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THE INFLUENCE OF SENSORY AND MOTOR SET ON EARLY ATTENTION-SENSITIVE VERS

Oakley, Marta Valerie Tlapova', Ph.D.

The University of North Carolina at Greensboro, 1987

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THE INFLUENCE OF SENSORY AND MOTOR SET ON EARLY ATTENTION-SENSITIVE VERs

by

Marta Tlapova' Oakley

A Dissertation submitted to
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The University of North Carolina at Greensboro
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Approved by

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APPROVAL PAGE

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ABSTRACT

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The study examined whether motor set, along with perceptual set, produces precortical short-latency poststimulus effects in the visuo-motor system. Eighteen subjects participated in a spatial selective attention paradigm developed by Eason, Harter, and White in 1969. Spots of light were presented concomitantly 30 degrees peripherally in the right and left visual fields. The stimuli were presented either as a single flash or as two flashes (doublets). Subjects were required to make one of three types of responses to the doublets presented in the relevant field: (1) an eye movement, (2) a foot lift response, or (3) silent counting. VERs were recorded at frontal and parietal areas of each hemisphere.

VER deflections in the 40-70 msec latency range were dependent on the relevancy of the visual field; type of response made; and the scalp region from which recordings were obtained. These short-latency deflections were relatively more negative under the attend condition when subjects were set to make an eye movement, whereas they were positive under the attend condition when the subjects were set to silently count doublets. The absolute magnitude of the deflections were very small, compared to later components, and had a shallow gradient across the frontal

and parietal recording regions.

These findings were interpreted as evidence that both perceptual and motor set can influence the responsivity of visuomotor neurons very early following the presentation of a trigger stimulus, such influence being manifested precortically. Likely structures responsible for the observed effects were discussed within the context of anatomical and physiological data derived from animals, particularly from cats and monkeys. Data obtained from later VERs generally considered to be of cortical origin were also presented and discussed.

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A dissertation is not a product of one person. It is a piece of work which reflects the sharing of knowledge among many individuals; knowledge which takes generations to accumulate. I would like to thank the faculty of the Department of Psychology at the University of North Carolina at Greensboro for sharing their knowledge with me. I particularly wish to thank Drs. Harter, Nelson, Salinger, and Muir who served as committee members. I feel priveledged to have worked under the supervision of my mentor, Dr. Robert Eason, without whose support, encouragement, and trust this work would have never materialized.

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CHAPTER I

INTRODUCTION

Background and Rationale

To date most of the evoked potential research with humans has treated sensory and motor set as two independent, nonoverlapping entities wherein it is assumed that sensory set precedes motor set (Broadbent, 1970; Hillyard, 1981; Naatanen, 1982). However, information obtained from animal studies by Evarts, Shinoda and Wise (1984), Hikosaka and Wurtz (1983a,b,c,d), Wurtz and Goldberg (1972), and others suggest that sensory and motor set concomitantly impact on the responses of neurons to a relevant stimulus at very early, and probably precortical, stages of processing. Preliminary data collected in our laboratory with humans are consistent with the animal data, and suggest that motor, as well as sensory set, may affect the neural response to a relevant stimulus as early as 40 msec poststimulus (Oakley, Eason, & McCandies, 1986).

Cognitive neuroscientists have traditionally taken the view that before any differential neural processing of sensory information can occur, the information must first contact memory; and in order for this to occur, the information must reach the cortex (Donchin, 1979; Hillyard, 1981; Hillyard & Kutas, 1983; Hillyard, Munte, & Neville, 1984; Naatanen, 1982). Thus, the view proposed in the 1950s by Hernandez-Peon and associates (Hernandez-Peon, Sherrer, & Jouvet, 1956), Linsdley (1960), Livingston (1958) and others that, depending on the behavioral state of the organism, the flow of sensory information can be altered very early in the sensory pathways due to higher level influences (presumably cortical) being centrifugally imposed on synapses in these pathways, has been resisted by these neuroscientists despite the mounting body of evidence which has accrued in the past two decades in support of such a mechanism.

Eason, Harter, and White (1969) were the first to demonstrate an intramodality selective attention effect on an early negative component (onset/offset latencies of 90 and 130 msec) of the visually evoked response (VER). The paradigm consisted of presenting small flashes of light concomitantly in the periphery of both visual fields. With the eyes fixed straight ahead, the subject was instructed to attend from the corner of his eye to a specified location in the right (or left) visual field and to respond to flashes appearing in that field while attempting to ignore flashes presented at a homologous location. Subsequent data conducted by Eason and associates and others (Oakley & Eason, 1985; Oakley, Eason, Moore, & Conder, 1985; Oakley et al., 1986), Harter and Salmon (1972), VanVoorhis and

Hillyard (1977) have verified the earlier findings, and have provided an impetus for a host of current EP studies concerned with the effects of selective attention on early sensory transmission (Oakley et al., 1985; 1986).

Spatial selective attention, as used in the earlier work of Eason and associates, may be operationally defined as that location in a given visual field (e.g., right) to which the subject is required to make a specified response to designated ("target") stimuli, while not being required to make any response to stimuli appearing in the opposite field. A similar definition is used in the present study. The field requiring a response is designated the "relevant" or "attended" field; the opposite field is designated the "irrelevant" or "unattended" field. Within the context of this definition spatial selective attention is an independent variable, while variations in the magnitude and polarity of VER-components are dependent variables. That is, such variations are manifestations of biological correlates of spatial selective attention; they are not spatial selective attention *per se*.

The proposed research is an outgrowth of recent studies conducted by Eason and associates involving a concerted effort to demonstrate the existence of precortical gating in the visual system as a function of selective attention. Using a variation of the paradigm employed in the 1969 study, and with electrodes placed at the internal canthi of each eye, Eason, Oakley, and Flowers (1983) reported that the amplitude of a component believed to be the b-wave of the electroretinogram (ERG), as well as a later component believed to be the afterpotential of the ERG, was significantly enhanced when a given spatial location was being attended to. Followup studies conducted by Eason (1984) corroborated these observations, although Mangun, Hansen, and Hillyard (1986), who recorded with gold-foil electrodes folded over the lower eyelid, were unable to obtain positive results in an attempted "replication".

Although extensive evidence is available to indicate that centrifugal fibers exist in the optic nerve of mammals (Itaya, 1980; Itaya & Itaya, 1985; Larsen & Moler, 1985; Terubayashi, Fujisawa, Itoi, & Ibata, 1983) including humans (Reperant & Gallego, 1976; Wolter, 1979), considerable skepticism still remains among neuroscientists as to their existence. If they in fact do not, then the attention effects noted above could not have been of retinal origin. There is the possibility that the canthal electrodes recorded activity arising from subcortical generators located centrally to the retina, and that it was this activity, which algebraicaly summed with the electroretinogram, that was actually modulated by the attention manipulation. Subsequent experiments were therefore conducted in our laboratory (starting with

Oakley's Masters thesis) in an effort to further test the validity of the pre-cortical gating hypothesis, using flash stimuli too weak to elicit detectable ERGs. The purpose of these experiments was to determine whether (1) early (non-ERG) EP-components falling within the latency range of the b-wave and afterpotential of the ERG could be modulated by selective attention, and (2) whether such components are of subcortical origin.

In her Masters thesis project, Oakley placed bilateral chains of electrodes on either side of the midline of the scalp, and measured the effect of selective attention (using the Eason, et al, 1969 paradigm) on very short-latency components of the VER. She found that a component with a peak latency of approximately 50 msec was sensitive to the attention manipulation. The component was of relatively low amplitude and homogenously distributed across the scalp. With the aid of latency information garnered from animal studies (Goldberg & Wurtz, 1972; Hikosaka & Wurtz, 1983 a,b,c,d; Petersen, Robinson, & Keys, 1985; Wurtz, Goldberg, & Robinson, 1980) and on the basis of the low amplitude, flat distribution of the component across the scalp, it was concluded that the component was probably of subcortical origin. Information available in the animal literature suggested further that likely candidates for generating the component were the superior colliculus (SC) and pulvinar, since peripheral stimuli, such as were used in the thesis project, preferentially activated the tectopulvinar system via synaptic connections in the SC (Cowey, 1984). Other possible contributors include the lateral geniculate nucleus (LGN), inter medullary lamina, and paralaminar nuclei of the thalamus, since it is known that these structures also receive sensory input from peripheral retinal areas (Schlag & Schlag-Ray, 1984).

In an initial effort to determine whether the SC may have been a significant contributor to the component, a subsequent study (Oakley et al., 1985) was conducted wherein subjects were required to make an eye response when a target stimulus appeared in the relevant (i.e., attended) visual field in addition to making a finger lift response. Since research with monkeys has shown that certain neurons in the SC respond to a target stimulus presented at the relevant location only when the animal is set to make an eye movement to that location (Goldberg & Wurtz, 1972), it was reasoned that if these cells respond in a similar manner in humans, than the early (50-msec) component should differ in amplitude and/or polarity when both an eye movement and finger lift response are required compared to when only a finger lift response is required. No differences were observed; thus the hypothesis was not confirmed. However, the results did confirm earlier observations that the amplitude of the 50-msec component is affected by the selective attention manipulation. Other topographical studies conducted at UNCG have further confirmed this finding (Oakley, et al., 1986), while providing further topographical evidence that the component is of subcortical origin.

In addition to substantiating the 50-msec attention effect, the Oakley, et al (1986) study yielded data suggesting motor set may also have affected the amplitude and/or polarity of the early component. This study yielded interesting hemispheric asymmetries in the early attention effect as a function of the hand with which (left or right) the subject was prepared to make a response when the target stimulus appeared in the relevant visual field. At central, parietal and occipital recording sites the attention effect was relatively larger over the right hemisphere than over the left when subjects were set to respond to target stimuli with the left hand. At frontal recording sites (F3,4 and Fp 1,2), the attention effect also was relatively larger over the right hemisphere than over the left, but only when subjects were set to respond to target stimuli with the right hand. No significant attention effect was obtained over the left hemisphere at central, parietal and occipital electrode sites, regardless of the hand with which the subject was set to respond. Since the VERs to target stimuli were not included in the averaged responses, these results suggest that motor set (i.e., a readiness to respond with a particular hand) influenced neural generators of the early EP-component concomitantly with centrifugal influences associated with sensory set (i.e., spatial selective attention). This surprising observation provided an initial cue in our laboratory that motor set, as well as sensory set, may influence very short-latency, presumably precortical, responses to target stimuli presented at relevant (i.e., attended) locations in the peripheral visual field. A review of the animal anotomical and physiological literature has yielded information suggesting that it not only is possible but even quite probable that motor set may influence neural responses to attended stimuli at subcortical, as well as at cortical levels. Summaries of these studies are presented in the next section, but before turning to them, however, it is of some importance to describe two additional experiments conducted in our laboratory which provided significant methodological information utilized in the present project. These were control experiments designed to rule out the possibility that shifts in eye position may have been responsible for the early attention effects noted in our earlier studies, and to assess the neutrality of the mastoid as a reference point for recording the attention-sensitive early EP-component (since this site was used as reference in our most recent studies).

To test the possibility that the observed attention effect on the 50-msec component may have been due to shifts in eye position toward the relevant stimulus field, the effects of shifts in eye position on the amplitude and polarity of VER-components obtained over a 500-msec period were systematically studied, special emphasis being placed on the effects of such shifts during the first 130 msec poststimulus. With the eyes fixated straight ahead, the retina was stimulated at seven different eccentricities ranging from 20 to 40 degrees, thereby simulating various distances of shifts in eye position both toward and away from a peripheral location of 30 degrees (the latter being the location used in the attention studies). The effects of shifts in eye position on the amplitude and polarity of the early component were just the opposite of those observed for the attention manipulation. Thus the attention effect could not have been due to shifts in eye position (Oakley, Eason, & McCandies, 1986).

Since the mastoid was used as reference in the attention studies summarized above, a common practice among cognitive neuroscientists (Hillyard & Munte, 1984, Neville & Lawson, 1987), and since no information was available concerning the neutrality of this site on very early components of the VER, a study was conducted in our laboratory to assess whether and to what extent the mastoid may have contributed to the amplitude and polarity of VER-components occurring within 500 msec poststimulus, emphasis being given to any effects noted within the first 130 msec. The extent to which the mastoid recording site may have influenced early components has implications for the orientation of dipole(s) responsible for the generation of the attention-sensitive field potentials detected at various scalp locations, as well as for the location of the dipole(s). VERs were obtained between electrodes placed at the mastoid and the ipsilateral earlobe. On the assumption that an electrode placed on the earlobe is relatively more insensitive to scalp field potentials than one placed at the mastoid, due to the greater distance of the lobe from the generator source (and therefore greater resistance in current flow), it was reasoned that any consistent departure of the VER within a given latency range away from a zero voltage baseline would be indicative of a field potential change detectable at the mastoid location. The VER waveform, averaged across thirty-eight subjects, was found to be essentially flat for the first 60 msec. However, a positive deflection with a peak latency of 90 msec and a negative deflection with a peak latency of 120 msec were both found to deviate significantly from baseline. There were no discernible deviations from baseline at later points in time. These findings indicate that the mastoid seems to have contributed nothing to the 50-msec attention-sensitive component recorded over frontal, central, and parietal scalp locations. However, the site is substantially influenced by field potentials evoked by peripheral stimulation during a critical latency range of 70 (onset latency of a positive deflection) and 120 (offset latency of a negative component) msec. This finding has important implications for the interpretation of the location and orientation of dipole sources responsible for VER-components falling within this latency range.

Motor Set

The influence of motor set on the quality and quickness of an organism's response to various kinds and amounts of stimuli presented to various sensory modalities has a very long history (Boring, 1957; Herrnstein & Boring, 1965; Woodworth, 1958), but only in recent years have neuroscientists engaged in a concerted effort to understand the neural basis of such influences (Evarts, Shinoda, & Wise, 1984). The conceptual framework for the proposed project, in addition to our own work summarized above, relies heavily on the pioneering work of Evarts and associates (Evarts et al., 1984; Evarts, 1984), as this group of researchers has conducted the most sustained, systematic, and influential investigation of neural mechanisms of motor set to date. Two recent books are especially relevant to the dissertation project. One of them was authored by Evarts, Shinoda, and Wise, and is entitled Neurophysiological approaches to higher brain function (published in 1984 by Wiley); the other was edited by Kornblum and Requin, and is entitled Preparatory states and processes (published by Erlbaum in 1984).

Motor set-related activity. Set-related neuronal activity may be studied in at least two ways. One approach is to provide an instructional stimulus (IS) to the subject (e.g., a stimulus cue or verbal instruction to get set to respond to stimulus X by making response Y) and measure the activity occurring in one or more neurons during the interval following the IS and the presentation of stimulus X (the trigger stimulus; TS). Any changes noted in the monitored neuron(s) during the IS-TS interval, in comparison to that observed during the interval separating each IS-TS sequence, would constitute a manifestation of set-related activity. One example of this approach is the delayed response (DR) paradigm frequently used for studying memory mechanisms in monkeys. A commonly employed procedure involving the use of this paradigm is to (1) place food under one of two opaque covers while the monkey watches, (2) institute a delay interval, and (3) permit the monkey to make a response to retrieve the food. Evarts (1984) notes that within the framework of the IS-TS paradigm, placement of the food is the IS, and the elevation of a screen interposed during the delay interval (to block the animal's view of the two opaque covers) is the TS. Studies conducted by Fuster and Alexander (1971) and Kubota and Niki (1971) exemplify the usefulness of this paradigm in assessing the set-related activity of neurons in prefrontal cortex. These studies were among the first to show that during the delay between the IS and TS the discharge frequencies of prefrontal cortex neurons were dramatically affected by the IS. Their results suggested to Evarts and associates (Evarts, 1984) that the sustained activity of prefrontal cortex neurons might underlie the set of the monkey to make a movement (i.e., motor set) specified by the IS. A later study conducted by Weinrich and Wise (1982), using a paradigm which permitted examination of single neuronal activity during the IS-TS interval in a visuospatial task, demonstrated that set-related neurons exist in the premotor cortex (area 6) of the monkey. Furthermore, most of the set-related neurons showed specificity for the direction of the upcoming movement. The utility of studying neuronal activity during the IS-TS interval as a means of disclosing neural mechanisms of motor set has even been demonstrated in the invertebrate <u>Pleurobranchaea</u> (Kovac & Davis, 1977). Indeed, because of the simplicity of this organism's nervous system, Evarts (1984) proposed that it constitutes a valuable model for formulating hypotheses about motor set which may be studied in more complex organisms, including mammals.

A second approach for studying set-related activity is to measure changes in neural and behavioral activity (such as EPs and reaction time) following the TS as a consequence of variations in the IS. Among the first to use this approach was Hammond, who demonstrated over three decades ago (1956) that motor set can have very short-latency effects on the manner in which a subject reacts to a trigger stimulus. Subjects were asked to flex the forearm, and instructed to respond to a sudden pull on the forearm by "resisting" or "letting go". In this paradigm the instruction to "resist" or "let go" was the IS, the sudden pull on the forearm was the TS. The biceps EMG was recorded following the TS for the two different types of IS. Since typical reactions to auditory and visual stimuli in well practiced subjects are about 150 and 180 msec respectively, Hammond was surprised to find that an EMG response with a latency of only 50 msec was elicited when the IS was "resist" and that this response was absent when the IS was "let go". An earlier (18 msec) stretch reflex response was observed in the EMG for both types of IS. Since the 50-msec response, which responded differentially to the two types of IS, was less than half the latency of typical voluntary responses to simple visual and auditory stimuli, Hammond (1956) concluded that it was largely an involuntary, reflex-like response; yet, the set induced by the IS to "let go" drammatically interfered with (i.e., inhibited) the occurrence of the response. It appears that the IS, "let go", altered the readiness of neurons which normally participate in a reflex response to a TS producing muscle stretch so as to attenuate or totally inhibit their participation. This was the first demonstration that motor set can alter a TS-elicited movement which cannot be classified as being either all reflex or all voluntary in nature.

Hammond's observations were essentially ignored for nearly 20 years, primarily because the very short latency of the set-related response could not be reconciled with the existing literature. It was not until the mid 1970s that Evarts and Tanji (1974) conducted a study of set-related responses with monkeys, using a paradigm analogous to that of Hammond. In their study, the IS was a red or green light; the red light instructing the monkey to pull a lever in response to a TS, the green instructing him to push the lever in response to the TS. Following the IS, the monkey witheld making a movement until a torgue motor moved the lever toward or away from the animal (TS). EMGs were obtained from biceps muscle following each TS under each of the four experimental conditions generated by the two types of IS and TS. When the IS was "pull" and the TS was "away", a 20 msec stretch reflex response was manifested in the EMG. This was followed by a potent EMG response with an onset latency of about 80 msec (comparable to the 50-msec response obtained by Hammond from humans). When the IS was "push" and the TS was "toward", no discernible EMG response was recorded at any latency. The first of these two conditions was optimal for eliciting both a stretch reflex and a set-related response produced by the instruction to "pull". The second of the two conditions produced a set-related neural pattern which eliminated both the stretch reflex response and the 80-msec discharge. Recordings concomitantly obtained from pyramidal tract neurons in motor cortex resulted in changes which paralled those noted in the EMG responses. These observations, along with the set-dependent prefrontal cortex activity observed by Fuster and Alexander (1971) and Kubota and Niki (1971), as well as the set-related activity observed in premotor cortex by Weinrich and Wise (1982), suggested to Evarts and Tanji (1974) that the occurrence of such activity in the IS-TS interval plays a role in the altered responses to the TS.

<u>Visuomotor animal studies having implications for motor set effects on short-latency TS evoked EPs</u>. A number of studies on monkeys in recent years, and in some instances on cats, primarily for the purpose of defining neural circuits and mechanisms pertaining to ocular movement and fixation, have yielded data which strongly suggest that motor set may

influence short-latency responses (both cortical and subcortical) to a TS. Studies by Goldberg and Wurtz (1972) and Wurtz and Mohler (1976) have revealed neurons in the SC which give an enhanced response to a TS only if the monkey is set to move the eyes toward a location in space to which it had previously been instructed (with an appropriate cue) to attend (the IS). If the eyes are set to move to a location other than that in which the TS appears, the response of these neurons to the TS is not enhanced. This likewise is the case if the animal is set to respond to the TS upon its occurrence in the attended field by some means other than an eye movement (e.g., a hand-withdrawal response). These investigators observed that approximately 51% of the SC neurons tested were of this response-specific type. The units had a relatively short response latency to the TS, the onset of response enhancement (i.e., increased firing rate) being about 40 msec in most instances. Although these investigators did not discuss the implications of their findings for motor set, their observations are consistent with the interpretation that IS-dependent, motor set-related activity occurring during the IS-TS interval biased the responsivity of neural elements in the SC such that a short-latency, enhanced response was elicited by these units only when the eyes were set to move toward the attended location in response to the TS.

Units which respond in similar fashion have been identified in the reticular part of the substantia nigra (Hikosaka & Wurtz, 1983 a,b,c,d), which is known to receive extensive input from the corpus striatum (Graybiel & Ragsdale, 1979), and to send projections to the superior colliculus, central gray, reticular formation, and thalamus (Anderson & Yoshida, 1977; Hikosaka & Wurtz, 1983d; Hopkins & Niessen, 1976). These cells typically responded to a visual stimulus by a reduction in firing rate (just the opposite of SC cells), the latency of reduction onset being about 80 msec. Over half of the cells from which responses were obtained (58%) reacted to visual stimulation, strongest reactions occurring to relatively small stimuli (0.2-1.0 degrees visual angle). Forty-eight of 114 visually responsive cells (42%) gave enhanced responses (i.e., firing rate reduction of greater amount and duration) when the monkey was set to make (and made) a saccade toward the location in which the TS appeared. Concomitant recordings from nigral and SC cells, which had been found to be functionally connected through antidromic stimulation of nigral units by electrical stimulation of units located in the SC, revealed that the reduction in firing rate by nigral units was highly correlated with an increase in firing rate of SC units (Hikosaka & Wurtz, 1983d). The known anatomical and functional connections between prefrontal cortex and the frontal eye fields to the basal ganglia (e.g., Allen &

Tsukahara, 1974), in conjunction with the striatonigrotectal pathways just described, provide one possible route whereby motor set-related cortical activity occurring during the IS-TS interval might influence the responses of SC neurons to a TS.

Visually responsive, saccade dependent thalamic responses also have been obtained from units in the pulvinar (Petersen, Robinson, & Keys, 1985) of the monkey, as well as from units located in the internal medullary lamina (IML) of both cats (Schlag & Schlag-Rey, 1971; Schlag, Lehtinen, & Schlag-Rey, 1974) and monkeys (Schlag-Rey & Schlag, 1984; Schlag & Schlag-Rey, 1984). Petersen et al. found that 60% of the cells tested in the lateral pulvinar (PL) gave a greater response to a peripheral stimulus (TS) when the monkey was cued (IS) to make a saccade in response to the TS, compared to responding with the hand while maintaining fixation. Responses obtained from the inferior pulvinar (PI) also were enhanced by the saccade condition. The authors concluded that the enhancement "...indicates that an eye movement is about to occur and does not signal the attention shift that preceded the eye movement." This seems to be another way of saying that the saccade-dependent enhancement of these cells is a manifestation of motor set-dependent activity established by the IS, which produced a bias in cortico-pulvinar pathways during the IS-TS interval favorable to response enhancement to the TS. In short, the conclusion implies that the observed enhancement was due to motor set rather than to sensory set (i.e., selective attention). The vast majority of these units had an onset response latency between 40 and 100 msec, the average being about 65 msec. In addition to receiving visual input from pretectal (Benevento, Rezak, & Santos-Anderson, 1977) and tectal (Benevento & Fallon, 1975) nuclei, the pulvinar also receives input from striate, prestriate, and temporal cortex (Benevento & Miller, 1981; Chalupa, 1977). Various nuclei of the pulvinar project to striate cortex (Benevento & Rezak, 1976), prestriate cortex (Benevento & Miller, 1981; Chalupa, 1977), inferotemporal cortex (Benevento & Miller, 1981), and the frontal eye fields (Trojanowski & Jacobson, 1974). Thus, as for the SC, it would appear that adequate circuitry exists for imposing motor set-induced cortical influences on PL and PI regions of the pulvinar wherein Petersen et al. observed saccade-dependent enhancement effects.

Studies conducted on single units located in the inter medullary lamina (IML) of the central thalamus of both cats and monkeys, alluded to in the preceding paragraph, are strongly suggestive that motor set-related subcortical (if not precortical) gating mechanisms probably exist. The Schlags conducted these studies for the purpose of further elucidating the neural mechanisms of ocular movement and gaze, and interpreted their findings within the context of this objective (Schlag & Schlag-Rey, 1971; 1984). However, their observation that some units in the IML show enhancement only when the animal was required to make a saccade to the visual stimulus make these studies relevant to the motor set gating issue. The latency of most of these units (80%) fell between 77 and 135 msec, the mean latency being about 100 msec. These observations have particularly important implications for set-related activity (including motor set) in view of the extensive reciprocal connections of the IML with other thalamic structures as well as with other structures located both caudally and rostrally which are involved in sensory and/or motor information processing. Inputs to and outputs from the IML are widely shared with adjacent thalamic nuclei, including the dorsomedial (CD) and centrolateral (CL) nuclei (Kievit & Kupers, 1977; Schlag-Rey & Schlag. 1984). Indeed the IML is predominantly a region of passing fibers. There are inputs from the cerebellum, brainstem reticular formation, tectum, pretectum, vestibular nuclei, substantia nigra, and adjacent thalamic nuclei (Schlag-Rey & Schlag, 1984). Although there is evidence that some IML neurons project caudally (Scheibel & Scheibel, 1967), most of them project rostralward with the majority reaching the striatum (Royce, 1978; Schlag-Rey & Schlag, 1984). Neurons located in prefrontal cortex, including the frontal eye fields, project downward to the IML, where they send collaterals to both the IML and the MD, before reaching the superior colliculus. This transthalamic pathway directly links the frontal eye fields to the IML and SC (Leichnez, Spencer, Hardy, & Astruc, 1981; Schlag-Rey & Schlag, 1984).

The numerous connections of the IML to other structures led Lindsley (1960) and others to postulate that the region was a diffuse projection and receiving system which played a major role in alerting and attention. Studies by the Schlags and others have verified that attention-related neurons exist in abundance in the IML, but although the connections are complex, they are not general, and IML cells appear much more specific than was thought to be the case by activation and attention theorists of the 1950s and 60s (Schlag-Rey & Schlag, 1984). The important point for the present project is that the rich variety of inputs and outputs to the IML make this region particularly well suited to participate in the gating of both sensory and motor activity as a function of the behavioral state of the organism.

Single unit studies of frontal eye field (FEF) neurons in the monkey have disclosed that the response of many neurons in this area to a peripheral visual stimulus (TS) is enhanced, provided the animal has been cued (IS) to make a saccade in response to the TS (Bruce & Goldberg, 1985;

Goldberg & Bushnell, 1981; Mohler, Goldberg, & Wurtz, 1973). The majority of these units have an onset latency between 40-120 msec, the median being 80 and the mean 87 msec. Bruce and Goldberg (1985) have proposed that this enhanced activity reflects a mechanism which channels selected visual information to the oculomotor system. Since it is known that the FEF sends projections either directly or indirectly to all layers of the SC in cats, and to the intermediate and deep layers in the monkey, if not also to superficial layers (Sparks, 1986), it is our contention that this process may be motor-related.

