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Attention-related evoked potential correlates of precortical gating in the human visual system

Harding, J. Michael, Ph.D.

The University of North Carolina at Greensboro, 1987

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ATTENTION-RELATED EVOKED POTENTIAL CORRELATES OF PRECORTICAL GATING IN THE HUMAN VISUAL SYSTEM

by

J. Michael Harding

A Dissertation Submitted to
the Faculty of the Graduate School at
The University of North Carolina at Greensboro
in Partial Fulfillment
of the Requirement for the Degree
Doctor of Philosophy

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Approved by

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The precortical gating hypothesis was tested by having subjects selectively attend to points in space under conditions wherein the saliency (size) of the evoking stimulus and motivation level of subjects were manipulated in an attempt to further elucidate relative contributions of retinal and neural components to visually evoked responses (VERs) occurring within the 40-70, 70-130, and 40-130 msec latency intervals poststimulus. A large, relatively salient stimulus was expected to elicit relatively more retinal than neural contributions in canthally recorded VERs. A small, relatively nonsalient stimulus was expected to elicit relatively more neural than retinal contributions in both canthally and frontally recorded VERs. All VERs recorded from frontal scalp were expected to reflect more neural than retinal contributions regardless of the size of the evoking stimulus. Attention-related enhancement of the b-wave of the ERG was expected to be revealed in only the canthal VERs for the large stimulus. The attention effect was expected to be revealed as enhanced negativity over most, if not all, of the 40-130 msec latency interval for canthal recordings evoked by the small stimulus, and frontal VERs evoked by both the large and small stimuli. Any effect of motivation was expected to be manifested as increased VER amplitude in a late component having a peak latency of about 180 msec.

A significant interaction between attention and stimulus size was revealed for the canthal, but not the frontal, recordings. The VERs evoked by the large and small stimuli were more negative under the attend than under the unattend condition. An ERG response was elicited by the large stimulus in only half the subjects. For these subjects, the attention

effect on the b-wave was in the expected direction, but it was not statistically significant. The attention effect on the b-wave afterpotential (within the 70-130 msec latency interval) was as expected (i.e., increased negativity for the attend condition), as was the attention effect for all frontal recorded VERs. There was no significant feedback (motivation) effect revealed in any VERs within the first 100 msec poststimulus. These results were interpreted as evidence of precortical gating of sensory input as a function of selective attention. In addition, they were interpreted as providing some evidence for separation of retinal and neural VER components in half the subjects.

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TABLE OF CONTENTS

CHAPTER

Page

CHAPTER

LIST OF TABLES

LIST OF FIGURES

TABLE OF ABBREVIATIONS

Auditory Evoked Potentials	AEPs
Electrencephalogram	EEG
Electroretinogram	ERG
Event Related Potentials	ERPs
Evoked Potentials	EPs
Frontal Eye Fields	FEFs
Latency Interval	LI
Lateral Geniculate Nucleus	LGN
Left and Right Frontal Combined	FLR
Left and Right Internal Canthi Combined	ICLR
Left Frontal	FL
Left Internal Canthus	ICL
Left Visual Field	LVF
Mesencephalic Reticular Formation	MRF
Olivocochlear Bundle	OCB
Right Frontal	FR
Right Visual Field	RVF
Superior Colliculus	SC
Visual Evoked Responses	VERs

CHAPTER I

INTRODUCTION

Attention has been described as "the process by which the brain selects stimuli from the environment for further investigation or action" (Goldberg & Bruce, 1985). One outstanding feature of attention is its selective nature. In general, models for selective attention propose that individuals select specific stimulus features in their environment to which they direct or focus their attention. At the neural level, transmission of sensory input from attended stimulus features is said to be enhanced or facilitated, relative to transmission of such input from unattended stimulus features.

The differential facilitation of transmission of sensory input from attended and unattended stimulus features has been said to involve a filtering or gating process wherein sensory input from the unattended stimulus features is inhibited, input from attended stimulus features is facilitated, or both inhibition and facilitation of input from unattended and attended stimulus features, respectively (Broadbent, 1970; Eason, 1981, 1984; Eason, Harter, & White, 1969; Eason, Oakley & Flowers, 1983a; Hernandez-Peon, Scherrer, & Jouvet, 1956; Hillyard, Picton, & Regan, 1978; Lukas, 1980, 1981; Mangun, Hansen, & Hillyard, 1986; Naatanen, 1975, 1979, 1982; Oakley, 1984; Oakley, Eason, Moore, & Conder, 1985; Oakley, Eason, & McCandis, 1986; Oatman, 1971, 1976, 1982; Oatman & Anderson, 1977, 1980;

Posner, 1982; Posner & Presti, 1987; Skinner & Yingling, 1977; Weinberger, 1971; Yingling & Skinner, 1977).

There is little doubt that, at the neural level, transmission of sensory input from attended stimuli is differentially facilitated. Furthermore, this attention-related enhancement or facilitation of sensory transmission is manifested in scalp-recorded evoked potentials (EPs) under certain conditions. Controversy stems from the various theoretical positions concerning the level within the sensory pathways at which such attention-related filtering can conceivably take place. In general, there is experimental evidence supporting two broad theoretical positions concerning this issue. On the one hand is evidence which supports the position that such filtering can occur at both precortical and cortical levels (i.e., subcortical relay nuclei and the cerebral cortex) (Eason, 1981, 1984; Eason et al., 1969; 1983a; Hernandez-Peon et al., 1956; Lindsey, 1959; Livingston, 1978; Lukas, 1980, 1981; Oakley, 1984; Oakley et al., 1985, 1986; Oatman, 1971, 1976, 1982; Oatman & Anderson, 1977, 1980). On the other hand is evidence in support of the position that selective filtering of attended and unattended stimulus features can occur only at the level of the cerebral cortex (Deutsch & Deutsch, 1963; Naatanen, 1975, 1982; Naatanen & Mitchie, 1979; Woods & Hillyard, 1978).

A subset of the evidence in support of attention-related filtering at precortical levels within the sensory pathways suggests that such filtering can possibly occur at the periphery (i.e., at synaptic junctions peripheral to subcortical relay nuclei). Such evidence is mounting (Eason, 1984; Eason et al., 1983a; Hernandez-Peon, 1956; Livingston, 1978; Lukas, 1980, 1981; Oatman, 1971, 1976, 1982; Oatman & Anderson, 1977, 1980). However, only Eason (1984) and Eason et al. (1983a) have demonstrated possible differential filtering of attended and unattended sensory input at the periphery of the visual system humans using scalp-recorded visual evoked potentials (VEPs). Lukas (1980, 1981) demonstrated possible attention-related filtering at the periphery of the human auditory system, when subjects attended to visual stimuli, using auditory evoked potentials (AEPs). These significant findings suggest that measurement of scalp-recorded evoked potentials may be a method for demonstrating attention-related filtering of sensory input at varying levels within sensory pathways. Naatanen (1975) reports a relative increase in the use of scalp-recorded event related potentials (ERPs) for studying selective attention in humans.

Scalp-Recorded Event Related Potentials (ERPs)

General Recording Procedure

There are essentially two types of electrical activity in the brain which can be recorded by electrodes placed about the scalp. The first type is ongoing, spontaneous electroencephalographic (EEG) activity due entirely to endogenous brain activity. The second type occurs at a fixed time following the presentation of a stimulus; therefore, it is said to be time-locked to the stimulus (Goff, 1974; Lindlsey, 1984). The nature of the time-locking between the stimulus and subsequent electrical brain activity implies that brain electrical potentials are evoked by the stimulus.

The voltage of EEG activity is typically greater than that of stimulus-related (i.e., event-related) activity. Unless amplified, the small ERP will remain embedded within the larger EEG and other artifactual activity. The task, then, is to extract the small stimulus-related electrical signals from the background noise created by the EEG activity. This is accomplished by presenting the stimulus many times, while averaging or algebraically summing the small evoked signals over the many trials. Since the signals are not occurring randomly (with respect to the stimulus), their voltage eventually exceeds the background noise, which tends to cancel itself due to its random occurrence. Increasing the number of stimulus presentations improves the signal-to-noise ratio. In order to obtain a reasonably good ERP measurement, the stimulus should be presented at least 48-64 times (Goff, 1974).

Averaged ERPs cannot be recorded without the use of special electronic equipment to detect, amplify, store, and average the signals. Metal electrodes, usually made of gold, silver, or platinum are used to initially detect signals. In the process of applying electrodes, several steps are taken to minimize the resistance to current flow across electrode pairs. An electrolyte cream is usually placed between the electrode and skin surface to ensure good contact. The skin is usually rubbed clean with alcohol, warm soapy water, or some other cleanser to remove oils, dirt, and dead tissue. A sticky tape is sometimes applied to hold the electrode firmly in contact with the skin. Two electrodes are required to measure ERPs, since an electrical potential at a given point must be measured in reference to another point (Goff, 1974). Electrodes are usually placed in accordance with the standard 10-20 system adopted by the International Federation of Societies for Electroencephalography and Clinical Neurophysiology in 1947 (Goff, 1974).

The recording and reference electrodes can be placed where both are capable of recording evoked activity. In this case, the resulting potential is bipolar and represents the algebraic difference between the two electrodes. If the reference electrode is presumed to be insensitive (inactive) to evoked activity, the recorded potential is said to be monopolar. Under real recording conditions, it is difficult to find a reference location which is totally inactive. There is always the possibility that the reference electrode will pick up myogenic, and possibly some far-field, potentials. However, the reference electrode can be located at places relatively free of evoked activity, or at sites where it picks up essentially the same artifactual activity as the recording (active) electrode. In this case, the artifactual activity will cancel itself, leaving the evoked activity unchanged. The location of the reference electrode should be determined in accordance to the location of the active electrode. Some popular places for locating reference electrodes are the ears, chin, nose (Goff, 1974) and the mastoid complex located just behind the ears. In some instances reference electrodes may be located on the neck or some other location.

Volume Conduction Theory

The source of origin of scalp-recorded ERPs cannot be precisely determined solely on the basis of their morphology. However, there is general agreement that their equivalent source of origin can be determined by applying electrical field theory to the conduction of current within biological tissue (Allison et al., 1983; Darcy et al., 1980; Goff, Allison, & Vaughan, 1978; Oakley, 1984; Vaughan, 1982; Wood & Allison, 1981). Typically, volume conduction theory makes the assumption that the same laws which apply to electrical field theory, are applicable to ionic current flow through the brain, meninges, skull, muscle, and scalp (Allison et al., 1983). Assuming that the conductive properties of the skull and its coverings are known, it is possible to apply volume conduction theory as a procedure for making inferences about the equivalent dipole sources of origin of intracranial electrical activity recorded at the scalp.

Dipole Model

The dipole model provides a conceptual framework for interpreting source of origin of potential fields generated intracranially, as recorded from the scalp. There are two categories of transmembrane current flow which gives rise to electrical potentials within the brain: (1) all-or-none action potentials, and (2) graded potentials resulting from depolarization and hyperpolarization of cell membranes (Allison et al., 1983; Goff et al., 1978). Depolarization and hyperpolarization give rise to excitatory postsynaptic (EPSP) and inhibitory postsynaptic potentials (IPSP), respectively. EPSP and IPSP intracranial activity are typically recorded at the scalp as negative and positive-going ERP deflections, respectively (Allison et al., 1983; Goff et al., 1978). However, this is not always the case. The polarity of the potential at the scalp depends upon the level of the generator source within the brain. For example, Goff et al. (1978) pointed out that potentials arising from locations deep within the brain have polarities at the surface which are the opposite of those arising from sources closer to the scalp. The orientation of cells within the various brain structures is another factor which determines the polarity of ERPs recorded at the scalp. Positive scalp-recorded ERPs generally reflect outward current flow (called the source), while negative ERPs generally reflect inward current flow (called the sink).

Allison et al. (1983) present several generalizations regarding potential fields generated by neuronal activity. One of the most important of these generalizations, with respect to volume conduction theory, is that the density of current flow decreases rapidly as the distance from the immediate vicinity of the depolarized region increases. This implies that the amplitude of the scalp-recorded potential decreases as the distance between the recording electrode and the neural activity increases.

There are, however, other factors which should be considered when the absolute amplitude of ERGs is used to make inferences about their sources of origin. For example, if electrodes are located near the source of the ERP (i.e., in the near field), absolute amplitude is larger than when they are in the far field. ERP amplitude decreases sharply with small deviations in electrode location when recording near field potentials. When recording far field potentials, changes in electrode location has less effect on ERP amplitude (Wood & Allison, 1981).

Direct vs. Inverse Methods of ERP Source Identification

Two methods are typically used to estimate the location of intracranial generators of scalp-recorded ERPs (Wood & Allison, 1981; Vaughan, 1982). The first is the direct (or forward) method wherein assumptions regarding the anatomical configuration and electrical properties of the generator sources are used to calculate equivalent field potentials. The distribution of the scalp-recorded ERPs is subsequently compared to the theoretically derived distributions to determine the goodness-of-fit between the two measures (Vaughan, 1982). Application of the inverse (or indirect) method involves recording ERPs from varying scalp locations, then making assumptions about their source of origin on the basis of their morphology (Wood & Allison, 1981).

Visual Pathways

Classical Afferent Visual Pathways

Two parallel afferent pathways have been identified in most vertebrates, including primates and humans: the (1) geniculostriate, and (2) tectopulvinar ascending pathways (Hall, 1972; Harting, Glendenning, Diamond, & Hall, 1973; Rodieck, 1979; Schiller & Malpeli, 1978; Schiller, Malpeli & Schein, 1979; Singer, Zihl, & Poppel, 1977; Tigges, Bos, & Tigges, 1977). In humans and other primates, the geniculostriate system consists of heavy projections from retinal X and Y cells, to the lateral geniculate nucleus (LGN) of the thalamus, and on to striate cortex (Berkley, 1978; Harting et al., 1973; Holstein, Pasik, Pasik, & Hamori, 1985; Ruddock, 1984; Tigges & O'Steen, 1974; Tigges et al., 1977; Wilson, 1978). The X and Y cells are known to be involved in fine pattern discrimination and spatial location, respectively (Schiller & Malpeli, 1978; Schiller et al., 1979). The geniculostriate system also subserves color vision and is more sensitive under photopic conditions than the tectopulvinar system (Schiller & Malpeli, 1978).

The tectopulvinar system in primates consists of projections from retinal Y and W cells to the superior colliculus (SC), to the pulvinar, and on to extrastriate cortex (Harting et al., 1973; Holstein et al., 1985; Holtzman, 1984; Schiller & Malpeli, 1978; Schiller et al., 1979). This system mediates saccadic eye movements and other visuo-motor integration, spatial location, night (or scotopic) vision, and peripheral vision (Schiller & Malpeli, 1978; Schiller et al., 1979; Singer et al., 1977).

The geniculostriate and tectopulvinar visual systems reflect cone and rod activity, respectively, and function in a complementary fashion. When one system suffers damage, the other can compensate for some, but not all, the lost functions. One system cannot completely assume the function of the other primarily because the residual vision subserved by the tectopulvinar system is very limited (Ruddock, 1984; Wilson, 1978).

A third ascending visual system has been identified in most mammals, humans included (Harting et al., 1973; Swadlow, 1983; Wilson, 1978). This system consists of sensori-motor connections in deep SC layers which project to the pons, mescencephalic reticular formation (MRF), and tegmentum.

Retinopetal Efferent Visual Pathways

There is considerable controversy regarding the existence of corticofugal fibers in primates and humans which terminate in the retina. Such fibers are known to exist in birds (Cowan, 1970; Cowan & Clark, 1976; Hayes & Holden, 1983; Miles, 1972a, 1972b, 1972c, 1972d; Ogden, 1968; O'Leary & Cowan, 1984; Reparent, Peyrichoux, Weidner, Micheli, & Rio, 1980; Rogers & Miles, 1972; Shkol'nik-Yarros, 1971; Shortess, 1970). There is evidence that they may exist in reptiles (Ferguson, Mulvanny, & Brauth, 1978; Fritzsch & Himstedt, 1981; Marchiafava, 1976; Reperant, Peyrichoux, Weidner, Miceli, & Rio, 1980; Weiler, 1985), fishes (de Craprona & Fritzsch, 1983; Ebbesson &

Meyer, 1981; Springer, 1982, 1983; Vanegas & Ito, 1983); the shark (Luiten, 1981), snakes (Hoogland & Welker, 1981), rats (Frank & Goldberg, 1983; Itaya, 1980; Itaya & Itaya, 1985; Molotchnikoff & Temblay, 1983, 1986), gerbils (Larsen & Moller, 1985), dogs (Terubayashi, Fujisawa, Itio, & Ibata, 1983), mice (Goldberg & Galin, 1973), and primates, including humans (Bogoslovskii & Semenovskaya, 1958; Honrubia & Elliott, 1968, 1970; Jacobson & Gestring, 1958; Noback & Mettler, 1973; Okun & Collins, 1962; Pfister & Wolter, 1963; Reparant & Gallego, 1976; Tigges & O'Steen, 1974; Wolter, 1955, 1960, 1961, 1965, 1966a, 1966b, 1968, 1979; Wolter & Knoblich, 1965; Wolter & Lund, 1968).

The investigations by Wolter (1979), Wolter and Knoblich (1965) and Sacks and Lindenberg (1969) provide relatively strong anatomical evidence for the existence of retinopetal fibers in humans. Fibers of apparent central origin were identified in the human optic nerve with an electron microscope (Wolter, 1979), and in the optic nerve, chiasm and tract of a woman with bilateral congenital cystic eyeballs, a degenerative disorder which prevents development of retinofugal fibers (Sacks & Lindenberg, 1969). Possible efferent retinal fibers were also identified in a man whose eyes had been removed 50 years earlier (Wolter & Knoblich, 1965). Based upon these findings alone, it seems reasonable to assume that retinopetal fibers do exist in the human visual system. Thus, the corticofugal projection in the human visual system consists of fibers terminating in the thalamus (i.e., LGN, SC, pulvinar), pons, basal ganglia, and most probably, the retina.

Nonretinopetal Efferent Visual Pathways

Generally, subcortical structures which give rise to ascending visual pathways are recipient of direct (or indirect) descending corticofugal projections in vertebrates (Baker & Malpeli, 1977; Leiby, Bender, & Butter, 1982; Singer, 1977; Singer et al., 1977; Spatz, 1975; Swadlow, 1983; Tigges et al., 1973; Weller & Kass, 1981). Visual cortical area 17 (i.e., primary visual or striate cortex) has been demonstrated to send descending fibers to the lateral geniculate nucleus (LGN), superior colliculus (SC), and inferior pulvinar nuclei (PI) in monkeys (Schiller et al., 1979; Spatz, 1975; Tigges et al., 1973). In addition, area 17 has been shown to project to the pons (Tigges et al., 1973) and reticular nucleus (Swadlow, 1983). Thus, the thalamus receives heavy afferent and efferent projections within the primate visual system.

Fibers arising in extrastriate cortex also project to subcortical areas. The superior colliculus (SC) is known to receive indirect projections arising in occipital cortex (Goldberg & Wurtz, 1972; Weller & Kass, 1981). The frontal eye fields (FEFs), located in the frontal lobes, project to intermediate and deep SC layers which are involved in eye movements (Busnell et al, 1981; Crowne, 1983; Lindsley et al., 1980). Connecting fibers have been shown to project from the FEFs to the basal ganglia (Bruce et al., 1985).

Function of Corticofugal Pathways

It is generally accepted that one function of corticofugal pathways is to modulate the flow of sensory input from more peripherally located structures (Bartlett, Doty, Pecci-Saavedra, & Wilson, 1973; Hull, 1968; Singer, 1977; Singer, Zihl, & Poppel, 1977; Skinner, 1984; Skinner & Yingling, 1977; Swadlow, 1983; Wilson, Pecci-Saavedra, & Doty, 1973; Yingling & Skinner, 1977). With the exception of olfactory sensory transmission, all afferent impulses are relayed via thalamic nuclei prior to reaching cortical levels (Singer, 1977). The descending visual pathways from visual cortical areas to the thalamas, in addition to ascending pathways to the thalamus from the reticular formation constitute mechanisms wherein transmission via the thalamic relay nuclei could be modulated or gated as a function of psychological and behavioral states (Singer, 1977). Both facilitation and inhibition of subcortical unit activity appear to be under centrifugal influences.

The modulation of neural activity in thalamic nuclei has been investigated in monkeys (Bartlett et al., 1973; Hull, 1968; Wilson et al., 1973). Hull (1968) employed a technique wherein the visual cortex was reversibly cooled, while simultaneously recording single unit activity in the lateral geniculate nucleus (LGN) of Maccaque monkeys. When the visual cortex was cooled, activity in some LGN cells increased, while it decreased in others. These results were interpreted as facilitation and inhibition of LGN unit activity due to removal of cortical influences. Activity in LGN cells projecting to noncooled cortical areas was not affected by cortical cooling.

Baker & Malpeli (1977) concluded that increased LGN and pulvinar unit activity observed following cryogenic blockage of striate cortex was possibly due to centrifugal influences. Stimulation of the mesencephalic reticular formation (MRF) or pretectal area has been shown to increase LGN unit activity in the squirrel monkey (Doty, Wilson, Bartlett, & Pecci-Saavedra, 1973). Increased LGN activity following electrical stimulation of the MRF was observed while the animal was under barbiturate anesthesia, however. These results were interpreted as evidence of differential gating of transmission through the LGN (Doty et al., 1973). The MRF influences on LGN activity suggest a possible mechanism for mediation of arousal-related influences on transmission through the thalamus.

According to Singer (1977), corticogeniculate fibers inhibit LGN activity via presynaptic inhibition of optic nerve fibers. This conclusion was based upon the demonstration of increased activity within the optic tract following electrical stimulation of visual cortex. It was concluded that the LGN serves as an "internal retina" from which the visual cortex selects relevant stimulus features (Singer, 1977). Swadlow (1983) also concluded that corticofugal fibers modulate LGN activity presynaptically.

The function of corticofugal fibers to the retina is unknown. If such fibers exist in primates, they could modulate retinal ganglion cell sensitivity (Miles, 1972a, 1972b). Since many neuroscientists view the existence of retinopetal fibers in human with some skepticism, it is generally agreed that the thalamus is the earliest level at which centrifugal influences may be manifested within the human visual system (Singer, 1977). However, the early selective attention effect demonstrated by Eason (1984) and Eason et al. (1983a), which will be discussed in the section dealing with electrophysiological evidence of precortical gating, suggests otherwise.

Centrifugal Influence in Visual Pathways as a Function of Selective Attention

Precortical Gating Hypothesis

A mechanism which selectively gates or filters sensory transmission through major thalamic relay nuclei has been proposed (Skinner & Yingling, 1977; Yingling & Skinner, 1977). The nucleus reticularis thalami, which surrounds the thalamus and connects with the mesencephalic reticular formation (MRF) and the mediothalamic frontal system (MTFCS), has been implicated as the selective regulator of thalamocortical activity (Skinner & Yingling, 1977; Yingling & Skinner, 1977). In general, the precortical gating hypothesis states that the flow of transmission through the thalamus is selectively regulated as a function of biological or behavioral states. Evidence which is consistent with this hypothesis will be reported in the following section. The body of evidence consistent with precortical gating at the thalamic level is substantial (Baker & Malpeli, 1977; Bartlett et al., 1973; Doty, 1973; Hull, 1968; Singer, 1977; Singer et al., 1977; Skinner & Yingling, 1975; & others); however, there is relatively little evidence for such selective gating of transmission at more peripheral locations within the visual system.

