmental disorders. With attention to attention, we may also someday be able to further elucidate not only the role that the thalamus and spontaneous neural rhythms play in perceptual binding, but the neural substrates underlying consciousness itself.

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