A case can be made for the existence of motor set-related mechanisms at a cortical level by returning to the work of Evarts and associates (Evarts & Fromm, 1977; 1978; Evarts et al., 1984; Fromm & Evarts, 1978), involving recordings from monkey motor cortex during the performance of a visual pursuit-tracking task. Through feedback applied to a handle grasped by the monkey, the animal was taught two types of tracking tasks: (1) to keep the tracking stimulus as still as possible, the "steady" condition, and (2) to move the tracking stimulus as quickly as possible toward a suddenly displaced target stimulus, the "balistic movement" condition. The IS in the first condition was to get set to hold the handle as steady as possible ; in the second, the IS cued the animal to be prepared to move the lever as quickly as possible toward the displaced target stimulus (the TS). Afferent responsiveness of pyramidal tract neurons located in the hand area of motor cortex (MI) was measured upon displacement of the handle under the two motor set conditions. Enhancement of these neurons to kinesthetic stimulation through handle displacement (TS) was obtained when the animal was set to maintain accurate positioning and controlled fine movement (the "steady" set condition), but their responsiveness to the sudden displacement was depressed when the animal was set to make a "ballistic" movement in the direction of the displacement.

While acknowledging that the difference in motor cortex responsiveness could have been due to alterations of sensory signals at subcortical levels, these investigators have proposed an intra-cortical gating process which functions as an "open loop" set under the "balistic" condition and a "closed loop" set under the postural stability and fine control condition. Drawing on a proposal by Allen and Tsukahara (1974), they postulate that a shift in motor set from "steady" to "balistic" requires a change of input from the interpositus nucleus (IP) of the cerebellum, which provides kinesthetic feedback to MI, to input from the dentate nucleus (DEN), which provides central commands to MI. Input from these two sources is provided through circuitry involving cerebello-thalamo-cortical pathways which converge upon individual MI PTNs (at least this is the case for the cat and presumably also true for the monkey). Evarts acknowledges that the gating could occur at any level of the circuit (i.e., the IP and DEN of the cerebellum, the VL of the thalamus, or at MI), but he has proposed a model (1984) which places the gate in MI where it is subject to modulation by "...cortico-cortical and/or nonspecific thalamic inputs." The model proposes the existence of an interneuron in MI which lies between VL terminals of the thalamus and MI PTNs. These MI interneurons are assumed to receive private line inputs from either IP or DEN neurons of the cerebellum via the VL of the thalamus. Also, there are "set cells" within MI and in areas projecting to MI (not specified) which impinge on these interneurons. It is assumed that these set cells can control the exitability of the interneurons. The convergence of two such interneurons (one receiving DEN and the other receiving IP input from the cerebellum with each being coupled with "set cell" input) onto a single pyramidal tract neuron in MI could conceivably produce an enhanced reaction to the TS under the "closed loop", steady-set condition, and a suppression of PTN activity under the "open loop", ballistic-set condition. Evarts acknowledges that this model is speculative, but it does exemplify at least one way in which neural gating due to motor set (at a cortical level) might produce short-latency effects on TS-elicited neural and motor activity.

It is not unreasonable to assume, as Evarts points out (1984), that gating based on similar kinds of switching models could occur at subcortical levels as well.

Statement of the Problem

The work of Evarts and associates, Wurtz and associates, the Schlags, and that of others summarized above, along with the work conducted in our laboratory, not only lends credibility to the possibility but suggests it is quite probable that motor set, along with sensory set (i.e., selective attention), may influence short-latency reactions (40-120 msec range), both neural and muscular, to a specified trigger stimulus (TS) as a consequence of set-related neural activity which occurs during the IS-TS interval. The neural biasing which occurs in the information processing units involved in the elicitation of an appropriate response during the IS-TS interval could be sustained or phasic, and could involve both subcortical and cortical elements.

Studies conducted in our laboratory in recent years (Oakley & Eason, 1985; Oakley et al., 1985; 1986) have consistently shown that very early components of scalp-recorded VERs (40-100 msec range) can be modulated by the instruction to respond to target stimuli (usually doublets) appearing at a specified location in the relevant (i.e., attended) visual field. An analysis of our paradigm within

Evart's IS-TS framework reveals that the subject is faced with a fairly complex perceptual-motor task involving two types of IS and two types of TS. The instruction to attend to a specified location in a given visual field (left or right) constitutes the first type of IS (designated IS1). The instruction to make a defined response to specified target stimuli (e.g., doublets) appearing in the attended field (e.g., finger lift, foot lift, eye movement, or counting response), while making no defined response to single flashes appearing in that field, constitutes a second type of IS (designated IS2). The stimuli to which the subject is required to make a designated response constitute one type of TS (designated TSr); the stimuli requiring the suppression of an active response (i.e., no response) constitute the other type of TS (designated TSnr).

The two types of instructional stimuli (IS1 and IS2) differ in two important respects in regard to their implications for perceptual and motor set-related biasing during early stages of sensory transmission and processing. The first difference is that IS1 involves the utilization of widely separated, non-overlapping receptor units and neurons due to the widely-separated physical location of stimuli presented in the relevant and irrelevant visual fields, whereas IS2 requires the utilization of the same receptors and sensory neurons (at least in the early stages of processing). The second difference is that IS1 leads the presentation of the TS, thereby providing an opportunity for perceptual and motor set-related neural bias to develop in the visual-motor system (wherever that may be) during the IS1 - TS interval; whereas for IS2 there is no opportunity for any perceptual or motor set-related neural bias to develop following its presentation, since IS2 and TS (single or double flash) are one and the same and the time interval between IS2 and TS (whether TSr or TSnr) is zero. Thus, any set-related effects on early components of VERs, using our paradigm, can only be observed by noting the effects of IS1 on responses elicited by the TS. In our paradigm, this consists of making a comparison of VERs obtained to stimuli presented in a specified visual field when relevant (i.e., attended) compared to when that same field is irrelevant (i.e., unattended). The effects of perceptual and motor set-related bias on VERs to the TS could be studied for both single (TSnr) and double-flash (TSr) stimuli. Our analyses, based on previous research, have been limited to responses to single flashes (TSnr) only, because these stimuli are presented more frequently than doublets (TSr), movement artifacts are avoided, and equipment constraints do not permit the recording of VERs to both types of stimuli during a data collection trial. In the present research, recording continued to be limited to VERs obtained to trigger stimuli of the TSnr type (i.e., single flashes).

Until fairly recently, we had assumed that the effects of the selective attention manipulation given by the instruction to respond to stimuli appearing in one visual field (either overtly by lifting the finger off a key or covertly by not lifting the finger in response to TSr or TSnr respectively) were entirely due to perceptual set (i.e., selective attention). It was not until we varied the type of response the subject was required to make (using either the right or left hand) that motor set was implicated as playing a role in the neural biasing process occurring during the IS1-TS interval, and thus possibly influencing early VER-components evoked by the TS (Oakley et al., 1986). Before embarking on a major investigation of this question, which was the primary purpose of the present study, a preliminary investigation was conducted to assess the feasibility of attempting to investigate this question through the use of scalp-recorded VERs obtained from humans.

In this preliminary study, stimulus flashes subtending 35' of arc were presented in either the right or left visual field on a given trial. One group of three subjects was required to respond to every single flash; a second group (four subjects) responded only to doublets randomly interspersed (33% probability of occurrence) among the single flashes. VERs were obtained to the single flashes (N=100) from frontal and parietal electrode sites over each hemisphere for both groups. The type of response made by the subjects (whether to single flashes or doublets) was varied across trials. The responses were: (1) an eye movement toward the target stimulus; (2) opening the mouth as quickly as possible; (3) making a finger lift response with the left hand; (4) doing likewise for the right hand; (5) making a left foot response as quickly as possible; and (6) doing likewise with the right foot. Grand VER averages, collapsed across both groups of subjects, were obtained for each recording site. The frontally-recorded VER waveforms in the 40-90 msec range tended to be more negative when the subjects responded (or were set to respond) to the target stimulus by making an eye movement response than by making any other type of response. T-tests performed on quantitative measures of the VER-deflections in the 40-50 msec range revealed this short-latency deflection was significantly more negative for an eye movement than for a mouth response; also for an eye movement than for a hand lift response. The eye movement vs foot lift condition did not reach statistical significance, although the observed difference was just as marked. Differences in this latency range also were observed between mouth vs hand, mouth vs foot, and hand vs foot, but only one of these comparisons reached statistical significance (the hand condition was significantly more positive than the foot condition at parietal recording sites). These preliminary results strongly suggested that the type of response the subject makes (or is set to make) to a TS may influence the neural response to the TS at a subcortical (or extremely early cortical) level, and that such influences can be detected with electrodes placed over frontal and parietal regions of the scalp.

Objectives

The primary purpose of this study was to establish whether motor set, along with perceptual set, produces short-latency effects (i.e., prior to 100 msec poststimulus) in the visuo-motor system when one engages in a task involving spatial selective attention. A closely related purpose was to establish whether such changes, if found, occur precortically. If it could be shown that EP-components with latencies as short as those of neural elements found in subcortical structures of monkeys could be modulated by perceptual and motor set, this would constitute one important line of evidence that the changes are in fact precortical. The absolute magnitude and scalp distribution of such components would constitute another line of evidence, since field potentials arising from subcortical sources tend to be of very low amplitude and are flatly distributed across the scalp (Nunez, 1981; Vaughan, 1974; Wood, 1982). A third purpose was to establish whether earlier demonstrations in our laboratory of spatial selective attention on short-latency EP-components deemed to be of precortical origin could be replicated. A definitive demonstration of the reliability of the attention effect on such components was considered to be important in view of the prevailing skepticism by neuroscientists concerning its reliability (Mangun, Hansen, & Hillyard, 1986), the failure of neuroscientists to demonstrate its existence in the auditory (Picton & Hillyard, 1974; Picton, Hillyard, Galambos, & Schiff, 1971) and somatosensory modalities (Desmedt & Robertson, 1977; Velasco, Velasco, & Olvera, 1980) and the general reluctance on the part of cognitive neuroscientists to incorporate such findings into information processing models of selective attention (e.g., Naatanen, 1982; Woods, in press). A fourth purpose was to examine later components of scalp-recorded potentials known to be of cortical origin, and about which an extensive literature currently exists, in order to assess the significance of any short-latency attention effects within the context of established effects on these later components. A comparison of set-related effects on these later components obtained in the present study to the effects previously reported in the literature would serve as a kind of indirect validity check of the effects of the perceptual and motor set manipulations employed in the present study on the very short-latency components for which no comparative information currently exists (except for that previously reported by our laboratory group). Also, examination of the later components would help provide information as to whether the observed effects on short-latency components could be due to variations in general activation level rather than to changes in perceptual or motor set.

Hypotheses. Based on anatomical and physiological information presented earlier, and prior findings obtained in our laboratory, including the preliminary findings of a pilot study, it was hypothesized that if motor set, along with perceptual set, influences the responsivity of neuronal activity in subcortical nuclei of the visual pathway prior to presentation of the trigger stimulus, then such influences should be manifested in the magnitude and /or polarity of very early (40-70 msec) poststimulus VER-components recorded at frontal and parietal scalp regions.

Based on the vast knowledge concerning the effects of selective attention on later VER-components considered to be of cortical origin (Eason et al., 1969; Eason, 1981; Harter & Aine, 1984; Harter & Salmon, 1972; Hillyard & Kutas, 1983; Picton et al., 1986; Van Voorhis & Hillyard, 1977; Woods, in press), it was further hypothesized that attention-induced variations in the responses of the cortical units involved in the processing of information contained in the TS will be manifested in these components (including those commonly identified as P1, N1, and P300).

Predictions. (1) Perceptual and motor set will have an effect on the responsivity of subcortical neurons, and such an effect will be manifested in EP-components with latencies in the 40-70 msec range. (2) The short latency components, being of subcortical origin, will be of relatively low amplitude (less than one microvolt) and have a shallow distribution across the scalp. (3) Using the spatial attention paradigm employed in our previous studies, if perceptual set (i.e., spatial selective attention) has an effect on the responsivity of subcortical neurons, the magnitude and/or polarity of EP-deflections in the 40-70 msec range obtained when a given visual field is relevant (i.e., being attended to) will differ from that obtained when that same field is irrelevant (i.e., not being attended to). (4) If motor set has an effect on the responsivity of subcortical neurons, EP-deflections in the 40-70 msec range will differ significantly in magnitude and/or polarity as a function of the type of motor task the subject is required to perform (e.g., being set to make an eye movement vs a foot-lift vs a counting response). Polarity differences will be observed if different populations of neurons are activated by different kinds of motor set, and the equivalent dipole sources generated by the different neuronal populations have different orientations.

With respect to later EP-components generated by cortical dipole sources, it was predicted that deflections corresponding to parietally-recorded P1, N1, and P300 will be significantly influenced by perceptual set; and that larger effects will be obtained over the right than over the left hemisphere, in accordance with the prevalent findings reported in the literature. It was further predicted that if general activation level varies across the various tasks used to induce different types of motor set, such variations will be reflected in the N1 component, since it has long been established that this component is sensitive to such changes (Eason, Aiken, White, & Lichtenstein, 1964; Eason, et al., 1969).

CHAPTER II

METHOD

Experimental Design

Eighteen subjects participated in three two-hour sessions each. Four data collection trials (or runs) were executed in each session; thus, each subject participated in a total of 12 trials. Over the 12 trials, two replications of data were obtained for each of six experimental conditions generated by which of two visual fields (right or left) the subject was instructed to attend to (IS1) and which of three types of response he/she was set to make (or withold) to stimuli appearing in the attended field (TS). The data collection time per subject was six hours. Thus, a total of 108 hours involving 54 2-hour recording sessions was required to collect data from all 18 subjects.

The visual field to which the subjects attended and the type of response made (or withheld) to the TS was varied across trials. The order in which the six experimental conditions were presented across the first six trials, as well as across the six replication trials, was randomly determined for each subject. This randomized order of presentation was selected over various designs which would have resulted in complete counterbalancing with respect to order of presentation of the experimental conditions within and across subjects for practical reasons.

During a given trial the subject attended to a given visual field (e.g., right) and responded to trigger stimuli (TS) appearing in that field by making a particular kind of response to TSr or witholding that response to TSnr. Depending on the experimental condition, the type of response made or witheld on a given trial was (1) an eye movement toward the attended (relevant) visual field, (2) a foot lift response, or (3) maintaining a silent cumulative count of the number of times TSr occurred during each quarter segment of a trial.

Subjects

Subjects were recruited from advanced undergraduate courses in psychology at UNCG and from the roster of psychology graduate students enrolled at UNCG. The subjects were selected primarily from biologically oriented courses and on the basis of their affiliation with and involvement in research-related activities in one or more of the psychobiology laboratories at UNCG. Recruitment was limited to these sources, because of the important requirement that the subjects be strongly interested in and highly motivated to perform the presribed tasks to the best of their ability;

otherwise, it was felt that, due to the low amplitude of field potentials generated at the scalp by subcortical generators, they may not maintain a sufficiently adequate degree of selective attention (i.e., perceptual set) and motor set to reveal the effects of these behavioral states on the early processing of information by the visual-motor system. Subjects with known, uncorrected eye or neurological problems were not used. However, those individuals wearing corrective lenses were permitted to participate. Since perfect visual acuity was not essential for the purposes of this study, rigorous measures of acuity were not performed. The subject was simply asked if he/she has normal vision (with or without corrective lenses). If the answer was yes the individual was not excluded. Eleven subjects were women; seven men. Their ages varied from 19 to 28 years (mean age 22). Clearance for the project was obtained from the Psychology Department's Human Subjects Research Committee, and the subjects were treated in accordance with UNCG IRB policies.

Pre-data Collection Procedures

Prospective subjects were indoctrinated and acclimatized to the laboratory, and given an opportunity to practice the various performance tasks prior to the first data collection trial. In most instances this was done in a special session which preceded the first recording session.

The subjects were briefed on the stimulus presentation and recording apparatus, on the nature of the tasks they were to perform, and on the procedure for attaching electrodes. When time permitted, a couple of electrodes were actually attached to the prospective subject in order that he/she could experience what it was like.

After having described the apparatus and procedures to the individual(s), each person received several practice trials while sitting in the subject's room and making specified responses to trigger stimuli appearing in the relevant visual field.

During the indoctrination and training period information was sought about the individual's visual acuity; whether he/she had any eye problems of any kind; and whether he/she presently had or ever had had any debilitating neural problems. During the practice period the individuals were asked if they felt claustrophobic; if their glasses (rims) blocked their view of the small stimuli appearing in their peripheral vision; and if they could discriminate between single and double flashes. Anyone experiencing discomfort or difficulty while performing the task, or who reported visual or neural problems, was not used.

Apparatus and Procedures

Stimulus presentation. The visual display consisted of a white 70 x 202 cm screen which was slightly curved to make all points along the horizontal meridian equidistant from the subject's eyes. The distance from the horizontal meridian of the screen to the midpoint of an imaginary straight line drawn between the corneas of the subject's eyes was approximately 40 cm. When viewing the display the subject's head was held in the appropriate position by placing his/her upper teeth on a sanitized bite board and closing the mouth gently against the board.

Stimuli of 10 microseconds duration were delivered from the back side of the screen 30 degrees peripherally along the horizontal meridian in each visual field by means of two Grass (PS-2) photostimulators. The flashed stimuli passed through circular, blue-filtered appertures in the screen subtending a visual angle of 35 minutes. Thus, from the subjects vantage point, the stimuli appeared as small (35' VA), momentary (10 microseconds) circular patches of blue light imposed on a screen dimly illuminated with red light. Blue stimuli imposed on a red background were used to maximaze the response of the rod system and to minimize that of the cones. The luminance of the background screen was approximately 1 millilambert. With the Grass photostimulators set at intensity level 4, the luminance of the stimuli, as viewed from the subject's perspective, was approximately 2.7 log units brighter than the background. When recording, the subject fixated a point lying midway between the two appertures in which the peripheral stimuli appeared, and approximately 2 cm below an imaginary horizontal line passing through the center of the appertures. The fixation point was so arranged to present the stimuli slightly in the upper quadrant of the right and left visual fields. Although limiting stimulation to the upper field may have had little effect on the scalp distribution of early EP-components, we did so on the assumption that the effect of such limitation would be to generate equivalent dipole sources which were more focalized and possess stronger "open field" properties than would have been the case if the stimuli had been permitted to overlap both the upper and lower fields. The upper field was chosen over the lower for practical reasons. Its selection was based on the observation from earlier experiments that time-locked myogenic artifacts in frontal EP recordings are progressively reduced as a function of the degree of downward eye rotation required to maintain gaze on the fixation point. Since stimulation within the upper field required placing the fixation point several degrees lower than would have been the case for lower field stimulation, the probability of time-locked myogenic activity associated with vertical eye position influencing early EP-components was appreciably reduced.

With the use of LVE and Coulbourn Instruments solid state modules, stimuli were presented concomitantly, but never simultaneously in each visual field. The visual field in which each sequential stimulus appeared was randomized, thus the subject could not predict above chance level in which field the next stimulus would appear. In general, the time interval between sequential stimuli varied from 1 to 2 seconds, the mean interval being approximately 1.5 seconds. Once in a long while the interstimulus interval (ISI) exceeded 2 sec, but the vast majority (over 90%) did not. The shortest ISI was never less than 1 sec.

The majority of the stimuli appearing in each visual field were single flashes which, from the subject's perspective had the characteristics described above. Interspersed among the single flashes were randomly presented doublets (two single flashes separated by 200 msec). These occurred 30% of the time, on the average. As specified by the instructions, flashes appearing in the unattended (i.e., irrelevant) visual field in a given trial were to be ignored and not responded to by the subject. Doublets appearing in the attended (relevant) visual field constituted the trigger stimuli (TSr) to be responded to by making one of the three types of responses indicated above (eye movement, foot lift, or counting), depending on the experimental condition.

The eye movement and foot lift response to TSr were to be made as quickly as possible, and if the subject did not respond within a specified time period (which was controlled by the LVE and Coulbourn solid state modules), a "beep" was presented through a speaker to signal to the subject that he/she responded too slowly or missed seeing the doublet altogether. Initially, the beep-delay interval was set at 600 msec. If the subject received no beeps during the presentation of the first block of 25 single flashes to each visual field (with interspersed doublets), the delay interval was decreased in 15-msec steps until the subject received a late reaction signal. The delay interval was thereafter adjusted by the experimenter during the course of the trial to reproduce a quasi-random set of from 2 - 8 beeps.

Based on previous research it was the experimenter's impression that late feedback beeps falling within this frequency range tended to have a facilitating effect on the subject's ability to selectively attend. Pilot work suggested that if no late feedback signals occurred during the course of a trial, some subjects seemed to get the impression that it was unnecessary to engage in intensive selective attention to perform the task effectively. If too many late signals occurred during the course of a trial, some subjects seemed to become discouraged and stop trying to selectively attend. Adjustment of the delay interval, in the present study in the manner indicated, during the course of the trial was to prevent these extremes from occurring.

The subject was given feedback at the end of each block of 25 single flashes (plus interspersed doublets) presented in each of the visual fields as to how many late reactions were made to TSr. This feedback served as a verbal reminder to the subject of the number of beeps which occurred during that trial segment, and the subject was encouraged to do as well (if there were none or only one or two beeps) or better (if more than two beeps) on the next segment. The purpose of this feedback was to reintensify the subject's efforts to selectively attend to the relevant field and to maintain a high level of readiness to respond in the specified manner (motor set).

For the count condition, late reaction time "beeps" were not a factor. The subject simply kept track of the number of doublets which were interspersed within each block of 25 single flashes, there being four such blocks per trial. After each block of flashes was presented, the experimenter deactivated the stimulus delivery system and asked the subject to report the number of doublets counted. The experimenter then gave the subject feedback as to the accuracy of his/her count.

The stimulus delivery system was under the direct control of the subject, and required the simultaneous closure of three switches which were wired in series. Two of these were microswitches, one of which could be engaged by pressing the switch lever with the finger and the other by pressing the switch lever with the ball of the foot. The third switch consisted of a solid state LVE Schmitt trigger which could be activated by the amplified output voltage recorded at the external canthus of the right or left eye relative to the ipsilateral earlobe. The latter switch was in the "closed" position when the canthal electrode voltage was below the minimal level required to engage the Schmitt trigger. That is, the Schmitt trigger switch <u>disengaged</u> whenever the canthal amplified voltage exceeded a specified level (the latter of which could be set by the experimenter). The switch was set to disengage when the subject blinked or made a horizontal eye movement of approximately 3 degrees or more in either direction. It also disengaged when any other type of bodily response (e.g., exessive EMG activity due to applying too much pressure to the bite board, raising the eye brows, increased tension in frontalis muscle for other reasons, etc.,) exceeded a critical value. The purpose of this switch was to instantaneously disengage the stimulus delivery system whenever such events occurred to prevent their contaminating scalp-recorded VER-components time-locked to the trigger stimuli. The length of the disengagement interval was controlled by an LVE timer which was set for 2 seconds. If the artifact was still present at the end of the two-second interval, the system instantenously disengaged for another 2 seconds without the occurrence of a stimulus. The system remained disengaged until the artifact-induced voltage level dropped below the threshold level of the Schmitt trigger.

To ready the stimulus delivery system, the experimenter set two LVE predetermining counters which specified the number of single flashes (plus an indeterminant number of randomly interspersed doublets) to be presented. These counters were each set to present 25 single flashes. With these counters preset, the system began to deliver flashes concomitantly in each visual field when all three of the switches described above were engaged. Disengagement of any one of them at any time stopped the delivery system.

On those trials in which an eye movement response was to be made to the doublets appearing in the relevant visual field, the foot-operated microswitch was locked in the closed position by the experimenter. When the subject was ready to begin, he/she gazed steadily at the fixation point without moving or blinking (thereby permitting the Schmitt trigger switch to "close") and then closed the hand-operated microswitch by pressing on the lever with the forefinger of both hands (one finger on top of the other). Stimulus flashes were delivered until the subject made an eye movement in response to the appearance of a doublet in the relevant field; released the forefingers from the microswitch; or involuntarily blinked, moved, or tensed up. After making an eye movement to a doublet the subject re-established his/her gaze on the fixation point, and after 2 seconds, the delivery system was re-engaged. If the subject wished to take a break, he/she released the hand-operated microswitch. When the two predetermining counters counted down to zero the system was automatically deactivated.

On those trials in which a foot lift response was called for, the hand-operated switch was locked in the closed position, and if the subject was properly fixating, the delivery system was engaged upon pressing the foot-operated switch. Breaks could be taken at any time by releasing the foot from the lever.

When the counting task was being performed the foot-operated switch was locked in the closed position, and if the subject was properly fixating, the delivery system became engaged when the two forefingers were pressed against the hand-operated switch. The subject could take a break at any time by releasing the forefingers from the microswitch lever.

The subject was encouraged to take frequent breaks in order to avoid eye tension, reduce the probability of artifacts appearing in the records, and to regain concentration to selectively attend to the relevant visual field and maintain a high degree of readiness to make the appropriate response to the doublets (TSr). An experimenter-imposed break occurred after each block of 25 single flashes were presented concomitantly in each visual field (plus any doublets), as was implied in the discussion of providing feedback on late reaction-time responses above. The length of the break imposed between each block of flashes lasted about 2 minutes during which time the experimenter talked to the subject, who remained in the stimulus presentation room. During this period the subject was given verbal feedback of his/her performance; was reminded of the experimental conditions under which he/she is working; was reminded to take frequent breaks; and was encouraged to keep trying to selectively attend, maintain readiness to respond to the doublets appearing in the relevant field, and to try to reduce or avoid getting late response (beep) signals.

Between-trial breaks lasting approximately five minutes were imposed between the first and second as well as between the third and fourth trials of each session. The subject remained in the recording room during these breaks. A longer break lasting about 10-15 minutes was imposed between the second and third trials (a mid-session break) during which time the subject left the stimulus presentation room and engaged in conversation with the experimenter. At least a 24-hour break was imposed between each 2-hour recording session.

The break patterns described above were considered to be extremely important, because observations from earlier experiments had revealed that any attention effect on early EP-compoonents is markedly affected by the presence, absence, and duration of breaks imposed within and across trials and across sessions. The break patterns utilized in this study had previously been found to be more conducive to the attainment of an early EP-attention effect than patterns having shorter and less frequently imposed rest intervals (Eason, 1984).

Recording

Scalp-recorded EPs were obtained from four locations, two frontal (F3 and F4) and two parietal (P3 and P4). Each of the recording sites was referenced to the ipsilateral earlobe. The earlobe references were considered preferable to the mastoids in this study, because earlier observations from pilot studies established that even though the mastoid is relatively neutral for recording EP-deflections in the 40-60 msec range, this is not the case for deflections in the 80-110 msec range. Since a primary purpose of the present study was to obtain as much information as possible as to the locus of the generators responsible for the deflections not only in the 40-60 msec range but also in the 80-110 msec range, the earlobes were selected as the more neutral reference sites.

The electrode application procedure consisted of scrubbing the skin with alcohol, permitting it to dry, and placing Grass gold-cup EEG electrodes filled with Grass (type EC2) electrode cream at the scrubbed locations. The electrodes were held in place by the electrode cream, which had a semi-adhesive quality, and covered with approximately 2-inch square pieces of thin plastic sheeting to keep the cream from drying out. After attachement, the resistance of the electrodes was checked with an ohmmeter. If the resistance exceeded 10,000 ohms, the electrode was removed, the skin preparation procedure was repeated, and the electrode was reattached. This procedure was repeated until all electrode sites had a resistance of 10,000 ohms or less.