Electrophysiological Evidence of Precortical Gating

Hernandez-Peon et al. (1956) demonstrated the early filtering of irrelevant auditory stimuli in cats. While recording neural activity from electrodes implanted in the dorsal cochlear nucleus, these researchers stimulated the animals with three types of stimuli: a mouse, fish scent, and somatic shock. Auditory evoked potentials (AEPs) were recorded while the animals were exposed to a tone, or a tone paired with one of the above stimuli. The amplitude of the AEPs decreased markedly when animals were presented with any combination of an extraauditory stimulus with the tone, and returned to normal levels when the extraauditory stimuli were removed. These results were interpreted as evidence for the blocking of afferent impulses in response to the unattended (irrelevant) auditory stimuli. When the extraauditory stimuli were presented, the animals shifted their attention to them and away from the tones. The blocking effect reportedly occurred in the subcortical portions of the auditory pathway. It was suggested that the response to the tones was inhibited by centrifugal mechanisms when the animals shifted their attention to the nonauditory stimuli (Hernandez-Peon et al., 1956).

Oatman (1971) provided further support for selective attention effects on sensory transmission, using auditory and visual stimulation in cats. The animals were trained to make a visual discrimination for food. AEPs were recorded from three locations in the auditory pathway: (1) the auditory cortex, (2) cochlear nucleus, and (3) round window before, during, and after the animals performed the discrimnation task. The amplitude of the AEPs decreased markedly at all recording locations when the animals performed the visual discrimination task. These results were interpreted (Oatman, 1971) as reductions in AEP amplitude as a function of the attentional state of the animals.

Two systems were suggested as playing a role in the suppression of responses to the irrelevant stimuli. The reticular feedback system was said to have suppressed irrelevant auditory stimuli by way of middle ear contractions, while the olivocochlear bundle (OCB) was said to have suppressed the irrelevant stimuli at the hair cell level in the cochlea (Oatman, 1971). It has been firmly established that the OCB projects to the cochlea from the brain (Broadal & Walberg, 1959; Guinan, Warr, & Norris, 1983; Rossi, 1968; Sala, 1968; Werall, 1966).

Oatman (1976) essentially replicated the Oatman (1971) study. In the later study, it was determined that the intensity of the irrelevant stimuli influenced the magnitude of its suppression during periods when the animals engaged in the visual discrimination task. The greatest degree of suppression of the irrelevant stimuli was observed when the intensity of the auditory stimulus (a click in this case) was lowest. As the intensity of the auditory click increased, the degree to which it was suppressed during the visual discrimination condition decreased.

Oatman and Anderson (1977) provided evidence which strongly suggests that the OCB was involved in suppression of irrelevant auditory stimuli as a function of the animals' selective visual attention. The animals' muscles to the middle-ear were cut to prevent possible middle-ear influences on AEPs. The procedure for this study was very similar to the procedure used in the earlier studies (Oatman, 1971; 1976) and the results were essentially the same. In a later study (Oatman, 1982), it was determined that the hippocampus was also involved in the suppression of irrelevant auditory stimuli during selective visual attention.

Precortical filtering of irrelevant stimulus information has been demonstrated in the human auditory system. Lukas (1980) demonstrated the attenuation of AEPs in humans who were selectively attending to visual stimuli. Brainstem auditory evoked potentials (BAEPs) were recorded from subjects under two conditions. In the "look" condition, subjects were instructed to mentally count the number of randomly presented visual target stimuli. In the "listen" condition, they attended to auditory stimuli in the absence of visual stimulation. Wave V of the BAEP was significantly lower in amplitude under the look, relative to the listen condition. It was concluded that the irrelevant auditory stimuli were inhibited at the level of the inferior colliculus when subjects focused their attention on the visual discrimination task (Wave V was said to be primarily generated by the inferior colliculus).

Lukas further demonstrated that irrelevant auditory stimuli were differentially filtered as a function of their frequency (Lukas, 1980). He used two tone frequencies (2000 and 8000 Hz) as auditory stimuli, and found that both stimuli elicited smaller Wave I components of the BAEP during the look condition. This result was interpreted as an indication of the filtering of irrelevant stimuli at the periphery of the auditory pathway via the OCB. The 2000 Hz stimulus was apparently filtered only at the inferior colliculus level during the look condition, as revealed by the decreased amplitude of Wave V.

In order to be more certain that the decreased BAEP amplitudes in response to the irrelevant auditory stimuli were a result of shifts in attention, Lukas (1981) conducted another investigation. In this study, visual stimuli were presented during both the look and listen conditions. Target stimuli were designated for each modality; however, AEPs were recorded in response to nontarget stimuli only. Subjects were required to shift their attention from the visual to auditory target stimuli upon request. Target stimuli were presented randomly to control for nonspecific arousal effects. Since both visual and auditory stimuli were presented for each condition (look and listen), subjects received equal amounts of stimulation across conditions.

An attention effect was observed for those subjects with the fewest errors on the visual discrimination task (i.e., there was a significant reduction in the Wave I amplitude during the look condition) but not for those subjects with the greatest number of errors. The results were interpreted as evidence for the filtering of irrelevant stimuli at the periphery via the OCB. Lukas (1981) suggested that the filtering of irrelevant stimuli may take place at various levels within the sensory pathway as a function of organism and environmental conditions.

Using scalp-recorded visual evoked responses (VERs), Eason et al. (1983a) demonstrated a selective attention effect when human subjects selectively attended to visual stimuli presented in the periphery of the right (RVF) and left visual field (RVF). Selective attention was manipulated by requiring subjects to respond to flash stimuli presented at one spatial location, while ignoring such stimuli presented concomitantly at a homologous location. Flashes of light were presented in the peripheral RVF, LVF, and numerals (digits) were presented at a foveal fixation point. When stimuli in the RVF were relevant, those in the LVF were irrelevant and vice versa. In a third condition, stimuli presented foveally were relevant, while peripheral stimuli were irrelevant. VERs were recorded from the left and right internal canthi, and over the occipital lobe.

A significant attention effect was demonstrated for both the b-wave and afterpotential occurring within the 20-120 msec latency interval for the right canthal recordings. The attention effect was manifested in the VERS as increased negativity for the afterpotential under the attend condition relative to the unattend condition. The b-wave amplitude was greater under the attend than under the unattend condition for the right eye. A significant attention effect was also demonstrated for a late positive-going deflection peaking at about 200 msec poststimulus. The attention effect for this component was manifested as increased amplitude for the VER under the attend relative to the unattend condition. The attention-related modulation of the ERG was not evident in the recordings from the occipital region.

Eason (1984) essentially replicated the Eason et al. (1983a) study. In the follow-up investigation (Eason, 1984), the attention effect at the retina was more pronounced than for the earlier study. In addition to observing increased amplitude of the b-wave as a function of attention, Eason (1984) also observed decreased latency of the same component when subjects were selectively attending. The enhanced attention effect observed in the ERG responses in the 1984 study was attributed to more rigorous experimental control and the use of central-peripheral rather than peripheral-peripheral attentional shifts.

Mangun, Hansen, and Hillyard (1986) conducted a study similar to those by Eason (1984) and Eason et al. (1983a), and failed to demonstrate attention-related modulation of the b-wave component of the ERG. There were several differences between their study and the Eason (1984) and Eason et al. (1983a) studies which might account for their negative findings. For example, Mangun et al. (1986) used a slightly smaller evoking stimulus at a lower intensity than Eason (1984) and Eason et al. (1983a). Other differences between the investigations by Mangun et al. (1986) and Eason (1984) and Eason et al. (1983b) were: (1) length of interstimulus intervals, (2) method of recording ERG's, and (3) number of subjects used.

Eason (1984) and Eason et al. (1983a) interpreted their findings as evidence of precortical gating, and possible selective filtering of irrelevant visual information at the retina. With the exception of the ERG effect, these results were consistent with those obtained from a similar study (Eason, 1981) in which an attention effect was demonstrated for occipitically-recorded VER components occurring within the 70-100 msec latency range. The amplitude of the VER deflection was more negative for the attend relative to the unattend condition.

Increased negativity for VERs recorded under attend conditions relative to those recorded under unattend conditions appears to be the usual manner in which selective attention is manifested within the 20-120 msec latency interval, except for ERG b-wave attention effects. The increased negativity of deflections within this latency interval under attend conditions is generally thought of as a neurophysiological manifestation of selective attention (Naatanen, 1975, 1979, 1982).

Oakley et al. (1985) recorded VERs from electrodes placed on the frontal scalp. Selective attention to peripherally-presented stimuli too small to elicit ERGs was used to manipulate attention. A significant attention effect was manifested as relatively increased negativity for VERs recorded under the attend relative to the unattend condition over the 40-60 msec latency range. In a follow-up study (Oakley et al., 1986) similar results were obtained.

The studies by Eason (1984) and Eason et al. (1983a), which demonstrated possible centrifugal modulation of retinal responses (i.e., significant attention effects for the b-wave and afterpotential) have important implications for the precortical gating hypothesis. Such an effect implies that selective filtering of irrelevant sensory input can occur as early as the retinal level under some conditions. This implies the existence of a retinopetal pathway in the human visual system. These appear to be the only two studies in the literature reporting such an attention effect in scalp-recorded VERs.

Arousal Factors and Selective Attention

It is possibile that the demonstration of early attention effects is, in part, due to arousal or motivational factors. Eason et al. (1969) demonstrated that some VER components were enhanced as a result of both attention and arousal manipulations. It was pointed out in the earlier section dealing with the function of corticofugal visual pathways, that connections which could possibly mediate interactions between attentive and motivational states exist. The fact that stimulation of the reticular formation (MRF) influences unit activity in various thalamic nuclei which are known to receive direct input from the retinas and visual cortical areas (Doty et al., 1973; Pecci-Saavedra et al., 1966; Singer, 1977; Swallow, 1983) suggests a possible mechanism wherein both attentional and arousal factors could influence transmission within the visual pathways. Evidence exists which is consistent with the position that arousal factors possibly influence selective attention as manifested in scalp-recorded VERs (Eason, 1985). Based upon these findings, it appears as if motivational factors might influence the ability to selectively attend.

Statement of Purpose

Eason et al. (1983b) determined that in order to record ERGs of sufficient magnitude to permit reliable measurement of the b-wave and afterpotential from periorbital locations, the evoking stimulus should be relatively large and of high intensity (i.e., relatively high in saliency). In subsequent studies, Eason (1984) and Eason et al. (1983a) used relatively large circular stimulus flashes (subtending 6 1/2 degrees of visual angle) of relatively high intensity to demonstrate attention-related modulation of the ERG b-wave and afterpotential. The selective attention effect on the ERGs evoked by the large, salient stimulus was manifested in canthal recordings as greater b-wave amplitude (i.e., more positivity at peak latency) under the attend than under the unattend condition. The amplitude of the afterpotential was also greater (i.e., was more negative at peak latency) under the attend than under the unattend condition.

The results of these ERG-attention studies were interpreted as evidence that centrifugal neural influences associated with the behavioral state of the individual may alter sensory transmission at the level of the retina. Although this may have been the case, it is possible that the canthal recordings which revealed ERG activity may have also been influenced by field potentials generated in subcortical brain structures during the same latency interval of the b-wave. Thus, it may have actually been this subcortical neural activity which was modulated by the attention manipulation rather than retinal b-wave activity. To test this possibility, Oakley (1984) recorded the field potential activity occurring within the 40-100 msec interval poststimulus evoked by stimuli too small (35 minutes of visual angle), and too dim to elicit discernible ERGs, even at canthal sites. Simultaneous recordings at scalp locations too far removed from the eyes to detect ERG activity, in the event any should occur, were also obtained. An attention effect was manifested within the latency interval of the b-wave; however, the polarity of the deflections were relatively more negative under the attend than under the unattend condition.

The attention effect demonstrated by Oakley (1984) within the 40-70 msec interval, using the relatively nonsalient, non-ERG-evoking stimulus was opposite that demonstrated by Eason (1984) and Eason et al. (1983a) within the same latency interval, using the relatively salient, ERG-evoking stimulus. When a b-wave was elicited, the attention effect within the 40-70 msec interval was manifested as greater positivity under the attend, relative to the unattend condition. Conversely, when no b-wave was elicited, the attention effect was manifested as greater negativity associated with the attend condition within the same latency interval. The results obtained by Oakley (1984) were corroborated in subsequent studies (Oakley, et al., 1985, 1986) using stimuli too nonsalient to elicit discernible ERGs at canthal recording sites. These findings were interpreted as evidence that spatial selective attention influences sensory transmission at subcortical levels of the visual system. The scalp field potentials associated with such attention influences was relatively more negative under the attend than under the unattend condition.

Oakley did not obtain recordings at canthal sites in her studies employing the relatively nonsalient stimuli (Oakley, 1984; Oakley et al., 1985, 1986), nor did Eason et al. (1983a) obtain VER recordings from frontal scalp locations in response to the larger, relatively more salient stimuli in their initial ERG-attention study. Thus, it is presently unknown how the field potentials elicited by relatively salient and relatively nonsalient stimuli influence recordings obtained simultaneously at canthal and frontal scalp locations. By varying stimulus saliency in a single study, while using the attention paradigm of Eason (1984), Eason et al. (1969, 1983a), and Oakley et al. (1985, 1986), it should be possible to elucidate further the relative influences of retinal and subcortical generators of the field potentials for VER deflections occurring within the latency interval of the b-wave and afterpotential of the ERG (i.e., approximately 40-130 msec from b-wave onset to afterpotential offset).

Retinal and Subcortical Contributions Within the 40-70 Msec Latency Interval

The ERG b-wave is typically manifested within the interval of about 40-70 msec poststimulus. One of the objectives of this study was to assess the effects that relatively salient and relatively nonsalient stimuli have on VERs recorded from canthal and frontal scalp sites, in a single experiment, in an effort to delineate the relative contributions of retinal and subcortical activity to such recordings within the b-wave interval. Considering the findings discussed earlier in this section, one would predict that use of a relatively salient evoking stimulus would elicit clearly discernible and measurable ERGs in VERs detected by electrodes located at the internal canthi. In such case, the retinal contribution to the canthal recordings, relative to contributions of a more remotely located subcortical generator, should be substantial. When a small, relatively nonsalient stimulus which is too small to elicit discernible ERGs at canthal sites is used, the retinal contribution to VERs within the 40-70 msec interval should be minimal. In this case, the influence of the subcortically generated activity should be relatively more substantial at the canthal sites than retinal activity.

The attention effect in response to a relatively large, salient evoking stimulus should be manifested within the 40-70 msec interval as a relatively more positive b-wave peak latency under the attend compared to the unattend condition. Conversely, the attention effect for the small, relatively nonsalient stimulus should be manifested as relatively more negative deflections under the attend compared to the unattend conditions within the same latency interval. Moreover, when the respective voltages of the deflections for the attention effects for the large and small stimuli are compared, the deflections evoked by the large stimulus (within the 40-70 msec interval) should be more positive than those for the small, relatively nonsalient stimulus. Thus, one would predict an interaction between selective attention and stimulus size (i.e., saliency) whereby the magnitude, and possibly the direction, of the attention effect in the latency interval containing the b-wave (40-70 msec) would vary as a function of the size of the evoking stimulus. Such an interaction would constitute evidence for differential contributions of retinal and subcortical influences in deflections occurring within the b-wave latency interval. Accordingly, selective attention would drive the retinal contribution to canthal recordings in a relatively more positive direction. Conversely, selective attention would drive the subcortical contribution in a more negative direction. Under conditions in which retinal and subcortical contributions are approximately equal, their combined influence on the deflections would tend to offset one another, since the field potentials detected at canthal sites from these two sources are of opposite polarity (the retinal source being positive; the subcortical source being negative).

Frontal scalp recording sites are unfavorably located to detect retinal activity, except under conditions in which the evoking stimulus is extremely salient (i.e., very large, intense flash stimuli). Consequently, one would expect subcortical activity to be the dominant contributor to field potentials obtained at frontal scalp recording sites for both the large and small stimuli used in this study. Thus, one would predict that any attention-related effect for frontal scalp recordings would be manifested as increased negativity within the 40-70 msec latency interval under the attend, relative to the unattend condition, for both large (relatively salient) and small (relatively nonsalient) stimuli. Consequently, the type of interaction between attention and stimulus size predicted for canthal recordings would not be expected in frontal scalp recordings. If frontal scalp recordings were to reveal an interaction between attention and stimulus size, it should be in the opposite direction of the predicted effect for canthal recordings; that is, one would expect the attention effect to be associated with greater negativity between the attend and unattend conditions for the large than for the small stimulus.

Retinal and Subcortical Contributions Within the 70-130 Msec Latency Interval

The afterpotential of the ERG is known to occur within the 70-130 msec latency interval poststimulus. Eason et al. (1983a) found canthal recordings of the ERG afterpotential evoked by relatively salient stimuli (6 1/2 degrees of visual angle) to be enhanced in magnitude as a function of selective attention. The polarity of the component was relatively more negative at its peak latency under the attend than under the unattend condition. In a subsequent study using the same size stimulus, Eason (1984) observed increased negativity within the 70-130 msec interval as a function of selective attention in VER deflections recorded at frontal scalp locations. Since it is highly unlikely that retinal activity (i.e., the b-wave afterpotential) contributed to the attention-related enhanced negativity observed in the frontal scalp recordings, it follows that the dominant contributors to the field potentials registered at the scalp during this latency interval were of subcortical (for the earlier part of the interval) and early cortical origin (for the latter part of the interval).

The effect of selective attention is manifested as relatively more negative field potentials at canthal and frontal scalp recording sites within the 70-130 msec interval, regardless of whether they arise from retinal, subcortical, or cortical generator sources. Therefore, one would predict that responses obtained simultaneously from canthal and frontal scalp locations would be relatively more negative under attend than under unattend conditions within the 70-130 msec latency interval for both large (relatively salient) and small (relatively nonsalient) stimuli. If the magnitude of the attention effect is dependent on the saliency of the stimulus, one would expect the increased negativity observed at canthal sites under the attend condition to be relatively greater for a large (6 1/2 degrees) than for a small (35 minute) stimulus, since the combined influence of both retinal and more centrally located generators would be additive. Frontal recordings are minimally affected, if at all, by the retinal influences for either large or small stimuli. Therefore, an attention by stimulus size interaction for frontal scalp VERs, if observed, would have to be due to the differential impact of the large and small stimuli on the responsivity of the subcortical and/or cortical generators responsible for the VER deflections occurring within the 70-130 msec latency interval. No prior predictions were made regarding the possibility of such an interaction, but it would not be surprising if one were to occur. In such case, one would expect the magnitude of the attention effect to be relatively greater for the large than for the small stimulus.

Possible Interaction Between Selective Attention and Motivation

Eason et al. (1969) observed that variations in general arousal level influences the magnitude of VERs. Arousal was manipulated by having subjects selectively attend under the threat of shock for late reaction times, or without such threats. It was found that VER amplitude was greater, and reaction times were shorter, for the shock-threat than for the no shock-threat condition. The latency intervals for which the arousal-related enhancement of the VERs was demonstrated were those in which mostly cortical activity is generally thought to occur.

Although Eason et al. (1969) did not examine whether the attention effect interacts with arousal level, inspection of their figures suggests this may have been the case. Also, it is possible that such an interaction may exist in VER deflections falling within the 40-130 msec interval, given the findings of the animal studies discussed in the introduction. By manipulating the motivation level of subjects, it should be possible to ascertain whether any attention effects demonstrated within the 40-70, 70-100, and 100-130 msec latency intervals are enhanced by psychological states which increase general arousal. Should this be the case, it would provide further support for centrifugal influences on sensory transmission at subcortical locations above and beyond that induced by the attention manipulation alone.

Eason et al. (1969) used shock as an incentive for altering arousal level. Since this method is no longer used, it may prove to be difficult to vary arousal level sufficiently to produce a measurable effect in early VER components, even if arousal level influences early sensory transmission. Using the Eason et al. (1969) attention paradigm, there may be a near ceiling effect with respect to motivation level, due to the subjects' desire to perform the task as best they can under all conditions. Nonetheless, a secondary purpose of this study was to attempt to assess the effects of motivation on early VER components, along with effects of selective attention.

Interaction Between Selective Attention and Visual Field

Since the visual system is symmetrical, no apriori predictions were made regarding possible interactions involving the visual field in which attended and unattended stimuli are presented. This does not rule out the possibility of obtaining such interaction effects, however. Eason (1984) found that recordings from the right internal canthus contained significantly more positive b-waves under the attend than under the unattend condition, but no such effect was revealed in recordings from the left eye. If an interaction involving the visual field to which subjects attend were obtained in the present study, one would expect it to involve differences in relative magnitudes rather than polarity, due to the symmetrical nature of the visual system and the display of visual stimuli in the present study.

CHAPTER II

METHOD

Subjects

Eight adults, four females and four males, served as subjects, seven of whom were affiliated with the UNC-G Psychology Department. They included a professor of psychology, five graduate students, and an undergraduate psychology major. The remaining subject was the spouse of a UNC-G graduate student of psychology. Three of the subjects were naive to the recording of visually evoked responses (VERs).

Subjects were recruited on a voluntary basis. Although pay was offered for participation, not all subjects accepted payment. It was observed, however, that whether or not subjects accepted payment made no difference in their responses, or their effort to perform. All subjects appeared to be highly motivated to participate in the study, and each was cooperative with the experimenter.

Independent Variables

Five variables were manipulated: (1) attentional state, (2) feedback, (3) stimulus size, (4) visual field, and (5) VER recording site.

Attention Manipulation

The attention condition consisted of two levels: attend and unattend. Attention was manipulated by experimenter instructions to attend to a given visual field - right or left - wherein target stimuli to which the subject was required to respond occasionally appeared, while attempting to ignore stimulus flashes presented concomitantly, but never simultaneously, at a homologous location in the opposite field. From the subjects' perspective, the attended field was relevant; the unattended one was irrelevant. The spatial locations in which the relevant and irrelevant stimuli appeared constituted the visual field manipulation.

Feedback Manipulation

The feedback manipulation was employed in an effort to systematically vary the subject's motivational state. Implicit in the manipulation was the assumption that a relatively high motivation level should be created by providing periodic feedback on the quality of performance, whereas a relatively low motivation level would result in the absence of such feedback. Feedback was provided by a loud tone when the subject failed to respond to a target stimulus appearing in the relevant visual field within a specified time limit (approximately 500 msec), or failed to respond at all. The feedback manipulation thus consisted of two levels: feedback (FB) and no feedback (NFB).

Stimulus Size Manipulation

Stimuli presented to subjects were of two sizes. The large stimulus subtended at 6 1/2 degrees of visual angle (VA), while the small stimulus subtended 35 minutes of VA. Stimulus intensity was approximately four log units above a background luminance level of about one millilambert.

VER Recording Sites

Visually evoked responses (VERs) were obtained with surface electrodes placed at four different locations: (1) the internal canthus of the left eye (ICL), (2) the internal canthus of the right eye (ICR), (3) the frontal scalp of the left hemisphere midway between the FP1 and F3 positions (FL), and (4) the frontal scalp of the right hemisphere, midway between the FP2 and F4 positions (FR). VERs were recorded simultaneously from all four location sites. All recording electrodes were referenced to the right earlobe, with the left earlobe serving as a ground.

Dependent Variables

Three latency intervals of the recorded VERs falling within the first 130 msec poststimulus were selected for measurement and subsequent statistical analysis. The average vertical distance of the VER deflections falling within each latency interval, relative to a zero baseline was measured in millimeters (mm), and subsequently converted to microvolts (μV). The peak-to-trough of a positive-going deflection, with a peak latency of approximately 180 msec, was also measured.

Behavioral data were obtained by observing the number of late or missed responses committed by subjects on the reaction time task. The task consisted of having subjects release a microswitch as quickly as possible following each presentation of a target stimulus.

The behavioral data were used to provide systematic feedback to subjects at periodic intervals during feedback trials, and to cue the experimenter that the subject was performing the task appropriately. Since these data had no direct relevance to the question of early sensory processing in the visual system, they were not subjected to quantitative analysis. However, the data were examined in order to verify that each of the subjects did in fact perform the tasks as they were instructed.

Experimental Conditions

Eight experimental conditions were created by combining the various levels of the attention, feedback, stimulus size, and visual field variables (Table 1). These eight experimental conditions were presented over two consecutive sessions, and each session consisted of four trials.

Display of Experimental Conditions

A schematic drawing of the stimulus display is shown in Figure 1. Stimuli were presented on a background screen formed by a 70 x 102 centimeter piece of white poster board. From the subject's perspective, the screen had a concave surface, which placed all points along the horizontal meridian equidistant from the eyes. The stimulus delivery setup consisted of the white screen, a foveal fixation point, appertures for presenting flashes of light in the subjects' LVF or RVF, a chin rest, and a bite board.

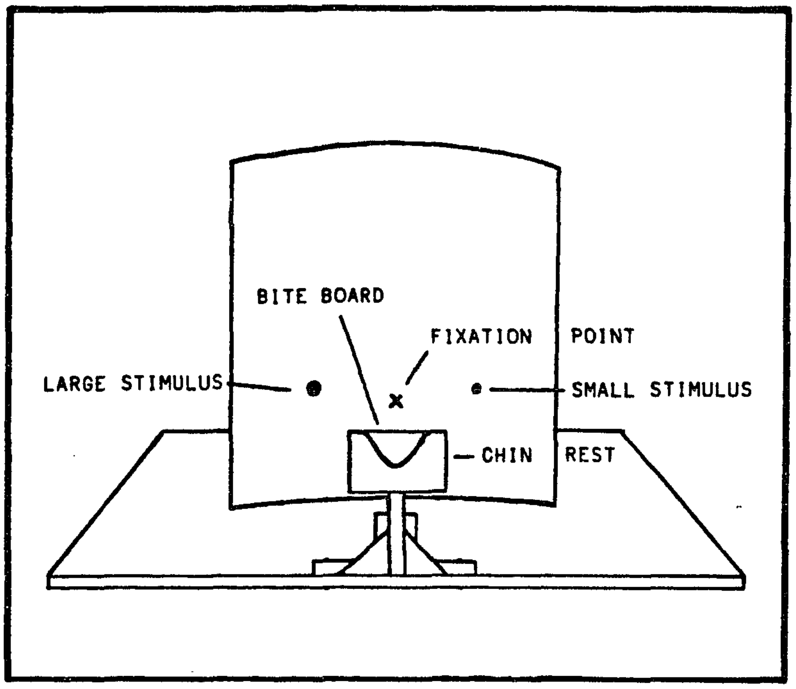

Figure 1

Schematic Drawing of the Physical Display

Not shown in the figure is the microswitch with which subjects activated and deactivitated the stimulus delivery system. This switch, which also served as the reaction time key, was placed on the table immediately in front of the subject. It could be moved about to allow for more comfort, if desired. In the schematic drawing, the large stimulus is appears in the LVF, the small one in the RVF.

The chin rest and bite board stabilized the subject's head, which was oriented toward the foveal fixation point. Subjects were instructed to place their upper teeth firmly on the bite board, while bringing their lower teeth gently against its lower surface. They were specifically instructed not to bite the board hard, as this would generate undesired myogenic activity. Observations from previous studies (Eason, 1985) have shown that myogenic activity generated by the frontalis muscles can enter VERs when subjects look in an upward direction. Consequently, the chin rest was adjusted to permit the subjects to look at the fixation point with the eyes rotated slightly downward. Each subject was provided with a personal bite board.

The appertures through which stimulus flashes were presented were located approximately 20 centimeters to the right and left of the fixation point. From the subject's perspective, they were located 30 degrees away from the fixation point.

Apparatus

Photostimulators

Two Grass Model PS-2 photostimulators were used to present the stimulus flashes, one for each visual field. Lehigh Valley Electronic (LVE) solid state programming modules were used to control the timing and order of presentation of the stimuli. White noise, generated by a Granson-Stadler Model 901-B amplifier, masked the sounds associated with the electronic equipment during the presentations of stimuli.

The tone used to provide feedback to the subjects was controlled by LVE solid state equipment. The tone was emitted 250 msec following late or missed responses to double flash stimuli presented in the relevant (attended) visual field.

Background Illumination

Three 60-watt light bulbs were used to illuminate the visual display area. Light generated by these bulbs passed through red acetate filters, which created a red background in order to increase the responsivity of the rods. The lights were located on either side, and above the display area.

Display Cubicle

While recording, subjects sat in a copper shielded cubicle approximately six feet wide on all sides, and eight feet high. The copper shielding, which was connected to ground, minimized the occurrence of electrostatic interference in the VER records. The cubicle walls were covered with soft fiber board.

Electrodes

Gold cup electrodes were used for recording VERs from canthal and frontal scalp locations. Clip-on type electrodes which were attached to the two earlobes, served as reference and ground for the active canthal and frontal electrodes. All electrodes were filled with electrically conductive cream to lower contact resistance. Other measures taken to establish and maintain low contact resistance were: (1) thoroughly cleaning the skin first with water, and then with rubbing alcohol; (2) taping the electrode firmly in place, and (3) checking the resistance after attachment. Contact resistance was kept below 10,000 ohms. If an attached electrode exceeded this value, it was removed and the skin preparation procedure was repeated.

Preamplifiers and Amplifiers

A Grass Model 7 polygraph equipped with 7P5A EEG voltage preamplifiers coupled to a 7P1 driver amplifier was used to amplify the signals detected at each electrode location. The 1/2 amplitude low and high frequency dials were set at one and 35 Hz respectively.

Signal Averaging Computers and VER Plotters

Two averaging computers were used to store and average signals picked up by the four active electrodes in response to the relevant and irrelevant stimulus presentations. One was a Technical Measurement Corporation (TMC) Computer of Average Transients (CAT); the other was an IBM XT, used in conjunction with a Modular Instruments M1000 Laboratory Signal Processing Program (Version 1.5).

The two computers were calibrated with respect to the initiation and termination of each averaging sweep, and their amplification factor. This calibration ensured that the averaging characateristics of the two computers were identical. On a given trial, one computer recorded VERs elicited by stimuli appearing in the relevant (i.e., attended) visual field, while the other recorded VERs elicited by stimuli appearing in the irrelevant (i.e., unattended) field. The computers were systematically switched across trials with respect to the relevancy of the field from which averages were obtained (i.e., they were counterbalanced).

A Moseley Model 2D2 X-Y plotter, and an IBM printer were used to plot the VERs recorded and averaged by the TMC-CAT and IBM XT, respectively. The vertical and horizontal scales used by the two plotters were calibrated, making them identical with respect to voltage and time units. Thus, the amplitude and latency of VERs plotted by the two machines could be compared directly.

Oscilloscope Used to Monitor EEG Activity

A Farchild Model 708-A oscilloscope was used to monitor ongoing EEG activity during data collection. This activity was routinely monitored for signs of excessive myogenic activity or other artifacts which might contaminate the VERs.

Procedure

Introduction of Study to Subjects

Prior to data collection, subjects were brought to the laboratory and shown the various equipment used to record VERs. The purpose of the study and the general procedure to be used were explained. Subjects were then shown the visual display area, where they had an opportunity to practice responding to relevant stimuli without moving their eyes. Each subject was given ample time to practice responding to the stimuli under all conditions.

Following the initial practice, subjects were shown how to prepare their skin for attachment of the electrodes. Once the electrodes were in place, and their resistance tested, subjects returned to the display area for more practice. Data collection was begun only after the subjects demonstrated a thorough understanding of the experimental procedures, and the ability to perform the task without making eye movements or blinking.

Before beginning the recording sessions, the delay interval preceding the late response feedback tone was adjusted for each subject so as to make the task equally difficult across sessions and subjects. The interval was set at a point where subjects responded late to target stimuli approximately 30% of the time.

Procedure for Data Collection

Soon after reporting for a session, subjects began preparing for electrode placement. After the electrodes were placed and checked, subjects were given instructions for the first of the four within session trials (e.g., "You are to attend to the large stimulus, in the LVF. You will get feedback on your performance for this trial").

When ready subjects began presentation of stimulus flashes by depressing the microswitch. Stimuli were presented as long as the switch was depressed, or up to 20 stimulus presentations. After 20 stimulus presentations, a 10 second break was imposed by the experimenter. Subjects could initiate a break at any time during the session, however, by releasing the microswitch. Observations from previous studies (Eason, 1985) have indicated that when subjects fail to take adequate breaks, their ability to selectively attend is impaired. For this reason, they were encouraged to take as many breaks as desired. During breaks, subjects were free to move about, to the extent that the electrode leads allowed. At the end of each trial, subjects exited the shielded cubicle for a relatively long break. When indicated, feedback was given at the end of a trial.

Design

Sessions

Table 2 shows the eight sessions, four within session trials, and the order in which the experimental conditions were presented within each session, for each subject. Sessions appear in the row at the very top of the figure. The four within session trials appear in the row immediately under the session row. An experimental condition is shown for each trial, and subject. Subjects are listed in the first column. Each subject completed a total of eight sessions, and 32 trials. Four replications were obtained for each experimental condition. Figure 2 also depicts the experimental design.

Counterbalancing Experimental Conditions Across Sessions

As indicated in Table 2, the eight experimental conditions were counterbalanced across sessions. Half the subjects received feedback on their performance during the first session, and half did not. The feedback conditions were reversed for the next session. The counterbalancing procedure was followed throughout the next six sessions. The size of the stimulus to which subjects were instructed to attend also was counterbalanced, as was the visual field in which the attended stimulus was presented.

Replications of Experimental Conditions

The presentation of each experimental condition was replicated four times for each subject. During sessions one through four, the first two replications were completed. The last two replications were completed during sessions five through eight.

Designation of Target Stimuli

Stimuli consisted of flashes of light with a duration of ten microseconds. Some of the stimuli consisted of single flashes with a duration of ten microseconds, and others consisted of double flashes, separated by 200 msec, with a duration of 10 microseconds each. The flashes, both single and double, were either large (6 1/2 degrees of visual angle) or small (35 minutes of visual angle). Subjects were instructed to attend to double flashes occurring in one visual field

SUBJECTS	ATTEND								UNATTEND							
	NO FEEDBACK				FEEDBACK				NO FEEDBACK				FEEDBACK			
	LVF		RVF		LVF		RVF		LVF		RVF		LVF		RVF	
	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S
1																
2																
3																
4																
5																
6																
7																
8																

LVF: LEFT VISUAL FIELD
RVF: RIGHT VISUAL FIELD
L : LARGE STIMULUS
S : SMALL STIMULUS

Figure 2

Schematic Representation of Experimental Design

		SUBJECT PROVIDED WITH ______, AND INSTRUCTED TO:	
EXPERIMENTAL CONDITION	A	NO FEEDBACK	ATTEND TO SMALL STIMULUS IN LEFT VISUAL FIELD
	B	NO FEEDBACK	ATTEND TO LARGE STIMULUS IN LEFT VISUAL FIELD
	C	NO FEEDBACK	ATTEND TO SMALL STIMULUS IN RIGHT VISUAL FIELD
	D	NO FEEDBACK	ATTEND TO LARGE STIMULUS IN RIGHT VISUAL FIELD
	E	FEEDBACK	ATTEND TO SMALL STIMULUS IN LEFT VISUAL FIELD
	F	FEEDBACK	ATTEND TO LARGE STIMULUS IN LEFT VISUAL FIELD
	G	FEEDBACK	ATTEND TO SMALL STIMULUS IN RIGHT VISUAL FIELD
	H	FEEDBACK	ATTEND TO LARGE STIMULUS IN RIGHT VISUAL FIELD

Table 1

Experimental conditions created by combining the two levels of the Attention, Stimulus Size, Feedback, and Visual Field Manipulations.

SESSIONS		1	2	3	4	5	6	7	8
TRIALS		1 2 3 4							
SUBJECTS	1	A B C D	E F G H	B D A C	F H E G	C A D B	G E H F	D C B A	H G F E
	2	B D A C	F H E G	G E H F	C A D B	H G F E	D C B A	E F G H	A B C D
	3 *	C A D B	G E H F	C A D B	G E F H	H G F E	D C B A	E F G H	A B C D
	4	B D A C	H G E F	A B C D	E F G H	B D A C	F H E G	G E H F	C A D B
	5	E F G H	A B C D	B D A C	F H E G	C A D B	G E H F	D C A B	H G F E
	6	F H E G	B D A C	C A D B	G E H F	D C B A	H G E G	A B C D	E F G H
	7	G E H F	C A D B	D C B A	H G E F	E F G H	A B C D	B D A C	F H E G
	8	H G F E	D C B A	A B C D	E F G H	F H E G	B D A C	C A D B	G E H F

*COMPLETE COUNTERBALANCING WAS NOT ACHIEVED FOR SUBJECT NUMBER THREE. DUE A DECISION TO USE DATA OBTAINED IN TWO PREVIOUS SESSIONS, AFTER HAVING COLLECTED DATA ACROSS TWO SESSIONS USING THE SAME ORDER OF PRESENTATION OF EXPERIMENTAL CONDITIONS. OBSERVATIONS INDICATED THAT THE ORDER IN WHICH DATA WERE COLLECTED FROM EACH SUBJECT HAD LITTLE OR NO EFFECT ON VER WAVEFORMS.

Table 2

Counterbalancing procedure used to achieve four complete Replications of the eight experimental conditions for each of the eight subjects. Sessions appear in the row at the very top. The four within session trials appear in the row immediately under the session row. Subjects are listed in the first column.

only (either the right or left). VERs elicited by single flashes were recorded from both the attended and unattended visual fields during each trial. VERs were not recorded to the doublets. Stimuli were presented binocularly at all times.

Behavioral Task

Upon the observation of a double flash in the attended visual field, subjects were instructed to release the microswitch (which deactivated the stimulus delivery system) as quickly as possible. If they did not respond at all, or responded too slowly, a tone (signifying a late response or a miss) was amplified to about 60-70 decibles and transmitted to the subject through a speaker. The tone was not presented when late responses or misses occurred under the no feedback conditions, or when double flashes occurred in the unattended visual field.

CHAPTER III

RESULTS

PREPARATION OF DATA FOR STATISTICAL ANALYSIS

Single Subject Averaged Analog Tracings

Averaged responses, collapsed across the four replications, were obtained for each experimental condition and recording site for each subject. This averaging process generated a total of 64 VERs for each subject (two for each experimental condition and recording site), each VER being the composite average of four separate VERs. Quantitative measures were obtained from these composite averages, each of which was based on a total of 400 stimulus flashes (100 per individual average).

Since VERs were recorded in response to the attend and unattend stimuli concomitantly for each of the eight experimental conditions, a complete single subject analog record consisted of 16 separate composite averaged VER waveforms for each recording site. The waveforms, corresponding to the two attentional states of the subject, were superimposed on a common zero baseline for each experimental condition and recording site. The VER for the attend and unattend conditions were constructed with a solid and dashed line, respectively. Such superimposition permits a direct visual comparison of the two waveforms obtained under attend and unattend conditions with respect to all other experimental conditions for each recording site.

The zero baseline was determined by averaging through the first 30 milliseconds (msec) following stimulus onset (time 0 msec) of each composite response for each subject. Following the neuroscience convention, negative VER deflections extend above baseline; positive ones extend below the baseline.

Determining VER Latency Intervals for Statistical Analysis

Latency intervals for which quantitative measures were obtained were selected on the basis of results of previous research, the primary objectives of the current study, and from visual inspection of the grand averages of the waveforms collapsed across the eight subjects for each experimental condition and recording site. The latency interval (LI) of 40-100 msec poststimulus was of particular interest in this study, because it constitutes the range in which both retinal and subcortical activity is known to occur (Eason, 1984; Eason et al., 1983b), and thus, is most closely linked to the precortical gating hypothesis. However, later components were also measured and subjected to statistical analyses.

Three latency intervals (LIs) were selected for quantitative measurement: 40-70 msec; 70-100 msec; and 100-130 msec. In addition, integrated measures were obtained across the first two latency intervals (40-70 and 70-100), and across all three intervals (40-70, 70-100, 100-130). This yielded latency intervals of 40-100 and 40-130. Finally, a peak-to-trough measure was obtained of a relatively late positive-going component having a peak latency of approximately 180 msec.

Quantification of Analog Data

Measurements within each of the VER latency intervals (LIs) selected for analysis (with the exception of the peak-to-trough measure) were made at 10 msec intervals and summed to obtain quantitative data for statistical analysis. Measurements consisted of determining the vertical distance (in mm) of the VER deflections from baseline. Deflections above baseline were assigned negative values, while those below baseline were assigned positive values. Deflections mostly above baseline yielded negatively summed values; those mostly below yielded positively summed values.

The peak-to-trough quantitative data were obtained by measuring the vertical distance from the peak (the greatest point in the negative-going direction) and the trough (the greatest point in the positive-going direction) within the 150-180 msec range. All measurements were converted from mm to microvolts (μV) using the following conversion factor: 12.5 mm = 1 μV.

All quantitative measurements were made from single subject composite averaged analog tracings, which had been separated by recording site (ICL, ICR, FL, and FR), attention (attend, unattend), stimulus size (large, small), feedback (feedback, no feedback), and visual field (LVF, RVF).

Group Averaged Analog Tracings

Group averaged analog tracings for each experimental condition and recording site were obtained by averaging across the single subject composite averages. The group averaged tracings constitute an analog display of group means for each of the VER LIs subjected to statistical analysis.

The group averaged tracings for the ICL and ICR recording sites were averaged to produce analog tracings collapsed across the two internal canthi recordings. These tracings also depict (in analog form) the quantitative data obtained by averaging the values for the composite group averaged tracings for the FL and FR recording sites. These combined data, which shall hereafter be referred to as ICLR and FLR, were obtained for each experimental condition. Figures 3a, 4a, 5a, 6a, 7a, and 8a show the composite group averaged analog tracings for the ICL, ICR, FL, FR, ICLR, and FLR recording sites, respectively.

Basic Data Format

Waveforms corresponding to each experimental manipulation are shown in Figures 3a-8a. The first pair of VERs located in the upper most portion of the left and right figures represent the responses to the large stimulus under the no feedback (NFB) condition. The left figure depicts responses to stimuli in the LVF; the right depicts responses to stimuli in the RVF. The VERs, located immediately below the previously described pair, constitute responses to the small stimulus flashes under the NFB condition for the LVF and RVF.

The tracings in the extreme lower portion of each figure constitute responses to the small stimulus under the feedback (FB) condition, those located immediately above these tracings depict responses to the large stimulus under the same condition. The horizontal distance between vertical lines in each figure represent 100 msec intervals, starting at the time of stimulus onset (time 0). The latency intervals from which quantitative data were obtained for statistical analysis are readily discernible in each figure.

Figures 3b, 4b, 5b, 6b, 7b, and 8b depict the group mean deviations from baseline for the six VER LIs from which quantitative data were obtained (Figures 3a-8a). VER LIs are represented in horizontal rows; feedback and visual field are represented in the vertical columns. Stimulus size and attention are plotted in each individual graph. The two left columns represent responses from the LVF and RVF, respectively, under the NFB condition. The two columns on the right show equivalent responses under the FB condition. The horizontal bar in each graph represents baseline. The mean deviations from baseline are plotted in μVs for each experimental condition and VER component.

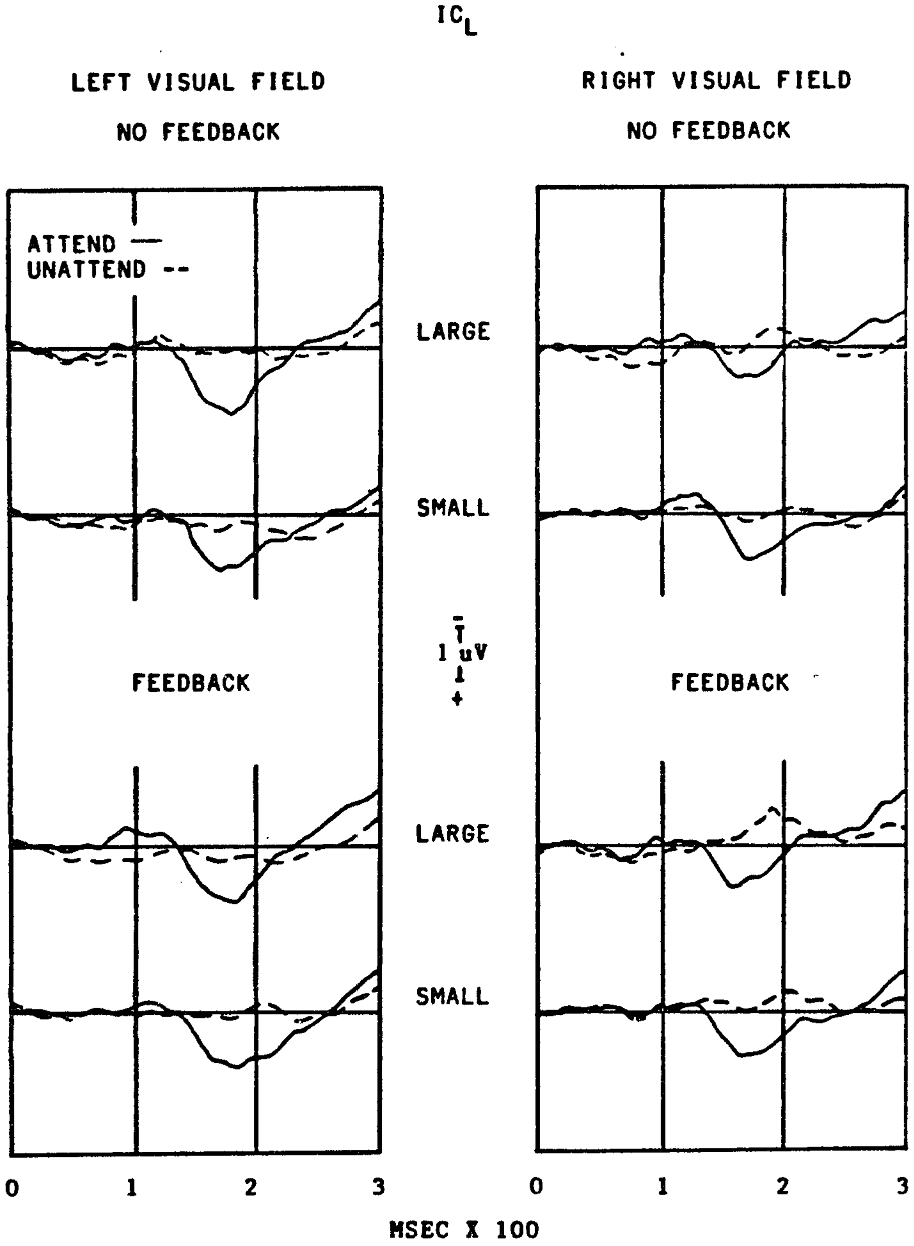

Figure 3a

Group averaged analog tracings for left internal canthus recordings. VERs are depicted for each of the experimental manipulations.