The subject was grounded with an electrode placed in the center of the forehead. An electrode used for recording horizontal eye movements, eye blinks, frontalis muscle twitches, mandibular tension, and other muscular artifacts was placed at the external canthus of one or both eyes. If on a given trial the subject was required to make eye movements toward the right (relevant) visual field when a doublet appeared, the electrode was placed by the external canthus of the right eye. If the requirement was to move the eyes toward the left visual field, the electrode was placed by the external canthus of the left eye. When eye movements were to be made to the left and right visual fields on different trials in a given session, an electrode was placed next to each eye during the preparation procedure, but recordings were obtained from only one of these electrodes in a given trial. The reason for the shift in electrode placement from the external canthus of one eye to that of the other eye when the direction of the required eye movement shifted from one visual field to the other was to generate an electro-oculographic voltage shift in the same direction whether the eyes moved toward the right or toward the left visual field. This was necessary in order to disengage the Schmitt trigger switch at the same instant that an eye movement was initiated toward the relevant visual field. The deflection associated with eye blinks was always in the correct direction for disengaging the Schmitt trigger switch without delay regardless of which of the two external canthi the electrode was placed beside.

Field potentials detected at each of the frontal and parietal electrode sites were amplified with Grass PS-5 preamplifiers. The voltage-amplified signals were fed into Grass PS-1 driver amplifiers for further amplification. The low and high 1/2 amplitude settings of the amplifiers were 1 and 35 Hz respectively. The output of these amplifiers was constantly monitored for signs of artifact contamination in polygraphic recordings of the amplified activity. The amplified output of the driver amplifiers was channeled in parallel to two computers, one of which registered the evoked responses over a 500-msec epoch to single flashes presented in the attended (relevant) visual field while the other registered the responses over the same epoch to single flashes presented in the unattended (irrelevant) field. One of the averaging systems was a 1965 model Computer of Average Transients (CAT); the other was a 1985 modular unit system manufactured by Modular Instruments Incorporated (MI2). The latter system utilized an IBM-PC, with appropriate software, for signal averaging.

Averaged evoked responses were obtained only to the single-flash stimuli presented in each visual field (i.e., to TSnr). Each average was based on 100 stimulus presentations. Responses evoked by the doublets were not averaged. Thus the EP data subjected to analysis were limited to those instances in which the subject withheld making a particular type of response to TSnr while being set to make that response to TSr (i.e., to doublets).

VERs averaged with the CAT were written out on graph paper with a Moseley X-Y plotter. Those obtained with the MI2 device were printed out with an IBM Proprinter. The two printout devices were calibrated so as to make a given horizontal distance correspond to the same time units and to make a given vertical distance correspond to the same degree of voltage change.

This was accomplished by feeding the same signal into both averaging devices and adjusting their horizontal and vertical sensitivities until both units generated the same deflections along both the horizontal and vertical axes. Even though the units had been matched in sensitivity, recordings obtained from the attended and unattended visual fields were counterbalanced across the two devices for each of the response conditions. This procedure assured there could be no possibility of a bias in the VERs due to slight, undiscernible differences in the sensitivity of the two averaging units.

During each data collection trial white noise was channeled into the stimulus presentation room to prevent extraneous sounds from affecting the VERs. The presentation room was electrically shielded to protect the subject from electrostatic disturbances which might also have affected the VERs.

CHAPTER III

RESULTS

Identification of EP Components and Measuring Procedure

Group analog waveforms for the 18 subjects (collapsed across replications, visual fields, and hemispheres) are presented in Fig. 1 as a function of attention (attend vs unattend), scalp location (frontal vs parietal), and tasks (eye movement vs fool-lift vs counting). The waveforms span a post-stimulus interval of 360 msec. Corresponding difference potentials are shown in Fig. 2. All figures and a table summarizing results are contained in appendix A.

Qualitative Description of VERs and Difference Potentials

Each of the analog tracings in Fig. 1 is a group average based on a total of 7,200 separate stimulus presentations. The waveforms obtained over frontal and parietal regions (left and right side of the figure respectively) bear some marked similarities as well as some differences. Both manifest a short-latency negative-going deflection with a peak latency of approximately 55 msec. This is followed by a positive-going deflection which peaks at approximately 100 msec for the frontal and at 120 msec for the parietal region. This positive deflection is succeeded by a large negative one which peaks at approximately 160 msec for the frontal and at 170 msec for the parietal region. The latter is followed by a large positive deflection at the frontal region which peaks at approximately 270 msec. At the parietal region this positive-going deflection is interrupted at approximately 220 msec by a small negative-going deflection with a peak latency of approximately 260 msec. Finally, a late positive-going deflection with an onset latency of about 320 msec is manifested in the waveforms obtained at both the frontal and parietal regions.

A cursory comparison of the superimposed solid and dashed lines reveals that most of these deflections, including the earliest one, tended to differ as a function of the attentional state of the subject; and in some instances, they tended to differ as a function of the type of response the subjects were set to make to the trigger stimulus.

The apparent effects of perceptual and motor set are manifested even more clearly in the difference potentials of Fig. 2. In the frontal recordings (left side of the figure), beginning at about 40 msec the waveform obtained under the attend condition when subjects were set to make an eye movement (top row) can be seen to be relatively more negative than that obtained under the unattend condition (the latter condition being represented by the straight horizontal baseline). Although there are peaks and troughs in the difference potential, it remains biased in a negative direction until about 300 msec. At this time the potential becomes relatively positive in comparison to the unattend baseline. After about the first 100 msec, the frontally recorded difference potentials obtained for the foot and counting tasks (second and third rows on the left) are seen to resemble that obtained for the eye task (top row). As for the eye task, these difference potentials remain negatively biased until about 300 msec poststimulus. However, in contrast to the eye task condition, within 40 msec poststimulus, the difference potentials for both the foot and counting tasks deviate from the unattend baseline condition in a positive rather than in a negative direction, such positivity reaching a peak at about 55 msec.

With respect to the parietally recorded difference potentials (right side of Fig. 2), deviations from baseline in the 40-70 msec range resemble those noted for the frontally recorded deviations (with slight variations). As for the frontal recordings, the deviation from baseline can be seen to be negative for the eye and positive for the counting task condition. There is, however, little deviation from baseline for the foot condition. In contrast to the frontal recordings, beginning at about 100 msec the parietally recorded difference potentials can be seen to be more positive, relative to the unattend baseline condition, such positivity peaking out at about 120 msec. This positivity can be seen to be of about the same degree of magnitude for all three types of tasks.

40-70 Msec Latency Window (C-55)

The latency ranges chosen for quantitative measurment and statistical analysis within the first 100 msec poststimulus were based on visual inspection of the maximal deviations which occurred between the waveforms under the two attend conditions. As noted above, the differences associated with the two attention conditions within the first 100 msec were most pronounced in the latency range of about 40-70 msec for both the frontal and parietal scalp regions, and for the three types of tasks the subjects were set to perform. Thus, this latency interval was selected as the critical zone of analysis for assessing the influences of perceptual and motor set on the very early responsivity of the visuo-motor system.

The following procedure was employed for obtaining data points for the 40-70 msec interval. Ten-msec windows at 40-50, 50-60, and 60-70 were demarcated on the tracings obtained under each experimental condition for every subject. A horizontal line representing the average distance from baseline to the VER-segment lying within each 10-msec window was drawn through each of the segments; then the distance from baseline to each of these horizontal lines was measured in millimeters (20mm = 1.0 uv). To assess the feasibility of integrating the data across two or more of the 10-msec windows, correlated t-tests were performed on the 10-msec measures (after collapsing across replications, visual fields, and hemispheres) for each latency interval, task, and frontal and parietal scalp region. Statistically significant deviations ranging from $p<.001$ to $p<.08$ were obtained for at least one task and one electrode pair at all three latency ranges (40-50, 50-60, and 60-70). Therefore, the deviation measures were integrated across all three latency windows to yield a single data point across the 40-70 msec range for each subject, task, attention condition, visual field, and electrode location.

VER-segments falling within this latency range will be referred to in this report as C-55, where C stands for component and 55 represents the mid-way point in the 40-70 msec range. Since the polarity of the deflection in this latency range can be either positive or negative; depending on the experimental condition, recording site, and subject; symbols denoting polarity will not be used. The term, component, is being used in a purely descriptive sense and is not intended to imply a single generator source or the peak or trough of a deflection.

100-130 Msec Window (Cf-115 and Cp-115)

The next segment of the VER-waveforms to be subjected to quantitative analysis fell within the 100-130 msec range poststimulus. This latency window encompasses the leading edge and peak latency of a positive-going deflection observable in the parietal tracings (right-hand side of Fig. 1), and commonly referred to as P1. The same latency window was used for the frontal tracings (right-hand side of Fig. 1), although the deflection recorded at this location tended to go in a negative rather than in a positive direction. As with the 40-70 msec window, the 100-130 msec window was broken into 10-msec segments, and the average distance from baseline to the segment of the waveform falling within each 10-msec interval was measured on the individual tracings of each subject for each experimental condition, using the same procedure described above for the 40-70 msec window. The segment of the waveform falling within this latency window will be referred to hereafter generally as Component 115 (C-115) and specifically as Cf-115 for frontal and Cp-115 for parietal recordings.

160-170 Msec Latency Window (N-165)

The third latency range to be subjected to quantitative analysis fell within 160-170 msec poststimulus. This is the latency at which the large negative going potential peaked out for virtually all of the subjects. The average distance from baseline to the segment of the VER-waveform falling within this 10-msec interval was measured for each subject for every experimental condition. This deflection is commonly referred to as N1. It will be identified in this report as N-165, with N denoting negativity and 165 denoting the midpoint of the peak latency interval.

350-360 Msec Latency Window (P-300)

The fourth and final measure to be subjected to quantitative analysis was a late component falling within a latency window of 350 to 360 msec. As noted in the preceding section, this deflection can be seen to be considerably more positive under the attend than under the unattend condition. As with the other measures, the average distance from baseline to the segment of the VER-waveform falling within the 350-360 msec latency window was measured in millimeters. This late deflection is commonly referred to as P-300. It will be identified as P-355 in this report in order to make explicit the latency at which it was measured.

Statistical Analyses

Several sets of analyses were performed on each of the measures, using all or some combination of six variables as factors. The variables of interest were: Location (L), which refers to frontal vs parietal recording regions; Tasks (T), which refers to subjects' being set to make an eye movement vs foot-lift vs counting response; Attention (A), which refers to the subjects' attending to or not attending to a given visual field; Hemisphere (H), right vs left; Visual field (V), right vs left; and Subjects (S). While some of the specific analyses performed on the data varied somewhat for the four components, the same general procedure was used throughout.

First, a comprehensive 6-way ANOVA was performed, treating all six variables as factors (L, T, A, H, V, S). These analyses consisted of a 2x3x2x2x2x18 repeated measures model involving a total of 863 degrees of freedom. Second, a 5-way ANOVA was performed for each location separately (frontal recordings only and parietal recordings only), using the remaining five variables as factors (T, A, H, V, S). This generated a 3x2x2x2x18 repeated measures model with 431 degrees of freedom. Third, a 4-way ANOVA was performed for each task separately (eye; foot; counting) and for each location separately (frontal; parietal), using the remaining four variables as factors (A, H, V, S). Each of these analyses entailed a 2x2x2x18 repeated-measures model with a total of 143 degrees of freedom. In some instances post hoc Scheffe analyses were performed on the mean deviations from baseline to aid in the interpretation of significant interactions obtained in the ANOVAs. The lesser analyses were performed in each case in order to aid in the interpretations of interactions found to be significant in larger analyses. The entire set of ANOVAs provided a comprehensive picture of the reliability of the observed effects of the variables of primary interest (frontal vs parietal recording site; motor set; selective attention; hemispheres; and visual field) on the measures obtained at each of the four latency windows. Appendix B contains the results of all the statistical analyses performed.

Effects on C-55

Findings Involving Tasks and Attention

6-way ANOVA. The 6-way ANOVA revealed a significant tasks x attention (TxA) interaction [F(2,34)=5.45, p<.01]. Also, two second-order interactions approached significance. These were tasks x attention x hemispheres (TxAxH) [F(2,34)=2.38, p<.10] and tasks x attention x location [F(2,34)=2.49, p<.10]. The mean deviation of C-55 from baseline is plotted in Fig. 3 as a function of: tasks, attention, hemispheres, and location (Panel A); tasks, attention, and hemispheres (Panel B); and tasks, attention, and location (Panel C). By visually integrating across hemispheres and location in Panel A and across hemsipheres in Panel B, one can readily see the TxA interaction. The interaction also is manifested in the group VERs of Fig. 1, as well as in the difference potentials between the attend and unattend conditions for the three different tasks (Fig. 2). Inspection of any of these sources reveals that C-55 was relatively more negative under the attend than under the unattend condition for the eye task; relatively more positive under the attend than under the unattend condition for the counting task; and slightly more positive under the attend than under the unattend condition for the foot-lift task.

By visually collapsing across location in Panel A and by direct inspection of Panel B, one can observe the nearly significant TxAxH interaction revealed by the 6-way ANOVA. This nearly significant interaction appears to be reflecting a greater attention effect over the right hemisphere for the eye and counting tasks, with the magnitude of the attention effect being slightly greater over the left hemisphere for the foot-lift task. The nearly significant TxAxL interaction is manifested in Panel C wherein the attention effect for the eye and foot tasks appears relatively greater for the frontal than for the parietal region, while for the counting task the attention effect appears slightly greater over the parietal region.

5-way ANOVA for each location separately. A significant task x attention interaction was obtained for both the frontal [F(2,34)=5.06, p<.01] and parietal [F(2,34)=4.27, p<.02] recording sites. This finding is consistent with the significant TxA interaction for the two sites combined, revealed by the 6-way ANOVA (summarized above); and as stated earlier, is readily apparent upon inspection of Panel C of Fig. 3. In addition to the first-order interaction, a significant second-order interaction involving tasks, attention, and hemispheres was obtained for the frontal [F(2,34)=3.97, p<.03] but not for the parietal recording site. This finding indicates that the nearly significant TxAxH interaction obtained in the 6-way analysis was largely due to the frontal recordings. A comparison of the differences in the slopes of the lines between left and right hemispheres for each task in the frontal recordings of Fig. 3 (left side of Panel A) to those manifested in the parietal recordings (right side of the panel), reveals the differences are about the same in both the frontal and parietal recordings. Apparently, there was less error variance associated with the frontal than with the parietal recordings.

4-way ANOVAs for each task and location separately. For the eye task, a significant attention x hemisphere interaction was obtained for the <u>frontal</u> [F(1,17)=14.79, p<.05] but not for the <u>parietal</u> recording area. A significant main attention effect also was obtained for the frontal [F(1,17)=59.48, p<.04] but not for the parietal region. Examination of Panel A of Fig. 3 reveals that for the eye task the attention effect was greater for the frontal than for the parietal area (compare slopes of solid lines). The significant AxH interaction obtained for the frontal region (left-hand side of Panel A) reflects the fact that a larger attention effect was obtained over the right than over the left hemisphere. Although a larger attention effect also was obtained over the right than over the left hemisphere for the parietal region (compare solid lines in right-hand side of Panel A), the AxH interaction was not significant.

For the <u>counting</u> task, a significant main attention effect was obtained for both the frontal [F(1,17)=8.95, p<.01] and parietal [F(1,17)=10.33, p<.01] recording sites. The significant attention effect for the counting task is revealed in all of the graphs of Fig. 3 (dotted lines). As stated earlier, the direction of the attention effect on C-55 for the counting task was just the opposite of that for the eye task, the polarity being relatively more positive under the attend condition for the counting and more negative for the eye task. It should be noted that the attention effect was equally pronounced over both hemispheres and at both the frontal and parietal recording sites for the counting task, whereas for the eye task, the effect was most pronounced in frontal recordings obtained over the right hemisphere, with the left hemisphere and parietal areas contributing relatively little.

No significant attention effects of any kind were obtained for the foot task. Thus, all of the analyses summarized above provide consistent evidence that the attention manipulation had no reliable effect on C-55 when the subjects were set to make a foot-lift response to target stimuli. In fact, for approximately half of the subjects, the C-55 component was relatively more negative under the attend than under the unattend condition, whereas for the other half, it was relatively more positive.

A post hoc Scheffe test revealed that, at the frontal scalp, the mean deviations from baseline under the attend condition for the eye and counting tasks differed significantly (error rate = .01), as did the mean deviations from baseline for the eye and foot tasks (error rate = .05). The differences in the baseline mean deviations obtained at the frontal scalp under the unattend condition for the eye and foot tasks, as well as for the eye and counting tasks, were significant (error rate = .01 in both cases). For the parietal scalp recordings, the differences in the mean deviations from baseline under the attend condition differed significantly for the eye vs the counting task (error rate = .05) and for the foot vs counting task (error rate = .01). The differences obtained under the unattend condition also were significant for the eye vs counting (error rate = .01) and foot vs counting (error rate = .05) tasks. These effects may be viewed pictorially in Panel C of Fig. 3.

A second post hoc Scheffe test revealed that the mean deviations from baseline obtained from the left frontal hemisphere under the attend condition differed significantly between the eye vs foot and eye vs counting tasks (error rate = .05). For the same hemisphere under the unattend condition a significant difference was obtained for the eye vs foot task (error rate = .05). For the right hemsiphere under the attend condition, a significant difference was obtained between the eye and foot tasks (error rate = .05); for this hemisphere under the unattend condition significant differences were obtained between the eye and foot, and between the eye and counting tasks (error rate = .01 in each case). These effects are graphically depicted in the left-hand side of Panel A, Fig. 3.

Findings Involving Tasks and Variables Other Than Attention

6-way ANOVA. The 6-way ANOVA revealed three significant effects involving location, visual field, and hemispheres. There was a significant LxV interaction [F(1,17)=9.02, p<.01], a significant main effect for location [F(1,17)=5.46, p<.03], and a main effect for hemispheres [F(1,17)=26.20, p<.001]. There was no significant main effect for visual field, nor did tasks interact significantly with location, visual field, or hemispheres. The LxV interaction is dramatically revealed in Fig. 4, Panel A, wherein it can be seen that for the parietal recording site, the polarity of C-55 was considerably more negative to left than to right visual field stimulation, whereas for the frontal site there was no difference. The significant main effect for location is very discernible in Panels A & B of Fig. 3 as well as in both panels of Fig. 4. Inspection of any of these reveals that C-55 was relatively more negative over the parietal than over the frontal region. The significant hemisphere effect is most clearly depicted in Fig. 3, Panel B, wherein one can see that C-55 was relatively more negative over the right than over the left hemisphere. This hemsiphere effect also is apparent in Panel A of Fig. 3, as well as in Panel B of Fig. 4.

5-way ANOVAs for each location separately. The 5-way ANOVA performed on each location separately revealed a significant main hemisphere effect for both the frontal [F(1,17)=15.13, p<.001] and parietal regions [F(1,17)=15.23, p<.001]. These findings are consistent with the main effect obtained in the 6-way analysis (see above), and indicate that both regions contributed to the significant effect obtained in that analysis. The hemisphere effect for each location separately is clearly depicted in Fig. 3, Panel A. For both locations, C-55 was relatively more negative over the right than over the left hemisphere.

A significant main effect for visual field was obtained for the parietal [F(1,17)=7.61, p<.01] but not for the frontal recording region. This effect is apparent upon inspection of Panel A of Fig. 4 wherein a large difference is observable between visual fields in the parietal but not in the frontal region. This finding, in conjunction with the significant L x V interaction obtained in the 6-way ANOVA, indicates the parietal region was markedly affected in the 40-70 msec range poststimulus as a function of the visual field in which the evoking stimulus appeared whereas the frontal region was not. It may be pointed out that even though C-55 was more negative to right than to left visual field stimulation in the parietal recordings, this polarity shift apparently was unrelated to the magnitude and direction of the significant attention effect obtained during the counting task. At least, the 4-way analysis which was performed on the parietal recordings for the counting task (summarized in the preceding section) revealed no significant interaction between attention and visual field.

4-way ANOVAs for each task and location separately. For the eye task, a significant main hemisphere effect was obtained for the frontal [F(1,17)=5.80, p<.03] but not for the parietal region.

For the foot task, a significant main hemisphere effect was obtained for the frontal region [F(1,17)=5.37, p<.03], while the effect for the parietal region was marginally significant [F(1,17)=4.11, p<.06]. Also, a significant main effect for visual field was obtained for the parietal [F(1,17)=4.77, p<.04] but not for the frontal area.

For the counting task, a significant main hemisphere effect also was obtained for the frontal region [F(1,17)=11.74, p<.003], while that for the parietal region approached significance [F(1,17)=3.79, p<.07].

The results of these analyses for each task and location taken separately suggests a rather consistent tendency for a stronger hemisphere effect at the frontal than at the parietal region, however, a significant LxH interaction was not manifested in either the 6- or 5-way ANOVAs. Thus, it would be inappropriate to offer more than a suggestion, based on these observations, that a stronger hemisphere effect may exist over the frontal region. The more striking and consistently reliable demonstration (across all analyses) is that C-55 was relatively more negative over the right than over the left hemisphere at both locations for all three tasks.

Summary of C-55 Findings

The VER-waveforms falling within the 40-70 msec range poststimulus (C-55) were affected by the experimental manipulations as follows:

(1) The relative polarity of C-55 was dependent on both the relevancy of the visual field (attended vs unattended) and the type of response the subject was set to make to target stimuli presented in that field.

(2) When subjects were set to make an eye movement, C-55 was relatively more negative under the attend than under the unattend condition.

(3) When the subjects were set to quietly count target stimuli, C-55 was relatively more positive under the attend condition.

(4) A significant attention effect was not obtained when subjects were set to make a foot-lift response.

(5) The dependency of the attention effect on the type of response the subject was set to make was manifested as a highly significant task x attention interaction at both the frontal and parietal recording sites.

(6) When subjects were set to make an eye movement, a significant main attention effect was obtained for the frontal but not for the parietal region. Also, at the

frontal region the attention effect was found to be significantly greater over the right than over the left hemisphere.

(7) When subjects were set to silently count target stimuli, a significant attention effect was obtained for both the frontal and parietal sites.

(8) For the frontal region, significant differences in the mean deviation from baseline were obtained under the attend condition when subjects were set to make an eye movement vs a silent counting response, and also when they were set to make an eye movement vs a foot-lift response.

(9) For the frontal region, significant differences in mean deviation from baseline were obtained under the unattend condition when subjects were set to make an eye movement vs a silent counting response, as well as an eye movement vs a foot-lift response.

(10) For the parietal region, significant differences in mean deviation from baseline were obtained under the attend condition when subjects were set to make an eye movement vs silent counting response, as well as a foot-lift vs a silent counting response.

(11) For the parietal region, significant differences in mean deviation from baseline were obtained under the unattend condition when subjects were set to make an eye movement vs a silent counting response, as well as a foot-lift vs a silent counting response.

(12) For the parietal region, the polarity of C-55 was significantly more negative to left than to right visual field stimulation, whereas for the frontal site there was no significant difference.

(13) For both the frontal and parietal regions, C-55 was significantly more negative over the right than over the left hemisphere.

Effects on Cf-115 and Cp-115

Findings Involving Tasks and Attention

6-Way ANOVA. The 6-way ANOVA revealed a significant main effect for attention [F(1,17)=6.51, p.<02], a significant attention x location (A xL) interaction [F(1,17)=14.13, p<.0002], and a marginally significant main effect for tasks [F(2,34)=3.10, p<.06]. These effects are graphically depicted in Fig. 5A and 5E. Graph A shows the mean deviation from baseline plotted as a function of tasks, location, and attention. As is apparent in the EP-tracings of Fig. 1, Cf-115 deviated in a negative direction from baseline whereas Cp-115 deviated in a positive direction. The main attention effect is depicted in Fig. 5A as a heavy line connecting the mean deviations from baseline under the two attention conditions, after collapsing across tasks and location. It is evident that the attention effect was primarily manifested at the parietal recording site, with the frontal site contributing little or nothing. The significant AxL interaction reflects this fact.

The marginally significant main effect for tasks is manifested in Fig. 5E by the heavy line which represents the mean deviation from baseline collapsed across frontal and parietal regions. It can be seen that the polarity of the waveform was relatively more positive for the eye than for the foot or counting tasks, being most negative for the counting task. Also, it can be seen that the differences in polarity with respect to tasks was about the same for both recording locations even though the 100-130 msec segments of the waveforms obtained at frontal and parietal locations deviated in opposite directions from baseline.

5-Way ANOVAs for each location taken separately. The 5-way ANOVAs yielded findings consistent with the AxL interaction obtained in the 6-way analysis. As suggested by the slopes of the lines in Fig. 5A, no significant attention effect was obtained for the frontal recording site, whereas a highly significant one was obtained for the parietal site [F(1,17)=14.60, p<.002]. No other significant effects involving attention were obtained for either recording site.

4-way ANOVAs for each task and location separately. For the _frontal_ recording site, a significant attention x hemisphere (AxH) interaction was obtained for the _counting_ task [F(1,17)=7.07, p<.02]. This count-related interaction is revealed upon inspection of the dotted lines in the upper part of Fig. 5B. For the left hemisphere, a relatively more negative Cf-115 was generated under the attend than under the unattend condition whereas for the right hemisphere a relatively more positive Cf-115 was generated under the attend condition. No such interaction was obtained for the eye and foot tasks, as the nearly parallel lines obtained across hemispheres for each of the two tasks suggest (compare the two solid lines to one another; also the two dashed lines in the upper part of Fig. 5B). Since the 5-way ANOVA conducted on the frontal recordings revealed no significant interactions involving tasks, attention, and hemispheres, it is not clear why such an interaction should have occurred for the counting task. This may simply be an instance in which the criterion for rejecting the null hypothesis was reached even though the hypothesis was true. Until the finding can be substantiated in subsequent experiments, this would seem to be the most parsimonious interpretation to assign to it at the present time. No other significant effects involving the attention manipulation were obtained at the frontal recording site for any task. There was a tendency for Cf-115 to be relatively more negative under the attend than under the unattend condition for the eye task (see upper-left tracings in Fig. 1 and solid line in upper part of Fig. 5A), but the effect was not significant.

For the parietal location, a significant main attention effect was obtained for each of the three tasks [for the eye, F(1,17)=8.09, p<.02; for the foot, F(1,17)=10.00, p<.01; for the counting task F(1,17)=13.65, p<.01]. The effect for each task is very apparent in the lower part of Fig. 5A (note slopes of solid, dashed, and dotted lines). In addition to these main effects, for the counting task only, a significant attention x hemisphere (A x H) interaction was obtained [F(1,17)=8.43, p<.01], the magnitude of the attention effect being greater for the right than for the left hemisphere. This effect can be seen in the lower part of Fig. 5B (compare slope and length of dotted lines). For the other two tasks (eye and foot), the magnitude of the attention effect was essentially the same over each hemisphere.