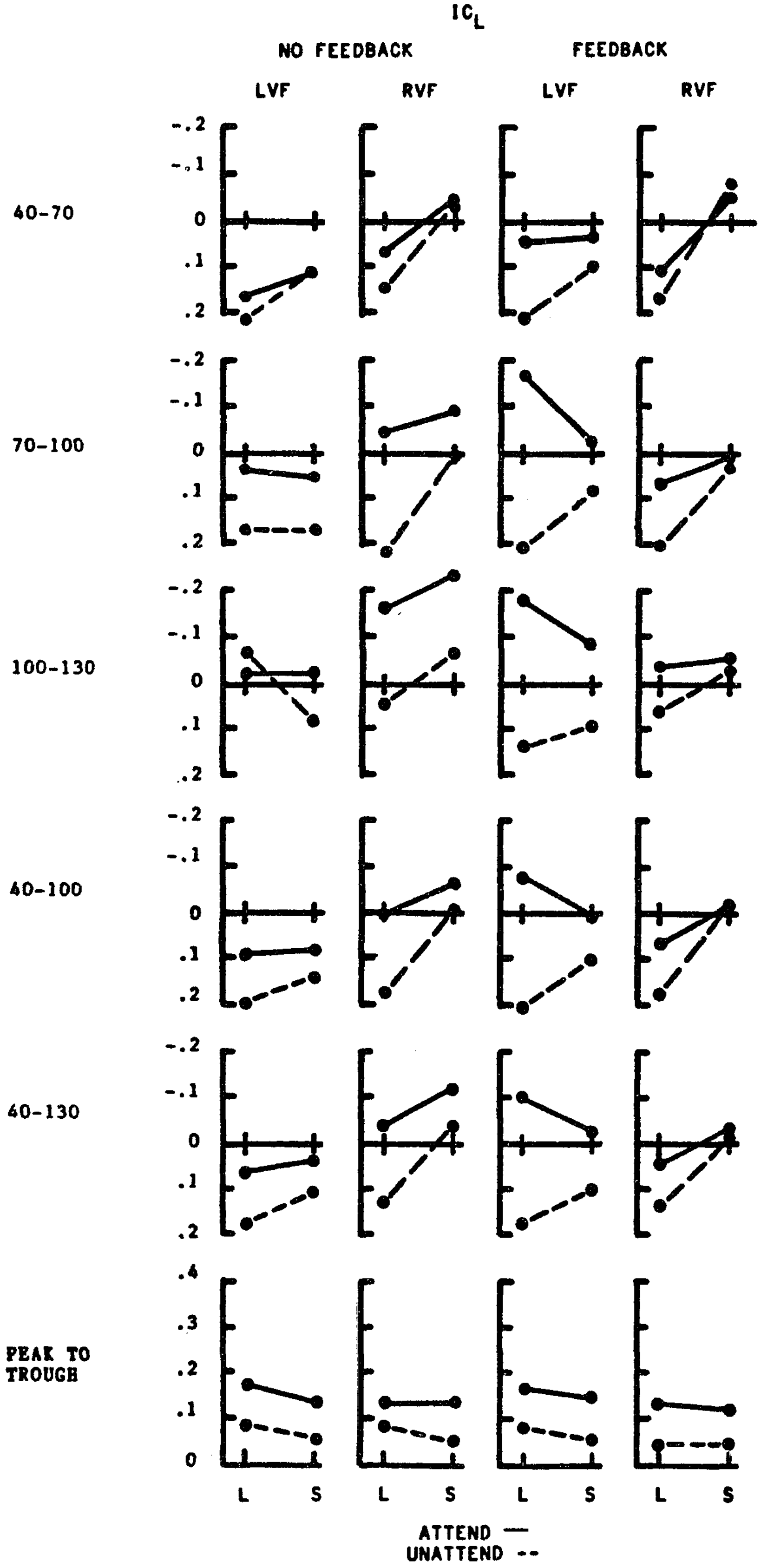

Figure 3b

Graphic representation of group averaged analog tracings for left internal canthus recordings as a function of Attention and Stimulus Size.

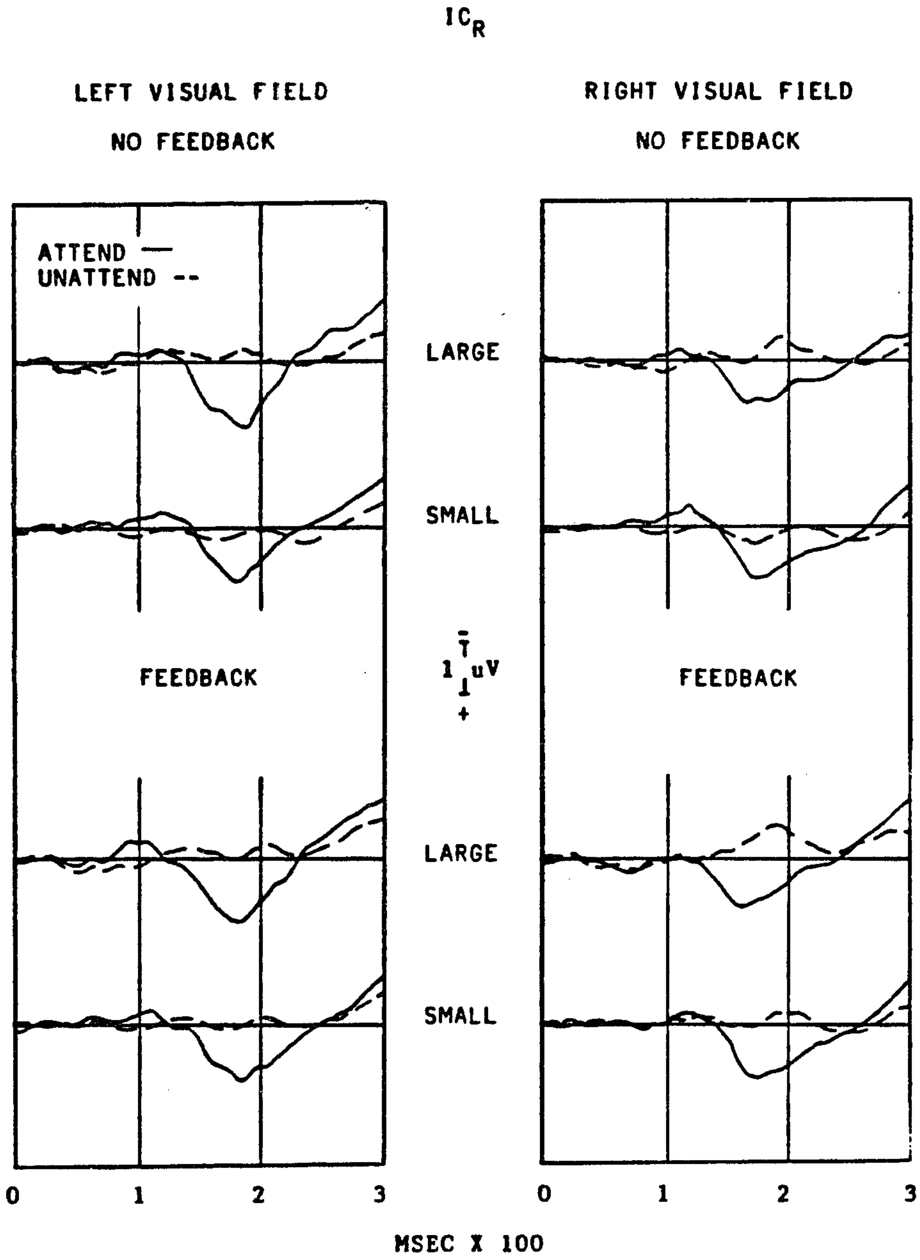

Figure 4a

Group averaged analog tracings for right internal canthus recordings. VERs are depicted for each of the experimental manipulations.

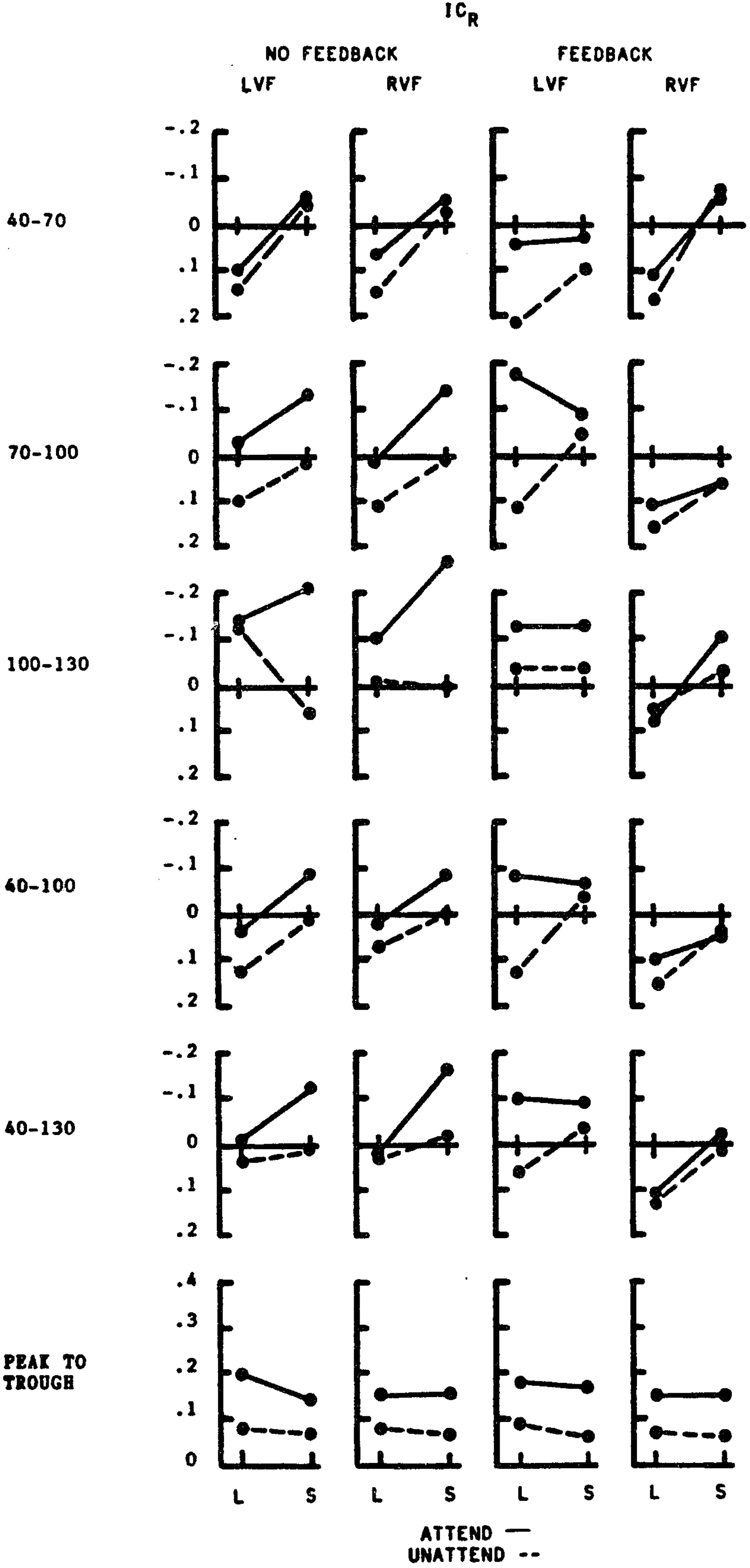

Figure 4b

Graphic representation of group averaged analog tracings for right internal canthus recordings as a function of Attention and Stimulus Size.

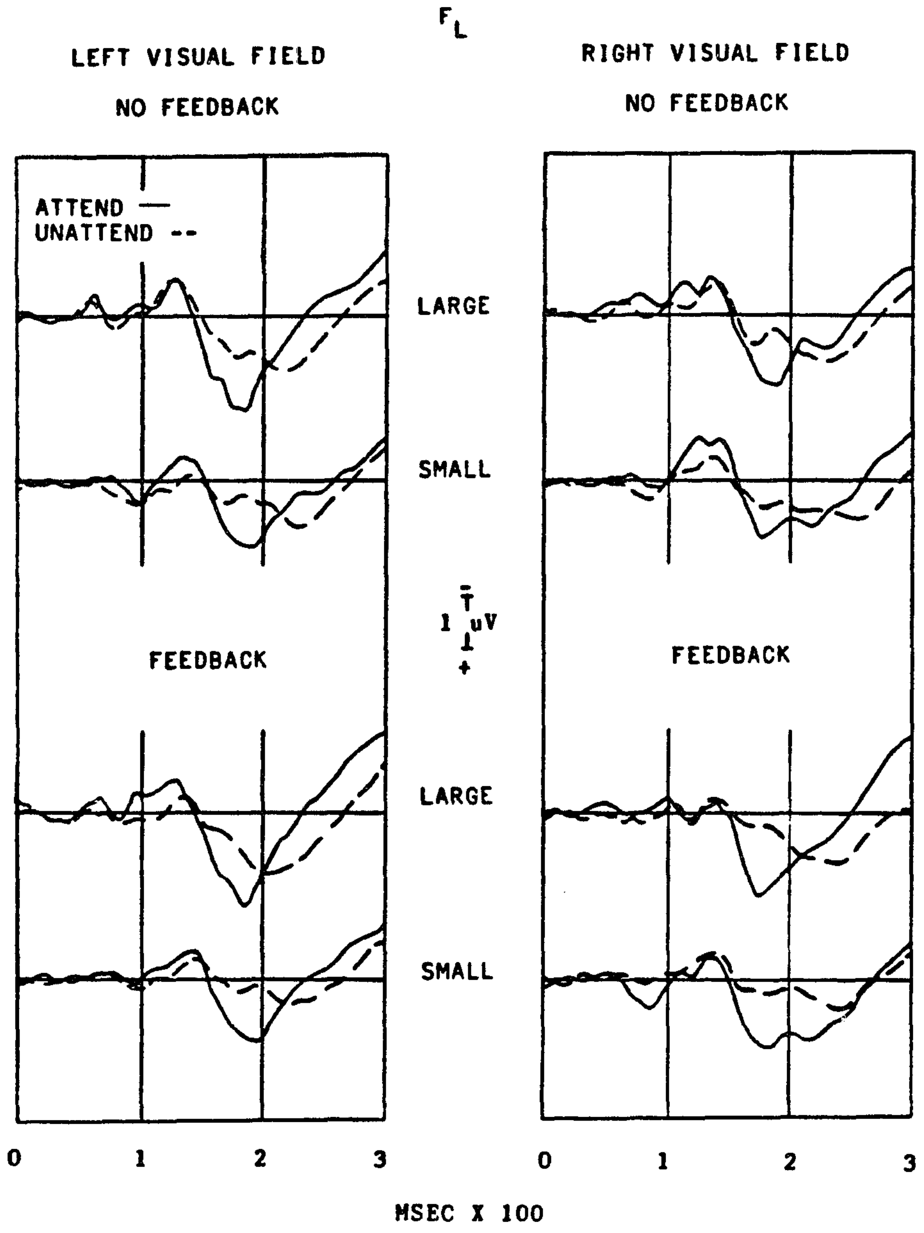

Figure 5a

Group averaged analog tracings for left frontal recordings. VERs are depicted for each of the experimental manipulations.

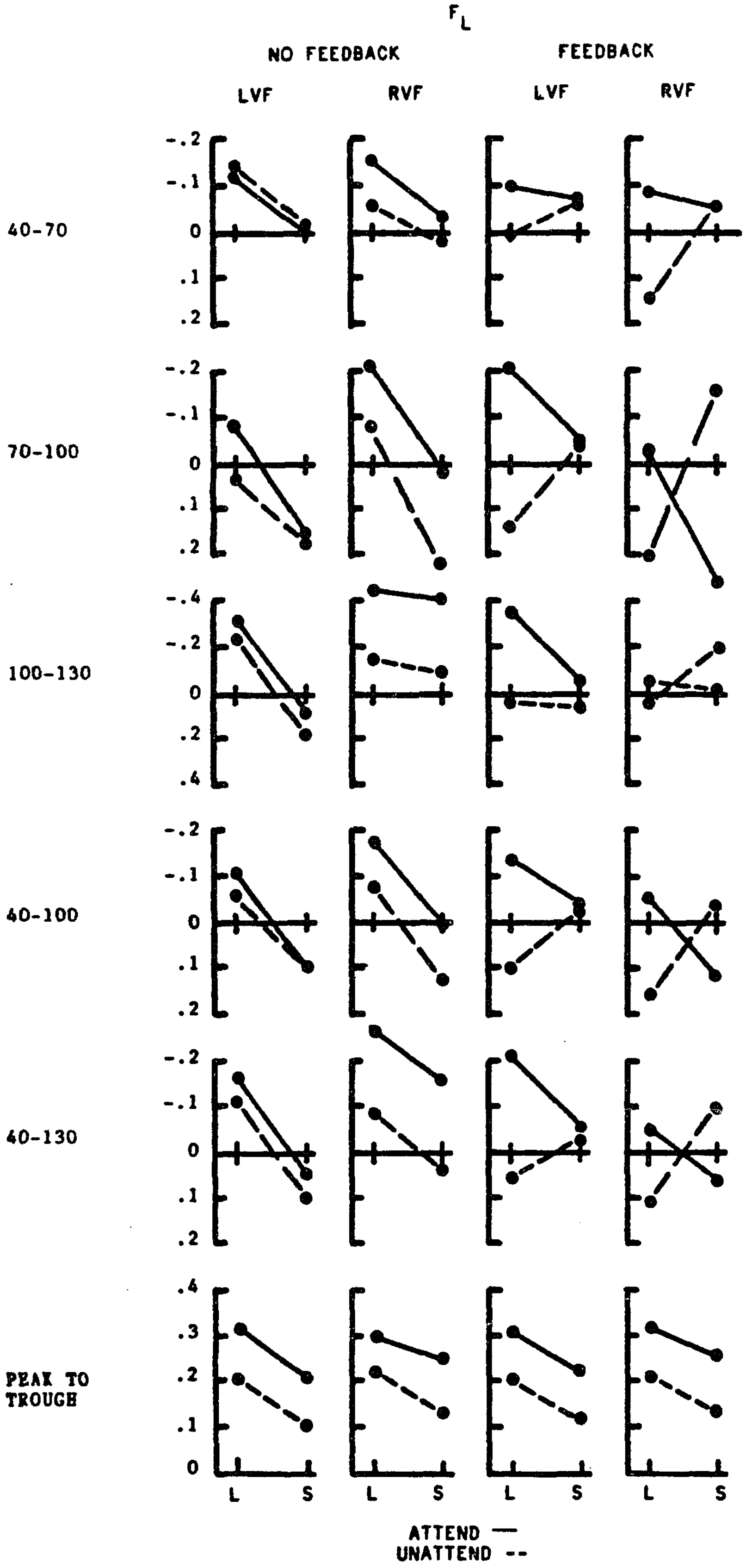

Figure 5b

Graphic representation of group averaged analog tracings for left frontal recordings as a function of Attention and Stimulus Size.

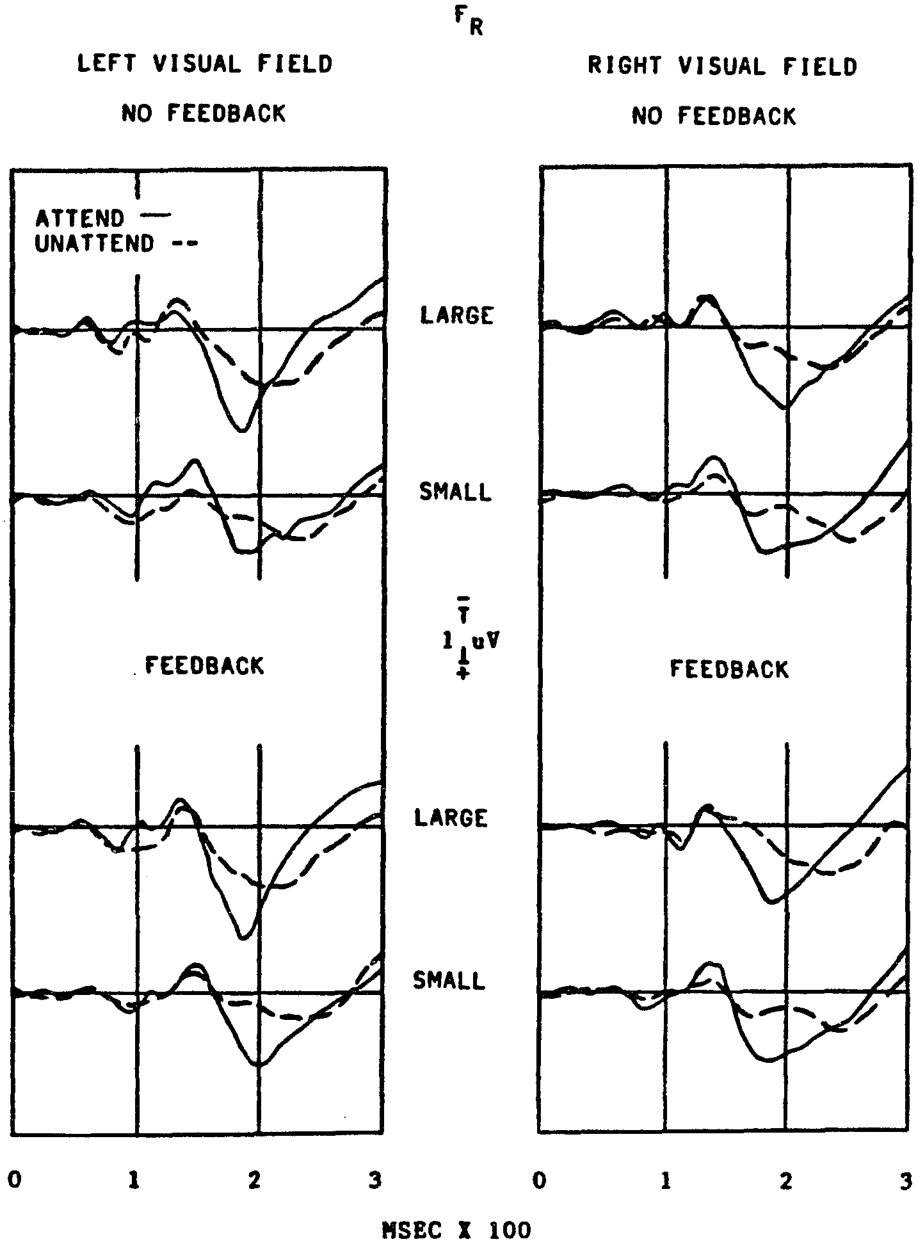

Figure 6a

Group averaged analog tracings for right frontal recordings. VERs are depicted for each of the experimental manipulations.