Findings Involving Tasks and Variables Other Than Attention

6-Way ANOVA. In addition to the attention effects summarized above, the 6-way ANOVA revealed a significant main effect for location [F(1,17)=29.43, p<.0001], a significant location x visual field (LxV) interaction [F(1,17)=5.54, p<.04], and a significant location x hemisphere x visual field (LxHxV) interaction [F(1,17)=26.29, p<.0001]. The main location effect is obvious in every graph of Fig 5, as well as in Fig. 1. It simply reflects the fact that the VERs obtained at frontal and parietal sites deviated from baseline in opposite directions in the 100-130 msec range, the frontal recordings going in a negative and the parietal recordings in a positive direction (note direction of deviations from baseline in the graphs). The significant LxV interaction is depicted in Fig. 5C in which mean deviations from baseline have been plotted as a function of tasks, location, and visual field. Inspection of this graph reveals that the negative-going Cf-115 deflection deviated more from baseline during right than during left visual field stimulation, as did the positive-going Cp-115 deflection. The interaction reflects the fact that the frontal and parietal VER-segments went in opposite directions in the 100-130 msec latency range. The three-way interaction involving location, hemispheres, and visual field (LxHxV) is depicted in Fig. 5D which shows mean deviations from baseline as a function of tasks, location, hemispheres, and visual field. Perusal of this graph reveals that the effect of visual field was greater over the left than over the right hemisphere. Also, the effect was in opposite directions for the two hemispheres. The mean deviation from baseline was greater during right than during left visual field stimulation in left-hemisphere recordings, while such deviation was greater during left than during right visual field stimulation in right-hemisphere recordings. The relative deviations from baseline as a function of visual field and hemispheres can be seen to be in opposite directions for frontal and parietal recording sites, thus producing the three-way interaction with hemisphere and visual field.

5-way ANOVAs for each location taken separately. A 5-way ANOVA conducted on the frontal recordings revealed a significant hemisphere effect [F(1,17)=4.64, p<.05] as well as a significant hemisphere x visual field (HxV) effect [F(1,17)=8.77, p<.01]. These effects are easily discernible in the upper part of Fig. 5D. It is evident that the mean deviation from baseline after collapsing across visual field (main hemisphere effect) was greater for the left than for the right hemisphere at both the frontal and parietal locations. It is also evident that the visual field effect was much greater for the left than for the right-hemisphere, in addition to being in opposite directions (HxV interaction).

A 5-way analysis conducted on the parietal recordings revealed no main hemisphere effect, contrary to that obtained in frontal recordings. However, as for the frontal recordings, a significant hemisphere x visual field (HxV) interaction was obtained [F(1,17)=16.44, p<.001]. This interaction is vividly manifested in the lower part of Fig. 5D. For the left hemisphere, the mean deviation from baseline was much greater during right than during left visual field stimulation, whereas the opposite was the case for the right hemisphere. Further examination of the lower part of Fig. 5D makes it clear why no significant main hemisphere effect was obtained at the parietal location. The mean deviation from baseline, after collapsing across visual fields, can be seen to be about the same for both hemispheres.

4-way ANOVAs for each task and location separately. At the frontal region, a significant main hemisphere effect [F(1,17)=4.95, p<.04] and a marginal hemisphere x visual field (HxV) interaction [F(1,17)=4.21, p<.06] was obtained for the eye task; also, significant hemisphere x visual field (HxV) interactions were obtained for both the foot and counting tasks. The HxV interactions are consistent with the findings obtained in the 6-way and 5-way ANOVAs summarized above, and indicate all three tasks contributed to the previously described interactions. The main hemisphere effect for the counting task can be discerned in the upper part of Fig. 5D when one compares the mean deviation for the eye condition (collapsed across visual fields) obtained from the left hemisphere to that obtained from the right (dotted lines). It is clear the mean deviation from baseline was greater for the left than for the right hemisphere. Although in the same direction, no main hemisphere effect was obtained for either the eye or foot tasks. Thus, the significant main hemisphere effect noted above in the 5-way analysis for the frontal region was heavily weighted by the counting task.

At the parietal region, significant H x V interactions were obtained for each task [for the eye, F(1,17)=16.71, p<.001; for the foot task, F(1,17)=14.48, p<.01; for the counting task, F(1,17)=10.32, p<.01]. These interactions are evident for each task in the lower part of Fig. 5D, and indicate that each contributed substantially to the HxV interaction noted above in the 5-way ANOVA for the parietal location. For each task, the mean deviation from baseline was greater during right than during left visual field stimulation in left hemisphere recordings while the opposite was the case in the right hemisphere recordings.

Summary of Cf-115 and Cp-115 Findings

Findings involving tasks and attention are as follows:

(1) The mean deviation from baseline, collapsed across all variables except attention, was significantly more positive under the attend than under the unattend condition (Fig. 5A).

(2) A main effect for tasks approached significance, reflecting that both Cf-115 and Cp-115 were relatively more positive for the eye than for either the foot or counting tasks; both Cf-115 and Cp-115 were most negative for the

counting task (Fig. 5E). This is an interesting finding, if it can be replicated, in view of the fact that the absolute deviation from baseline for Cf-115 was in a negative direction whereas such deviation for Cp-115 was in a positive direction.

(3) There was a significant attention x location interaction, reflecting the fact that a large attention effect was obtained at the parietal electrode site with little or no effect being manifested at the frontal site (Fig. 5A).

(4) A significant attention x hemisphere interaction was obtained at the frontal recording site for the counting task only (Fig. 5B). Since a non-significant interaction involving tasks, attention, and hemispheres was obtained in a 5-way ANOVA of the frontal recordings, this AxH interaction for the counting task is to be interpreted with extreme caution.

(5) At the parietal recording site, a significant main attention effect was obtained for each task, Cp-115 deviating more from baseline under the attend than under the unattend condition in each case (Fig. 5A).

(6) Also at the parietal site, a significant attention x hemisphere interaction was obtained for the counting task, but not for the eye or foot tasks. For the counting task, the magnitude of the attention effect was greater for the

right than for the left hemisphere (Fig. 5B).

(7) No other significant interactions involving tasks and attention in relation to any other variables, were obtained.

Findings involving tasks and variables other than attention may be summarized as follows:

(1) A significant main effect for location (frontal vs parietal recording sites) was obtained, reflecting the fact that Cf-115 deviated from baseline in a negative direction whereas Cp-115 deviated in a positive direction (manifested in all graphs of Fig. 5).

(2) A significant location x visual field interaction was obtained, indicating that frontal and parietal VER-segments went in opposite directions in the 100-130 msec range, and that the deviations from baseline were more pronounced for the right than for the left visual field (Fig. 5C).

(3) A significant location x hemisphere x visual field interaction was obtained, indicating the effect of visual field was greater over the left than over the right hemisphere, and that the direction of the effect was reversed for the two hemispheres (Fig. 5D). The mean deviation from baseline was greater during right than during left visual field stimulation in left-hemisphere recordings, while being greater during left than during right visual field stimulation in right-hemisphere recordings.

(4) A significant main hemisphere effect was obtained at the frontal but not at the parietal recording site (Fig.

5D). At the frontal location, the mean deviation from baseline was greater for the left than for the right hemisphere.

(5) A significant hemisphere x visual field interaction was obtained at both the frontal and parietal sites (Fig. 5D). For both sites, the mean deviation from baseline was greater for right than for left visual field stimulation in left-hemisphere recordings, whereas just the opposite was the case for right-hemisphere recordings.

(6) At the frontal recording region, a significant main hemisphere effect was obtained for the eye task but not for the foot and counting tasks (upper part of Fig. 5D). For the eye task, the mean deviation from baseline was greater for the left than for the right hemisphere.

(7) Also at the frontal region, a significant hemisphere x visual field interaction was obtained for each of the three tasks, being marginal for the eye (upper part of Fig. 5D). The nature of the interaction for each task is the same as that described for the combined tasks in (5) above.

(8) At the parietal region, a significant hemisphere x visual field interaction also was obtained for each of the three tasks (lower part of Fig. 5D). The interaction specific to each task was found to be the same as that for the combined tasks summarized in (5) above.

(9) Tasks did not significantly interact with any of the

variables.

Effects on N-165

Findings Involving Tasks and Attention

6-way ANOVA. A 6-way ANOVA revealed significant main effects for tasks [F(2,34)=14.60, p<.0001] and attention [F(1,17)=85.25, p<.0001]. There also was a significant task x attention interaction [F(2,34)=3.83, p<.05]. A four-way interaction involving attention, location, hemispheres, and visual fields was significant [F(1,17)=9.68, p<.01], while a second four-way interaction involving attention, location, tasks, and visual fields approached significance [F(2,34)=3.02), p<.07]. The main effects for tasks and attention, as well as the interaction between them are manifested in Fig. 7A wherein mean deviations from baseline have been plotted as a function of tasks, attention, and recording sites. Mean deviations from baseline were much greater under the attend than under the unattend condition; the deviations were greatest for the eye and least for the counting task; and the differences in the magnitude of the deviations from baseline as a function of tasks were greater under the attend than under the unattend condition (compare slopes of lines in Fig. 7A for attend and unattend conditions). The four-way interactions involving attention are reflected in the upper and lower graphs of Fig. 6, although they are hard to discern. Suffice it to say here that the magnitude of the attention effect on N-165 appears to be dependent on both the location (frontal vs parietal) and hemisphere from which one records, as well as on the task the subject is set to perform and the visual field from within which the evoking stimulus is presented. The results of the 5-and 4-way ANOVAs to be presented below will help to clarify the nature of this dependency.

<u>5-way ANOVAs for each location separately</u>. At the <u>frontal</u> region, significant main effects were obtained for attention [F(1,17)=49.71, p<.0001] and tasks [F(2,34)=16.10, p<.0001]. A significant task x attention (TxA) interaction also was obtained [F(2,34)=5.01, p<.02]. The main attention effect is very evident in the group VERs of Fig. 1 (left side) wherein N-165 can be seen to deviate at least twice as far from baseline under the attend than under the unattend condition for all three tasks. The frontal attention effect also is very apparent in the upper part of Fig. 6, as well as in the left-hand side of Fig. 7A. The main effect of tasks also is manifested in the left side of Fig. 7A, as is the task by attention interaction. Inspection of the graph reveals the deviations from baseline were greatest for the eye and least for the counting task, and the differences in the deviations from baseline as a function of tasks were greater under the attend than under the unattend condition (compare slopes of lines in left side of Fig. 7A). These

frontal site findings indicate that this region contributed substantially to the significant effects noted in the 6-way ANOVA above.

A main effect for attention [F(1,17)=55.90, p<.0001] and tasks [F(2,34)=7.77, p<.002] also was obtained in the parietal recordings. These effects are evident in the group VERs (right side of Fig. 1), as well as in the lower part of Fig. 6 and in Fig 7A (right-hand graph). The direction of the effects was the same as noted for the frontal recordings above. Thus, the parietal region also contributed significantly to the main attention and task effects noted in the 6-way analysis. No significant interactions involving attention were obtained at the parietal region, thus, the T x A interaction noted in the 6-way analysis was due primarily to contributions from the frontal region.

4-way ANOVAs for each task and location separately. Significant main attention effects were obtained for each type of task [for the eye, F(1,17)=41.19, p<.0001; for the foot, F(1,17)=25.21, p<.0001; for the counting task, F(1,17)=53.02, p<.0001]. This also was the case at the parietal region [for the eye, F(1,17)=47.93, p<.0001; for the foot, F(1,17)=43.96, p<.0001; for the counting task, F(1,17)=25.78, p<.0001]. No significant interactions involving attention were obtained for any task at either recording region.

Findings Involving Tasks and Variables Other Than Attention

6-way ANOVA. A main hemisphere effect was obtained [F(1,17)=11.97, p<003] along with a significant hemisphere x visual field interaction [F(1,17)=27.13, p<.0001]. In addition, a location x hemisphere interaction approached significance [F(1,17)=4.37, p<.06]. The hemisphere effect is discernible in Fig. 6 as well as in Fig. 7B wherein mean deviations from baseline have been plotted as a function of location, tasks, hemisphere, and visual fields (collapsed across attention). By visually collapsing across all variables except hemispheres, it can be seen that the mean deviation from baseline was greater over the right than over the left hemisphere.

The significant hemsiphere x visual field interaction can best be seen in Fig. 7B. One can easily discern that the slopes of the lines derived from left hemisphere recordings are clearly different from those derived from right hemisphere recordings. The nearly significant location x hemisphere interaction also is discernible in Fig. 7B wherein it can be seen that the mean deviation from baseline (collapsed across all variables except hemispheres) was greater over the right than over the left hemisphere for the frontal recordings whereas the mean deviation was about the same over both hemispheres for the parietal recordings.

5-way ANOVAs for each location separately. At the frontal region, a significant main hemisphere effect was obtained [F(1,17)=13.16, p<.002]. This effect can be seen in the left-hand graph of Fig. 7B. The deviations from baseline were more pronounced over the right than over the left hemisphere. A significant hemisphere x visual field interaction also was obtained [F(1,17)=6.72, p<.02]. This interaction is evident in the left-hand graph of Fig. 7B wherein it can be seen that the visual field in which the stimulus appeared had little effect over the left hemisphere, whereas substantially greater deviations from baseline occurred during left visual field stimulation than during right field stimulation over the right hemisphere. These findings indicate the frontal region contributed significantly to both the main hemisphere effect and the HxV interaction noted in the 6-way analysis.

At the parietal region, there was no main hemisphere effect, although there was a significant hemisphere x visual field interaction [F(1,17)=35.66, p<.0001]. The HxV interaction is apparent in the right-hand graph of Fig. 7B wherein it can be seen that the left hemisphere mean deviations from baseline were greater during right than during left visual field stimulation, whereas the opposite was the case for the right hemisphere. While the possible significance of this observation will be discussed later, it may be noted here that the right visual field projects to the left hemisphere whereas the left field projects to the right hemisphere.

<u>4-way ANOVAs for each task and location separately</u>. At the <u>frontal</u> region, a main hemisphere effect was obtained for each of the three tasks [for the eye, $F(1,17)=6.57$, $p<.02$; for the foot, $F(1,17)=22.23$, $p<.0002$; for the counting task, $F(1,17)=12.87$, $p<.003$], indicating that each of the tasks contributed to the hemisphere effect noted in the 6-way ANOVA above. The hemisphere effect for each task separately can be readily observed in the left-hand graph of Fig. 7B. There also was a significant hemisphere x visual field interaction for the eye task [$F(1,17)=4.67$, $p<.05$] as well as a nearly significant effect for the foot [$F(1,17)=3.68$, $p<.08$] and counting tasks [$F(1,17)=3.90$, $p<.07$], indicating that all three tasks contributed in some measure to the significant HxV interaction noted in the 5-way ANOVA for the frontal region above. The HxV interaction for each task can be observed in Fig. 7B (left graph) by comparing the slopes of each pair of solid, dashed, and dotted lines.

Significant hemisphere x visual field interactions also were obtained at the <u>parietal</u> region for each task separately [for the eye, $F(1,17)=29.66$, $p<.0001$; for the foot, F91,17)=30.86, $p<.0001$; for the counting task, $F(1,17)=27.63$, $p<.0001$]. As depicted in the right-hand graph of Fig. 7B, the hemisphere-visual field relationship noted for the 5-way ANOVA above also holds for each task separately, indicating that each task constributed in like manner to the H x V interaction observed in the parietal 5-way analysis.

Summary of N-165 Findings

(1) A main attention effect was obtained in all analyses, the deflections deviating farther from baseline under the attend than under the unattend condition.

(2) A main effect for tasks was obtained in the 6-way, as well as in both 5-way analyses, indicating that the extent of the deviations from baseline varied across tasks at both the frontal and parietal regions. The deviations were greatest for the eye and least for the counting task.

(3) A significant task x attention interaction was obtained for the frontal but not for the parietal region, the differences in deviation from baseline across tasks being greater under the attend than under the unattend condition at the frontal region.

(4) A significant main hemisphere effect was obtained for the frontal but not for the parietal region. At the frontal region, larger deviations were obtained over the right than over the left hemisphere.

(5) There was a significant hemisphere x visual field

interaction over both regions. At the frontal region, right hemisphere recordings were greater during left than during right visual field stimulation, whereas left hemisphere recordings yielded baseline deviations of about the same magnitude for both visual fields. At the parietal region, deviations in baseline for the right hemisphere recordings were greater during left than during right visual field stimulation whereas the opposite was the case for the left hemisphere recordings.

Effects on P-355

Findings Involving Tasks and Attention

6-way ANOVA. The 6-way ANOVA revealed a significant main effect for attention [F(1,17)=10.37, p<.005], a significant attention x location (AxL) interaction [F(1,17)=7.98, p<.01], and a significant attention x location x task x hemisphere x visual field (AxLxTxHxV) interaction [F(2,34)=6.8, p.003]. These effects are graphically represented in Fig. 8. The main attention effect is manifested clearly in Graph A. By visually collapsing across all other variables, it also is apparent in all segments of Graph B. As is evident from these graphs and from Fig. 1, both scalp locations generated larger positive deflections (positive is down) at 350-360 msec under the attend then under the unattend condition. As reflected in the AxL interaction, the overall attention effect was due primarily to the large effect obtained at the parietal location, there being only a slight contribution from the frontal region. The 5-way interaction is embedded in Graph B of Fig. 8.

5-way ANOVAs for each location separately. The 5-way analyses revealed that the main effect of attention and the interactions involving attention derived from the 6-way ANOVA were primarily due to the parietal site recordings. This is shown in Graph B of Fig. 8 in which the 5-way interaction is plotted as a function of location, task, hemisphere, visual field, and attention. Parietal recordings (lower portion of Graph B) resulted in a main attention effect [$F(1,17)=16.38$, $p<.0008$]; a marginally significant interaction involving tasks, attention, and hemispheres [$F(2,34)=2.7$, $p<.08$],and a 4-way interaction involving tasks, attention, hemispheres, and visual fields [$F(2,34)=5.69$, $p<.007$]. The only effect involving attention in the frontal recordings (upper portion of Graph B) was a marginally significant attention x hemisphere interaction [$F(1,17)=3.59$, $p<.07$]. This interaction can be discerned by visually averaging across tasks and visual fields for each hemisphere. Such averaging yields a steeper slope as a function of attention for the left hemisphere than for the right.

The 4-way interactions obtained at the parietal region indicate the magnitude of the attention effect either is subtly dependent on which task the subject is set to perform, the hemisphere from which recordings are obtained, and from within which visual field the stimulus is presented; or the finding is an isolated instance of a Type I error.

4-way ANOVAs for each task and location separately. At the frontal region a significant effect involving attention was obtained for only one task. This involved a significant attention x hemisphere interaction for the foot [F(1,17)=9.99, p<.006]. This interaction can be seen in the upper part of Graph B of Fig. 8 by visually averaging across the dashed lines for the two visual fields of the left hemisphere, and comparing them to the slopes of the similarly averaged dashed lines for the two visual fields of the right hemisphere. It is evident that the left hemisphere yielded a larger attention effect than the right. At the parietal recording region a main effect of attention was obtained for the eye [F(1,17)=10.28, p<.005]; also, an attention x hemisphere x visual field interaction approached significance [F(1,17)=3.28, p<.08]. The main attention effect can be seen in the lower portion of Graph B after visually collapsing across hemispheres and visual fields; by visually collapsing across the left hemisphere-right visual field plots (for the solid lines only) and the right hemisphere-left visual field plots, and then comparing the slope of the line to that obtained by collapsing across the left hemisphere-left visual field and right hemisphere-right visual field plots, it is apparent that the attention effect was greater over the hemisphere receiving direct projections from the retinal areas stimulated. A significant main effect of attention also was obtained at the parietal region for the foot task [F(1,17)=21.82, p<.002], along with a significant attention x hemisphere interaction [F(1,17)=4.50, p<.05]. The lower portion of Graph B depicts these effects. Notice that the effect of attention was larger for the left hemisphere than for the right.

As for the eye and foot tasks, a significant main effect of attention was obtained at the parietal region for the counting task [F(1,17)=12.16, p<.003]. There were no significant interactions. The attention effect is clearly manifested in the lower part of Graph B (dotted lines); also the absence of any interactions are evident, as the slopes of the lines are essentially parallel for each of the two hemispheres and visual fields.

Findings Involving Tasks and Variables Other Than Attention

6-way ANOVA. In addition to the main attention effect and the location x attention interaction described above, the 6-way ANOVA revealed several significant interactions not involving attention. A significant four-way interaction involving location, tasks, hemispheres, and visual fields [F92,34)=5.79, p<.007] is depicted in Fig. 9A. A significant 3-way interaction involving location, tasks, and visual fields [F(2,34)=3.34, p<.05] also is evident in the figure. At the parietal recording region, stimulation from within the right visual field resulted in a larger positive mean deviation from baseline (collapsed across hemispheres) than was the case when the stimulus occurred in the left visual field. Also, there was a tendency for the visual field effect to go in opposite directions at the two locations. The deflections were greater (i.e., more positive) over the parietal region during right than during left visual field stimulation. At the frontal region, the deflections were slightly greater during left than during right visual field stimulation.

Several significant two-way interactions also were obtained. A significant location x visual field (LxV) interaction was obtained [F(1,17)=7.14, p<.01], reflecting the fact that at the parietal region, right visual field stimulation resulted in a greater positive deflection than left field stimulation, whereas at the frontal region the magnitude of the deflections was about the same for both visual fields (Fig. 9B).

A significant task x hemisphere interaction also was obtained [F(2,34)=4.22, p<.02], reflecting the fact that task-related differences in P-355 were dependent on the hemisphere over which recordings were obtained. The task-related differences for each hemisphere can be seen in Fig. 9A (after visually collapsing across frontal and parietal plots for each hemisphere). The interaction appears to result primarily from hemispheric differences associated with the foot task. For this task, P-355 was considerably more positive over the left than over the right hemisphere, whereas the deflection was of about equal magnitude over both hemispheres for each of the other two tasks.

A significant hemisphere x visual field (HxV) interaction was obtained [F(1,17)=5.05, p<.04], reflecting the fact that the visual field in which the stimulus appeared had a greater impact on left than on right hemisphere recordings. Largest P-355s were obtained over the left hemisphere at the parietal region during right visual field stimulation. The interaction can be seen in Fig. 9A (after visually collapsing across tasks and locations).

<u>5-way ANOVAs for each location separately</u>. At the <u>frontal</u> region only one interaction, task x hemisphere, approached significance [F(2,34)=2.94, p<.06]. This interaction reflects a tendency for P-355 to be of greater amplitude over the left than over the right hemisphere when

set to make a foot response, the opposite being the case when set to make an eye movement. The amplitude was symmetrical over the two hemispheres when set to count target stimuli.

For the parietal region, several main effects and interactions involving hemispheres, visual fields and tasks were disclosed. A significant main effect for hemisphere was obtained [F(1,17)=5.16], reflecting the fact that P-355's recorded over the left hemisphere were larger than those recorded over the right. A significant main visual field effect was derived [F(1,17)=12.45, p<.002], reflecting the fact that larger P-355's were generated by right than by left visual field stimulation.

A significant task x hemisphere x visual field (TxHxV) interaction was obtained [F(2,34)=5.87, p<.006], the complex relationships of which are manifested in the right-hand side of Fig. 9A. For the eye task, P-355 was larger over the left hemisphere than over the right during right visual field stimulation, whereas just the opposite was the case over the left hemisphere. This inversion did not occur for the foot and counting tasks, P-355 being greater during right than during left visual field stimulation over both hemispheres.

4-way ANOVAs for each task and location separately. For the eye task, a significant hemisphere x visual field interaction [F(1,17)=6.61, p<.02] was obtained for the parietal but not the frontal region. This effect is shown in Fig. 9A. At the parietal region, stimulation within the right visual field resulted in a larger deflection over the left hemisphere than over the right, while stimulation within the left visual field produced just the opposite effect.

For the foot task, a significant main hemisphere effect was obtained at both the frontal [F(1,17)=4.41, p<.05] and parietal [F(1,17)=11.56, p<.003] regions. In addition, a significant main effect of visual field [F(1,17)=18.35, p<.0005] was obtained at the parietal region. All of these effects are manifested in Fig. 9A.

For the counting task a significant main hemisphere effect [F(1,17)=4.83, p<.04] and a significant main effect of visual field [F(1,17)=4.55, p<.05] was found over the parietal region only (Fig. 9A).

The hemisphere and visual field findings are consistent with the 6- and 5-way ANOVAs wherein it was noted that larger P-355's were obtained over the left hemisphere during right visual field stimulation than were obtained over the right hemisphere during left visual field stimulation.

Summary of P-355

(1) A significant main attention effect was obtained in a 6-way ANOVA.

(2) The 5-way ANOVAs revealed a significant main attention effect for the parietal, but not for the frontal region.

(3) Over the parietal region, a significant attention effect was obtained for each task.

(4) Over the parietal region, P-355's obtained over the left hemisphere were larger than those obtained over the right hemisphere; the deflections also were larger during right than during left visual field stimulation.

(5) When subjects anticipated making an eye movement the magnitude of P-355 varied inversely with respect to hemisphere and visual field. During right visual field stimulation, larger deflections were recorded over the left hemisphere, while the opposite was true during left visual field stimulation.

(6) When subjects were prepared to make a foot response, P-355 also was asymmetrical with respect to hemispheres, but not in the same manner as for the eye task. For the foot task, larger responses were obtained over the left hemisphere than over the right regardless of the visual field in which the stimulus occurred, while this was not the case for the eye task.

(7) Larger P-355's were generated during right than during left visual field stimulation.

(8) For the counting task, the main effects of hemisphere and visual field were in the same direction as in the foot

task noted in (6) above.

Comparison of Findings Across Components

A two-dimensional matrix of significant effects obtained in the 6-, 5-, and 4-way ANOVAs for each component (i.e., at each latency range) is shown in Table 1. The various analyses and components are arranged across columns; sources of variance are arranged across rows. The first 15 rows contain sources of variance involving the attention manipulation; the remaining 15 contain sources not involving attention. The number of ●'s (filled circles) in each cell represents level of significance (●●●● = $p<.0001$; ●●● = $p<.001$; ●● = $p<.01$; ● = $p<.05$). A o (open circle) in a cell designates a nearly significant effect ($.05<p<.10$).

Findings Involving Attention

Row 1 summarizes main attention effects. For C-55, an attention effect was obtained for the eye and counting tasks at the frontal region and for the counting task at the parietal region. For C-115, an effect was obtained at the parietal region for all three tasks, there being no effect at the frontal region for any task. For N-165, there was an attention effect at both frontal and parietal regions for all three tasks. For P-355, the effect of attention was significant at the parietal region for all tasks and at the frontal region for the foot task only. These main effects can be reviewed upon perusal of Fig. 10 wherein the attention-related effects depicted in Figs. 3, 5, 6, and 8 have been reproduced on a single page to enable a quick visual comparison across components.

The LxA interactions obtained in the 6-way analysis (row 2) reflect the fact that for C-115 the attention effect was manifested at parietal cortex only, while for P-355, the effect was manifested much more strongly and uniformly across all tasks at the parietal region but was significant only for the foot task at the frontal location. The attention effect for C-55 and N-165 was not found to be dependent on recording location. These findings are manifested in Fig. 10.

The nature of the attention effect on both C-55 and N-165 was found to be dependent on the type of task (TxA) the subject was set to perform (see Fig. 10) whereas this was not the case for C-115 and P-355 (row 3 of Table 1).

The effect of attention on C-55 was found to be dependent on the hemisphere over which frontal, but not parietal, recordings were obtained for eye and counting tasks (HxA interaction). Such dependency also was found for C-115 in both frontal and parietal recordings (for the counting task only), and for P-355 in frontal recordings (for the foot task only). N-165 was not influenced by hemisphere at either the frontal or parietal region. These results are summarized in row 4 of Table 1, and visually displayed in Fig. 10.