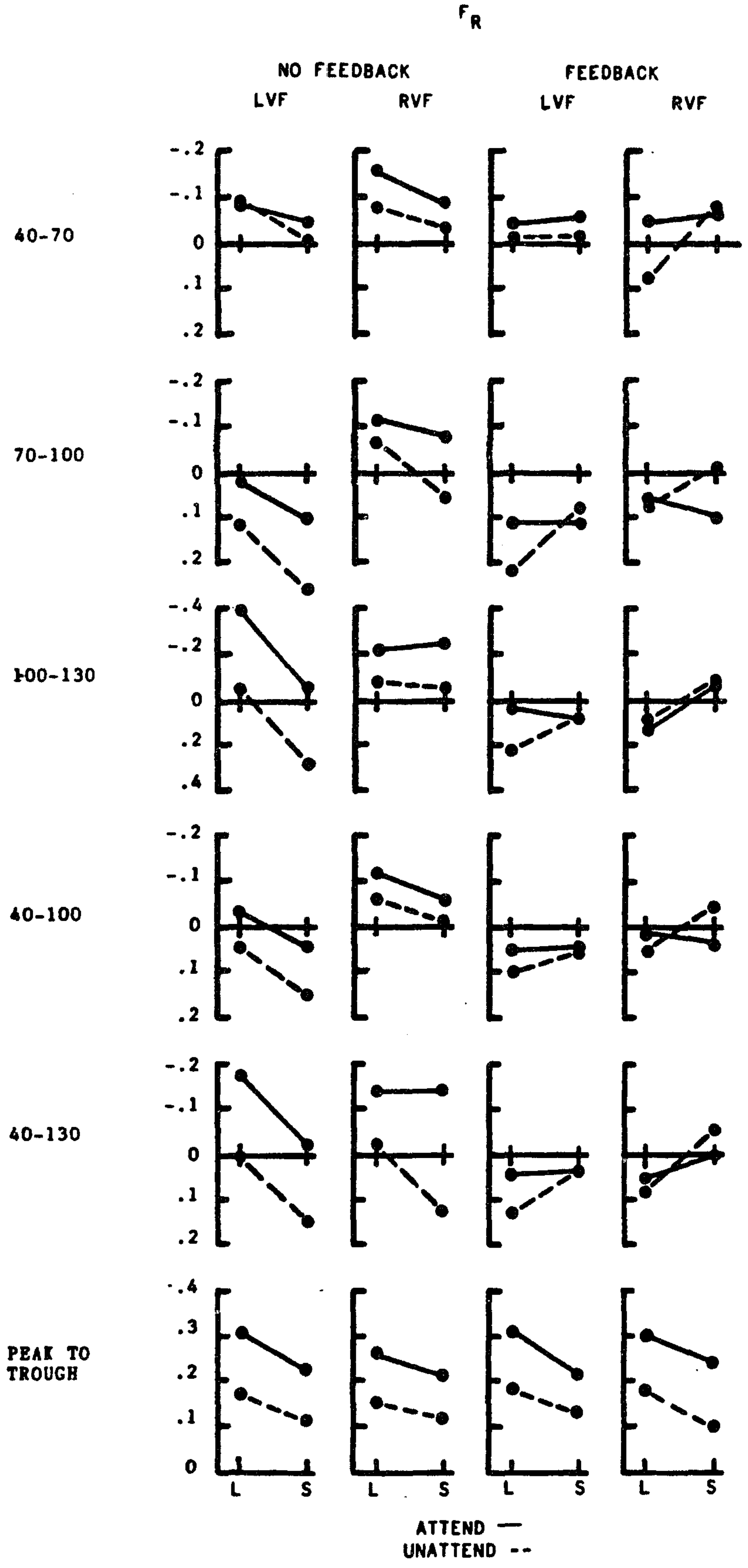

Figure 6b

Graphic representation of group averaged analog tracings for right frontal recordings as a function of Attention and Stimulus Size.

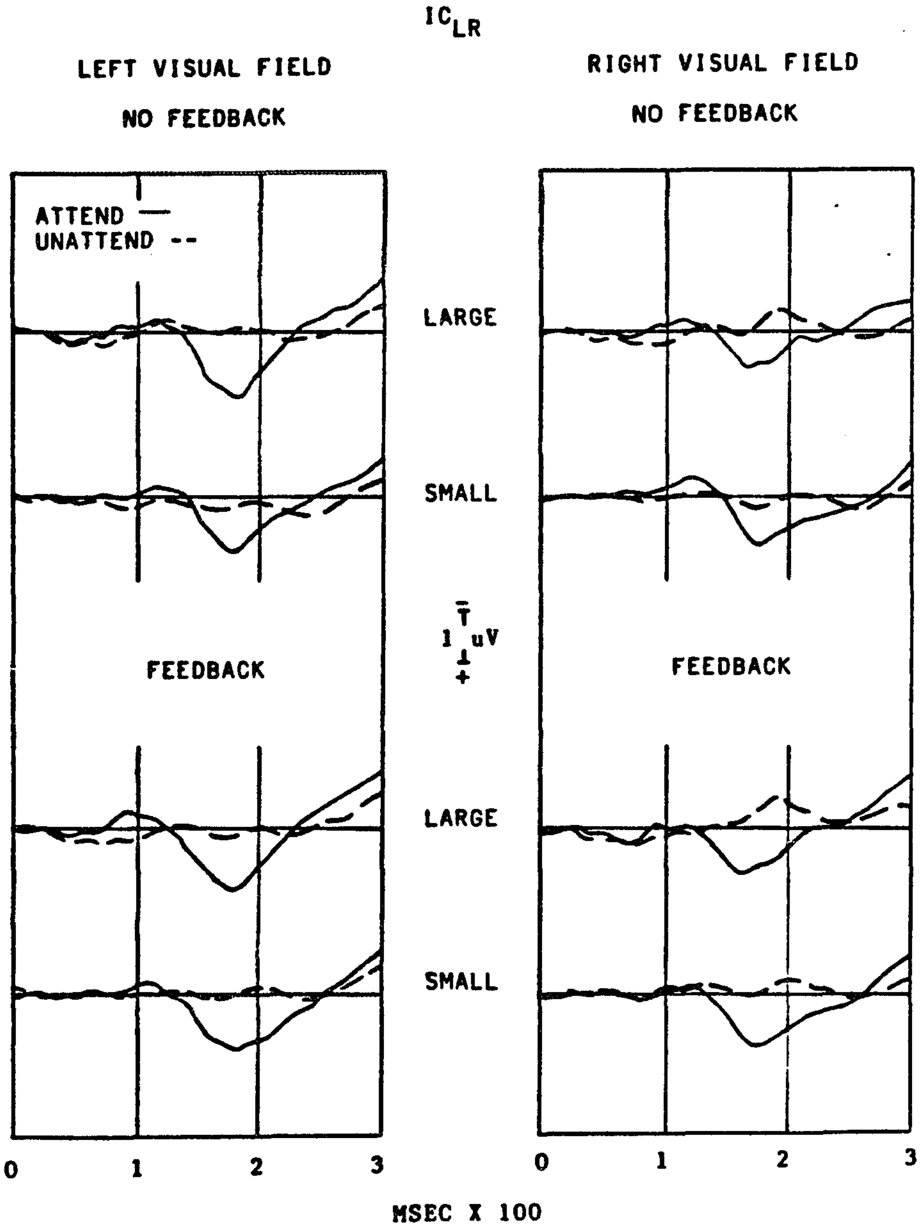

Figure 7a

Group averaged analog tracings for left and right internal canthus recordings combined. VERs are depicted for each of the experimental manipulations.

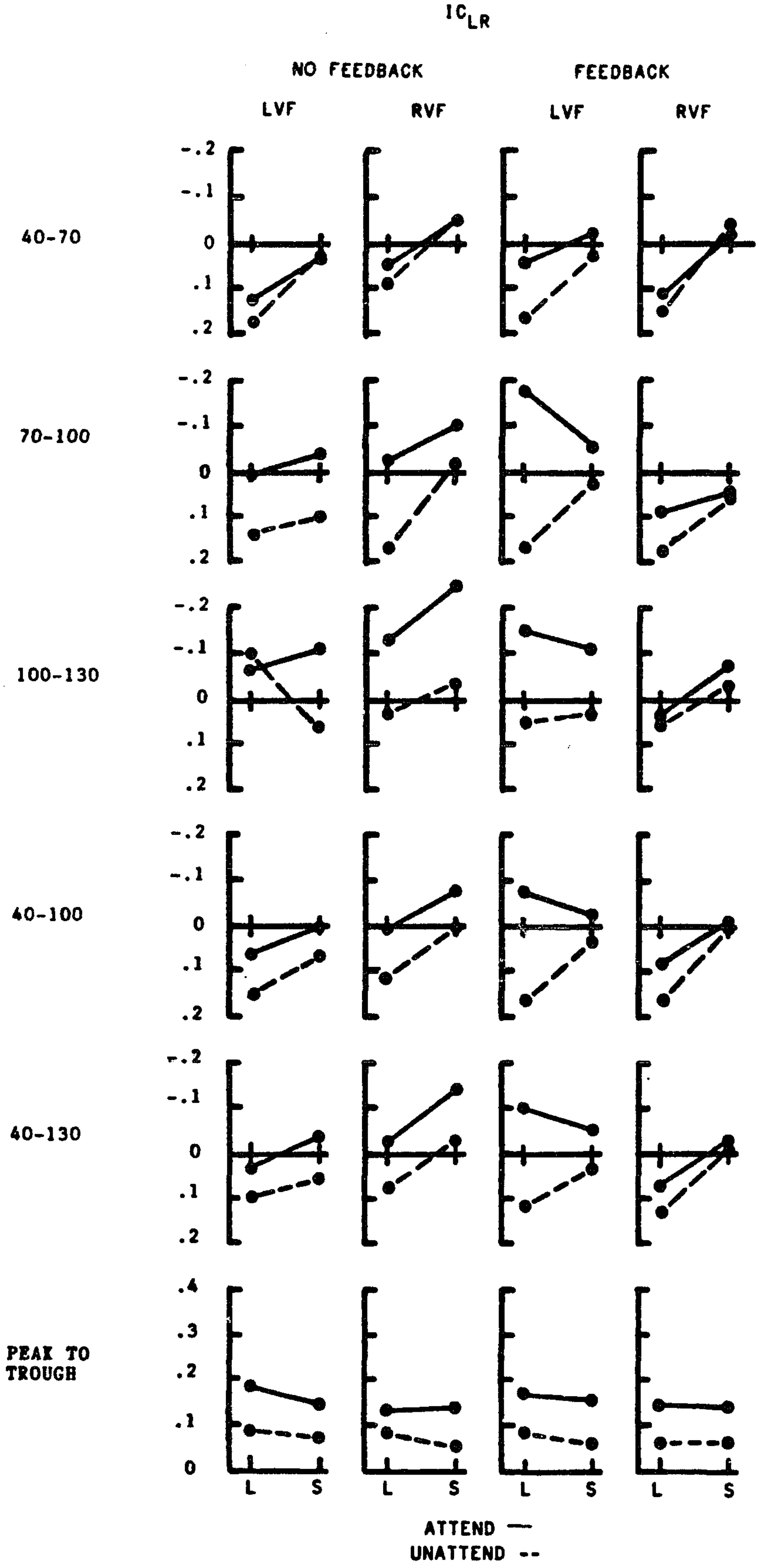

Figure 7b

Graphic representation of group averaged analog tracings for left and right canthus recordings combined as a function of Attention and Stimulus Size.

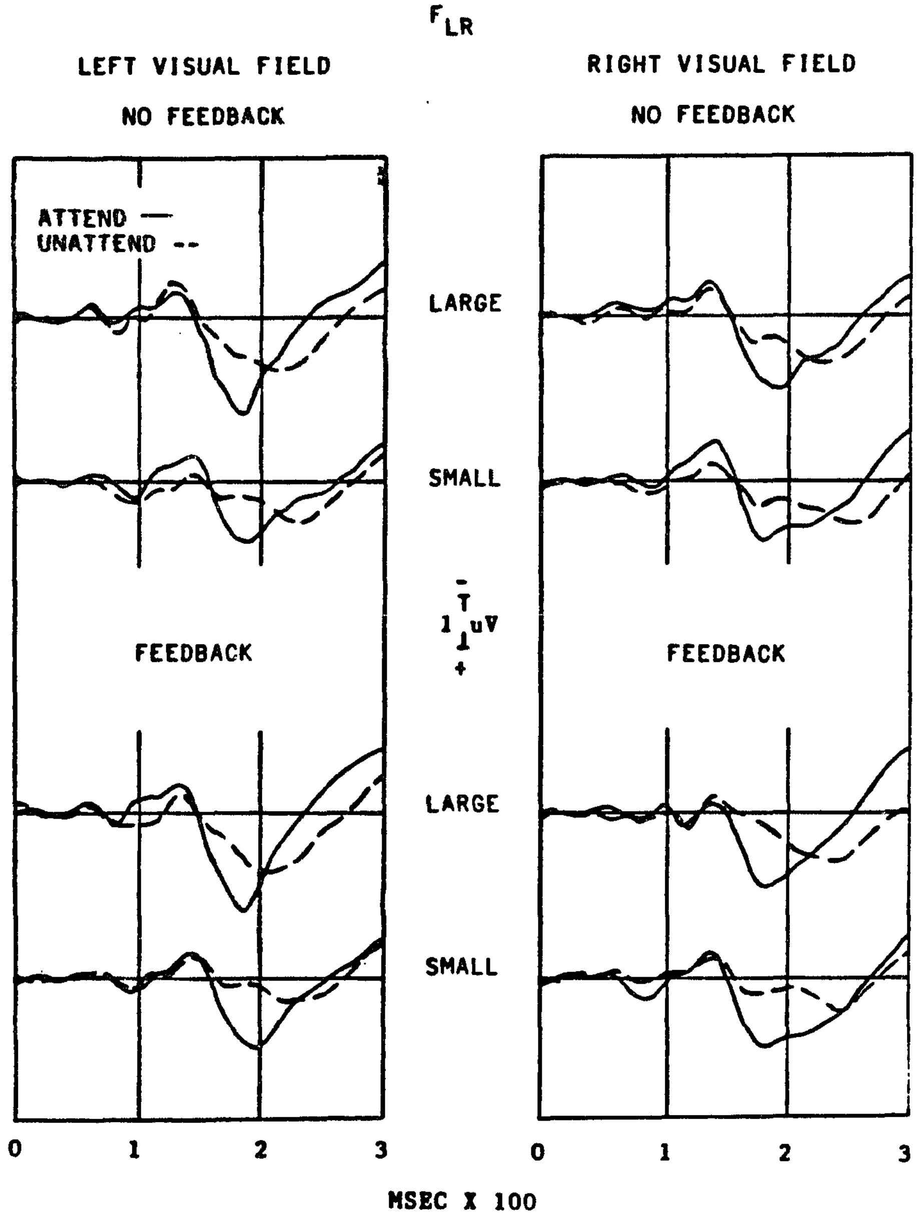

Figure 8a

Group averaged analog tracings for left and right frontal recordings combined. VERs are depicted for each of the experimental manipulations.

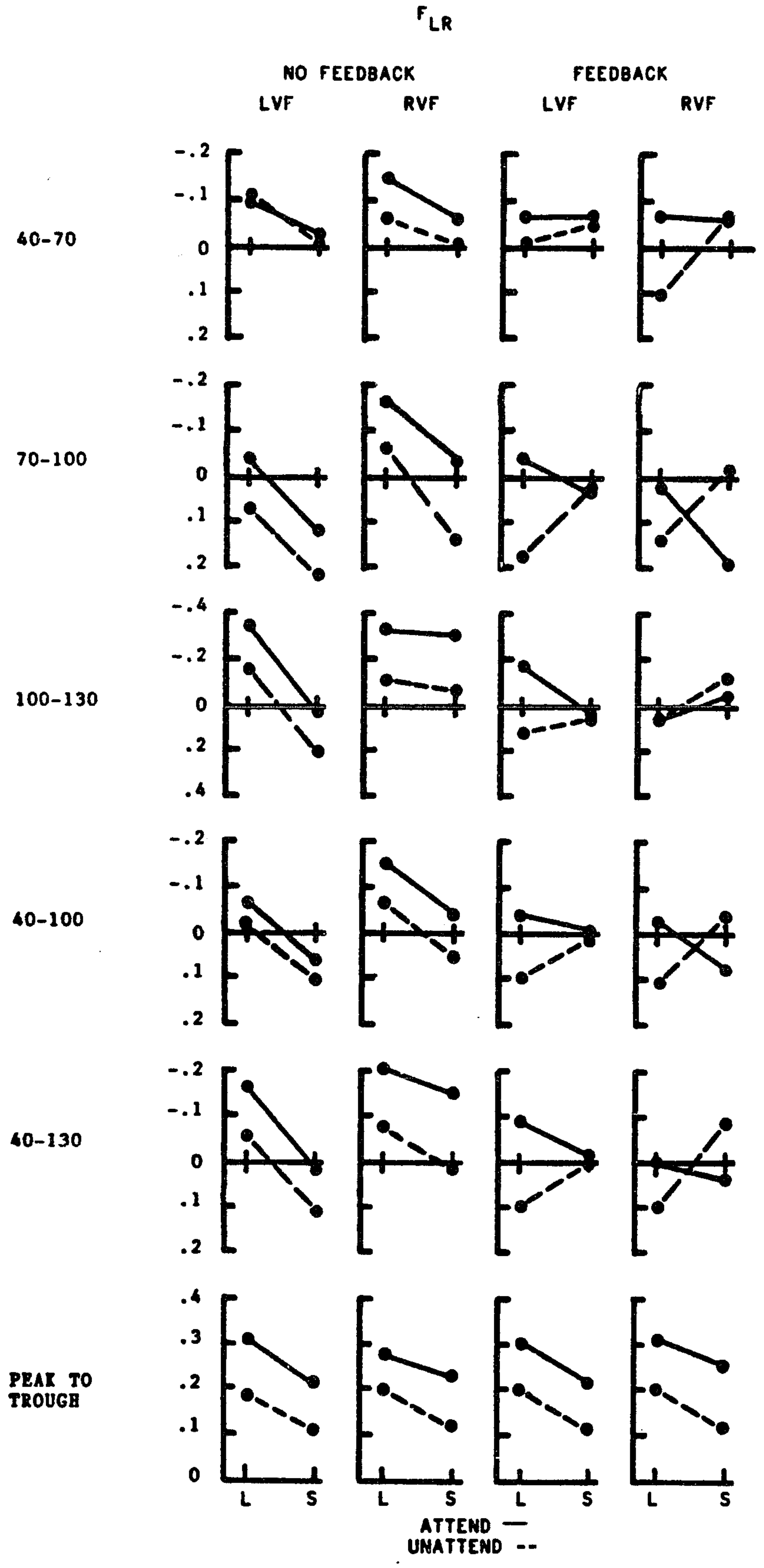

Figure 8b

Graphic representation of group averaged analog tracings for left and right frontal recordings combined as a function of Attention and Stimulus Size.

Data Analysis

Using a VAX computer system and the SAS statistical package, a five-way analysis of variance (ANOVA) statistical procedure was performed on the quantitative data for each recording site. Several significant main effects and interactions were obtained. These are summarized in Table 3. Starting at the left, the table sequentially lists (1) Sources of variation, (2) Recording sites, (3) VER components, (4) Degrees of freedom, (5) F values, and (6) P values. The degrees of freedom for each source of variation were 1 and 7.

Analog and Graphic Illustrations of Significant Effects

Figures 9 and 10 depict the group averaged analog tracings for those recordings wherein statistical significant effects were obtained. The left and middle panels of Figure 9, depict group averaged analog tracings for those recording sites at which significant main effects were obtained for attention and stimulus size, respectively. The upper right panel contains group averaged analog tracings for which significant main effects for feedback were obtained (sites FL, FR, and FLR). The lower right panel shows the group averaged analog tracings obtained at ICL for which a significant visual field main effect was obtained.

The group averaged analog tracings for which significant main effects were obtained have been collapsed across all other variables. The VERs recorded when subjects were attending and not attending have been superimposed on a common baseline. The time of stimulus onset and subsequent poststimulus segments up to 250 msec is represented (in 100 msec intervals), by the horizontal distance between vertical lines in each panel.

The group averaged analog records for which significant attention by stimulus size, attention by feedback, and visual field by stimulus size interactions were obtained are shown in Figure 10. These tracings were derived by averaging across all conditions except those involved in the significant interactions. The format for displaying the tracings follows that described for Figure 9.

Table 4 contains group mean amplitudes (in µVs), and Tukey post hoc analysis summary tables, for each VER latency interval and recording site for which a significant interaction was revealed. Interactions significant at the .05 and .01 levels are denoted by single and double asterisks, respectively. The experimental conditions for the listed mean amplitudes are indicated in the top row of each separate summary segment of the table. The second and third rows of each segment show the mean deviations from baseline amplitudes for each experimental condition, and the number of steps separating the means, respectively.

Figures 11 through 13 depict group mean deviations from baseline for each latency interval and recording site plotted as a function of attention and stimulus size (Figure 11), attention and feedback (Figure 12), and visual field and stimulus size (Figure 13). These plots reveal the nature of the interactions found to be statistically

SOURCE OF VARIANCE	RECORDING SITE	COMPONENT	DF	F VALUE	PR > F
ATTENTION	IC_L	70-100	1,7	7.19	.031
		100-130		6.55	.037
		40-100		5.46	.052
		40-130		9.36	.018
		PEAK-TROUGH		68.90	.0001
	IC_R	100-130		5.14	.057
		PEAK-TROUGH		53.84	.0002
	F_L	40-130		5.50	.051
		PEAK-TROUGH		102.71	.0001
	F_R	40-130		11.34	.012
		PEAK-TROUGH		59.67	.0001
	IC_{LR}	100-130		7.30	.030
		40-130		6.83	.035
		PEAK-TROUGH		63.94	.0001
	F_{LR}	40-130		7.65	.023
		PEAK-TROUGH		109.06	.0001
STIMULUS SIZE	IC_L	40-70		16.62	.004
	IC_R	40-70		14.45	.007
		40-100		5.60	.050
	F_L	PEAK-TROUGH		28.98	.001
	F_R	PEAK-TROUGH		15.99	.005
	IC_{LR}	40-70		19.99	.003
	F_{LR}	PEAK-TROUGH		25.80	.001
FEEDBACK	F_L	100-130		14.94	.006
	F_R	100-130		39.89	.0004
		40-130		25.71	.001
	F_{LR}	100-130		80.97	.0001
		40-130		10.21	.015
VISUAL FIELD	IC_L	40-70		6.12	.042
ATTENTION X STIMULUS SIZE	IC_L	70-100		7.74	.027
		40-100		13.88	.007
	IC_{LR}	40-100		6.78	.035
ATTENTION X FEEDBACK	IC_L	PEAK-TROUGH		18.20	.004
	IC_{LR}	PEAK-TROUGH		6.47	.038
VF X STIMULUS SIZE	IC_L	PEAK-TROUGH		7.72	.027

Table 3

ANOVA Summary Table for significant main effects and interactions.

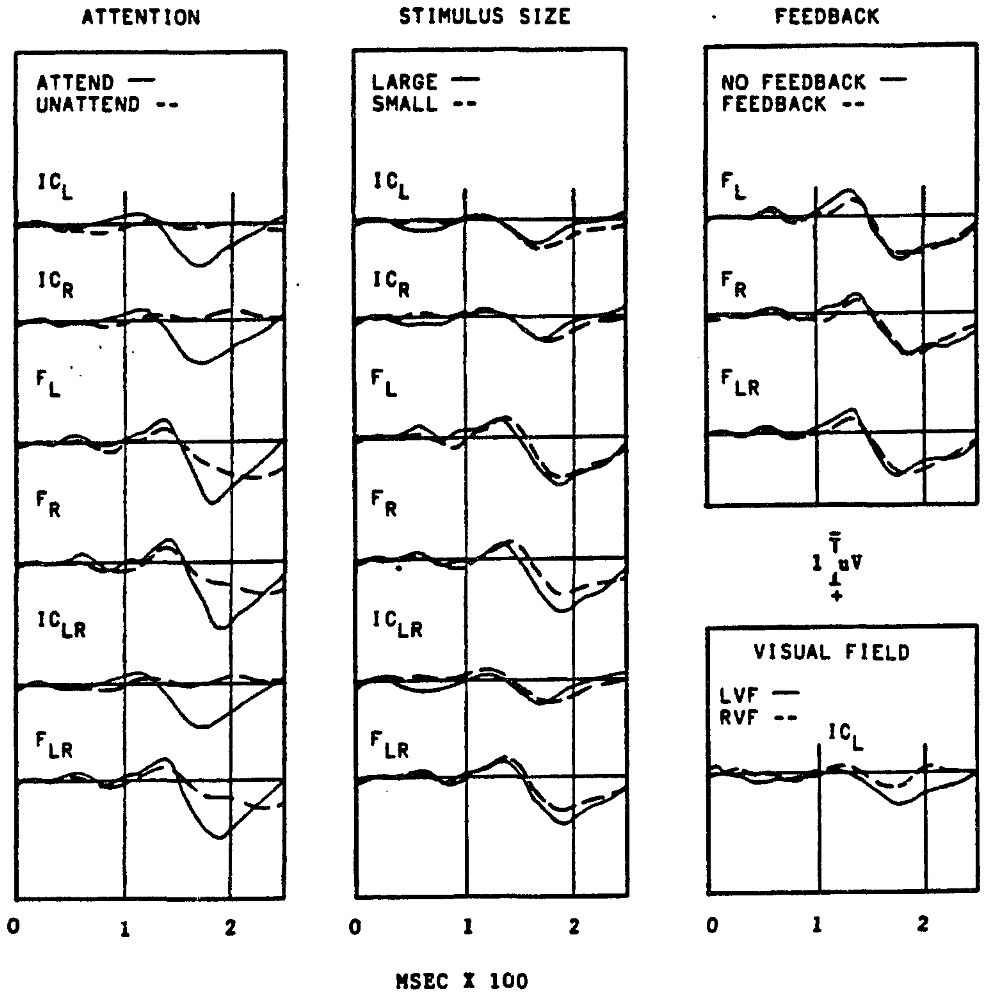

Figure 9

Group averaged analog tracings for significant main effects. Depicted are the group averaged analog tracings for significant effects for the Attention, Stimulus Size, Feedback, and Visual Field manipulations.

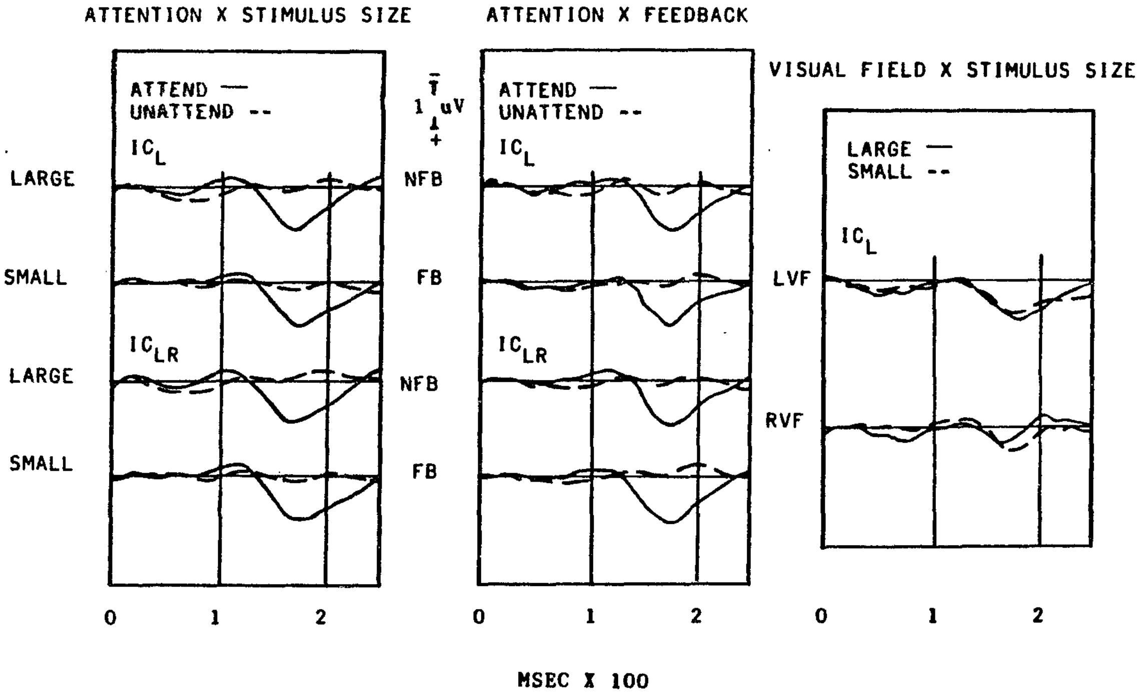

Figure 10

Group averaged analog tracings for significant interactions. Depicted are group averaged tracings for the Attention by Stimulus Size, Attention by Feedback, and Visual Field by Stimulus Size interactions.

ATTENTION AND STIMULUS SIZE INTERACTIONS

IC_L (70-100 MSEC)

EXPERIMENTAL CONDITION	ATTEND LARGE	ATTEND SMALL	UNATTEND SMALL	UNATTEND LARGE
R STEPS AWAY	1	2	3	4
MEAN µV	-.03	-.01	.07	.20
-.03	--	.02	.10*	.23**
-.01	--	--	.08*	.21**
.07	--	--	--	.13*

IC_L (40-100 MSEC)

EXPERIMENTAL CONDITION	ATTEND SMALL	ATTEND LARGE	UNATTEND SMALL	UNATTEND LARGE
R STEPS AWAY	1	2	3	4
MEAN µV	0	.02	.05	.19
0	--	.02	.05	.19**
.02	--	--	.03	.16*
.05	--	--	--	.14*

IC_{LR} (40-100 MSEC)

EXPERIMENTAL CONDITION	ATTEND SMALL	UNATTEND SMALL	ATTEND LARGE	UNATTEND LARGE
R STEPS AWAY	1	2	3	4
MEAN µV	-.03	.01	.02	.16
-.03	--	.04	.05	.19*
.01	--	--	.01	.15*
.02	--	--	--	.14*

ATTENTION AND FEEDBACK INTERACTIONS

IC_L (PEAK TO TROUGH)

EXPERIMENTAL CONDITION	UNATTEND-FB	UNATTEND-NFB	ATTEND-NFB	ATTEND-FB
R STEPS AWAY	1	2	3	4
MEAN µV	.55	.70	1.42	1.46
.55	--	.15*	.87**	.91**
.70	--	--	.72**	.76**
1.42	--	--	--	.04

IC_{LR} (PEAK TO TROUGH)

EXPERIMENTAL CONDITION	UNATTEND-FB	UNATTEND-NFB	ATTEND-NFB	ATTEND-FB
R STEPS AWAY	1	2	3	4
MEAN µV	.63	.72	1.54	1.57
.63	--	.09	.91**	.94**
.72	--	--	.82**	.85**
1.54	--	--	--	.03

VISUAL FIELD AND STIMULUS SIZE INTERACTION

IC_L (PEAK TO TROUGH)

EXPERIMENTAL CONDITION	RVF-SMALL	RVF-LARGE	LVF-SMALL	LVF-LARGE
R STEPS AWAY	1	2	3	4
MEAN µV	.92	.97	1.01	1.25
.92	--	.05	.09	.33*
.97	--	--	.04	.28*
1.01	--	--	--	.24*

* SIGNIFICANT AT .05 LEVEL
** SIGNIFICANT AT .01 LEVEL

Table 4

Tukey Post Hoc Summary Table for significant interactions.

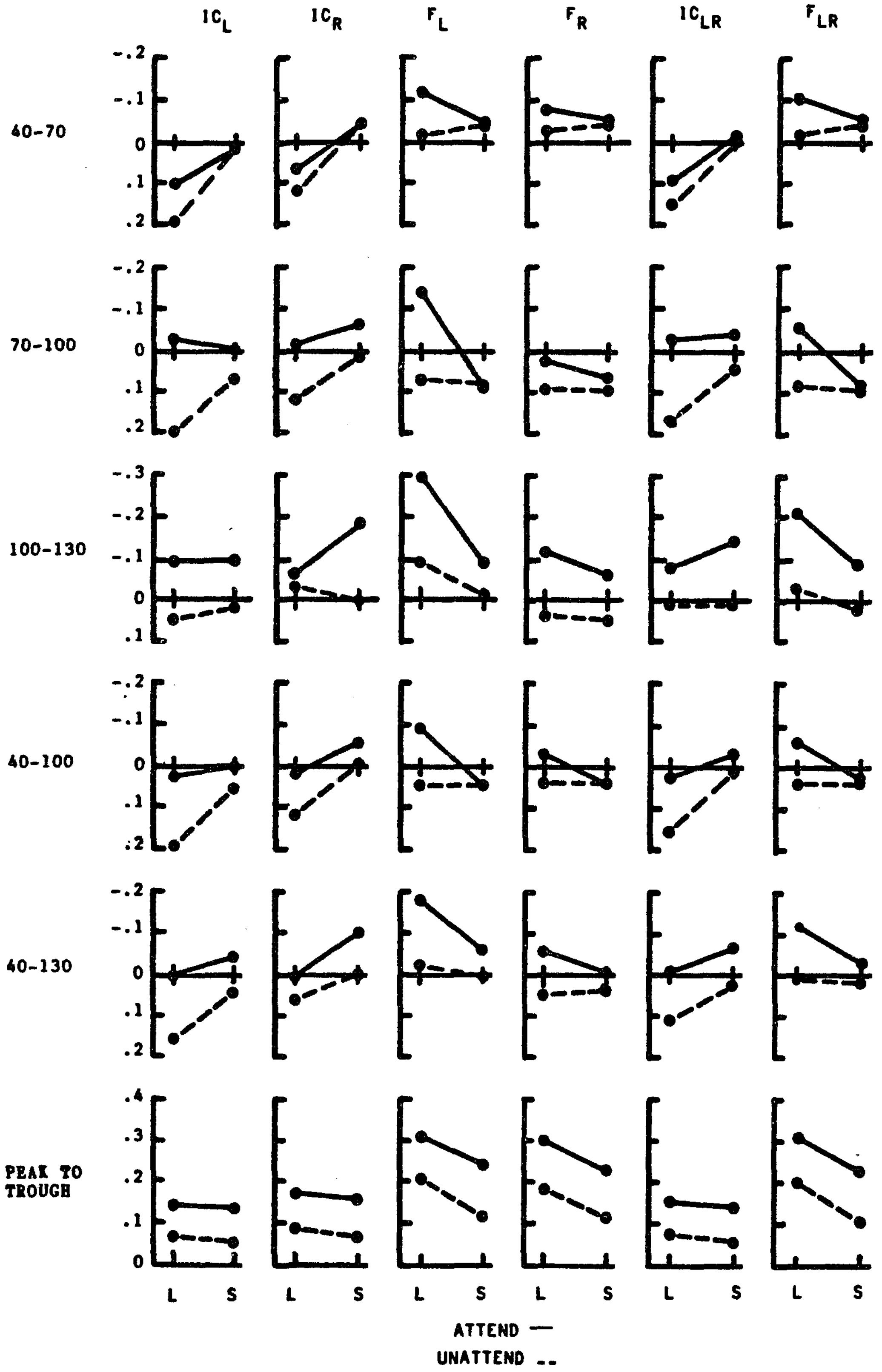

Figure 11

Graphic representation of Attention by Stimulus Size interaction. This figure also provides graphic representation of the main effects for Attention and Stimulus Size.

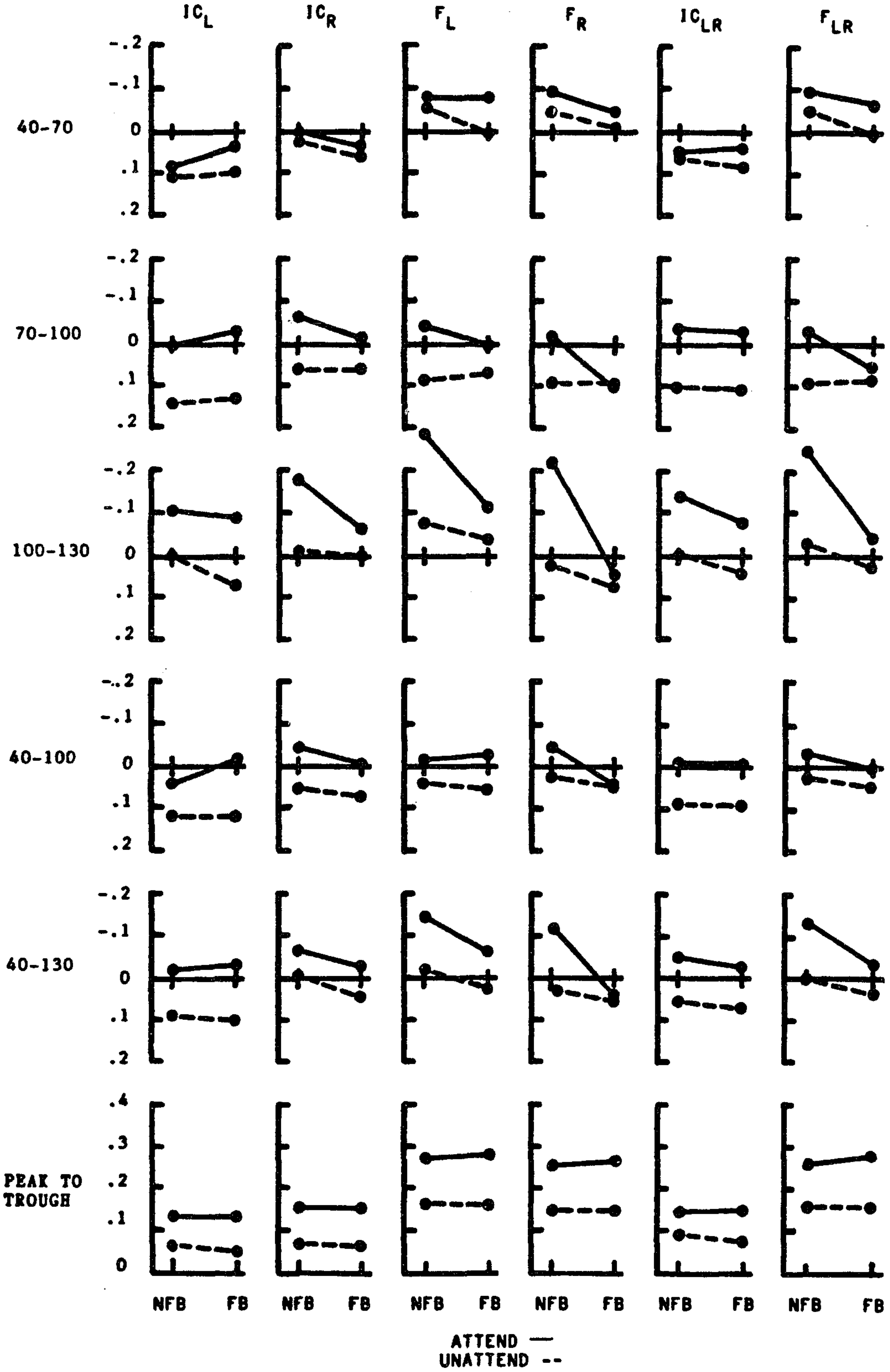

Figure 12

Graphic representation of Attention by Feedback interaction. This figure also provides graphic representa- of the main effects for Attention and Feedback.

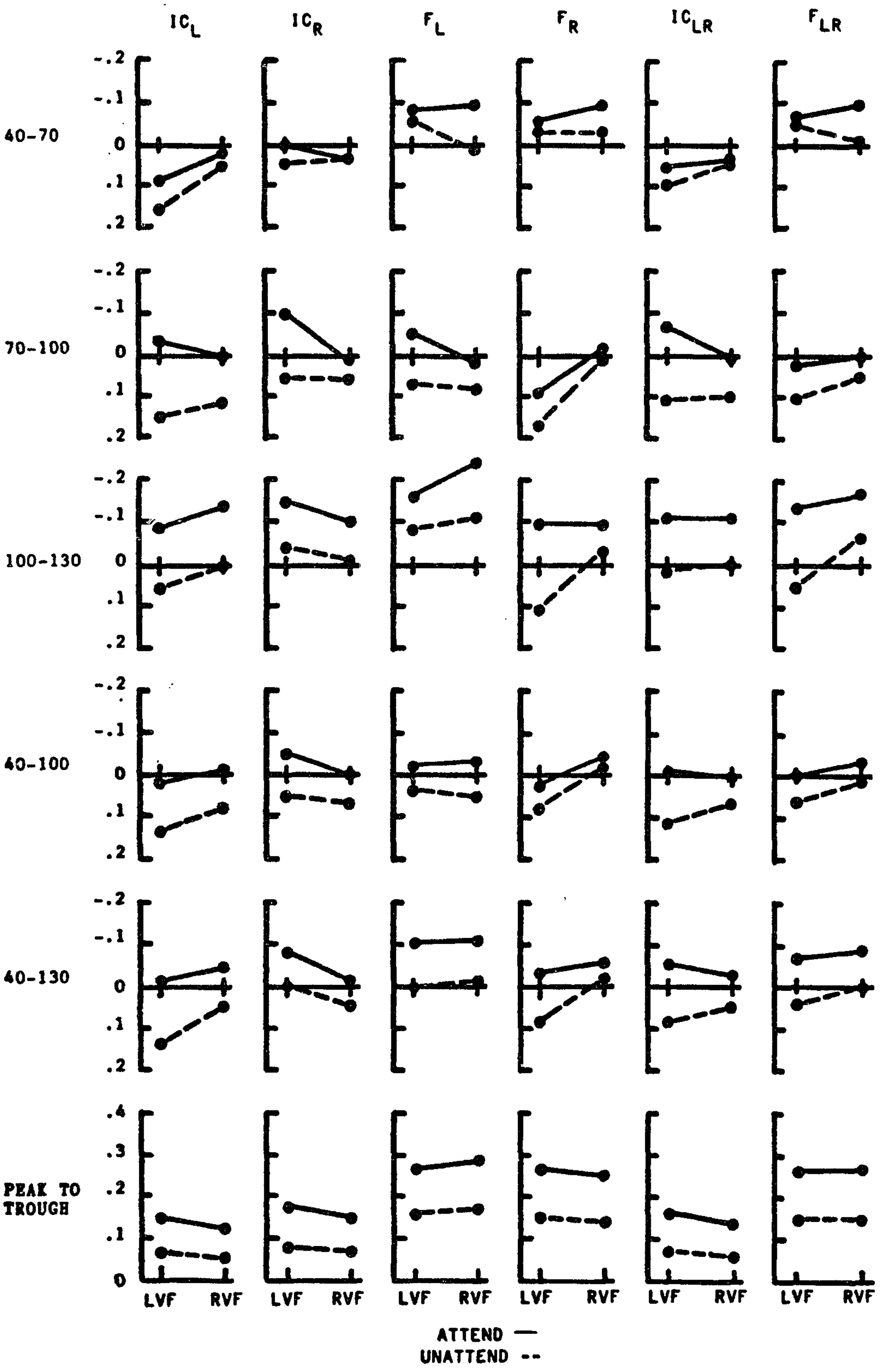

Figure 13

Graphic representation of Attention by Visual Field interaction. This figure also provides graphic representation of the main effects for Attention and Visual Field.

significant for attention by stimulus size, attention by feedback, and visual field by feedback (previously described in relation to Figure 10 and summarized in Tables 3 and 4). In Figures 11 and 12 the attend condition is depicted by solid lines; the unattend condition by dashed lines. In Figure 13 the large stimulus is represented by solid lines; the small stimulus by dashed lines.

Although Figures 11 through 13 were constructed to depict two-way interaction effects, main effects also are readily observable by visually averaging across one of the two variables plotted in each graph. For example, visually averaging across the stimulus size variables in Figure 11 provides an indication of the attention main effect for the various recording sites and latency intervals (LIs). Similarly, graphic manifestations of the main effects for stimulus size (Figure 11), feedback (Figure 12), and visual field (Figure 13) are provided when one visually averages across the attention conditions.

Significant Main Effects for Attention

Left Canthal (ICL) VERs

With the exception of the 40-70 msec LI, a significant main attention effect was obtained for all the VER latency intervals recorded from the ICL site. Table 4 summarizes these effects. The earliest latency interval for which a significant attention effect was obtained was 70-100 msec (F=7.19, p.= .031). Inspection of the group analog tracings of Figure 9 reveals that the polarity of the VER waveform in this latency interval was relatively more negative under the attend (solid line) than under the unattend condition (dashed lines). A similar effect is manifested for this latency interval in Figures 11-13. The mean deviation from baseline during this latency interval was -.02 µV for the attend condition, compared to a mean of .14 µV for the unattend condition.

A significant attention effect also was obtained for the 100-130 msec LI of the ICL recordings (F=6.55, p.=.037), with the attend condition again producing a more negative deflection than the unattend condition. The mean deviations from baseline for the attend and unattend conditions were -.10 µV and .03 µV, respectively. This effect is clearly manifested in the group averaged VERs, as well as in the quantitatively derived means (Figures 9 and 11-13). Although a significant attention effect was not obtained for the 40-70 LI, integration of this interval with the 70-100 msec LI (i.e., over a 40-100 msec LI) was significant (F=5.46, p.=.052). The respective mean deviations from baseline for the attend and unattend conditions for this longer latency interval were .01 and .12 µV. Finally, a significant effect was obtained for measures integrated across the entire 40-130 msec latency interval (F=9.36, p.=.018). The mean deviation from baseline over this 90-msec interval was -.03 µV for the attend and .10 µ for the unattend condition.

The effect of attention on the peak-to-trough measure of the deflection peaking out at 180 msec was highly significant (F=68.90, p.=.0001). The mean amplitude of this measure recorded at ICL under the attend and unattend condition was 1.45 µV and .62 µV respectively.

A significant attention effect was also obtained for the peak-to-trough measures derived from all other recording sites (see Table 3). All the significant attention effects summarized above are manifested in the group averaged VER tracings and graphs of the mean deviation from baseline depicted in Figures 8 and 11-13).

Right Canthal (ICR) VERs

Only the peak-to-trough measure of the late positive-going deflection (peak latency 180 msec) revealed a significant attention main effect at the ICR recording site (F=53.84, p.=.0002). The more negative voltage under the attend condition for the right canthal recordings within the 100-130 msec LI approached significance at the .05 level (F=5.14, p.=.057).

Left Frontal (FL) VERs

Statistically significant effects were obtained for two of the measures derived from recordings at the left frontal (FL) site. The VER voltages averaged across the 40-130 msec LI were more negative under the attend than under the unattend condition (F=5.50, p.=.051). The peak-to-trough measure of the late positive-going deflection was significantly greater under the attend than under the unattend condition for the FL recordings (F=102.71, p.=.0001). The group analog tracings of Figure 9 reflect the significant attention effect for these two measures, as do the group means in Figures 11-13. The mean deviation from baseline during the 40-130 msec interval was .11 μV for the attend and -.01 μV for the unattend condition.

Right Frontal (FR) VERs

There also was a significant attention effect on the VER waveforms obtained at the right frontal (FR) site during the 40-130-msec interval (F=11.34, p.=.012), as well as on the peak-to-trough measure of the late positive-going deflection (F=59.67, p.=.0001). The mean deviation from baseline during the 40-130 msec latency interval was -.05 μV for the attend and .03 μV for the unattend condition.

Combined Left and Right Canthal (ICLR) VERs

Significant attention effects were obtained for three of the measures derived from averaged evoked responses collapsed across canthal recording sites (ICLR). The deflections in the 100-130 msec latency interval were significantly more negative under the attend than under the unattend condition (F=7.30, p.=.030). The mean deviations from baseline were -.11 μV for the attend and -.02 μV for the unattend condition. A significant attention effect was also obtained over the longer latency interval of 40-130 msec (F=6.83, p.=.035), the mean deviation from baseline being .04 and .07 μV for the attend and unattend condition, respectively. Finally, a significant attention effect was obtained for the peak-to-trough measure of the late positive-going deflection for the ICLR recordings. Figures 9 and 11-13 reflect these significant attention effects for combined canthal recordings.