For C-55, the nature of the HxA interaction obtained over the parietal region was found to be dependent on the task (TxHxA) the subject was set to perform (row 9). An AxTxHxA interaction also approached significance in parietal P-355 recordings. These effects are depicted in Fig. 10.

An HxVxA interaction (row 11) approached significance for parietally recorded N-165 and P-355 (for the eye task only), but not for frontally recorded deflections. If this three-way interaction is real for these two components, it is at best very weak. No such interaction approached significance for C-55 and C-115 at either the frontal or parietal site.

Complex 4-way interactions involving attention were obtained in three instances. A TxHxVxA interaction was obtained for parietally recorded P-355 (row 12); an LxTxVxA interaction approached significance for N-165 (row 13); and an LxHxVxA interaction was obtained for N-165 (row 13). These interactions are depicted in Fig. 10; however, they are subtle and difficult to discern. The N-165 interactions might most parsimoniously be treated as isolated instances of sampling error which approached or reached the criterion for rejecting the null hypothesis. The P-355 interaction may be real, given the high significance level, but no attempt will be made in this report to unravel the significance of any subtle relationships which may exist among these four factors at this latency interval.

Findings Involving Variables Other Than Attention

Main task effects were obtained for N-165 at both the frontal and parietal regions (row 16). A task effect approached significance for C-115 (collapsed across frontal and parietal sites) but not for either C-55 or P-355. These findings are summarized in Fig. 11 which is a composite of Figs. 4, 7, and 9.

A significant HxT interaction (row 18) was obtained only for P-355, and this was limited to the 6-way analysis wherein measures were collapsed across frontal and parietal recording sites. The interaction approached significance in the 5-way analyses for the frontal site only. It did not approach significance for any of the other components. Fig. 11 pictorially summarizes these findings.

Significant 3-way interactions involving LxVxT (row 21) and HxVxT (row 22), along with a 4-way interaction involving LxHxVxT (row 23), were obtained for P-355 only. With careful scrutiny, these interactions are discernible upon inspection of the appropriate graphs in Fig 11. In general, the graphs suggest the complex interactions reflect a greater degree of responsiveness for the left hemisphere than for the right, the degree of which depends both on the visual field in which the evoking stimulus appears and the type of response the subject is set to make.

A main hemisphere effect (row 24) was obtained at the frontal region for _C-55_, being more negative over the right than over the left hemisphere (Fig. 11). A similar effect approached significance over the parietal region (for the eye and counting tasks). A hemisphere effect also was obtained for _C-115_ at the frontal region, but the magnitude of this component was greater over the left than over the right hemisphere (Fig. 11). No hemisphere effect was obtained for this component over the parietal region. A significant hemisphere effect likewise was obtained for _N-165_ in frontal, but not in parietal, recordings, being greater over the right (as for C-55) than over the left hemisphere. A significant effect was obtained for _P-355_ at the frontal recording site for the foot task only, and at the parietal site for both the foot and counting tasks. In each case P-355 was larger over the left than over the right hemisphere (as was the case for C-115). Fig. 11 depicts these effects.

There was a hemisphere x visual field interaction (row 26) for _C-115_ over both the frontal and parietal regions, the response generally being greater over the right hemisphere during left visual field stimulation and over the left hemisphere during right visual field stimulation. A similar result was obtained for N-165, the effect being more symmetrical over the parietal than over the frontal region. For P-355, an HxV interaction was obtained at the parietal region for the eye task only, the nature of which was like that observed for C-115 and N-165. No such interaction was obtained for C-55. See Fig. 11 for a graphic summary of the effects.

A 3-way interaction involving location, visual field, and hemispheres was obtained for C-115 (row 27), reflecting the fact that the VxH interaction summarized in the preceding paragraph for this component was highly symmetrical at the parietal region, while being quite asymmetrical at the frontal region (see Fig. 11). No significant LxVxH interaction was obtained for any of the other components.

A main visual field effect was obtained for C-55 in the parietal 5-way analysis, which appears to have been solely due to a significantly greater response having been obtained during left than during right visual field stimulation for the foot task only (row 28). A main effect also was obtained for P-355 over parietal cortex for all tasks combined and for each task separately. P-355 was larger during right than during left visual field stimulation. Fig. 11 provides a visual summary.

A significant LxV interaction was obtained for <u>C-55</u>, <u>C-115</u>, and <u>P-355</u> (row 29), reflecting the fact that for C-55 and P-355, the effect of visual field was limited to the parietal region. The significant effect for C-115 appears to be a reflection of a relatively greater visual field effect at the <u>frontal</u> than at the parietal region (Fig. 11) even though there was no main visual field effect.

Finally there was a main location effect (row 30) for <u>C-55</u>, which was more negative in polarity at the parietal than at the frontal region (Fig. 11); and also for <u>C-115</u>, indicating negative displacement from baseline at the frontal and positive displacement at the parietal region.

CHAPTER III

DISCUSSION

C-55 (40-70 msec)

VER deflections in the 40-70 msec latency range (C-55) were found to be dependent on the relevancy of the visual field from within which evoking stimuli were presented (i.e., on whether the subject's attention was or was not focussed on a given visual field); the type of response subjects were set to make to target stimuli; and the region (frontal vs parietal) and hemisphere (right vs left) from which recordings were obtained.

When subjects were set to count target stimuli, C-55 was relatively more positive at both the frontal and parietal regions under the attend (i.e., relevant field) than under the unattend (i.e., irrelevant field) condition. In contrast to this observation, when subjects were set to make an eye movement to target stimuli, C-55 was more <u>negative</u> at both regions under the attend condition (although the attention effect reached statistical significance only for the frontal region). When set to make a foot-lift response, C-55 was not significantly affected by visual field relevancy at either recording region, although at the frontal region there was a tendency for the component to be more positive under the attend (i.e., relevant) condition. For both the eye movement and counting task conditions there was a tendency for the visual field relevancy effect to be greater over the right than over the left frontal hemisphere, although the attention x hemisphere interaction reached significance only for the eye task. There was a similar interactive tendency at the parietal region for the eye task, but the effect did not reach statistical significance.

When a given field was relevant, C-55 was relatively more negative when subjects were set to make an eye movement than when set to make either a foot-lift or counting response. When that same field was irrelevant, C-55 was relatively more positive when subjects were set to make an eye movement compared to either of the other two task conditions.

The absolute magnitude of C-55 was very small, compared to later components, and tended to have a shallow gradient across the four recording locations. The polarity of C-55 at the parietal region was relatively more negative to left than to right visual field stimulation. A similar trend was seen at the frontal region, but the difference in polarity was not statistically significant. The polarity of C-55 also was more negative over the right than over the left hemisphere, being more so at the parietal than at the frontal region.

These findings indicate that early short-latency components falling within the 40-70 msec range can be modulated by the relevancy of the visual field from within which evoking stimuli are presented, and that the type of response the subject is set to make influences EP-components in the same latency range. The inversion in the direction of the relevancy effect for the eye movement and counting tasks suggests that the equivalent dipole sources activated by the two tasks were of opposite polarity. In addition, the fact that for the eye movement task C-55 deviated from baseline in a negative direction when a given visual field was relevant and in a positive direction when that same field was irrelevant, whereas the opposite was the case for the counting task, suggests that both facilitatory and inhibitory mechanisms were at work. That is, the C-55 deflection did not simply return to baseline under the unattended condition, but went beyond baseline in a direction opposite to the displacement observed under the attend condition for each task, suggesting active inhibition under the unattend condition. The greater negativity (responsivity?) of C-55 to left than to right visual field stimulation coupled with the greater negativity over the right than over the left hemisphere suggests prestimulus priming of neural elements responsible for the generation of C-55 (subcortical?) was greater in the right than in the left hemisphere. This observation is consistent with hemispheric differences involving later components (Harter & Aine, 1984; Hillyard et al., 1985; Neville & Lawson, 1987).

Confirmation of Earlier Findings

The finding that visual field relevancy affects VER deflections in the 40-70 ms range is consistent with earlier observations from our laboratory, dating back to an observed enhancement of the b-wave of the ERG when the evoking stimulus appeared in the relevant field (Eason, Oakley, & Flowers, 1983). The basic findings of these earlier studies have been summarized in the introductory section of this paper (pp. 2-7). As noted in that section, due to the long controversy as to whether centrifugal fibers project to the retina, Oakley and Eason (1985), along with other investigators (Mangun, Hansen, & Hillyard, 1986), have questioned whether the short-latency attention effect observed in the "ERG" study actually occurred at the level of the retina. The actual site of differential processing of spatial information as a function of visual field relevancy may have involved tectal and/or thalamic nuclei, the "far-field" activity of which may have been recorded at the internal canthi of the eyes. Recent new evidence, based on HRP tracing procedures, indicates that centrifugal fibers exist in the optic nerve of rats (Itaya, 1980; Itaya &

Itaya, 1985) and monkeys (Itaya & Van Hoesen, 1983; Perry, Oehler, & Cowey, 1984). These anatomical findings strengthen the plausibility for the existence of endogenously controlled differential processing of spatiovisual information at the level of the retina; thus, the issue remains an open one. In any case, the short-latency attention effects observed in the present study are consistent with those observed in canthal recordings in that they involve the modulation of components falling within the same latency range.

The attention-induced effects on C-55 in the present study are of particular significance with respect to the repeatibility of the observations made in the series of studies conducted in our laboratory in recent years. The first indication that an early component of subcortical (but non-retinal) origin could be modulated by spatial selective attention emerged from Oakley's Masters Thesis (1984) wherein she recorded from arrays of electrodes placed on either side of the midline of the scalp. She observed that an early component of low amplitude and with a flat scalp distribution falling within the same latency range as C-55 was relatively more negative when evoking stimuli appeared in the relevant (i.e., attended) visual field, the effect being most pronounced in frontal recordings. In a subsequent study Oakley, et al (1985) again observed that a frontally-recorded component falling within the same latency range was more negative when the evoking stimulus fell within the relevant visual field. This increased negativity was observed when subjects responded to target stimuli by either making a finger-lift response or a combined finger-lift and eye movement response. In another study designed to assess the topographical distribution of the attention-induced effect on early components falling within the same latency range, Oakley, et al (1986) observed increased negativity under the attend condition at scalp locations ranging from the frontal to the occipital region. Since subjects were required to respond with either the right or left hand, it was this study which provided the first cue that the type of response the subject was prepared to make seemed to influence the magnitude and direction of the visual field relevancy effect on the early EP deflection.

Motor set effects will be discussed later. The primary point being made here is that the same kind of attention-related negativity observed in four different experiments conducted in our laboratory, including the present one, was found when subjects were set to make an eye movement and/or finger-lift response to the target stimulus appearing in the relevant field. The effect was statistically significant in every case. While one might legitimately question whether the rejection of the null hypothesis in any single experiment taken in isolation is an instance in which the null hypothesis actually is true and a Type I error was therefore committed, the probability of this being the case for four sequential experiments is so infinitesimal, that such an explanation cannot reasonably be applied to the consistently positive outcomes.

The consistency with which the early attention effect has been obtained across experiments in our laboratory cannot be overly emphasized in view of the fact that a number of prominent cognitive neuroscientists have been loath to accept the proposition that any type of selective processing may occur precortically as a function of endogenously imposed centrifugal influences on subcortical centers (Hillyard et al., 1985; Naatanen, 1982; 1986; Picton et al., 1986; Woods, in press). Some have continued to question the reliability of findings which tend to support this proposition; others question their importance on the grounds that such effects can only be demonstrated under highly restricted conditions (Mangun et al., 1986; Picton et al., 1986); while still others have simply choosen to ignore such positive findings entirely (e.g. Woods, in press).

A number of investigators have reported attention-induced effects on short-latency components for both the auditory and somatosensory system in recent years, while others have consistently obtained negative results. Lukas (1980, 1981) observed that the auditory nerve component of the AEP was lower in amplitude and of longer latency to unattended than to attended tone pips in humans. McCallum et al (McCallum, Curry, Cooper, Pocock, & Papakostopoulos, 1983) observed that an early auditory component with an onset latency of 26 msec, and a difference potential with an onset latency as short as 15 msec were influenced by instructions to respond to sounds coming from a particular location among an array of locations in front, behind, and on either side of the subject. The latencies of these components fall within the range of medium latency AEP deflections believed to arise in part from the thalamus (Picton, Hillyard, Krausz, & Galambos, 1974). Woldorff, Hansen, and Hillyard recently reported (1986) that an auditory component with a latency range of 20-50 msec was more positive in polarity when the evoking stimulus was presented in the attended ear. They interpreted this component as reflecting activity of primary auditory cortex, but concluded the finding provides strong evidence for the hypothesis that selective auditory attention can bias processing of auditory signals at an early stage. Hackley, Woldorff, and Hillyard (in press) have very recently reported that activity mediated in the <u>upper</u> brainstem may be modulated by selective attention. To the writer's knowledge this is the first report to emerge from Hillyard's laboratory which suggests that selective attention may influence subcortically mediated auditory activity. In so doing, they emphasized that such mediation occurred at upper levels of the brain-stem while holding to the view that lower brainstem activity is "obligatory and invariant with attention". McCarthy and Wood (1986) recently have reported that a somatosensory deflection with an onset latency of 22 msec became more positive in polarity when subjects attended to the location at which a mild shock was applied (right or left wrist) and responded with a foot-press to target stimuli. Although this early latency response is deemed to be of cortical origin (Desmedt, et al., 1977; Picton, et al., 1986) it constitutes yet another demonstration of an attention effect at a very early stage of neural processing.

In contrast to the above findings, a host of EP experiments conducted on both the auditory and somatosensory systems have failed to reveal selective attention effects on early components of sufficiently short latency to be considered indicative of precortical activity (Desmedt & Robertson, 1977; Desmedt, et al., 1977; Hillyard & Debecker, 1977; Hillyard et al., 1985; Michie, 1984; Picton & Hillyard, 1974; Picton, Stapells, & Campbell, 1981; Velasco, Velasco, & Olvera, 1980; Woods & Hillyard, 1978) At least one study, an attempted "replication" of the ERG study conducted by Eason et al (1983), failed to obtain evidence for the attention-modulation of subcortical activity in the visual modality (Mangun, Hansen, & Hillyard, 1986).

In view of the wealth of anatomical and physiological information garnered from monkeys, cats, and other animals (to be discussed later) indicating that changes in attentional state can alter the responsiveness to incoming sensory information of a number of mesencephalic and diencephalic structures via a variety of pathways, it seems likely that the same or similar mechanisms responsible for such alteration also exist in humans. Thus, the failure of EP selective attention studies to demonstrate such modulatory activity should not be taken as conclusive evidence of its non-existence. Based on negative results obtained primarily in the cat (Brindley, 1970), for years it was thought that centrifugal fibers most probably do not exist in the cat or any other mammal, including humans (Rodieck, 1973; Shortess, 1978). But as noted earlier, recent findings based on new, powerful anatomical tracing techniques have indicated their existence in both rats (Itaya, 1980; Itaya & Itaya, 1985) and monkeys (Itaya & Van Hoesen, 1983; Perry et al., 1984), making highly credible the earlier anatomical observations of their existence in the optic nerve of humans by Honrubia and Elliot (1968), Wolter (1965) and others (Livingston, 1978; Van Hasselt, 1972/73).

It is not the purpose of this discussion to attempt to explain why a substantial number of auditory and somatosensory EP studies have been unsuccessful in demonstrating attention-induced modulation of neural activity at a subcortical level. Rather, the purpose is to point out that the detection of changes in subcortical activity with scalp electrodes is difficult, even when the changes in the structures involved is substantial, due to the massive attenuation which occurs between the subcortical locus of the equivalent dipole source(s) and the scalp. Due to such attenuation, the amplitude of subcortically generated EP-components typically are less than a microvolt (Nunez, 1981; Vaughan, 1969, 1974, 1982; Wood, 1982; Wood & Allison, 1981). If the primary longitudinal axis of the equivalent dipole source is poorly directionalized, due to wide variations in the orientation of the dendritic processes contributing to the dipole, the scalp field potentials will be attenuated even more. If the dipole orientation becomes too defocalized, a "closed field" results (Lorente de No, 1947) and no field variations associated with the subcortical activity will be detected at the scalp. Thus, under the best of recording conditions, it is clear that scalp-recorded EP activity is a relatively insensitive means of detecting changes in subcortical activity, but as the present study demonstrates, along with preceding ones conducted in our laboratory, such activity can be detected and measured under certain conditions.

We have been most successful in modulating short-latency EP components, using the peripheral visual field attention paradigm, when (1) employing small, near-threshold, punctate spots of light widely separated in the two visual fields; (2) selecting highly motivated subjects; (3) running as many subjects as possible as few times as possible; (4) imposing frequent breaks within a trial, (5) giving periodic reminders and encouragement to the subject to try very hard to "tune in" on the relevant field and to ignore the irelevant one, (6) instructing the subject to avoid reactivating the system until "ready"; (7) providing feedback; (8) providing at least 5-min breaks between trials within a session; (9) limiting any given session to not more than eight trials and two hours; (10) requiring the subject to leave the recording room midway through a 4-trial session for at least 10 minutes; (11) limiting a given subject to not more than one session per week; (12) limiting the interstimulus interval to not less than 800 msec; and (13) presenting a fairly high percentage of targets within each trial (25-33%). On the whole, these procedures enhance the subject's capacity to selectively attend when the data collection system is engaged (sustained attention). By the same token, they help to minimize refractory, inhibitory, habituative, and general arousal reduction effects produced by fatigue or boredom; any one of which could contribute to the attenuation, or possible obliteration, of any attention-induced effects on short latency components of scalp-recorded potentials believed to arise from subcortical generators.

Having failed in their attempt to "replicate" the ERG attention study by Eason et al (1983), Mangun, Hansen and Hillyard (1986) concluded their "...results raise questions about the replicability of the ERG attention effect and suggest that such effects, if they exist, may depend on a narrow range of stimulus parameters and/or instructional sets." The latter part of this statement has validity. Given the intrinsic difficulties embedded in the recording of subcortical activity with scalp electrodes, it is probably true that the definitive demonstration of attention-induced modulation of subcortical activity in the auditory and somatosensory system will depend on a narrow range of stimulus parameters and/or instructional sets, as well as on other variables which may affect the behavioral state of the subject during the data collection process. Except for the studies conducted by Lukas (1980, 1981), it would appear that the appropriate parameters and instructional sets have not yet been employed which permit a convincing demonstration of such subcortical modulation in these sensory systems.

Subcortical Generators of C-55

It previously has been noted that the absolute magnitude of C-55 is very small and has a relatively flat distribution across the scalp, suggesting that the generator(s) of the deflection is/are of subcortical origin. Furthermore, the latency range of the component overlaps that obtained from single units in various subcortical structures of the visual pathway of monkeys (and cats in some instances). Although latency measures vary as a function of stimulus intensity (Baker, Sanseverino, Lamarre, & Pogio, 1969) and across species (Arezzo, Vaughan, Kraut, & Legatt, 1986), the extensive overlap in latency between C-55 and the single unit records in cats and monkeys suggests the component is largely a manifestation of subcortical activity which precedes the arrival of sensory information at the cortex.

Recording from single units in the monkey superior colliculus, Goldberg and Wurtz (1972) observed that a particular class of cells located in the superficial and intermediate layers responded within 40-50 msec poststimulus to one-degree spots of light of moderate intensity presented in the cell's receptive field. In a subsequent study, Wurtz and Mohler (1976) observed SC cell onset latencies ranging from 35-60 msec, with most of them falling within the 40-50 msec range as noted by Goldberg and Wurtz.

Recording from units in the LGN of the cat, Baker et al., (1969) observed that stimulation of the eye with small spots of light at near threshold intensity resulted in onset latencies of approximately 55 msec; with higher intensities yielding onset latencies as short as 25 msec. Modal latencies for near-threshold and higher intensity flashes varied from approximately 60 msec (for high) to 100 msec (for near threshold intensities). In averaged evoked potential recordings from the LGN of alert squirrel monkeys to both diffuse flash and pattern (checkerboards or vertical stripes) stimulation, Perryman and Lindsley (1977) obtained biphasic (positive-negative) potentials of approximately 70 msec duration. The positive leg of the biphasic potential had an onset latency of approximately 30 msec and a peak latency of about 60 msec. The negative leg had an onset latency of 60 msec and a peak latency of 100 msec.

In single unit recordings from the inferior, lateral, and dorsomedial pulvinar, Peterson, Robinson, and Keys (1985) obtained mean onset latencies of 67, 64, and 86 msec respectively. For the inferior and dorsal regions, most of the onset latencies fell within a 40-80 msec range. In averaged evoked potential recordings from the pulvinar of alert squirrel monkeys Perryman and Lindsley (1977) obtained responses consisting of an initial positive deflection with an onset latency of approximately 40 msec and a peak latency of about 80 msec. This was followed by a negative deflection with an onset latency of 80 msec and a peak latency of approximately 130 msec. A second positive deflection had a peak latency of 200 msec or more.

In contrast to the latencies obtained in single unit and evoked potential recordings from these subcortical structures, the latencies of visually responsive units located in cortex tend to be considerably longer. An exception are the latencies of units found in striate cortex of monkeys which range from 40-80 msec (Wurtz & Mohler, 1976). However, Wurtz and Mohler observed the striate cells do not respond differentially as a function of selectively attending to specific points in space. Thus, even if this cortical area may have contributed to the field potentials responsible for C-55, it seems unlikely that they contributed to the observed perceptual and motor set effects on this component. In evoked potential recordings from area 17 of alert squirrel monkeys, Perryman and Lindsley (1977) obtained an initial negative deflection with onset and peak latencies of approximately 60 and 90 msec respectively. A subsequent positive deflection had onset and peak latencies of approximately 90 and 160 msec respectively. Both deflections were much larger to pattern than to diffuse stimulation. In recordings obtained from area 19, an initial deflection of positive polarity had onset and peak latencies of approximately 60 and 120 msec. A subsequent negative deflection had respective onset and peak latencies of approximately 120 and 250 msec.

Attention-related visually responsive units in the frontal eye fields (FEF) have median onset latencies of 80 msec, the vast majority falling between 60-120 msec. Attention-related units in posterior parietal cortex have modal and mean latencies of 76 and 98 msec respectively (Bushnell, Goldberg, & Robinson, 1981). Robinson, Goldberg, & Stanton (1978) observed that 73% of the latencies of parietal cortex units lie between 69 and 139 msec. Recordings obtained from units in pre-straite cortex of the monkey (i.e., in the prelunate gyrus), which show spatially selective, saccade-related enhancement, have a mean onset latency of 80 msec with peak enhancement of 120 msec to an eye movement related TS (Fisher & Boch, 1981). Visually responsive units in the inferior temporal cortex (Richmond, Wurtz, & Sato, 1983) have a latency range of 70-220 msec the majority falling between 70-160 msec. The observed enhancement in these units when the monkey performs a pattern discrimination task is not related to spatial attention, but rather to the pattern discrimination process. Thus, it is highly unlikely that this cortical area could have contributed to the field potentials responsible for the set-related effects on C-55 even if some of its units responded within the appropriate latency range.

Since the latencies of the visually responsive units in those cortical areas which exhibit set-related properties (namely the frontal eye field and parietal regions) tend to lie beyond the 40-70 msec range of C-55; and since the latencies of attention-sensitive cells located in subcortical structures to which the vast majority of the retinal ganglion cells project (LGN, SC, and pulvinar) do fall within this latency range, it is probable that C-55 is comprised primarily of field potentials arising from one or more of these subcortical structures.

It should be noted that the response latencies of subcortical and cortical structures in the human visual system are believed to be 10-20 msec longer (depending on the structure) than those observed in monkeys (Arezzo, et al., 1986). However, even if this should prove to be the case, the substantially longer latencies of cortical units, compared to subcortical units, in monkeys (and cats) still support the conclusion that C-55 arises from subcortical generator sources. The latencies of cortical units in humans would be considerably longer (10-20 msec) than those reported for monkeys, making it even more likely that C-55 is of subcortical origin.

Anatomical Considerations

An assessment of the neural elements which might be involved in the generation of C-55 requires an anatomical analysis of the interconnections of those subcortical structures which receive retinal input from the region stimulated in the present study (30 degrees peripherally in the right and left visual fields), along with input from other brain areas, both subcortical and cortical, which might be involved in set-related activity.

Recent studies conducted on monkeys indicate the existence of four morphologically distinct types of ganglion cells: alpha, beta, gamma and epsilon (Perry, Oehler, & Cowey, 1984). In comparison to the cat, the alpha cells are similar to Y cells, beta cells to X cells, and gamma and epsilon cells to W cells. Alpha and beta cells, which project to the magno and parvocellular layers of the LGN respectively, are found throughout the periphery in both monkeys (Perry et al., 1984) and in humans (Rodieck, Binmoeller, & Dineen, 1985). In monkeys about 10% of the ganglion cells are of the alpha type and 80% of the beta type. The remaining 10% are of the gamma and epsilon type, and the vast majority of these project to the superior colliculus (Perry & Cowey, 1984). Unlike in the cat, there are very few cells projecting to the LGN which also send collaterals to the superior colliculus. As for alpha and beta cells, gamma and epsilon cells also tend to be distributed throughout the retina, although their precise distribution remains to be established.

Given current knowledge about the distribution of alpha, beta, gamma, and epsilon cells, it follows that all four types were activated to some degree by the peripheral stimuli used in the present study, resulting in the parallel activation of neural elements in both the parvo- and magnocellular layers of the LGN, and in both superficial and intermediate layers of the superior colliculus (Goldberg & Wurtz, 1972; Goldberg & Robinson, 1978; Goldberg, Bushnell, & Bruce, 1986; Wurtz & Goldberg, 1972). Since the superior colliculus projects to the pulvinar (Fries, 1984; Sparks, 1986; Wurtz & Albano, 1980), and in addition, some ganglion cells project directly to the inferior and medial pulvinar (Itaya & Van Hoesen, 1983), it is likely that neural elements in that structure also were activated directly and /or indirectly by the peripheral stimuli. It is clear, then, that the signals generated by the peripherally-presented stimuli travelled through segregated, parallel pathways to several subcortical visual nuclei; any or all of which may have been primed to respond in a particular manner as a function of set-related activity which preceded the presentation of each stimulus.

The SC, LGN, and pulvinar are all richly endowed with projections from various cortical and subcortical structures, some of which are known to be involved in set-related activity.

SC. In the monkey, the superficial layers of the SC receive projections from striate (area 17) and prestriate cortex (areas 18 and 19), the frontal eye fields (area 8), and the adjacent premotor cortex; and in almost if not in every case a topographic alignment is maintained with the retinal input (Wurtz & Albano, 1980; Fries, 1984; Sparks, 1986). Subcortical areas projecting to the superficial layers include the ventral LGN, the pretectum, and the parabigeminal nucleus (Wurtz & Albano, 1980; Sparks, 1986). The superficial layers send efferent projections to at least three thalamic nuclei; the dorsal LGN, the pregeniculate (ventral lateral geniculate) nucleus, and the inferior pulvinar; and to the parabigeminal and pretectal regions of the midbrain (Wurtz & Albano, 1980; Sparks, 1986).