Combined Left and Right Frontal (FLR) VERs

Significant attention effects were obtained for two of the measures derived from VERs collapsed across frontal recording sites (FLR): (1) the 40-130 msec interval, and (2) the peak-to-trough measure of the late positive-going deflection (F=7.65, p.=.023; and F=109.06, p.=.0001; respectively). The mean deviation from baseline during the 40-130 msec interval was -.08 μV for the attend and .02 μV for the unattend condition. The magnitude of the peak-to-trough measures was greater under the attend than under the unattend condition. These effects are observable in Figures 9 and 11-13.

Significant Main Effects for Stimulus Size

Left Canthal (ICL) VERs

A significant stimulus size effect was obtained for the 40-70 msec interval at the ICL recording site (F=16.62, p.=.004). As indicated by the analog tracings of Figure 9, the polarity was more negative for the small than for the large stimulus. This effect is also manifested in Figure 11. The respective mean deviations from baseline for the small and large stimuli .02 and .15 μV.

Right Canthal (ICR) VERs

A significant stimulus size effect was also obtained at the 40-70 msec LI (F=14.45, p.=.007) and the more extended interval of 40-100 msec (F=5.60, p.=.050) for the ICR recordings. The mean deviations from baseline for the 40-70 msec interval were -.04 for the small and .10 μV for the large stimulus. The corresponding mean deviations for the 40-100 msec were -.04 μV for the small and .07 μV for the large stimulus. Thus, the small stimulus consistently produced relatively more negative deflections than the large stimulus during the 40-70 and 40-100 msec latency intervals at the internal canthi recording sites. Figures 9 and 11 depict these effects.

Frontal VERs (FL, FR, and FLR)

A significant effect for stimulus size was obtained for the peak-to-trough measures of the late positive-going deflections at both frontal recording sites (Table 3). In each case, the deflections for the large stimulus were greater than for the small stimulus (see Figures 9 and 11).

Combined Left and Right Canthal (ICLR) VERs

A significant stimulus size effect was also obtained for the 40-70 msec range of the canthal recordings collapsed across the left and right sites (F=19.99, p.=.003). The mean deviation from baseline was -.02 μV for the small and .12 μV for the large stimulus. The more negative voltages for the small stimulus is reflected in Figures 9 and 11, respectively.

Significant Main Effects for Feedback

Frontal VERs

A significant feedback effect was obtained for the 100-130 msec range at the FL site (F=14.94, p.=.006). The mean deviations from baseline for the no feedback (NFB) and feedback (FB) conditions were -.20 and -.06 μV, respectively.

At the FR site, a significant feedback effect was obtained for the 100-130 msec latency interval (F=39.8, p.=.0004), as well as for the more comprehensive 40-130 msec latency interval (F=25.71, p.=.001). Mean deviations from baseline for the NFB and FB conditions within the 100-130 msec interval were -.10 and .06 μV, respectively. Mean deviations from baseline for the deflections within the longer 40-130 msec interval were -.07 and .04 μV for the NFB and FB conditions, respectively. Thus, in each case, the polarity for the NFB condition was relatively more negative than for the FB condition.

For the frontal recordings collapsed across both frontal recording sites, a significant feedback effect was obtained for the 100-130 msec interval, and also for the longer 40-130 msec interval (F=80.97, p.=.0001; and F=10.21, p.=.015, respectively). Mean deviations from baseline for the deflections occurring within the 100-130 msec interval for the NFB and FB conditions were -.14 and .01 μV, respectively. The corresponding mean deviations for the 40-130 msec interval were -.07 and .01 μV. These effects are depicted in Figures 9 and 12.

Significant Main Effects for Visual Field

Left Canthal (ICL) VERs

A significant visual field effect was obtained for the 40-70 msec latency interval in the left canthal recordings (F=6.12, p.=.042). The VER deflections in this latency interval were more negative for the RVF than for LVF. Mean deviations from baseline were .02 and .15 μV for the RVF and LVF tracings, respectively. This effect is depicted in Figures 9 and 13.

Significant Interactions

Attention and Stimulus Size

Left Canthal (ICL) VERs

The interaction between attention and stimulus size was significant for the 70-100 and 40-100 msec intervals of VERs recorded at the left canthal (ICL) site (F=7.74, p.=.027 and F=13.88, p.=.007, respectively). For the 70-100 msec LI, the deflections were more negative for the attend condition than for the unattend condition for both stimulus sizes; however, the magnitude of the attention effect was greater for the large than for the small stimulus. This difference in the magnitude of the attention effect for the two stimulus sizes is reflected in the group averaged analog tracings depicting significant interaction effects (Figure 10), the graphic representations of interactions between attention and stimulus size (Figure 11), and the Tukey post hoc summary table (Table 4). The post hoc analysis revealed that the attention effect for the large and small stimulus (within the 70-100 msec LI) was significant at the .01 and .05 level, respectively.

For the 40-100 msec interval, the post hoc analysis revealed a significant attention effect for the large stimulus only (Table 4). The group analog tracings of Figure 10 reflect this finding. The graph of the attention and stimulus size interactions (Figure 11) reflect a difference between the attend and unattend VERs for the 70-100 msec LI for both the large and small stimuli, but the difference between the attend and unattend VERs is observable within the 40-70 msec LI for the large stimulus only.

Combined Left and Right Canthal (ICLR) VERs

There was a significant attention by stimulus size interaction for the 40-100 msec interval of VERs collapsed across the canthal recording sites (F=6.78, p.=.035). The post hoc analysis revealed a significant attention effect for the large stimulus only (Table 2). The analog and graphic representations of this significant interaction (Figures 10 and 11, respectively) show that the VER for the large stimulus under the attend condition was more negative than under the unattend condition within the 40-100 msec LI.

Attention and Feedback

Canthal VERs

For left canthal recordings, and for recordings collapsed across both canthal sites, a significant attention by feedback interaction was obtained for the peak-to-trough measure of the late positive-going deflection (F=18.20, p.=.004; and F=6.47, p.=.038, respectively). The magnitude of this deflection was greater for the attend than for the unattend condition for both the NFB and FB conditions; however, magnitude of the attention effect was relatively greater for the FB than for the NFB condition (see Table 4 and Figures 10 and 12). This was true both for the ICL and ICLR recordings. The ICL recordings contributed more than the ICR recordings to the significant ICLR attention by feedback interaction.

Visual Field and Stimulus Size

Left Canthal (ICL) VERs

A significant visual field by stimulus size interaction was obtained only for the peak-to-trough measure of the late positive-going deflection recorded from the ICL site (F=7.72, p.=.027). Both the group analog tracings and the post hoc summary table (Figure 10 and Table 4, respectively) reveal that the LVF VERs evoked by the large stimulus were of greater magnitude than those evoked by LVF small stimuli or RVF stimuli of either size. There was no significant visual field by stimulus size interaction for the small stimulus.

Behavioral Results

As noted in the Methods Section, the behavioral data were recorded in order to monitor whether the subjects were performing the task as instructed, and to give them periodic feedback (under the feedback condition) as to the quality of their performance. These data were not subjected to quantitative analysis as they were not directly relevant to the purpose of the study. However, they were carefully examined. As anticipated, the subjects responded more slowly to target stimuli under the no-feedback than under the feedback condition. Even if both motivation level and the intensity with which subjects selectively attended had remained constant across the two feedback conditions, this result would still have been expected, since the subjects had no way of knowing how fast they were responding under the no-feedback condition.

Individual Differences

As expected, individual differences were observed in both the physiological and behavioral data. Highly significant between-subject differences have been observed consistently in ERG studies (Armington, 1974) as well as in VER studies (Eason, 1984, Eason et al., 1969; Goff et al. 1978; Hillyard, 1981; Hillyard et al., 1985). Such differences also have been observed consistently in behavioral data obtained concomitantly in VER studies (Eason, et al., 1969; Harter & Aine, 1986; Harter & Salmon, 1972; Harter, Aine, & Schroeder, 1982; Hillyard, et al. 1978).

Summary of Results

Significant attention main effects were obtained for at least one of the VER latency intervals (LIs) at each recording site. The earliest significant attention effect observed in canthal recordings was at the 70-100 msec LI at the ICL site. The effect was greater for the large stimulus, although it was significant for the small stimulus as well. The effect of the attention manipulation during the longer 40-100 msec latency intervals on the left canthal (ICL) and collapsed canthal recordings (ICLR) was significant only for the large stimulus. The magnitude of the attention effect on the peak-to-trough measures of the late positive-going deflection in the VERs recorded at the ICL and ICLR sites was more pronounced for the feedback than for the nofeedback condition. In each case, the magnitude of the deflection was greater under the attend than under the unattend condition.

There was a significant stimulus size effect for some latency intervals. In each case, the polarity for the VERs in response to the small stimulus was more negative than for the large stimulus. For the ICL and ICR recording sites, there was a significant stimulus size effect at the 40-70 msec interval. The effect of stimulus size was not significant at later latency intervals; however, the magnitude of the peak-to-trough measure of the late positive-going deflection recorded at ICL was greater for the large stimulus when presented from within the left visual field.

CHAPTER IV

DISCUSSION

SUMMARY OF ATTENTION MAIN EFFECTS

Canthal Recordings

A selective attention effect was demonstrated within the 40-130 msec latency interval on VERs obtained from the left internal canthus as well as on the recordings collapsed across both internal canthi. Significant effects were obtained across latency intervals of 40-100, 40-130, 70-100, and 100-130 msec. Although no significant attention effects were demonstrated at any of these latency intervals in the right internal canthus recordings, the differences observed between the two attend condition was in the same direction as those observed for the left canthal recordings.

The attention manipulation also significantly interacted with the size of the stimulus within the 40-130 msec latency interval of the canthal recordings. This interaction appears to reflect the fact that the attention effect for the large stimulus within the 40-70 msec latency interval was of greater magnitude than for the small stimulus. This also appears to have been the case for the longer latency interval (40-130 msec), though to a lesser degreee. The nature of the attention by stimulus size interaction for the canthal recordings is revealed in the group averaged analog tracings (Figure 10), the graphic representation of the attention by stimulus size interaction (Figure 11), and the post hoc summary table (Table 4).

While the above interpretation of the attention by stimulus size interaction may be consistent with the group data, it may not adequately reflect the nature of this interaction, as revealed in composite analog tracings of individual subjects (Figure 14). Inspection of the composite tracings of individual subjects revealed that for half the subjects, the peak deflections obtained from the left internal canthus within 40-70 msec latency interval for the large stimulus were more positive under the attend than under the unattend condition. The averaged analog tracings for these four subjects clearly revealed a retinally generated b-wave response of positive polarity within the 40-70 msec latency interval. This b-wave response was not apparent in the tracings of the other four subjects under any of the stimulus conditions. For the four subjects who did not generate a discernible b-wave response, an attention effect was manifested within the 40-70 msec interval as relatively more negativity for deflections under the attend than under the unattend condition. Thus, for half the subjects, it appears that a retinally generated b-wave response of positive polarity may have algebraically summed with an attention-related negative field potential arising from one or more subcortical generators, thereby masking the attention effect at the canthal recording sites. A case will later be made that two generator sources, one of retinal origin, and a second of subcortical origin, generated field potentials of opposite polarity which tended to cancel one another at canthal recording sites of some subjects under certain conditions. Such cancellation was not observed at frontal recording sites, since they were too far removed from the eyes to be influenced by retinally generated field potentials.

Frontal Recordings

A selective attention effect was demonstrated for VER components occurring within the 40-130 msec interval for both frontal recording sites. Although the attention effect was evident by 50 msec poststimulus (Figure 9), maximum separation occurred within the 100-130 msec latency interval. As was the case for the canthal recordings, deflections in the frontal recordings tended to be more negative under the attend than under the unattend condition throughout most of the 40-130 msec interval.

Late Attention Effect

The effect of selective attention on the peak-to-trough measure of the late positive-going deflection (respective onset and peak latencies of approximately 150 and 180 msec) was highly significant. The group averaged analog tracings (Figure 9) clearly shows the attention effect for this cortically generated potential at all recording sites. Its magnitude was markedly greater for the attend than for the unattend condition, a finding which has been repeatedly demonstrated under a relatively wide range of attention conditions (Eason et al., 1969; 1983a; Eason, 1981; 1984; Hillyard et al., 1985); Mangun et al., 1986; Oakley, 1984). The relative ease with which such attention effects can be demonstrated is an indication of the robustness of an attention effect on late VER components. The late attention effect in the present study serves as a kind of neural validation that the subjects did indeed selectively attend. There is little doubt that this late component is of cortical origin, based on animal research regarding the latency of cortical activity following stimulus presentation (Bushnell et al.,1981; Crowne, 1983; Kraut, Arezzo, & Vaughan, 1983; Wurtz et al., 1980).

Interpretation of Attention Main Effects

Retinal Responses

Following a description of the classical ERG, evidence will be presented which suggests that the attention-related early oscillations in the canthal recordings of some subjects reflect ERG activity (Figures 9, 10, and 12).

The classical ERG consists of five components which are typically referred to as "waves": the (1) a-wave, (2) b-wave, (3) b-wave afterpotential, (4) c-wave, and (5) d-wave (Arminton, 1974; Charles, 1980; Miller & Dowling, 1970; Weinstein, 1980). The stimulus conditions of the present study were not suitable for eliciting c- and d-waves. Therefore, they are of no significance to the present discussion.

The a-wave is a negative-going component which peaks at about 20-40 msec poststimulus, and is generated by the hyperpolarization of the photoreceptors (Armington & Brigell, 1981; Carr & Siegel, 1985; Eason, 1984; Eason et al., 1983a; 1983b; Weinstein, 1980). Since this component precedes any stage of synaptic transmission and, therefore, cannot be influenced by central neural activity, it also is of no interest to the present study.

The b-wave is a positive-going deflection measured from the negative peak of the a-wave (representing b-wave onset) to a positive peak at about 50-80 msec (b-wave offset). This component is generally believed to be generated by depolarization of the Muller cells within the retina (Armington & Brigell, 1981; Carr & Siegel, 1985; Eason, 1984; Eason et al., 1983a; 1983b; Weinstein, 1980). Following the b-wave is a negative-going afterpotential which peaks at about 100-200 msec (Eason et al., 1983a; Weinstein, 1980).

Observation of the group averaged canthal tracings (Figures 9 and 10), particularly those obtained at the left internal canthus in response to the large stimulus, reveals a relatively small positive-going deflection with onset and peak latencies consistent with the b-wave of the ERG. The negative peak is at about 30 msec (N30); the positive peak is at about 60 msec (P60). A negative-going potential, starting at 60 msec (P60), and peaking at about 120 msec (N120) corresponds in polarity and latency to the afterpotential component. These minute, but distinguishable deflections will be hereafter referred to as the b-wave (or canthal P60 component), and the afterpotential (or canthal N120 component).

These retinally generated potentials are too minute to be registered at the frontal recording sites. However, there is a negative-going component in the frontal recordings which had to arise from a non-retinal generator which overlaps the retinal afterpotential in time. This is the same generator source discussed earlier, which tends to cancel the ERG b-wave in canthal recordings. However, it has an enhancing effect on canthal recordings in the afterpotential latency interval (approximately 60-120 msec), since both it and the afterpotential dipole sources generated potentials of negative polarity. It has been pointed out that recordings of ERGs with electrodes placed at periorbital locations, such as the internal canthus, result in the attenuation of the amplitudes of the various ERG components relative to those recorded from the corneal surface of the eye. Eason et al. (1983b) list the following factors as contributors to the attenuation of skin-recorded ERGs: (1) increased resistance in current flow from the eye to extraorbital areas, (2) increased sensitivity of extraorbital electrodes to nonretinal potentials arising from nearby neural or myogenic sources, and (3) the need for higher amplification of electrical signals for extraorbitally recorded ERGs.

Evidence will be presented which suggests that the skin-recorded ERGs in this study were influenced by some, if not all, of the above factors. It would appear that for those subjects whose canthal recordings revealed no discernible ERGs, the canthal electrodes detected relatively more nonretinal than retinal activity. Conversely, it is likely that retinal potentials had a greater impact on canthal recordings in those four subjects whose canthal recordings did manifest discernible ERGs.

Nonretinal Responses

Four components were discernible within the first 140 msec poststimulus in the frontal recordings (Figure 9). The first had an onset latency at about 30 msec and a negative peak latency at about 70 msec; the second a positive peak latency at about 90 msec; the third a negative peak latency at about 110 msec; and fourth a negative peak latency at about 140 msec. The latter two negative peaks were pronounced for some subjects and small for others. These four nonretinal components manifested in frontal recordings will be referred to as frontal N70, P90, N110, and N140, respectively.

Probable Generators of Nonretinal Components

Evidence suggesting the components identified in the frontal recordings were of nonretinal origin comes primarily from animal research wherein neural activity within visual pathways has been recorded directly from different levels within the brain. Latency information garnered from single unit recordings of the activity evoked in various structures of the visual pathway to a stimulus can be used as an aid in the determination of equivalent generators of human scalp-recorded activity within the visual system. The high degree of similarity between the visual systems of humans and primates renders latency information from primates suitable for determining equivalent sources of human scalp-recorded potentials. Factors such as the behavioral state of the animals, stimulus parameters used to elicit activity within the visual pathways, and locations of recording electrodes within the brains of the animals, determine the degree to which this information can be generalized to humans. Even under the most favorable conditions, some care must be exercised when determining the origin of scalp-recorded potentials. However, as latency information from animal research obtained from direct recordings brain activity accumulates, the origin of scalp-recorded potentials in humans can be ascertained with increasing levels of confidence.

Recording directly from the visual cortex and the lateral geniculate nucleus (LGN) in monkeys, Kraut, Arezzo, and Vaughan, (1983) concluded that activity within the 30-70 msec latency interval reflects both presynaptic depolarization within the thalamocortical afferents and postsynaptic activation of lamina IV stellate cells. Based upon this information, it appears as if the frontal N70 component is a reflection of both precortical and cortical activity. Other support for this interpretation comes from work done on unanesthetized monkeys wherein scalp-recorded ERGs, mass unit activity of localized cortical areas, and current source density were obtained simultaneously (Kraut et al., 1985). In this study, it was concluded that increased mass unit activity in the 20-60 msec range originated in lamina IV of the cortex. Thus, the modulation of the N70 component by attention could possibly be due to centrifugal gating of afferent transmission from the thalamus to the cortex via the geniculostriate pathway.

The response latency of single units in the superior colliculus (SC) of behaving monkeys to the presentation of peripherally presented stimuli also overlaps that of the frontal N70 component recorded in the present study (Crowne, 1983; Hikosaka & Wurtz, 1986; Wurtz et al. 1980). In addition, electrical stimulation of the mesencephalic reticular formation (MRF) results in increased thalamic (LGN) activity within the 40-80 msec range (Pecci-Saavedra, Wilson, & Doty, 1966), as well as in the 70-120 (Doty, Wilson, Bartlett, & Pecci-Saavedra, 1973) msec range. Based in part on such latency information, Eason et al. (1983a) concluded that an attention modulated component occurring within the 40-70 msec latency interval in human scalp-recorded VERs may have been a manifestation of both subcortical and early cortical activity.

The frontal P90 component recorded in the present study overlaps the latency interval of single unit responses obtained from extrastriate areas of monkeys. Neural activity has been recorded in the frontal eye fields (FEFs), located in visual area 8 of the frontal lobes, within 80-120 msec following stimulation (Bruce & Goldberg, 1985; Crowne, 1983; Wurtz et al., 1980). Increased activity in the parietal cortex of monkeys (visual area 7) has been recorded from 40-236 msec following stimulation (Bushnell, Goldberg, & Robinson, 1981). Hillyard, Munte and Neville (1985) have concluded that increased neural activity within the 70-80 msec range probably reflects early cortical activity. They have further suggested that scalp-recorded activity within the 110-140 msec range most probably reflects parietal cortical activity in humans. This latency interval encompasses that observed for frontal N110 and N140 components.

Based on the latency information garnered from the studies summarized above, it seems probable that most of the scalp-recorded field potentials with latencies of 70 msec or less are almost, if not entirely, of subcortical origin (Bruce & Goldberg, 1985; Bushnell et al., 1981; Crowne, 1983; Hikosaka & Wurtz, 1986; Wurtz et al., 1980). The evidence suggesting that any activity occurring prior to 40 msec arises from subcortical generators is even more compelling (Cracco & Cracco, 1978; Kraut et al., 1983). It appears, therefore, that the frontal N70 component identified in the present study reflects predominantly subcortical activity, especially in its earliest portion, although the possibility exists that the latter portion of this component may reflect very early cortical activity as well (Cracco & Cracco, 1978; Siegfried & Lukas, 1981; Whittaker & Siegfried, 1983). It is likely that frontal P90, and the later negative components observed in frontal recordings, primarily reflect cortical activity, although ongoing subcortical activity which overlaps such cortical activity may also contribute to the components.

Evidence suggesting the canthal and frontal recordings differentially reflect retinal and nonretinal activity comes from several lines of research. Numerous studies have demonstrated that ERGs can be recorded from the internal canthus and other periorbital regions (Armington, 1974; Carr & Siegel, 1985; Eason, 1984; Eason et al., 1983a; 1983b). In addition to demonstrating that ERGs could be recorded from canthal electrodes, Eason et al. (1983b) demonstrated that the amplitude of the retinal components was influenced by the favorableness of the alignment of the recording electrode with the retinal dipole source. Charles (1980) points out that the retinal layers are arranged in similar orientation with one another which allows for the recording of retinal activity extraorbitally.

An averaging computer should be considered essential for recording ERGs from periorbital sites, especially if low intensity stimuli are used to elicit the retinal responses. The increased resistance to current flow from the retina to periorbital recording sites, the interference from volume conducted neural and muscle generated potentials arising from locations central to the retina, and the relatively small responses elicited by low intensity flashes all serve to make the recording of ERGs from locations outside the eye difficult (Eason et al., 1983b). For these reasons recording electrodes must be placed as close to the eyes as possible, the resistance across the active and reference electrode must be as low as possible, subjects must refrain from extraneous movement, and stimuli must be presented many times when recording ERGs from periorbital regions.

The procedures required to record ERGs periorbitally make it highly probable that field potentials of nonretinal origin will contribute to the evoked responses obtained at such recording sites. Thus, it is likely that, in the present study, the canthal electrodes (in addition to detecting any ERG activity) detected field potentials of neural origins which also were the primary contributors to the frontal recordings. Conversely, it is unlikely that the frontal recordings contained any retinal contribution, because: (1) the peripheral stimuli were too small in size and too dim to elicit a strong ERG response, (2) the frontal electrodes were not favorably aligned with the longitudinal axis of the retinal dipole sources responsible for the ERG, and (3) the electrodes were too far removed from the eyes to detect a weak ERG, even if they had been favorably aligned with the retinal generators. Unless they are of large magnitude, ERGs are generally not volume conducted to locations far from the eyes (Siegfried & Lukas, 1980).

A third line of evidence suggesting the differential recording of retinal and nonretinal activity at the canthal and frontal sites, comes from close examination of the shape, latency, and polarity of the early components (20-70 msec) for each of the recording sites. The frontally- and canthally-recorded components falling within the 20-70 msec latency interval do not share the same morphology. Armington (1981) recorded ERGs directly from the eye with a contact lens electrode, while simultaneously recording VERs from electrodes placed on the scalp (on the midline three cm above the inion, and on the left earlobe). Except for differences in amplitude, the morphology of the contact lens-recorded ERGs (Armington, 1981) is virtually identical to the ERGs discernible in the canthal recordings for half the subjects in the present study. It is the case that ERGs recorded from the corneal surface are several magnitudes greater than those recorded from periorbital sites. The morphology of the frontal recordings obtained in the present study resemble the morphology of the scalp-recorded VERs recorded at a more posterior site by Armington (1981). These observations further suggest the canthal and frontal electrodes were differentially sensitive to retinal and nonretinal activity, respectively.