In addition to receiving projections from striate and prestriate cortex, and the frontal eye fields, the intermediate and deeper layers of the SC of the (Macaque) monkey receive projections from posterior parietal cortex, inferotemporal cortex (areas 20 and 21), auditory cortex (area 22), the SII area of somatosensory cortex (area 2), upper insular cortex (area 14), motor cortex (area 4), premotor cortex (area 6), and prefrontal cortex (area 9) (Fries, 1984). Indeed, the only cortical areas for which no projections to these layers of the SC have been found are the SI region of somatosensory cortex, and infraorbital cortex. Thus, these SC layers are heavily endowed with projections from all sensory cortical areas and from virtually all associational and motor areas. These layers also receive numerous projections from subcortical structures in both cats and monkeys, including the zona incerta, reticular nucleus, and pregeniculate nucleus of the thalamus; the posterior commissure, pretectal nucleus, and optic tract nucleus of the pretectum; the substantia nigra, parabigeminal nucleus, inferior colliculus, locus coeruleus, and raphe nucleus of the midbrain; several nuclei in the pons and medulla; several cerebellar nuclei; and from the cuneate and gracile nuclei of the spinal cord (Hikosaka & Wurtz, 1983a,b,c,d; Wurtz & Albano, 1980; Fries, 1984; Sparks, 1986; Schlag & Schlag-Rey, 1984). The intermediate and deep layers in turn send efferents to numerous nuclei located in the same subcortical regions, including the oculomotor nuclei which drive the 12 eye muscles (Wurtz & Albano, 1980; Bruce & Goldberg, 1985; Fries, 1984; Goldberg, Bushnell, & Bruce, 1986; Sparks, 1986).

Based on these massive reciprocal connections between the various layers of the SC and sensory and motor structures located at all levels of the brain, the conclusion is inescapable that this structure is exquisitely equipped to play a major role in the integration of sensory and motor information required for the adaptive programming of eye movements. This includes not only the capacity to assess the behavioral state of the organism in order to make an appropriate eye movement response to a stimulus, but also the capacity to preset the motor programming system for making a specific kind of eye movement in the event an anticipated stimulus should occur. How this presetting may occur and the manner in which it may have influenced C-55 in the present study will be discussed following a brief description of the connections between both the LGN and pulvinar in relation to other brain structures. As we will see, circuitry exists which implicates both of these structures along with the SC, as probable contributors to the effects observed on C-55.

Pulvinar. Until fairly recently there has been no definitive proof for the existence of direct retinal projections to the pulvinar in primates; thus, it has generally been assumed that this structure receives its visual input indirectly via the pretectal nuclei and the SC (Chalupa, 1977). However, the development of anterograde HRP tracing techniques has led to the recent demonstration of such connections (Itaya & Van Hoesen, 1983; Mizuno, Itoh, Uchida, Uemura-Sumi, & Matsushima, 1982). These retinal fibers project to the inferior (PI) and medial (PM) regions. In addition to direct ganglion cell input, much of which is from the peripheral retina (Itaya & Van Hoesen, 1983; Mizuno, et al., 1982), the pulvinar receives projections from (and projects to) several cortical and subcortical structures.

PI receives retinotopically organized projections from striate and prestriate cortex, and the SC; and sends reciprocal connections in retinotopic fashion to striate and prestriate cortex (Itaya & Van Hoesen, 1983; Petersen, Robinson & Keys, 1985). The lateral pulvinar (PL) likewise receives retinotopically organized projections from striate and prestriate cortex, but without any apparent input from the SC (Petersen, et al., 1985; Benevento & Fallen, 1975). A third major region of the pulvinar, the dorsomedial region (Pdm), is interconnected with areas 5 and 7 of the parietal lobe, but has little, if any, direct connections to striate and prestriate cortex or to the frontal eye fields (Petersen et al., 1985). A medial region of the pulvinar (Pm) does, however, project to the frontal eye fields (Chalupa, 1977). Other projections to the pulvinar originate in the ipsilateral claustrum, the thalamic reticular nucleus, and the LGN (Trojanowski & Jacobson, 1974), as well as the temporal lobe of the cortex (Chalupa, 1977). Most of the pulvinar's efferent fibers project rostralward (Trojanowski & Jacobson, 1974), with terminations in association areas of the occipital, parietal, temporal, and frontal cortex, as well as in striate cortex (Chalupa, 1977). Subcortical projections are primarily to the reticular nucleus of the thalamus (Trojanowski & Jacobson, 1974). The three subdivisions of the pulvinar (PI, PL, and Pdm) do not seem to have extensive internal circuitry (Trojanowski & Jacobson, 1974), suggesting they may be involved in different types of visual processing.

At least one HRP study has shown a direct projection from the LGN to all three pulvinar regions (Trojanowski & Jacobson, 1974). This is only one of several locations at which the retino-geniculo-striate system can interact with the retino-colliculo-pulvino-prestriate system. Geniculo-prestriate fibers are known to project to areas 18 and 19 of visual association cortex (Benevento & Yoshida, 1981), while extra-geniculate thalamic nuclei have been demonstrated to project to striate cortex (Benevento & Rezak, 1976; Rezak & Benevento, 1979). The demosntration of retino-pulvinar fibers by Mizuno et al (1982) and Itaya and Van Hoesen (1983) provides further evidence of overlap between the so-called "first" and "second" visual system (Schneider, 1973). The degree of anatomical overlap between the two systems at all levels suggests that both systems probably contributed to the observed set-related effects on C-55.

<u>LGN</u>. Only 10-20% of the afferent connections to the LGN originate in the retina; thus the vast majority of the

afferent input to this structure is of non-retinal origin, suggesting that it does considerably more than simply relay visual information from the retina to higher visual areas for further processing (Sherman & Koch, 1986). Indeed it has been known for many years that the output of geniculate cells can be gated by signals received from the mesencephalic reticular formation as well as by cortical centrifugal influences (Lindsley, 1960; Livingston, 1978; Magoun, 1963; Scheibel & Scheibel, 1966; Singer, 1977); and more recently, anatomically and physiologically specific models have been developed to account for such gating (e.g., Skinner & Yingling, 1977; Sherman & Koch, 1986). The LGN consists of a dorsal (LGNd) and ventral portion (LGNv), the latter being known as the pregeniculate nucleus in primates (Rodieck, 1979). The LGNv receives bilateral input from fine retinal fibers, and non-retinal inputs from the visual cortex, SC, pretectum, and deep cerebellar nuclei. Although it receives input from visual cortex, all of its projections are to subcortical structures, including the pretectum, SC, pontine nuclei, suprachiasmatic nuclei, nucleus of the accessory optic tract, zona incerta, and the contralateral LGNv (Rodieck, 1979). The functional roles of this structure are poorly understood, but its lack of cortical input suggests it serves relatively low-level functions such as participating in pupillo-constrictor reflex activity and reflex-like, involuntary eye movements

(Rodieck, 1979). Since, based on current knowledge, it seems unlikely that it might play a role in voluntarily-induced set-related activity it will not be considered further.

Retinal projections to the LGNd were briefly described on page 124. In the cat, geniculate cells of the X-type project only to area 17; those of the Y-type project to both areas 17 and 18, and perhaps a small percentage to 19; and those of the W-type project to all three areas, with the vast majority projecting to area 19 (Rodieck, 1979; Stone, 1983). Since in the monkey, the vast majority of the retinal gamma and epsilon cells ("W"-type) project to the SC (Perry & Cowey, 1984), there are few, if any, geniculocortical connections of this type. The LGNd receives reciprocal connections from those cortical areas to which it projects, and in addition, receives indirect projections from frontal cortex via the thalamic reticular nucleus (Singer, 1977; Skinner & Yingling, 1977). In the cat, the LGNd receives projections from the perigeniculate nucleus which is often considered to be part of the thalamic reticular nucleus (Sherman & Koch, 1984). As previously noted, the LGNd also receives massive input from the mesencephalic reticular formation (Lindsley, 1960; Singer, 1977; Sherman & Koch, 1986), including the locus coeruleus, raphe nucleus, and parabrachial nucleus (Sherman & Koch, 1986), and from the superficial layers of the SC (Sparks, 1986; Wurtz & Albano, 1980).

Relative Contribution of SC, Pulvinar, and LGN to Set-related Effects on C-55

An accurate assessment of the extent to which the SC, pulvinar, and LGNd (along with other subcortical structures) contributed to the generation of C-55 would require localized recordings from these structures simultaneously with scalp-recorded VERs. Since such recordings are precluded in humans, except in specialized situations involving neurosurgery (e.g. Velasco, Velasco, & Olvera, 1980), one can only speculate as to their relative contributions to the early set-related effects on the basis of information garnered from monkeys and other mammals and from volume conduction theory.

The preceding section indicates that each of these subcortical structures has ample reciprocal connections with sensory, association, and motor cortical regions to be influenced by set-related activity immediately preceding the presentation of a trigger stimulus. Physiological data derived from monkeys and cats strongly suggest each of these structures is in fact influenced by set-related activity, and give credibility to the hypothesis that the inverted attention effect on C-55 observed between the eye movement and count conditions was due to differences in the prestimulus priming pattern brought about by differences in motor set.

SC. Single unit work conducted on the SC suggests this structure may have been strongly primed to respond to trigger stimuli presented in the relevant visual field when the subject was set to make an eye movement, and minimally primed or perhaps even inhibited when the subject maintained active fixation during the counting task. A lengthy series of single unit studies conducted on monkeys by the Laboratory Sensory Research Group at NIH, and their associates, have shown that cells in the superficial and intermediate layers of the SC are enhanced in their responsiveness to peripherally presented stimuli when the animal is attending to the spatial location in which the stimulus is presented and is set to make an eye movement to that location (Goldberg & Wurtz, 1972; Mohler & Wurtz, 1976; Wurtz & Albano, 1980; Wurtz, Goldberg, & Robinson, 1980). Similar studies conducted on the frontal eye fields have revealed that cells in this cortical region respond in a similar manner (Bruce & Goldberg, 1984, 1985; Mohler, Goldberg, & Wurtz, 1973; Wurtz & Mohler, 1976). Substantia nigra cells also change their responsiveness under the same conditions (Hikosaka & Wurtz, 1983a,b,c,d). Since the frontal eye fields send massive projections to the intermediate layers of the SC (Bruce, Goldberg, Bushnell, &

Stanton, 1985), as well as to the substantia nigra via the basal ganglia (Wurtz, 1985), which in turn sends projections to the same intermediate layers of the SC (Bruce et al., 1985; Hikosaka & Wurtz, 1983a,b,c,d), it is plausible that the frontal eye fields and adjacent cortical premotor regions (Schlag & Schlag-Ray, 1987) could preset the intermediate layer neurons of the SC so as to put them in a state of "readiness" to receive visual information from an attended location and initiate neural activity associated with making an eye movement to that location. Since at least one HRP study has shown intrinsic connections between the upper and intermediate layers of the SC (Grantyn, Ludwig, & Eberhardt, 1984), these intermediate neurons could in turn prime neurons in the superficial layers of the SC to be ready to receive visual information from the attended location. Thus, visually responsive neurons in both the superficial and intermediate layers of the SC could receive prestimulus priming brought about by cortical regions known to be involved in the planning and execution of purposive eye movements (Bruce, et al., 1985; Schlag & Schlag-Ray, 1987; Sparks, 1986).

When frontal eye field cells are activated by electrical stimulation, the threshold of visually responsive units with peripheral receptive fields is increased when the monkey actively fixates the central fixation point. Also, the latency of the eye movements induced by the stimulation is increased and movement velocity is decreased (Goldberg, Bushnell, & Bruce, 1986). It therefore appears that the frontal eye fields may not only enhance the responsivity of SC units when a monkey is set to make an eye movement to a relevant stimulus location, but this cortical region may also actively inhibit such activity when the animal is attending to another location with no intention of making an eye movement (with the possible exception of making a hand movement which frequently is coordinated with eye movement activity).

It is reasonable to postulate that a similar cortically induced priming effect on SC involving both facilitation and inhibition, depending on visual field relevancy, could have been largely responsible for the attention effect observed on C-55 when subjects were set to make an eye movement to a trigger stimulus presented in the relevant visual field. While it also is the case that both the pulvinar and dorsal LGN may have been differentially primed by stimulus relevancy (Chalupa, 1977; Petersen et al., 1985, 1987; Skinner & Yingling, 1977; Sherman & Koch, 1986), it seems likely that the SC may have been the primary contributor to the set-related effect observed under the eye movement condition.

In contrast to the eye movement task, evidence derived from single unit studies suggests the SC was not as strongly primed to be responsive to trigger stimuli presented in the relevant visual field when subjects were set to count doublets as when set to make eye movements. On the contrary, single unit data indicate that SC responses to relevant field stimulation not only fail to show enhancement when the monkey is not required to make an eye movement to the trigger stimulus appearing in that location (Goldberg & Wurtz, 1972; Wurtz et al., 1980), but such responses may even be actively inhibited if the animal is attentively fixating another location (Goldberg et al., 1986). Such findings suggest that when subjects were set to count doublets in the present study while maintaining steady fixation the SC contributed either relatively little to the equivalent dipole source responsible for the observed attention effect on C-55 or its influence was of opposite polarity to that contributed under the eye movement condition. In order for the subjects to maintain steady fixation, it is conceivable (although somewhat implausible) that the frontal eye fields and accessory motor regions, perhaps through prestimulus programming of the substantia nigra, primed the SC to respond in an inhibitory manner to target stimuli appearing in the relevant visual field, thus giving rise to a dipole source which was of opposite polarity to that generated under the eye movement condition. A perhaps more plausible possibility is that the SC was minimally affected by visual relevancy under the count condition, and that the observed effect on C-55, which was of opposite polarity to that observed under the eye movement condition, was due to relatively greater differential prestimulus priming of the LGN and/or the pulvinar.

Pulvinar. According to Petersen, et al (1985) that part of the pulvinar which contains attention-enhancement cells (Pdm) does not receive projections from the frontal eye fields (at least no direct ones), nor from striate or prestriate regions. This region does, however, project to the frontal eye fields as well as to other cortical regions (Chalupa, 1977). Primary subcortical projections of the pulvinar are to the reticular nucleus of the thalamus (Trojanowski & Jacobson, 1974). Petersen, et al (1985) state that the Pdm cells behave more like those found in parietal cortex, which show enhancement to trigger stimuli appearing in the attended location regardless of the type of response the animal is prepared to make (Mountcastle, Anderson, & Motter, 1981), than like attention-sensitive neurons found in SC or the frontal eye fields. If these observations are correct, then it is questionable whether the task-related attention effects on C-55 may have been due in part to the differential priming of visually responsive units in the Pdm of the pulvinar. However, it should not be overlooked that the pulvinar receives projections from the LGN and sends projections both to the reticular nucleus and

LGN (Trojanowski & Jacobson, 1976). It also should be kept in mind that the reticular thalamic nucleus which innervates the LGN, receives massive projections from frontal cortex (Skinner & Yingling, 1977), including the frontal eye fields (Crowne, 1983). Thus, despite the lack of direct input from the frontal eye fields to the Pdm, there is ample opportunity for this and other regions of the pulvinar to be primed to respond differentially to trigger stimuli appearing in the relevant visual field as a function of the type of response the subject was set to make. It therefore cannot be ruled out at this time that pulvinar cells did not contribute to the quivalent dipole source responsible for the task-related effects on C-55.

<u>LGN</u>. It is also possible that the LGNd contributed significantly to the equivalent dipole source responsible for the observed attention effect on C-55. Certainly the circuitry exists for the gating of visual input through this structure (Singer, 1977), and there is ample physiological evidence garnered from animals (especially cats) to indicate that such gating does occur (Sherman & Koch, 1986; Skinner & Yingling, 1977; Yingling & Skinner, 1977). Based on such evidence Skinner & Yingling (1977) developed a model which proposes that selective attention can gate visual input at the LGNd via fronto-cortical pathways terminating in the thalamic reticular nucleus. The differential activation of this structure in turn results in selective gating (i.e.,

selective inhibition) of information being conveyed by ganglion cells to geniculate relay cells. A similar model incorporating current neurochemical and biophysical data has been recently developed by Sherman and Koch (1986). Assuming these animal models apply to humans, which seems plausible, it is reasonable to postulate that the LGN may have been differentially primed to selectively gate stimulus evoked impulses as a function of visual field relevancy. Since the reticular nucleus receives extensive input from frontal cortex (including prefrontal, premotor, and frontal eye field regions) it is conceivable that the LGNd also could have been differentially primed to gate signals selectively as a function of the type of response the subject was set to make. However, since the LGNd does not appear to function as a sensory-motor integration center, but rather as a modulator of sensory input (Sherman & Koch, 1986), it is unclear as to how it may have been primed to differentailly transmit signals as a function of the type of response the subject was set to make. The mechanism whereby cortical areas 17 and 18, the immediate recipients of such gated activity, would be able to interpret the modulations as being motor related is unclear. Perhaps the most parsimonious conclusion to draw at this time is that the LGNd could have contributed to the equivalent dipole source responsible for the visual field relevancy and task-related effects on C-55, but the manner in which this may be accomplished remains obscure.

<u>Dipole strength of each subcortical structure</u>. To establish with precision the degree to which the SC, pulvinar, and LGNd may have contributed to the equivalent dipole source responsible for the observed effects on C-55, information would be required on the orientation of the dipole generated within each structure under each experimental condition, and the angular width of each dipole's primary axis (i.e., whether the dipole was highly directionalized or diffuse in its orientation). The more diffuse a dipole's orientation within a structure, the weaker its contribution would be to the equivalent dipole source generated by combined structures. If too diffuse, there would be no primary direction of current flow, and the activity within a given structure would become a closed field (Nunez, 1981). In such case, the structure, even though it may have been influenced by perceptual and/or motor set would have contributed nothing to the equivalent dipole source and to the field potential changes registered at the scalp. The degree to which the dipole source within a given structure is open or closed conceivably could vary across experimental conditions, in which case the variations in scalp recorded potentials across experimental conditions would not accurately reflect the degree of activity occurring within each structure. Thus, without detailed

knowledge of which cellular populations of neurons within each subcortical structure is active during the C-55 latency interval, the direction of current flow, and the degree to which the current flow is directionalized; the relative contributions of each structure to the scalp-recorded C-55 component under each experimental condition cannot be established with any degree of confidence.

Conclusion. Given our current knowledge of the anatomical connections of the SC, pulvinar, and LGNd to various cortical and to other subcortical structures; and single unit data obtained from animals; the most parsimonious conclusion which may be made at this time is that all three structures, along with others which have not been discussed, may have contributed in some manner to the attention effect observed on C-55 during the eye movement and counting tasks and to the attention-related inversion between the two tasks. Whatever may have been the relative contributions of the structures involved, the latency of the C-55 deflection, in conjunction with the inverted attention effect associated with the eye movement and counting tasks, strongly support the conclusion that precortical activity elicited by a trigger stimulus was influenced both by the relevancy of the visual field within which the trigger stimulus appeared (spatial attention or perceptual set) and by the type of response the subject was set to make (motor set).

Neuroanatomical Relationships Between Eye, Foot, and Finger Movements

In our previous study a negative difference potential with a peak latency of 45 msec was generated when subjects attended to the relevant visual field while being prepared to respond by lifting a forefinger from the microswitch key or by making both a finger lift and eye movement response (Oakley et el., 1985). The attention effect observed for the two tasks did not differ significantly, suggesting the neural generators activated by the two types of motor set were similar, if not the same (Oakley et al., 1985). Since the findings were replicated several times in the earlier studies, it seems reasonable to conclude that if a finger lift condition had been included in the present study the same results again would have been obtained. The anatomical and physiological data summarized above, in conjunction with supplementary information presented below, lend credibility to the view that the same or highly overlapping dipole sources in subcortical structures responsible for the set-related effects for the eye could have been responsible for effects observed for the hand task in the 40-70 msec range.

The anatomical connections of the SC strongly suggest that this tectal structure is involved in eye-hand coordination (Fries, 1984). The intermediate and lower layers receive projections from the somatosensory cortex (SII), primarily from regions corresponding to finger, arm, and head representations; and from motor and premotor cortex (Fries, 1984). Tanji and Kurata (1982, 1985), in a series of studies, investigated single unit responses of the premotor and supplemenatry motor area of the cortex (SMA) of the monkey in a discrimination task. The monkey learned to press a key in response to visual, auditory and vibrotactile trigger stimuli. An instructional stimulus (1000 Hz or 300 Hz tone) cued the animal as to which trigger mode to follow. It was found that single units in the SMA were selectively active during preparation for a hand movement in response to a sensory signal in one modality but not to a signal in the other modality. Half of the units tested (49%) responded to an instructional stimulus. Some cells showed continuous activity lasting until the occurrence of the movement (type I cells); some exhibited increased activity until the occurrence of a nontriggering signal (type II cells); and a small number responded with a short-latency burst after the instructional stimulus. Tanji and Kurata postulated that the SMA neurons are involved in the preparation to make a hand movement to a relevant sensory signal. The supplementary motor region may prepare the organism for a motor response by selecting the motor program in response to preselected sensory signals (type I cells), and by suppressing the motor program when the instruction does not call for a response (type II cells). The activity of motor cortex neurons was specific to the sensory signal which initiated a hand movement; therefore, the motor cortex seems to be at the end of the chain of events that lead to a hand movement (Lamare, Spidalieri, Busby, & Lund, 1980).

Sutton, Trachy, and Lindeman (1981) trained monkeys in a discrimination task to either press a lever to the presentation of a specified light stimulus, or to vocalize during the presentation of a different light stimulus. Ablation of the SMA affected the vocal response but not the lever-press. The results of Sutton et al, seem to indicate that it is the type of motor response, rather than the eliciting stimulus, which determines the deficit (Jurgens, 1984).

Another point about the SMA may be noted. Yamaguchi and Meyers (1972) reported that the deficits observed after SMA lesions in the monkey correlate with what they called the "volitional effort" exhibited during the performance of a specified behavior, such effort being greatly reduced in lesioned animals. Consistent with this observation, Roland, Larsen, Lassen, and Skinhoj (1980) demonstrated that cerebral blood flow increased in the SMA during voluntarily initiated finger movements but not during simple, repetitive movements.

From the various studies briefly described in this section, one of the functions of the SMA seems to involve the organization of volitional movement in response to a particular sensory stimulus. The SMA seems to be only one of the cortical areas involved in sensory-motor integration. Area 6 of the monkey also was found to contribute to the organization of visually guided hand movements (Haaxma & Kuypers, 1975; Moll & Kuypers, 1977, Rizzolatti et al., 1983). The activity of SMA cells described by Tanji and Kurata resembles the activity of frontal eye field neurons and other prefrontal regions involved in preparing the individual for an eye movement. Since signals from cortical areas involved in hand and eye movements converge on the SC, it seems plausible that preparation for either hand or eye responses may yield the same collicular activity.

Data suggesting common, or overlapping neural mechanisms involving hand and eye movements triggered by a sensory stimulus have been obtained in the monkey in another subcortical structure, the pulvinar (Acuna, Gonzales, & Dominguez, 1983; Yirmia & Hocherman, 1987). Yirmia and Hocherman trained monkeys to discriminate auditory and somatic stimuli and respond to them by moving a lever with their hands to the left or right. Eighty-one out of 101 cells (80%) responded prior to the movement; 70 out of 101 (70%) responded to the sensory stimulation; and most of the sensory cells were also movement related. The cells responded only when the stimulus was behaviorally significant to the animal, which confirms the findings of Petersen et al (1985). However, in contrast to Petersen's interpretation that only the dorsomedial pulvinar is related to attentive behavior, Yirmiya and Hocherman found that single units from all their electrode penetrations located in medial, lateral, and inferior pulvinar showed behaviorally contingent responses.

Acuna et al, (1983) trained monkeys to perform two tasks. One involved making saccadic eye movements to eccentrically placed visual targets; the other required projection movements of the arm and hand in order to touch the targets. Several types of cells were found in the lateral, medial and inferior regions of the pulvinar. Some responded only when the monkey made either an eye or hand movement; others (termed complex cells) were preferentially active when the animal executed both movements simultaneously (saccade and hand projection). Pulvinar neurons integrating sensory-motor activity also have been found in the human pulvinar (Straschill & Takahashi, 1981).

The supplementary motor cortex of the monkey projects to many cortical and subcortical regions (Jurgens, 1984), including the reticular nucleus of the thalamus. The point was made earlier (p. 138) that this nucleus seems to act as a "gate" of sensory information passing through the thalamus. Thus, the activity of motor-related cells in the supplementary motor cortex may modulate sensory activity at the level of the LGN via the thalamic relay nuclei.

The coordination of hand and eye movements is important for primates. The visual system locates an object within the subject's reach and motor commands direct the action toward the stimulus (Arbib, 1987). Eye-foot motor programs, although just as important and probably guided by the same principles as those discovered for eye-hand coordination, most likely converge on brain structures different from those mediating eye-hand coordination, and thus give rise to different EP configurations.

The above observations, taken collectively, suggest that being set to make a hand movement may prime the same subcortical regions in a similar manner as are primed when being set to make an eye movement, whereas being set to make a foot movement either primes the same regions dissimilarly or primes different regions. This would explain the similarity between the attention-related C-55 results obtained for the eye condition in the present study and the finger lift condition in our earlier studies, while the foot lift condition tended to show an attention effect (although non-significant) more like that of the count condition.

Relation to Earlier ERG Findings

In our initial ERG study (Eason et al., 1983), an early response believed to be the b-wave of the ERG was modulated by the spatial selective attention manipulation. Although the results were replicated in two subsequent experiments (Eason, 1984), the effects were less pronounced. Viewed within the context of the results obtained in the present study, the increased difficulty in demonstrating the effect in the replication studies may have been due to differences in the type of responses the subjects were required to make to target stimuli. In the 1983 study the subjects counted target stimuli while in the 1984 study they responded to target stimuli by lifting their right forefinger off a microswitch key. If the evoked responses obtained in the ERG studies contained volume conducted activity from subcortical structures, then, based on current findings, it can be postulated that in the count condition the positive polarity attention effect on the C-55 generator(s) summed with the positive polarity attention effect on the b-wave, thus enhancing the observed attention effect. On the other hand, in the finger lift task, the negative polarity attention effect on the C-55 dipole generator(s) would have summed algebraically with the positive polarity attention effect on the ERG b-wave, thus attenuating the observed attention effect at the canthal recording sites. If this were in fact the case, then the replication experiments involving a finger lift response (Eason, 1984) constituted a more rigorous test of a spatial attention effect at a retinal level than did the original study (Eason et al., 1983) utilizing a counting task.

Compatibility of C-55 Findings with Fronto-cortical Efferent Models of Sensory Selection (gating) and Sensory-motor Integration

Evart's theory. As stated in the introduction (pp. 12-26), Evarts (1984) postulated the existence of "set cells" in primary motor cortex (MI) and areas projecting to MI which control the excitability of interneurons impinging on pyramidal tract neurons (PTNs). The degree of excitability (or inhibition) imposed on the interneurons by the set cells during the IS-TS interval determines whether and to what extent PTNs will be responding to TS-elicited signals arriving via cerebello-thalamo-interneuronal MI circuits, and the latency of the response evoked by PTN activity. It was Evart's model which provided the basic rationale for the present study, the assumption being that if "set cells" located in motor cortex could alter the responsivity of cortical motor neurons to a trigger stimulus, then such cells might also exist in frontal cortex (and other regions) which could alter the responsivity of sensory and or sensory-motor cells (such as those found in the intermediate layers of SC and the dorso-medial pulvinar) at a subcortical level. The C-55 findings are consistent with this expectation.

Teuber's hypothesis. The idea that anticipation of making a particular response to a specified stimulus may generate efferent signals in frontal motor and premotor regions of the cortex which could alter the neural activity patterns evoked by a trigger stimulus was expressed in a model proposed by Teuber in the early 1960s (Teuber, 1964). Having observed profoundly disruptive effects of frontal lesions on the capacity of patients to assimilate environmental information and to respond adaptively to such information, Teuber concluded that such effects could never be understood by the classical approach of considering brain function initially from a sensory perspective and proceeding serially from sensory input to motor output. He postulated that the anticipation to make a particular response to a stimulus results in a discharge from motor to sensory structures "which prepares the sensory structures for an anticipated change" (Teuber, 1964, p. 418). He referred to such motor-to-sensory activity as "corollary discharge", meaning an endogenously induced discharge (reflecting voluntary or willed activity) which could alter the response pattern of those neural elements involved in the processing of incoming sensory information and the execution of the desired response. Teuber felt that such corollary discharges played an important role in making basic perceptual discriminations such as differentiating between the eyes moving while the environment remains stable. This discrimination breaks down if the eyes are moved passively. Teuber postulated the breakdown is due to the elimination of the corollary discharge from frontal cortex (the frontal eye fields in this case), a postulation that was later proven to be false (Sparks, 1986). While Teuber did not postulate (at least not in the articles reviewed by the writer) that the "corollary discharge" of motor and premotor cortical regions could also serve as an endogenous representation of attentional states, and that such discharge may subcortically gate incoming signals evoked by stimuli appearing at attended and unattended locations, this possibility seems at least as plausible as any of the examples given by him.

Theory of Skinner and Yingling. The fronto-reticulo-LGNd gating hypothesis of Skinner and Yingling (1977) is based on the same kind of idea as that proposed by Teuber. Their model is more elaborate in that it provides a more detailed anatomical and physiological analysis of how Teuber's corollary discharges might alter neural activity evoked by a trigger stimulus.

Theory of Goldberg and Segraves. Goldberg and Segraves (1987) have recently proposed a motor attention model which is analogous to visuo-spatial models of attention. Starting from the premise that visuospatial attention involves the selection of stimuli from the environment for further neural processing, they have proposed that motor attention involves the selection of approriate higher level motor signals from among an indefinite number of concomitantly occurring signals in order to execute a purposive response.

The Goldberg and Seagraves model is based primarily on ablation and lesion studies involving the frontal eye fields and the extensive single unit work conducted by their group at the NEI (e.g., Bruce and Goldberg, 1985; Bruce et al., 1985; Goldberg & Bushnell, 1981). When the frontal eye fields have been removed or damaged, both humans and monkeys tend to lose voluntary control over their eye movements; that is, their movements tend to become stimulus bound. Humans with FEF lesions have great difficulty suppressing saccades when the stimulus (to which they have been instructed not to respond) falls in the visual field contralateral to the lesion. Likewise, monkeys with ablated FEFs cannot refrain from looking at a peripheral stimulus when the task situation requires that they do not, although normals can do so with ease.

From such observations Goldberg and Segraves (1987) postulated that in the absence of the frontal eye fields, motor signals evoked by the stimulus in sensorimotor cells of the SC involved in making eye movements cannot be inhibited, and the eyes therefore move to the stimulus. They postulated that when the frontal eye fields are intact, the subcortical oculomotor system responds in accordance with the motor program imposed on it from higher levels. All other stimulus-driven motor activity is inhibited. Without endogenous prestimulus signals from the frontal eye fields, the "...more primitive stimulus-evoked or spontaneous motor signals would be sufficient to evoke the movement" (p. 117). They state further, "...when a form of behavior becomes important to an organism, for example a visually guided saccade crucial to the animal's ongoing behavior, then frontal motor signals would take control of the system, and adventitious signals would not result in behavior. The selection of an appropriate motor signal in the presence of conflicting motor signals is thus an analog of the selection of appropriate sensory stimulation in the external world, and ... that the selection of behavior is a motor attentional process analogous to the process of visuospatial attention" (p. 117).

An important implication of their theory is that prestimulus programming to make a particular type of response (motor set) works in parallel with prestimulus programming to receive information from a given spatial location (perceptual set), and that the neural response to a trigger stimulus of those subcortical structures subjected to such dual preprogramming will be dependent on their combined effects. The C-55 findings are consistent with this implication.

Theory of Rizzolatti et al. On the basis of data garnered from single unit studies of cats and monkeys and from lesion experiments, Rizzolatti (1983) has formulated a motor-oriented theory of attention which he refers to as the "premotor attentional hypotheis" (p. 285). His hypothesis is derived in part from observations in single unit studies that those cortical and subcortical areas which are closely linked to movement preparation also participate in selective attention, whereas those areas which do not participate in movement preparation show no relationship to either passive (orienting) or active (selective) attention. The hypothesis also is derived in part from observations in lesion studies which show that the difficulty animals experience in orienting toward stimuli presented at spatial locations contralateral to the lesion is accompanied by the incapacity to explore that same space.

Rizzolatti relies heavily on the work of Wurtz and associates (Wurtz et al., 1980), along with his own work on cats (Rizzolatti, Camarda, Grupp, & Pisa, 1973; 1974) in establishing an empirical basis and rationale for his premotor hypothesis. Since the attention-related enhancement effect occurs with highest frequency in the intermediate layers of the SC in cells which respond both to visual stimulation and impending eye movements (i.e., in visuomotor cells which Rizzolatti calls "premotor" cells), he postulates: "... when the animal expects a stimulus in a certain part of the visual field, the premotor collicular neurons will fire and facilitate both the motor neurons which determine a shift of the gaze toward the point in space where the stimulus is going to appear and the neurons of the superficial layers. These last become more sensitive and respond more strongly to the stimulus when it actually appears" (Rizzolatti, 1983; p. 285).

In their single unit work with cats, Rizzolatti et al (1973; 1974) observed that the responses of single units in the SC to stimuli appearing in the respective receptive field of each cell was strongly inhibited when a second stimulus was presented simultaneously from outside the cell's receptive field. The stimuli were most effective in inhibiting premotor neurons in the deep layers of the SC which, in turn, inhibited the responsivity of units in higher layers. From these observations, Rizzolatti et al concluded that the premotor collicular neurons are most likely responsible for both the enhancement and inhibitory effects observed in the superficial and intermediate layers.

In an effort to gain further support for the premotor hypothesis, Rizzolatti, et al (Rizzolatti, Matelli, & Pavesi, 1980) ablated a portion of cortical area 6 (a premotor area) in macaque monkeys to test whether any resulting motor deficits would be accompanied by attentional deficits. Such ablations disrupted the animal's capacity to make mouth biting movements when stimuli touched the side of the face contralateral to the lesion, and in accordance with the premotor hypothesis prediction, the monkeys tended to neglect food placed near their face (within 15 cm) in the visual field contralateral to the lesion. Rizzolatti, et al concluded these findings demonstrate the close tie between selective attention and overt movements, and in addition, serve as an illustration that selective attention is not a unitary process involving a signle neural mehanism (e.g., a parietal cortex mechanism), but involves multiple mechanisms distributed across several centers (perhaps the same centers involved in the programming of motor acts). In their words, "The attentional space controlled by the different centers coincide with their motor space, that is, with the space on which the effectors controlled by that area act."

To summarize, the premotor selective attention hypothesis proposes that premotor centers, both cortical and subcortical, play an active role in the spatial attention process. The neurons of these centers may be endogenously activated through an active attention process associated with the anticipation of a stimulus or exogenously through passive orienting of attention to an unexpected stimulus.

"...once a premotor neuron is activated it renders more responsive sensorial neurons which receive information from the part of the environment where the stimulus appeared or it is going to appear. Simultaneously it decreases the responses of the neurons which 'see' other parts of the visual space" (Rizzolatti, 1983; p. 289). The neural origin of the attentional process depends on the required response. If the response is oculomotor, the process will originate in the frontal eye fields or in the SC; if a grapsing response, in area 6 or 7b. If a complex response involving both eye and arm movements is required, then area 7a will be involved.

Harter and Aine's model. Although the neurophysiological model of selective attention proposed by Harter and Aine (1984) does not consider mechanisms of motor set, their basic premise that the processing of afferent neural information is modulated by efferent activity originating in higher cortical centers is supported by the C-55 findings in the present study. As their receptive field model would predict, such influence occurs at a subcortical level when spatial location is being selectively attended. Based on anatomical and physiological information obtained from monkeys (Bushnell, Goldberg, & Robinson, 1981; Motter, Steinmetz, Duffy, & Mountcastle, 1987; Robinson, Goldberg, & Stanton, 1978), it is plausible that centrifugal influences from the parietal cortex contributed significantly to the visual field relevancy effect observed on C-55, as Harter and Aine's model suggests. Although the task-related effects observed on C-55 cannot be handled within the context of the Harter and Aine model as presently formulated, expansion of the model to include frontocortical motor and premotor influences on lower visuo-motor centers would permit it to do so.

While it was not the purpose of the present study to subject any of the above models to experimental test, the set-related effects observed on C-55 are consistent with the notions expressed in each of them. With the possible exception of the Harter and Aine model, each of the models implies that the activity pattern elicited in subcortical structures by a trigger stimulus will be a function of both the attentional state of the subject and the type of response he/she is set to make. The model of Rizzolatti, et al perhaps comes closest to predicting the task-related effects on C-55 as a function of visual field relevancy. Recall that under the attended condition, C-55 was relatively more negative when subjects were set to make an eye movement than when set to count double flashes; while under the unattended condition, the relative polarities for the two tasks were reversed. Assuming the locus of the dipole responsible for this attention x task interaction was the SC, the results are consistent with the prediction suggested by the premotor hypothesis of Rizzolatti et al that the attention effect should be enhanced when subjects are set to make an eye movement but actively inhibited when engaged in active fixation while performing a counting task. The Goldberg and Seagrave model also suggests that both facilitatory and inhibitory processes could be involved in the motor attentional process; the Harter and Aine model similarly suggests that both kinds of processes could be involved in spatial attention.

The visual field relevancy and task related effects on C-55 take on considerable credibility when viewed within the context of frontocortical and parietocortical models which postulate mechanisms by which motor set, along with perceptual set, could conjointly influence the processing of spatiovisual information at lower levels.

Perceptual and Motor Set Interactions

A final point to be considered before leaving the C-55 component concerns the issue of whether the influence of perceptual and motor set on this component can be separated in selective attention experiments, and if so under what conditions. In the present study when subjects were set to make eye movements C-55 was relatively more negative under the attend (i.e., relevant visual field) condition. When they were set to make counting responses C-55 was relatively more possitive under the attend condition. When subjects were set to make a foot-lift response, C-55 tended to be relatively more positive under the attend condition, but not significantly so. In earlier experiments (Oakley et al., 1985, 1986), when subjects were set to make a finger-lift response, deflections falling with the latency range of C-55 were relatively more negative under the attend condition.

While traditional bottom-up models of information processing have assumed that sensory set precedes motor set (Broadbent, 1970; Triesman,1964), and a large body of findings obtained in the EP attention studies have been interpreted within this context (Hansen & Hillyard, 1980; Hillyard & Kutas, 1983; Hillyard et al., 1985; Michie, Bearpark, Crawford, & Glue, 1987), it is clear from the C-55 results obtained in the present and preceeding studies conducted in our laboratory that both processes occur in parallel and the observed EP effects are a manifestation of their combined influence.

Since all experimental attention paradigms require some kind of response to target stimuli, whether overt (e.g., pressing a button or lifting a finger) or covert (e.g., silently counting), it is reasonable to question whether spatial selective attention (or any other stimulus selection process) influences neural events independently of motor set. Recent neuroclinical observations made on humans undergoing operations indicate that stimulation of the superior pulvinar in the left hemisphere interferes with the patient's capacity to speak (Ojeman, 1977; 1982), suggesting the possibility that being set to count target stimuli might prime premotor neurons related to speech which could alter the processing of incoming visuospatial information. It is conceivable that every type of perceptual set is accompanied by some type of motor set. If so, some of the conflicting results reported in the selective attention EP literature may reflect differences in the types of tasks subjects were required to perform. An important implication of the C-55 findings is that due consideration should be given to the type of task to be performed as well as to the features of the environment to be selectively attended in future EP attention studies.

Later Components

As stated previously (pp.26-33), the focus of the present study was on the effects of perceptual and motor set on EP-components occurring within the first 100 milliseconds poststimulus. The primary objective was to investigate the hypothesis that visuospatial attention involves the differential gating at a subcortical level of incoming sensory information presented at attended and unattended locations, such gating being under the control of endogenously induced efferent signals occurring prior to stimulus presentation which arise from sensory and motor association cortex. Emphasis has been placed on the C-55 component, because it falls within the latency range required to provide the most direct proof of such differential gating.

Except for frontally recorded Cp-115, later components subjected to analysis in the present study have been extensively studied since the initial discovery by Eason, Harter, and White (1969) that they can be modulated by spatial selective attention. Thus, the observations made on these components for the most part are not new, and provide little additional insight concerning neural mechanisms of visuospatial attention. The changes observed in these later components are of some interest, however, in that they provide a kind of internal validity check on the observations and conclusions involving C-55. They also provide a basis for comparing the results of this study to previous findings reported in the literature on these same components.

C-115 (100-130 msec latency window)

Frontally recorded C-115 (Cf-115) deviated in a negative direction from baseline whereas parietally recorded C-115 (Cp-115) deviated in a positive direction. A significant attention effect was obtained at the parietal region for all three tasks, but no such effect was obtained at the frontal region for any task. A task-related effect approached significance, with both Cf-115 and Cp-115 being most positive when subjects were set to make an eye movement and most negative when they were set to make a counting response. For the counting task only, the magnitude of the attention effect was greater over the right parietal than over the left parietal region.

Both Cf-115 and Cp-115 deviated farther from baseline, and in opposite directions, during right than during left field stimulation. At the frontal location only, and only for the eye task, the mean deviation from baseline was greater for the left than for the right hemisphere. For both frontal and parietal recordings, the mean deviation from baseline was greater for contralateral than for ipsilateral visual field stimulation. Tasks did not significantly interact with any of the variables, including attention.

Although both Cf-115 and Cp-115 were measured over the same latency interval (100-130 msec) their peak latencies differed by several milliseconds. The frontal recordings peaked out at around 100 msec whereas the parietal ones peaked out at 110-115 msec. These latency differences indicate that at least two dipole sources were simultaneously active which differentially impacted on recordings obtained in the 100-130 msec range from frontal and parietal regions, since it is physically impossible for a single generator source to produce any latency differences on the order of milliseconds across the scalp (Nunez, 1981). The failure to obtain an attention effect at the frontal region while doing so at the parietal may have been a consequence of the differential impact of the overlapping dipole sources.

At the parietal region Cp-115 was highly consistent across subjects, and the attention effect was clearcut, with the deflection being relatively more positive under the attend condition. By contrast, at the frontal region Cf-115 was highly variable across subjects, with six of the 18 subjects either exhibiting no deflection during the 100-130 msec interval, or if one was exhibited, it went in a positive rather than a negative direction as though the electrodes were primarily sensing the same dipole source as was being sensed at the parietal region. It appeared, therefore, that the frontal recordings of these six subjects were either not sensing the dipole source that drove the polarity of the Cf-115 deflection for the remaining 12 subjects in a negative direction, or this negative dipole source was being overwhelmed in these six subjects by the more posteriorlly located positive dipole source. If this were the case, then inclusion of these six subjects in the sample for testing whether there was a significant effect on Cf-115 could conceivably have masked any attention effect associated with the more frontally located negative dipole source.

To check this possibility, a post-hoc analysis was performed on the Cf-115 data of only those 12 subjects showing a negative deflection from baseline in the 100-130 msec range. Analyses performed on each task separately yielded a borderline statistically significant attention effect for the eye task [F(1,11)=4.24, p<.06]. Also, there was a significant attention x hemisphere interaction for the counting task [F(1,11)=5.14, p<.04], with the left hemisphere showing an attention effect but not the right. No significant attention-related effects were found for the foot task. These attention effects were masked in the analyses involving all 18 subjects. With respect to visual field and hemisphere effect, the same results were obtained as with the entire sample of 18, the mean deviation from baseline being greater for the left hemisphere than the right and for the right visual field than for the left.

Consideration of these post-hoc findings based on 12 subjects exhibiting a negative Cf-115, in conjunction with the findings obtained from the complete sample of 18, strongly suggests that at least two dipole sources were simultaneously active during the 100-130 msec interval. One was of positive polarity and had a maximal field strength over posterior regions. This dipole is responsible for the classical P1 and is believed to arise from striatal cortex (Creutzfeldt & Kuhnt, 1973; Eason, 1981; Eason, et al., 1969; Eason & Dudley, 1971; Harter & Salmon, 1972; Hillyard, Munte, & Neville, 1985; Halliday, et al., 1977: Lesevre, 1982; Lesevre & Joseph, 1979; Van Voorhis & Hillyard, 1977). The other dipole was of negative polarity and had a maximal field strength over frontal regions.

Results obtained from the 12 subjects whose frontal recordings exhibited the negative dipole source suggest it is subject to modulation by both perceptual and motor set. The main attention effect obtained for the eye movement task suggests that the frontal eye fields may have been a major contributor to the dipole source, since it is known that the majority of attention sensitive neurons in this structure discharge to target stimuli within the 100-130 msec latency range of Cf-115 (Bruce & Goldberg, 1984; 1985; Bruce, et al., 1985; Mohler, et al., 1973).

The attention x hemisphere interaction for the counting task, reflecting the fact that the attention effect occurred only over the left frontal area, suggests that the dipole source responsible for this effect may have been located in or near Broca's area. As was proposed in the introduction, one would expect such an interaction to occur during the counting task if Broca's area were differentially influenced by the type of response the subject was set to make. The preferential activation of the speech area when subjects were set to count stimuli is supported by the fact that when subjects were set to make an eye movement there was no significant interaction between attention and hemispheres. In the latter case none would be expected since the frontal eye fields, which should be preferentially activated during the eye task, are located in both hemispheres.

The marginally significant task effect wherein both frontally and parietally recorded C-115 was most positive for the eye movement task and most negative for the counting task is puzzling. Since the dominant dipole source influencing Cf-115 is of negative polarity at the scalp whereas the dominant source influencing Cp-115 is of positive polarity, one would expect the two recordings to show inverted polarity shifts rather than parallel shifts as a function of tasks. Had the inverse relationship emerged, one could attribute the effects to variations in general activation level brought about by differences in task difficulty, but this explanation cannot handle the parallel polarity changes. This may be one of those instances in which the nearly statistically significant effect was a sampling error, and nothing more need be said about it unless or until a statistically significant finding emerges in subsequent experiments.

It also is puzzling that only for the eye task and only for the frontal region, C-115 was significantly more negative over the left than over the right hemisphere. Based on findings obtained at more posterior regions, one would have expected the frontal deflections to deviate farther from baseline over the right than over the left hemisphere. However, it must be kept in mind that a dipole source or sources seems to be preferentially influencing frontal recordings during the 100-130 latency range which is different from the source or sources influencing more posterior recordings. It is conceivable that the greater negativity observed over the left hemisphere actually is a manifestation of greater activity in the right hemisphere, and that the paradoxical effect is due to the more favorable alignemnt of the right hemisphere dipole toward the recording site over the left hemisphere. While this is a possibility, this kind of explanation is often used without foundation to account for puzzling hemispheric asymmetries. Perhaps it would be wisest to place this finding on "hold", along with the task effect noted in the preceding paragraph, until further data are available.

The finding that both Cf-115 and Cp-115 was greater over the hemisphere contralateral to the field of stimulation is consistent with earlier findings obtained in our laboratory (Eason, 1981; Oakley, et al., 1985; 1986), and also with those obtained by other investigators (Biersdorf & Nakamura, 1973; Cobb & Morton, 1970; Halliday, Barrett, Halliday, & Michael, 1977; Harding, Smith, & Smith, 1980; Lesevre, 1982; Lesevre & Joseph, 1979; Shagass, Amadeo, & Roemer, 1976). The findings are in contrast to those of Neville and Lawson (in press) who failed to observe greater responses over the hemisphere receiving direct retino-geniculate projections. The findings also are in conflict with an assertion made in a later paper by Hillyard, Munte, and Neville (1985) that, "The P1 wave tends to be bilaterally symmetrical whereas the later waves are usually larger over the scalp contralateral to the stimulus". The highly significant hemisphere by visual field interaction obtained in the present study, coupled with the positive findings of Biersdorf and Nakamura (1971), Cobb and Morton (1970), Lesevre (1982) and others, clearly indicate that C-115, whether recorded at frontal or more posterior cortical regions, is greater over the hemisphere receiving direct retinogeniculate input. It is not clear why Hillyard, Neville and associates have been unable to observe these hemispheric asymmetries. One reason may be that Neville and Lawson (1987) used linked mastoids as their reference electrode site, a practice generally followed by those affiliated with Hillyard's research group (Hillyard & Munte, 1984; Hillyard et al., 1985; Neville & Lawson, in press); whereas the ipsilateral earlobes were used as reference sites in the present study. As reported in the introduction (pp. 9-11), we investigated the effect of using the mastoid vs the earlobe as a reference, using the spatial attention paradigm, and found that the mastoids are not neutral between 50-130 msec poststimulus. According to Nunez (1981) linked mastoids (or earlobes) should not be used if one is interested in studying brain asymmetries. Although one cannot state with certainty why Hillyard, Neville, and associates have been unable to observe asymmetries in parietal and occipital recordings of C-115, one can only assume that if they used ipsilateral references and looked more carefully they would have been able to do so as we and others have done.

N-165 (160-170 msec)

Attention-related effects. N-165 was much greater under the attend than under the unattend condition for all tasks at both frontal and parietal regions. At the frontal region only, the magnitude of the attention effect interacted with tasks, being greatest for the eye and least for the counting task.

(Main attention effect). The robust main effect is consistent with earlier findings, dating back to the Eason, et al (1969) study. This effect has been repeatedly observed over the years (e.g., Harter et al., 1982; Hillyard & Mangun, 1986; Eason, 1981; Van Voorhis & Hillyard, 1977), and its occurrence was expected. Indeed, changes in this component have been so well established as an EP-correlate of selective attention, that its modulation in the present study can be taken as prima facie evidence that selective attention was in fact varied.

The nature of the neural processing manifested by this component has been interpreted in a variety of ways by cognitive neuroscientists. Hillyard and associates (Hillyard, Picton, et al., 1973; Hillyard et al., 1985; Woods, in press) have taken the position for many years that N1 (our N-165) is a manifestation of early sensory processing (stimulus set), whereas a subsequent positive wave (P-300 --- to be discussed later) is related to motor processing (motor set). This group has postulated that N1 is an "exogenous" (i.e., stimulus bound) component which can be modulated in amplitude much like changing the volume on a radio due to prestimulus priming of certain visual association cortical areas. Naatanen, Gaillard, and Mantysalo (1978) have proposed that the enhancement of N1 as a correlate of tonically maintained sensory set may be more apparent than real. Rather, the apparent enhancement may in fact be due to the modulation of "...an endogenous attention-related negativity being generated by a cerebral generator structure different from that responsible for the exogenous N1 component" (Naatanen, 1982, p. 610). The apparent change in N1 amplitude as a function of attention, therefore, could result from the processing negativity being added to the exogenous evoked potential (Naatanen & Michie, 1979). Naatanen (1982) proposed further that the processing negativity may be a manifestation of the comparison being made between incoming information and a sensory template of stimulus features being attended to, and the processing of the features which conform to the template. Harter & Aine (1984) have proposed that the negativity beginning within the latency range of N1 (at about 130 msec) is a manifestation of interlocation attention effects, i.e., it is an indicant of a selection process associated with spatial attention. They postulate that the neural level (and latency) at which various features of a stimulus can be selected for differential processing as a function of the attentional state of the subject is dependent on how far peripherally in the system the feature in question can be coded. If the information to be coded is spatial location, then it may be possible for selective processing to begin as far out as the retina (Eason, et al., 1983); if color, at the level of the LGNd; and if pattern, at the cortex (Harter & Aine, 1984). While the present study was not designed to test any of these cognitive models, the collective effects of attention observed on N-165, C-115, and C-55 seem to be most consistent with the physiologically oriented efferent model of Harter and Aine.

(Task x attention interaction and main task effects). A significant task x attention interaction was obtained for the frontal but not for the parietal region. Also, a significant main task effect was obtained at both frontal and parietal regions.

In contrast to C-55, for which the attention effect involving the eye and counting tasks was inverted, the magnitude of the attention effect on N-165 over frontal cortex was monotonically related, being greatest for the eye task and smallest for the counting task (Fig. 7A). Although not significant, a similar trend was observed in parietal recordings.

The polarity inversion associated with the attention x task interaction involving C-55 was attributed to different equivalent dipole sources activated by differing neuronal populations differentially primed by motor set neurons. The interaction involving frontally recorded N-165 cannot be interpreted in this manner, because the attention effect was in the same direction for all tasks. Since the absolute magnitude of N-165 was directly related to the magnitude of the attention effect observed for the three tasks, perhaps the most plausible explanation for both the interaction and the main task effect is that they were brought about by variations in general arousal due to differences in task difficulty. Although the subjects almost never counted the number of doublets with perfect accuracy, this task may have been least demanding. In both the eye movement and foot-lift conditions, the subjects had to respond to doublets very quickly to avoid receiving a late "beep" feedback signal. In the count condition they were not subjected to this time constraint. Thus, even though the subjects indicated they tried equally hard on all tasks, it seems probable that they were somewhat less aroused when performing the counting task. Most reported that they found the eye task the most difficult to perform.

The above interpretation is supported by a series of experiments conducted by Eason and associates (Eason, Aiken, White, & Lichtenstein, 1964; Eason, Harter, & White, 1969; Eason & Dudley, 1971) wherein they demonstrated that variations in task demands produce an alteration in N1 (our N-165) and later components of the occipitally recorded evoked response. The arousal interpretation also is supported by the single unit work of Singer, Tretter, & Cynader (1976) in which activation of the mesencephalic reticular formation (MRF) was found to produce a surface negative field potential in the visual cortex with a poststimulus latency interval of approximately 100-200 msec. During the period in which the field potential occurred, cortical responses to retinal stimulation were maximally facilitated. Their findings suggest that the poststimulus interval during which general arousal effects are maximally registered at the early scalp encompasses the latency at which N1 emerges. Although their work was based on recordings from visual cortex, while in the present study the significant task x attention interaction for N-165 was obtained over frontal cortex, it is extremely likely that frontal cortex, including premotor and prefrontal regions, also was activated by MRF stimulation in their single unit studies. Since the parietal cortical region also is influenced by MRF activity associated with arousal level, one might have expected N-165 recorded over this region in the present study to have exhibited a significant task x attention interaction, along with the frontal recordings. As indicated above, there was a trend in this direction although it was not significant.

Even though general arousal level may have varied across tasks, and the frontal N-165 findings are consistent with that possibility, the polarity inversion associated with the attention x task interaction observed for C-55 cannot be attributed simply to such variation. If this were the only variable influencing C-55 as a function of tasks, there should have been no inversion in the polarity of the attention effect between the eye and count condition, but merely a monotonic change in magnitude of the attention effect across tasks as was registered for N-165.

Other effects. At the frontal region, a main hemisphere effect was obtained for each task, N-165 being greater over the right hemisphere. No main hemisphere effect was obtained over the parietal region. A significant hemisphere by visual field interaction was obtained over both regions. At the frontal region the interactive effects were asymmetrical. That is, the right hemisphere recordings were greater during left than during right visual field stimulation, whereas the field of stimulation essentially had no effect over the left hemisphere. Over the parietal region the effects of visual field were highly symmetrical; that is, the responses to left field stimulation were greater over the right than over the left hemisphere, with opposite effects of equal magnitude being observed over each hemisphere to right field stimulation. The main hemisphere effect noted above for the frontal recordings is related to the asymmetrical effects of visual field over the two hemispheres at the frontal region. The absence of a main effect over the parietal region is due to the cancellation produced by the symmetrical effects of visual field over the two hemispheres (Fig. 7B).