A fourth line of evidence that retinal and neural generators differentially influence the responses recorded at canthal and frontal sites comes from a comparison of the recordings obtained at the two sites, in the present study, in response to the large and small stimuli (Figure 14). Without going into detail regarding the differential effects of the two stimulus sizes at this time (further discussion is given later in relation to size effects), only the large stimulus elicited clearly discernible ERGs, and even then for only half the subjects. The striking similarity between the early components in the canthal recordings evoked by the small stimulus, and the frontal recordings evoked by both stimulus sizes, suggests that early neural components were detected at both recording sites. However, for those subjects in which a discernible ERG was elicited, the neural components were masked or partially cancelled. Since the small stimulus did not elicit an ERG in any subjects, the morphology of the canthal recordings in response to this stimulus size is similar to the morphology of the frontal recordings. This further suggests that the nonretinal components were manifested at canthal recording sites in the absence of a relatively strong ERG response. The discrepancy between the canthal recordings evoked by the small and large stimulus will be discussed in greater detail in the sections dealing with stimulus size main effects and interactions.

Attention-Related Modulation of Early Components

Evidence of Precortical Gating

The results of this study are consistent with those obtained by other investigators who have demonstrated early selective attention effects in the human visual system under similar conditions (Eason, 1984; Eason et al., 1983a; Oakley et al., 1985; Oakley et al., 1986). In addition, the results are consistent with studies in the auditory system, wherein early precortical gating of sensory transmission along the auditory pathways has been demonstrated as a function of selective attention (Lukas, 1980; 1981). All these studies have shown that transmission of input from attended stimuli is enhanced relative to input from unattended stimuli, and that the differential transmission of input from attended and unattended stimuli can occur precortically.

To the extent that the neural activity within the 40-100 msec latency interval for the canthal recordings of the present study represent precortical activity, it can be concluded that the results of this study are consistent with the precortical filtering hypothesis. Evidence has been presented which suggests that, for half the subjects in this study, canthal recordings within the frost 120 msec primarily reflect retinal activity. Therefore it appears as if the results of this study are, at least, in agreement with those studies which have demonstrated attention effects at the level of the retina (Eason, 1984; Eason et al., 1983a).

It has been established that the b-wave of the ERG occurs within the 20-80 msec latency interval, depending on stimulus conditions. Since only half the subjects in this study generated clearly discernible ERGs, any significant attention effect on the b-wave amplitude (in those four subjects who generated discernible ERGs) may have been masked by averaging their responses with the four subjects whose recordings contained no discernible ERGs. Eason (1984) and Eason et al. (1983a) demonstrated that the b-wave was significantly greater when subjects attended to stimulus flashes than when they did not.

The amplitude of the afterpotential was also significantly greater under the attend than under the unattend condition in the present study. The deflection for the attend condition was more negative than for the unattend condition within the integrated segment which contains the afterpotential (40-130 msec). The effect was demonstrated only for the left canthal and the combined left and right canthal recordings, however. Attention-related enhancement of the afterpotential was also demonstrated by Eason (1984) and Eason et al. (1983a). As in the present study, the polarity of the afterpotential for the attend condition was more negative than for the unattend condition.

The attention effect for the frontal recordings was manifested as increased negativity for the deflections recorded under the attend condition over the long interval of 40-130 msec. This finding is consistent with the early attention-related enhanced negativity for VERs recorded from frontal electrodes demonstrated by Oakley (1984), Oakley et al. (1985, 1986). The similarity between the morphology of the frontal recordings in the present study, and those recorded by Oakley, et al. (1985) provides further evidence that the frontal recordings in this study primarily reflect neural activity. Oakley et al. (1985) carefully selected a stimulus which would not elicit an ERG.

To the extent that the frontal recordings in the present study reflect precortical activity, the present results are consistent with the precortical gating hypothesis. It has been established that the frontal N70, and possibly the frontal P90, component reflect mostly subcortically generated field potentials. The fact that the attend and unattend deflections in the frontal recordings begin to separate as early as 50-60 msec suggests the occurrence of some attention related precortical gating. The latency of this early separation is consistent with activity in the superior colliculus (SC) or LGN of monkeys (Crowne, 1983; Hikosaka & Wurtz, 1986; Wurtz et al., 1980). Oakley et al. (1985) demonstrated maximum early separation of the attend and unattend deflections at about 50 msec.

Summary of Stimulus Size Main Effects

Canthal Recordings

Significant stimulus size effects were demonstrated in the canthal recordings occurring within the early 40-70 msec latency interval, as well as for the longer 40-100 msec latency interval (for the right eye). When the recordings from both canthal sites were averaged, a significant effect for stimulus size was demonstrated for the 40-70 msec latency interval. The stimulus size effect for the frontal recordings was not significant for any deflections occurring within the first 130 msec. Therefore, the discussion of the effects of stimulus size will be limited to the canthal recordings.

Interpretation of Stimulus Size Main Effects

Separation of Retinal and Subcortical Neural Components

Since the large stimulus excited a larger area of the retina than the small stimulus, it was expected that it would elicit larger responses. In addition, it was expected that only the large stimulus would elicit an ERG, since stimuli of low salience are not likely to elicit ERGs which can be recorded periorbitally (Armington, 1974;

Oakley et al, 1985; Weinstein, 1980). As reflected in the group averaged analog data depicting the stimulus size effects (Figure 7), the canthal P60 and N120 components (i.e., the b-wave and afterpotential) are present only in the canthal recordings evoked by the large stimulus. Examination of the individual subjects' averaged analog tracings indicated that only half of them generated ERGs of sufficient strength to be recorded by canthal electrodes. These observations also provide further evidence that the frontal and canthal recordings differentially reflect neural and retinal activity, respectively.

Some of the most compelling evidence suggesting that the canthal and frontal recordings primarily reflect activity from different sources within the first 120 msec comes from observation of the morphology of the VERs recorded from the two sites (Figures 9 and 10). The canthal recordings evoked by the small stimulus have the same shape, polarity, and latency as the frontal recordings evoked by both the large and small stimulus. This suggests that VER components generated at sites central to the retina were volume conducted to the canthal recording sites. In the absence of an ERG, which appears to have cancelled the more central components (in those recordings in which they occurred), the canthal recordings reflect the activity from the more centrally located generators. This may account for the similarity between the canthal recordings evoked by the small stimulus and the frontal recordings to both large and small stimuli. In the absence of an ERG, the recordings from both sites reflect mostly the activity of the neural generators.

Even more compelling evidence that the canthal recordings differentially reflect retinal and neural activity as a function of the size of the evoking stimulus comes from the observation (in Figure 9) of the reversed polarity in the canthal recordings evoked by the large and small stimuli within the 40-70 msec latency interval (i.e., the deflections for the large stimulus are positive, while the deflections for the small stimulus are slightly negative in polarity). Since the location of the electrodes was the same while recording responses to the large and small stimuli, it is highly unlikely that this inversion of polarity reflects activity from different sides of the same dipole source, as is the typical interpretation of such polarity inversions when recording sites are varied. It is impossible that the polarity of the deflection from a single source can be both negative and positive simultaneously, when recording from the same location. The fact that there is no inversion in the polarity of the deflections in the frontal recordings evoked by the large and small stimulus within the 40-70 msec latency interval strengthens the case that activity from the more central neural generators was recorded at the frontal sites in response to both stimulus sizes. The frontal recordings to the large and small stimulus within the first 120 msec reveal that the magnitude of the VER was greater for the large than for the small stimulus. However, the shape of the deflections evoked by the two stimulus sizes is similar within the 40-70 msec latency interval.

It appears, therefore, that the positive peak of the ERG b-wave drove the deflections for the canthal recordings relatively more positive for the large than for the small stimulus within the 40-70 msec latency interval. For the frontal recordings, the deflection within the same interval, were relatively more negative for the large than for the small stimulus. This suggests that no b-wave was detected by the canthal electrodes in response to the small stimulus, nor was a b-wave detected by the frontal electrodes in response to either the large or small stimulus.

Summary of Feedback Main Effects

Frontal Recordings

A significant effect for the feedback manipulation was demonstrated for the frontal recordings within the 100-130 msec interval and for the integrated latency interval from 40-130 msec. The group averaged analog tracings for the feedback effects (Figure 9) demonstrate that the greatest degree of separation between the deflections for the feedback and no feedback conditions occurred within the 100-130 msec latency interval. The effect was manifested as enhanced amplitude for the no feedback condition.

Interpretation of Feedback Main Effects

Cortical Activity

Based upon the fact that there was essentially no separation between the deflections for the feedback and no feedback conditions except for the 100-130 msec latency interval, suggests that the significant effects for the 40-130 msec latency interval resulted from the process of averaging measurements obtained over the 40-100 msec interval with those obtained for the 100-130 msec interval. The effect was so great within the 100-130 msec latency interval, that it produced a significant effect summed over the entire 40 to 100 msec latency interval. The possibility exists that this significant effect was due to early cortical activity, based upon its latency and the fact that it was not demonstrated in the canthal recordings. Another possibility is that the canthal recordings represented a summation of retinal and neural activity with the same polarity within the 70-120 msec latency interval, which contributed to a ceiling effect on the absolute amplitude of the deflection within this latency interval for the canthal recordings.

The results of the feedback manipulation are unclear. Behaviorally, there was a tendency for subjects to make fewer late responses when feedback was provided. However, there was no consistent electrophysiological correlate of this enhanced performance which was demonstrable in the VERs. A logical interpretation of the feedback manipulation is that subjects were highly motivated both with and without feedback. However, when they did receive feedback, they were able to make behavioral adjustments which improved their performance on the reaction time task, but no consistent neural correlate of such adjustments was manifested in the VER recordings. Perhaps a more effective method of manipulating motivational levels would have influenced VERs to a greater extent.

Summary of Attention and Stimulus Size Interaction

Left Canthal Recordings

A significant interaction between the attention and stimulus size manipulations was demonstrated in the left canthal recordings for the 70-100 and 40-100 msec latency intervals. When the recordings for the left and right canthal sites were averaged, a significant interaction between attention and stimulus size was demonstrated only for the 40-100 msec latency interval. A Tukey post hoc analysis revealed that a selective attention effect was demonstrated for both the small and large stimulus within the 70-100 msec latency interval; however, the effect was greater for the large stimulus. Within the 40-100 msec latency interval, the attention effect was significant only for the large stimulus. The attention effect was greater for the left canthal recordings than for the left and right canthi recordings combined.

Interpretation of Attention and Stimulus Size Interaction

ERG Responders vs. Non-ERG Responders

Half the subjects generated clearly defined ERGs in the left canthal recordings evoked by the large stimulus. These subjects have been identified as ERG responders. The four remaining subjects have been identified as Non-ERG responders. The averaged analog tracings for the two groups are shown in Figure 14, wherein the attention and stimulus size interaction is depicted for all recording sites. The location of the recording site appears at the very top of the figure, with the recordings evoked by the large and small stimulus appearing directly underneath the headings. Right and left hemisphere responses are designated on the left column. The tracings for the ERG responders appear in the top half of the figure, while tracings for Non-ERG responders appears in the bottom half. The attend and

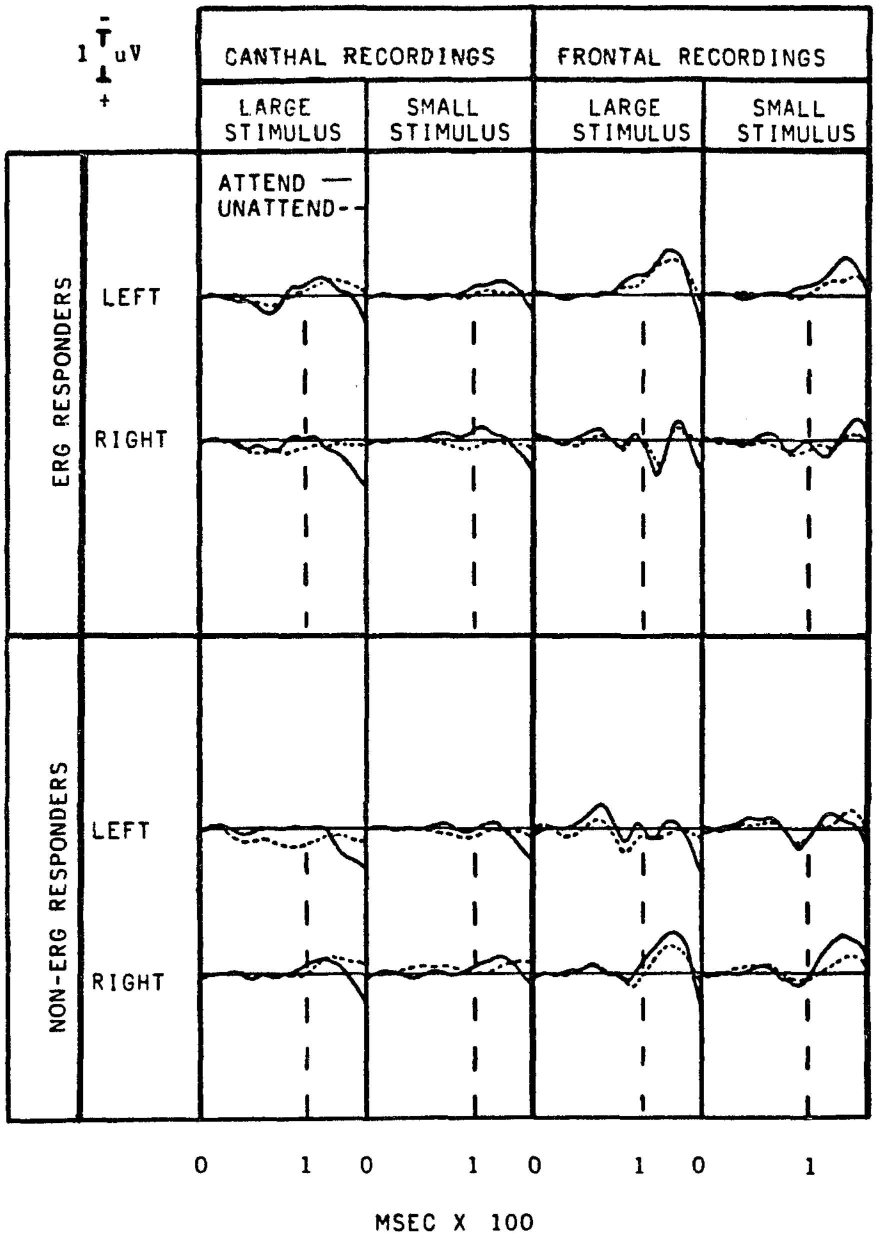

Figure 14

Attention by Stimulus Size interaction for ERG-responders and Non-ERG responders. VERs are separated as a function of Stimulus Size, Attention, and Recording Site.

unattend VERs are represented by solid and dotted lines, respectively.

The recordings for the ERG responders reveal a clearly defined ERG for the left canthal recordings evoked by the large stimulus. The ERG for the right canthal recordings is noticeable, but is not as pronounced as the one in the left canthal recordings. ERGs are conspicuously absent in all other recordings, including all frontal recordings evoked by the large stimulus. The attention effect reflected in the ERG responders' left canthal recordings is consistent with the ERG attention-related effect demonstrated by Eason (1984), wherein the b-wave and afterpotential were enhanced under the attend relative to the unattend condition. The attention effect was significant only for the afterpotential in this study; however, the trend toward a more positive b-wave for the attend relative to the unattend condition is consistent with the significant b-wave effect demonstrated by Eason (1984). Eason (1984) used more subjects and a more intense (i.e., more salient) stimulus than was used in the present study. This may account for the failure to demonstrate an ERG in all the subjects, and a subsequent b-wave attention effect in the present study.

In general, the deflections for the attend and unattend conditions appear to have separated earlier for the small stimulus recordings at all electrode sites. The overall tendency was toward increased negativity for the deflections recorded under the attend relative to the unattend condition. The implication of this observation is that the positive-going ERG and the negative-going more central components partially cancelled one another within the 40-70 msec latency interval. When a sufficiently large ERG was elicited, the more central components were completely suppressed within this latency interval. Thus, the recordings for both stimuli at all recording sites appears to have been a reflection of the algebratic summation of retinal and more central neural activity over the first 120 msec poststimulus. The relative contributions of the retinal and neural components to the overall VER waveforms within this latency interval depended upon the size of the evoking stimulus and the recording site. For the large stimulus at the canthal sites (for the ERG responders), the retinal components were dominant. When the small stimulus was presented to the same subjects at the same site, the neural components were dominant. For the frontal recordings, the neural components were dominant for all subjects and both stimulus sizes. For Non-ERG responders, neural components appeared to be dominant for both stimulus sizes at all recording sites.

There is general agreement between the findings for the canthal recordings evoked by the small stimulus, and the frontal recordings to both stimulus sizes in the present study, and the studies by Oakley (1984) and Oakley et al. (1985; 1986). In the latter studies, a Non-ERG-eliciting stimulus was used to demonstrate early attention-related negativity. This effect is suggested in the recordings for the Non-ERG responders. For these subjects, the deflections for the attend conditions are more negative than for the unattend condition over most of the 0-100 msec latency interval. This is even true for the recordings evoked by the large stimulus, since these subjects did not demonstrate ERGs. Although the attention effect for the Non-ERG responders over the 40-70 msec latency interval was not significant, the trend in the analog tracings is consistent with the findings of Oakley (1984) and Oakley et al. (1985; 1986). To this extent, it provides evidence for the precortical gating hypothesis.

Individual Differences

As noted in the Results Section, typical individual differences were observed in both the physiological and behavioral data. Such differences result from variations in the responsivity of the receptors to peripherally-presented stimuli, to variations in volume conduction of field potentials to the scalp due to differences in resistance to current flow, and to variations in the longitudinal axis of the equivalent dipole sources responsible for the field potentials (Vaughan, 1974; 1982). Differences in reaction time are related to variations in sensory and motor processing of signals to which the subjects are required to respond. The observed individual differences also could have been due in part to differences in the subjects' motivation levels and capacity to selectively attend to the peripheral stimuli. However, since such individual differences are in large measure due to physiological and anatomical variations which influence the amplitude, polarity, and the topographical distribution to field potentials recorded at the scalp (Vaughan, 1974, 1982), the correlation between VERs and behavioral measures such as reaction time tends to be quite low. Thus, the individual differences which occurred in the canthal and frontal recordings obtained in the present study cannot be interpreted as being a direct manifestation of between-subject differences in motivation level and/or degree of selective attention which occurred in the present study, although there would seem little doubt that such individual differences did occur. However, as stated in the Methods Section, an effort was made to minimize such between-subject differences by adjusting the late reaction time clock so as to make the task as nearly equal in difficulty as possible for all subjects (as measured by frequency of late reaction times).

CHAPTER IV

SUMMARY AND CONCLUSION

The following results were expected at the outset of this study: (1) the attention and stimulus size manipulations would interact significantly in the canthal (but not in the frontal) recordings within the 40-70 msec latency interval, (2) the large stimulus would elicit a b-wave response within the 40-70 msec interval which would be more positive under the attend than under the unattend condition, (3) the attention effect for the small stimulus would be manifested as increased negativity for the attend relative to the unattend condition for most, if not all, of the 40-120 msec latency interval for canthal and frontal recordings, (5) the magnitude of the attention-related negativity within the 40-70 msec latency interval would be greater for the small than for the large stimulus, (6) there would be no difference (except for possible increased amplitude for the large stimulus) between the frontal recordings in response to the large and small stimuli within the entire 40-130 msec latency range, (7) there would be little difference between canthal recordings in response to the small stimulus, and frontal recordings to both stimulus sizes, and (8) the attention effect might vary as a function of feedback.

While a significant attention by stimulus size interaction was obtained for the canthal (but not the frontal) recordings within the 40-100 msec latency interval, the attention-related enhancement of the b-wave was observed for only half the subjects. Thus, the large stimulus did not elicit reliable ERGs in all subjects' canthal recordings. When an ERG was elicited, the b-wave peak was relatively more positive under the attend than under the unattend condition, but the difference was not significant. The failure to demonstrate a significant b-wave effect in canthal recordings evoked by the large stimulus may have been due to the low intensity of the large stimulus (in this study) relative to the same sized stimulus used by Eason (1984). Although no b-wave attention effect was demonstrated in this study, the relative polarity of the deflections evoked by the large stimulus within the 40-70 msec latency interval was consistent with the expected results (Figure 11).

The magnitude of the attention effect was greater for the large than for the small stimulus with the 40-70 msec interval. This inconsistency with the expectation could be due to the insufficient saliency of the large stimulus. For half the subjects, the large stimulus elicited evoked responses of similar morphology to the VERs elicited by the small stimulus. In this case, the field potentials of the subcortical generators were relatively more influential than retinal generated field potentials (i.e., there was relatively little difference between the frontal and canthal recordings).

The expectation of greater negativity within the 40-70 msec interval for VERs in response to the small stimulus was apparently accurate. In general, the expectations regarding the relative contributions of retinal and nonretinal components to canthal recordings within the 40-70 msec latency intervals were upheld. This was especially true for half the subjects.

The outcome regarding the differential influence of the large and small stimulus on the afterpotential was consistent with the expectations. The attention effect within the 40-130 msec latency interval was consistently manifested as increased negativity for both the canthal and frontal recordings (for both stimulus sizes). The greater magnitude of the attention effect for the large stimulus (relative to the small stimulus) was also consistent with the expectations. The attention effect on the afterpotential supports the results obtained by Eason (1984) and Eason et al. (1983a). Thus, the canthal recordings appear to have been influenced by retinal activity in response to the large stimulus. The similarity between the outcome for the canthal recordings evoked by the small stimulus and the results of the studies by Oakley (1984) and Oakley et al. (1985, 1986) suggests that (for the small stimulus) the canthal recordings reflected more subcortical than retinal activity.

The failure to demonstrate a significant feedback effect is not surprising for several reasons. The feedback manipulation may not have increased subjects' motivational level to any significant degree, since they were already highly motivated. Another possible explanation for the failure to demonstrate a feedback effect is that it may not be possible for individuals to sustain very high levels of arousal over the duration of a two-hour session. Thus, there may have been a fatigue or habituation factor, which attentuated the feedback effect.

The results of this study provide a useful integrative function wherein the effects of relatively salient and relatively nonsalient evoking stimuli on recordings from near the eyes and frontal scalp have been examined in a single study. These results provide some evidence that VERs recorded from the frontal scalp mostly reflect the subcortical and early cortical activity within the 40-130 msec latency interval regardless of the saliency level of the evoking stimulus. Canthal recordings, on the other hand, differentially reflect retinal and neural activity as a function of the saliency level of the evoking stimulus.

The results of the study are at least consistent with the notion of precortical gating of sensory transmission at the level of the retina for half the subjects (see Eason, 1984; Eason et al., 1983a). The evidence of precortical gating at the thalamic level is more convincing, as the current results essentially replicate those obtained for the attention effect and for subcortically generated components within the 40-100 msec latency interval (Oakley, 1984; Oakley et al., 1985, 1986). Even stronger support for precortical gating as a function of psychological state could possibly be obtained if this study were to be replicated using a more salient large stimulus (i.e., more intense), and a more effective manipulation for varying motivational levels of subjects.

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