The N-165 results manifested in frontal recordings suggest that at this poststimulus latency the right hemisphere was more responsive to peripheral stimulation (such as was used in the present study) than was the same region of the left hemisphere. Furthermore, the less responsive left hemisphere was no more reactive to contralateral than to ipsilateral stimulation, whereas the more responsive right hemisphere responded considerably more vigorously to contralateral than to ipsilateral stimulation (see Fig. 7B).

In contrast to the frontal region, parietally recorded N-165 results suggest the responsivity of each hemisphere at this location was approximately equal; also, each hemisphere was more responsive to contralateral than to ipsilateral stimulation and approximately to the same degree.

Three observations, collectively considered, converge to strongly suggest that more than one equivalent dipole source was responsible for the generation of N-165 recorded at frontal and parietal locations. The observations are: (1) The presence of hemispheric asymmetries at the frontal region and their apparent absence at the parietal region; (2) the occurrence of a significant attention x task interaction at the frontal but not at the parietal region (see preceding section); and (3) a latency difference of at least 10 msec between frontal and parietal recordings, N-165 peaking out sooner over frontal cortex (see Fig. 1).

At least two dipole sources would be required to account for these observations; one located anteriorly, the other posteriorly. Hillyard and associates (Hillyard & Mangun, 1986; Van Voorhis & Hillyard, 1977) have proposed that N1 is a manifestation of a single generator source associated with cortical neural activity produced by sensory set, and that such activity occurs regardless of the sensory modality being used. This is in contrast to P1 (our C-115) which they say is specific to the sensory modality stimulated. The present results are in direct contradiction to their proposition that N1 arises from a single attention-related generator source which is common to all sensory modalities. If there is in fact such a generator operative at the time of occurrence of N1, then it must be operating along with at least one other generator.

Since both frontal and parietal N-165 recordings were influenced by attention (i.e., stimulus relevance) to the same degree and in the same direction, the effect being symmetrical across hemispheres at both regions; it is possible that a single generator source was responsible for the observed attention effect. Since the absolute magnitude of N-165, on the average, was about the same at both the frontal and parietal regions, it is possible that the locus of this dipole source is in the vicinity of the vertex, as Van Voorhis and Hillyard suggested (1977). However, the differences in the responses of the two hemispheres at frontal and parietal regions, and the visual field x hemisphere interactions observed at both regions, indicate that other generators were simultaneously active. The parietally recorded VF x H interaction, indicating that the response of each hemisphere was greater to contralateral than to ipsilateral field stimulation, suggests a generator source involved in the processing of sensory information specific to the visual system was active at the same time as the more centrally located, nonsensory specific, attention-sensitive generator postulated by Van Voorhis and Hillyard.

The VF x H interaction observed over frontal cortex of the right hemisphere, also reflecting a greater response to contralateral than to ipsilateral field stimulation, suggests the existence of still another dipole source which also was involved in the processing of information specific to the visual system. This generator could have been processing sensory information in parallel with the more posteriorly located (parieto-occipital) sensory processing generator. Such parallel processing in frontal cortex could facilitate making the appropriate response to the trigger stimulus. As Lindsley and associates (Lansing, Schwartz, & Lindsley, 1959) and Posner and associates (Posner, Nissen, & Ogden, 1977; Posner, Nissen, & Klein, 1976) have demonstrated, there are considerable savings in raction time when subjects know before hand where the trigger stimulus is going to appear. Such savings could be a consequence of the parallel processing occurring in frontal cortex in preparation for the appropriate response upon completion of sensory processing at more posterior cortical regions. Although no effects of motor set were clearly manifested in N-165 as a function of tasks (task effects were interpreted as reflecting variations in arousal level), as there were for C-55, the apparent parallel processing occurring at frontal cortex at the N-165 latency interval suggests that motor set-related activity was continuing at this time.

The hemispheric differences could have been due to differences in the orientation of the dipoles responsible for N-165. Further research is required in order to determine the physiological basis for and the functional significance of the more potent N-165 deflections recorded over right than over left frontal cortex.

P-355

A main attention effect was obtained at the parietal region only, P-355 being more positive under the attend than under the unattend condition for all three tasks. Although a main attention effect was not obtained at the frontal region for any task, there was a significant attention x hemisphere interaction for the *foot* task, reflecting the fact that the left hemisphere yielded a larger attention effect than the right. At the parietal region, no interactions involving attention and any of the other variables reached significance.

At the frontal region, a task-related hemisphere effect approached significance. For the *foot* task, P-355 was more positive over the left than over the right hemisphere whereas the opposite was the case for the *eye* task. No hemispheric asymmetries were observed for the counting task.

At the frontal region, a main hemisphere effect was obtained for the <u>foot</u> task only, P-355 being more positive over the left hemisphere. At the parietal region, a hemisphere x visual field interaction was obtained for the <u>eye</u> task only. When subjects were set to perform this task, stimulation from within the right visual field resulted in a larger deflection over the left than over the right hemisphere, while stimulation from within the left visual field produced just the opposite effect. At the parietal region, a main hemisphere effect, along with a main visual field effect, was obtained for both the <u>foot</u> and <u>counting</u> tasks, but not for the <u>eye</u> task. P-355 was more positive over the left than over the right hemisphere for both tasks; and it was more positive for both tasks during right than during left visual field stimulation.

<u>Attention effects</u>. The parietal scalp region provided a better vantage point for detecting the dipole source or sources responsible for the attention-related effect manifested by P-355 than did the frontal region. The very large attention effects manifested at the parietal region for all three tasks were symmetrical with respect to the two hemispheres. Only in one instance was the magnitude of the attention effect found to be dependent on the hemisphere over which recordings were obtained, and that was in frontal recordings for the foot task wherein a larger attention

effect was obtained over the left than over the right hemisphere.

In general, P-300 has been found to be largest over the central and parietal regions (Donchin, 1984; Parasuraman, 1985) and bilaterally symmetrical in tasks which do not require an overt response (Desmedt, & Robertson, 1977; Desmedt, Robertson, Brunco, Debecker, 1977). The modulation of P300 amplitude has been found to be related to higher cognitive processes; such as the subjective probability of the eliciting stimulus (Donchin, 1984), the reflection of a final stage in the hierarchy of stimulus selection (Hillyard & Munte, 1984), or post-decision closure (Desmedt, 1980). However, a major characteristic of P300 is its relation to selective attention (Picton, 1984).

The results obtained in the present study are consistent with the idea that P-355 reflects physiological mechanisms underlying attentive behavior. However, it is impossible to evaluate on the basis of the obtained results to what extent P-355 reflects higher cognitive functions, since the study was not designed for this purpose. Indeed, the experimental conditions were far from optimal for eliciting a P300. The subjective probability of the relevant stimulus was not varied; the targets (doublets) appeared quite frequently (about 33%) and the single flashes to which brain activity was obtained were presented with 100%

frequency.

Many workers (e.g., Desmedt, 1980; Hillyard & Munte, 1984) have suggested that P300 reflects the final selection of the relevant stimulus feature required for responding to a "target" stimulus. This conclusion is derived from studies in which ERPs are recorded both to "targets" and to "nontargets". In such situations nontargets generally do not elicit a P300 even though the subject must identify them in order to perform the required task (Desmedt, 1980). Based on such information, cognitive neuroscientists have generally agreed that P300 may be used as a "marker" as to when a decision has been made concerning whether a given stimulus was a target or a nontarget.

In the present study VERs were obtained only to single flash stimuli. Thus if the P-355 deflections were reflecting a decision making process, it would have to have been with regard to the decision not to respond (not to make an over response) to "nontargets". The separation between the doublets (i.e., "target stimuli") was 200 msec which means that the subject had to wait at least that long in order to assess on a given trial whether a single flash (a "nontarget") or a doublet (a "target") had been presented. One possible explanation of the enhanced P-355 response to "nontargets" under the relevant field condition is in terms of an "endogenous" response to an omitted second flash of a "target" stimulus. Such an explanation is based on the observation of Sutton and associates (Ruchkin & Sutton, 1979; Ruchkin, Sutton, & Tueting, 1975; Simson, Vaughan, & Ritter, 1976) that aperiodic omissions of a stimulus in a series of regularly presented stimuli will evoke a P300 response with a latency and scalp distribution similar to that evoked by physically presented stimuli. A difficulty with this explanation, however, is that P-355 occurs within 155 msec following the time that the second flash of each doublet should appear. This latency interval is only one-half as long as that of the endogenous positive potential normally elicited by the omission of a stimulus, casting doubt on whether the P-355 enhancement observed in the present experiment during relevant field stimulation was related to the omission of the second component of a "target" stimulus. Perhaps the most parsimonious explanation about the enhanced response of P-355 under the attend conditions is that it is a manifestation of a continuation of the same attentional mechanism being manifested very early after stimulus onset.

Other effects. At the frontal region, P-355 was more positive over the left hemisphere for the foot task; more positive over the right hemisphere for the eye task; and symmetrical for the counting task. The asymmetries were different at the parietal scalp where P-355 was more positive over the left hemisphere than the right, and to right field stimulation than to left, for both the foot and counting tasks. For the eye task, the responses obtained from each hemisphere were larger (i.e., more positive) to contralateral than to ipsilateral stimulation, and to approximately the same degree for each. P-355 was larger over the parietal than over the frontal region.

As mentioned earlier, P300 generally has been observed to be maximal over parietocentral regions (Parasuraman, 1985; Rosler, 1983). However, quite large frontal recordings can be obtained under certain conditions (Renault, Ragot, & Lesevre, 1980; Rosler, 1983). Rosler (1983) states that P300 tends to be larger over frontal cortex when new concepts are required for stimulus categorization, whereas a larger parietal P300 occurs when already existing concepts are appropriate for stimulus categorization. Certainly no new concepts were required to differentiate between single and double flashes ("nontargets vs targets") in the present study, and if the use of new categorization concepts were the sole reason for the generation of P300s at frontal cortex, then none should have been recorded in the present study. It also seems improbable that the generation of P-355 at parietal cortex was due to the use of already existing concepts for stimulus categorization, since the discriminations required in the present study (visual field in which stimuli appeared and single vs double flashes) do not appear to involve the use of concepts. In any case, the larger responses obtained over parietal cortex, compared to frontal cortex, is consistent with the results generally obtained in P300 studies.

The varied hemispheric differences observed at frontal and parietal regions on P-355 are difficult to explain, since the types of variables which are believed to have the most pronounced "endogenous" effects on P300 are higher level variables having little or nothing to do with the physical characteristics of the stimulus (Rosler, 1983). Since no "higher level" cognitive variables were manipulated in the present study, the observed asymmetries must be related to "lower level" factors, cognitive or otherwise. Various studies have shown that the scalp distribution is bilaterally symmetrical in tasks that require counting of targets (Desmedt & Robertson, 1977; Simson, Vaughan, & Ritter, 1977; Snyder, Hillyard, & Galambos, 1980), while motor responses produce relatively large positivities over the hemisphere ipsilateral to the responding hand (Ragot & Remond, 1979). In the present study asymmetries were found for all three types of tasks. Those for the foot and counting tasks were similar, both differing considerably from the asymmetries observed for the eye task. It is interesting to note that the effect of attention on C-55 was more similar for the foot and counting tasks than for the eye task. Thus, both early (C-55) and late (P-355) VER deflections seem to bear a close correspondence for the foot and counting tasks, both being different from the eye task; suggesting that factors common to both components may have contributed to the hemispheric differences observed on P-355. It seems plausible that the observed asymmetries may be more closely tied to the type of response the subjects were prepared to make than to higher level cognitive processes.

Since a lateralized negative component preceding P300 has been observed to be task-specific in earlier studies (Hillyard & Mangun, 1984; Ragot et al., 1980), and lateralized positive "readiness potentials" also are task-specific (Deecke, Eisinger, & Kornhuber, 1980), it is possible that the differential asymmetries observed in the present study for the eye in contrast to the foot and counting tasks was due to the summation of these two types of lateralized potentials with P-355.

Since generator source localization studies suggest that scalp-recorded P300 originates in non-sensory cortex (Vaughan, 1977), the hippocampal area being a strong possibility (Wood et al., 1984), it may be assumed that the asymmetries are unrelated to the physical characteristics of the stimulus. It should be recalled, however, that for the eye task, P-355 was larger over the hemisphere contralateral to the field of stimulation. If P300 is not related to the physical stimulus, then this effect must be related to differential processing occurring in visuo-motor processing regions. This possibility is supported by observations from single unit studies indicating that the majority of movement-sensitive cells in the right hemisphere of the parietal lobe respond before a saccade is made toward the left, whereas the majority of those located in the left hemisphere discharge prior to a saccade being made toward the right (Kurtzberg & Vaughan, 1980; Mountcastle, Andersen, & Motter, 1981).

These suggested explanations, along with any other post hoc explanations of the task-specific asymmetries on P-355, are highly conjectural. If the factors infuencing P300 are as complex as reports by Rosler (1983) and Renault et al (1983) suggest, numerous factors could be contributing to the observed asymmetries. The question can only be resolved through future research.

Comparative Findings Across Components

An attention effect was obtained at all latency ranges measured. For C-55 and N-165 the attention effect was task dependent but not for C-115 and P-355. The earliest attention effect (C-55) was more robust at the frontal than at the parietal region. The effect on C-115 was manifested only at the parietal region; on N-165 at both regions; and on P-355 primarily at the parietal region, being significant at the frontal region only for the foot task. A main task effect was obtained only for N-165. P-355 exhibited the greatest specificity, interacting significantly with all variables manipulated. C-55 and N-165 tended to be more negative in right- than in left-hemisphere recordings; C-115 and P-355 tended to be of greater magnitude in left- than in right-hemisphere recordings. For all components except C-55, visual field x hemisphere interactions were obtained, the recordings obtained over a given hemisphere being greater to contralateral than to ipsilateral stimulation. Main visual field effects were obtained for C-55 and P-355; C-55 being more responsive (at the parietal region only) to left field stimulation, and P-355 being greater during right field stimulation. C-55 was more negative in polarity at the parietal region; C-115 was of negative polarity at the frontal and of positive polarity at the parietal region.

The set-related findings, integrated across all of the components, indicate that the effects of prestimulus set were manifested very early upon presentation of a trigger stimulus to the peripheral retina (within 40 msec poststimulus), and continued for at least 300 msec. The long-duration set-related effects are clearly manifested in Fig. 12. This figure is comprised of the difference potentials depicted in Fig. 2. In addition, it contains visually-derived "best-fit" curves (dashed lines) depicting slow wave changes on which the higher frequency oscillations are riding. Inspection of the slow wave configuration indicate a negative bias occurred over a very long latency range, the bias being greater at frontal than at parietal regions. The negative bias peaked out at about 140 msec at the frontal and at 200 msec at the parietal region. At both the frontal and parietal regions, the negative bias was greater for the eye task and smallest for the counting task. At the frontal region the bias began at about 40 msec for the eye task and at about 100 msec for the foot and counting tasks. At the parietal region the bias began at about 130 msec for each of the tasks. The latency at which the negative bias developed is clearly related to whether and to what extent it was preceded by a positive bias required for its development. The longer latency at the parietal than at the frontal region is associated with a wave of positivity on which P1 (Cp-115) was riding. This early slow positive wave was minimal or nonexistent at the frontal region.

The slow shifts manifested in each of the tracings of Fig. 12, whether positive or negative, are like those generally characterized by cognitive neuroscientists as being "endogenous" (Donchin, Ritter, & McCallum, 1978; Rosler, 1983; Sutton, Braren, Zubin, & John, 1965). Unlike "exogenous" components, which are controlled by events external to the nervous system and are influenced by the physical characteristics of the stimulus, endogenous components (although partially related to physical stimulus parameters) are influenced primarily by the behavioral state of the subject brought about by variations in instructions and task demands.

Variations in P-300 have been attributed almost entirely to endogenous activity, i.e., internally generated neural activity (Sutton, et al., 1965; Donchin, et al., 1978; Naatanen, 1982; Ritter, et al., 1983; Renault, 1983; Picton, et al., 1986); whereas the modulation of earlier components, including P1 and N1 (Cp-115 and N-165), has been attributed to variations in the strength of incoming sensory information about the physical characteristics of the stimulus (Hillyard, 1981; Hillyard & Kutas, 1983; Hillyard & Mangun, 1986; Picton et al., 1986; Woods, in press). In the latter case, the effect of selective attention on these early components has been assumed to simply alter their amplitude (Hillyard & Munte, 1984; Hillyard et al., 1985; Hillyard & Mangun, 1986). The shape and the relative deviations of the positive- and negative-going segment of these "exogenous" waves remain unchanged. That is, selective attention has no biasing effect on the extent to which these "early" positive and negative EP-segments deviate from baseline. Rather, selective attention merely controls the intensity of the incoming sensory signal which activates the stimulus-bound generator(s) responsible for these early deflections (Michie, et al., 1987). To the extent that the positive and negative segments of an "exogenous" potential deviate asymmetrically from baseline as a function of attention and other state variables, the asymmetric deviation is considered to be due to endogenous generator sources whose field potentials are algebraically added to those responsible for the exogenous field potential.

Hillyard and associates (Hillyard, Hink, Schwent, & Picton, 1973) initially thought that the attention effect on N1 was due to an augmentation of the amplitude of this exogenous component, but based on findings by Naatanen and Michie (1979), and in their own laboratory (Hansen & Hillyard, 1980), they later concluded the apparent N1 enhancement could be and sometimes is (depending on task difficulty), due to the summation of an endogenously generated negative field potential with exogenous N1. The endogenous activity may last for several hundred milliseconds and is believed to be a manifestation of the processing of the information contained in the stimulus within the context of the instruction under which the subject is working. Since the polarity of the endogenous generator(s) is/are negative (within approximately a 100-300 msec latency range), the difference potentials derived by subtracting the EPs obtained under attend conditions from those obtained under unattend conditions tend to show a negative bias during this period. Such bias was termed "processing negativity" (Nd) by Naatanen and associates (Naatanen, 1982; Naatanen & Michie, 1979), and has been used in similar manner by Hillyard and associates and other cognitive neuroscientists. Based on their neural specificity model of selective attention, Harter and Aine (1984) labelled such activity "selection negativity".

Hansen and Hillyard (1983) have proposed that the "processing negativity" manifested in difference potentials is comprised of one or more dipole sources, the number depending on the number of relevant dimensions contained in a stimulus which are to be processed. Following the presentation of a stimulus, information pertaining to all features is transmitted forward for assessment by an appropriate "channel analyzer" as to its relevance, and whether there is a need for further processing. Although Hillyard and associates now acknowledge that certain information may be assessed subcortically (Hillyard, Munte, & Neville, 1985), their position has been that all such "analyzers" must reside somewhere in the cerebral cortex, since evidence for subcortical feature analysis has been lacking (Picton & Hillyard, 1974; Mangun, Hansen, & Hillyard, 1986).

Naatanen's view (1982) is similar to that of Hillyard and Hansen's in that he proposes that all of the information contained in a stimulus is processed within the context of an internal representation of a stimulus until a match or mismatch is made against this internal neural "template". It is clear from Naatanen's description of his model that the internal representations of stimuli reside in the cerebral cortex, as do Hillyard's channel analyzers.

In contrast to the models of Hillyard and Hansen (1983) and Naatanen (1982; 1986), the model proposed by Harter and Aine (1984) focuses "...on the efferent excitation (or inhibition) of the neural aggregates that process the features of the relevant (or irrelevant) stimulus <u>prior</u> to stimulation." This model does not assume that all information contained in a stimulus contributes to the earliest changes in "processing (i.e., selection) negativity" associated with selective attention. Instead, the selective attention process influences sequentially only those dipole generators located in structures capable of coding specific features of a stimulus. If, for example, spatial location can be coded at the level of the retinal ganglion cells, SC, LGNd, or pulvinar; then spatial selective attention could theoretically influence the response magnitude of dipole generators located in these structures. Any other information contained in the stimulus presented at the irrelevant location (e.g., orientation or pattern which is coded at the level of the cortex and therefore must be processed at that level) would be attenuated or blocked to the same degree as the irrelevant spatial information. To the extent that orientation and pattern was blocked at that level, it could not be processed later at the level of the cortex. On the other hand, the facilitation of transmission of spatial information through the attended channel at a subcortical level would result in the concomitant transmission of all other information contained in the stimulus for later processing at the appropriate level (the cortex in the case of orientation or pattern).

The extremely early negative deviation from baseline manifested in the difference potentials obtained at the frontal region for the eye task in the present study (upper-left tracing of Fig 12) is consistent with the view expressed by Harter and Aine (1984) and at variance with that of Hillyard and Hansen (1983), and Naatanen (1982; 1986). Since EPs were recorded only to "nontarget" stimuli (single flashes) in the relevant field, along with responses to single flashes in the irrelevant field, the negative bias expressed in the difference potentials of Fig. 12 for any given task reflect only spatial attention along with any motor set effects. Nothing can be said about the "processing negativity" required to differentiate between "target" (doublets) and "nontarget" (single-flash) stimuli. If an information processing interpretation is imposed on the slow negative waves manifested in Fig. 12, it follows that information transmitted through the relevant channel (with respect to spatial location) was processed to a greater extent than that transmitted through the irrelevant channel. Such processing appears to have reached a peak at approximately 160 msec at frontal cortex and at 180-200 msec at parietal cortex. The earliest processing negativity for the eye task (positivity for the counting task) reflects at a subcortical level the selection of the relevant spatial location. Selection with respect to response relevancy (motor set) previously has been extensively discussed (pp. 125-161). Since the selection process with respect to both spatial location and response relevancy began very early, the prolonged "processing negativity" could be a manifestation of (1) a continuation of these processes, (2) the processing of other stimulus features which cannot be assessed in the absence of EP-recordings to "target" stimuli, or (3) some combination of the two. Whatever the specific nature of the information being processed, the very early onset of the negative bias in frontal recordings suggests, contrary to the position of Hillyard et al (Hillyard & Mangun, 1986; Hillyard et al., 1985) that "endogenous" factors can influence the earliest (subcortical) components of the VER, and spatial selective attention is not simply manifested in terms of the amplitude modulation of "exogenous" components.

Hemispheric Asymmetries

The hemispheric and visual field effects summarized in the beginning of this section have been discussed earlier in relation to each component considered separately. Since the nature of the asymmetries varied across components in a complex manner, any theory offering a singular explanation for their occurrence is probably going to be inadequate. Some of the asymmetries observed in the present study were consistent with those observed by others; some were not. Eason and associates (Eason, Oden, & White, 1967; Eason & Dudley, 1971) have shown that the retinal area stimulated, stimulus size, and color have a significant impact on both early and late components of the VER. The retinal area stimulated (30 degrees peripherally) and the type of stimuli used (35' blue circles on a red background) set the present study substantially apart from most other studies reporting hemispheric asymmetries. It is quite likely that some of the asymmetries observed in the present study which have not been previously reported were specifically related to these variables.

There is a large body of literature which has long implicated the right hemisphere as playing a dominant attention-related role during the performance of visuospatial tasks (Heilman, Watson, & Valenstein, 1985). Recent VER studies have shown that larger response amplitudes are obtained over the right than over the left hemisphere (e.g., Hillyard, et al, 1985), and greater increases in blood flow have been observed in the right than in the left hemisphere during the performance of such tasks (Gur & Reivich, 1982).

Such asymmetric activity suggests that attention-induced endogenous activity tends to be greater over the right than over the left hemisphere. Further support for this hypothesis comes from patients suffering from hemispatial neglect, such neglect being more severe and frequent when the right hemisphere is damaged than the left. Areas involved include the inferior parietal lobule, dorsolateral frontal lobe, cingulate gyrus, neostriatum, and thalamus (Heilman et al, 1985). In monkeys, such neglect has also been produced through lesioning the superior colliculus (Sprague & Meikle, 1965).

The hemispheric asymmetry may also be related to the differential general activation of the two hemispheres independently of or in addition to selective attention. Patients with right hemisphere lesions have been shown to have a reduced activation level (Heilman et al, 1978; Howes & Boller, 1975). Also, the amplitude of VERs are often larger over the right than over the left hemisphere even when selective attention is not manipulated (Davis & Wada, 1974; Vella, Butler, & Glass, 1972). Greater activation of the right hemisphere, and therefore the greater capacity of that hemisphere to attend, may be related to the asymmetrical distribution of neurotransmitters generated by subcortical areas. Asymmetrical concentrations of dopamine (or dopamine receptors) are known to affect the motor behavior of lower mammals (Glick, Jerussi, & Zimmerberg, 1977). Although dopamine is only one neurotransmitter thought to be involved in the selective attention process (Picton, et al., 1986), it suggests the possibility that others may be similarly involved. In fact, injections of muscimol, a GABA agonist, into the pulvinar lowers a monkey's capacity to shift attention to the contralateral direction, suggesting the involvement of the GABA system in attentive behavior (Petersen, Robinson, & Morris, 1987).

Data derived from clinical studies also suggest that hemispheric asymmetries associated with behavioral state variables may be mediated in part by subcortical structures. Language function asymmetries have been observed in patients subjected to stimulation of the thalamus and pulvinar preliminary to undergoing thalamotomy for treatment of dyskinesia (Ojeman, 1982). Lesions of the left thalamus or pulvinar have been observed to disrupt verbal performance while lesions of these right-hemisphere structures do not (Rikland & Cooper, 1977). Also, parkinsonian patients with right-hemisphere lesions in the ventrolateral nucleus of the thalamus or in the pulvinar have been found to perform more poorly on a visuo-motor task than patients with left-hemisphere lesions in the same structures (Rikland & Cooper, 1977).

There are data to suggest that the right hemisphere can direct attention to visual stimuli presented to either visual field (right or left), whereas the left hemisphere apparently can do so only to the right (contralateral) field (Heilman et al., 1985; Mesulam, 1981). Single unit activity of the right pulvinar in human patients shows bilateral response to hand movement, while the left pulvinar shows response only to contralateral hand movements (Straschil & Takahashi, 1981). The ability of the right hemisphere to direct attention to either field may be by way of tectal commissural connections (Trevarthen, 1975). Apparently, split-brain patients make use of this pathway, which remains intact, since they can detect the presence of a stimulus projected to the contralateral hemisphere (Holtzman, 1984; Trevarthen, 1975; Zihl & Von Cramon,1979).

It is important to recognize that hemispheric asymmetries can arise from two different sources, one being related to the differential anatomical projections from the nasal and temporal halves of the retina to the two hemispheres; the other to differential endogenous priming due to hemispheric specialization of function. The larger

VERs generally observed over a given hemisphere to contralateral than to ipsilateral field stimulation may be attributed to the manner in which the incoming visual pathways are "wired". The larger attention effects generally observed over the right hemisphere, as well as the larger responses in terms of absolute magnitude, may be attributed to endogenous factors (general arousal and selective attention mechanisms) which, for whatever reason, seem to rely more heavily on right- than left-hemisphere structures. Results obtained for C-55 and N-165 are consistent with these speculations. The results obtained for Cp-115 (i.e., over parietal cortex) also are consistent with these ideas, but the asymmetries observed at the frontal region (Cf-115) are not. Recordings obtained over the left hemisphere for this component were greater than those obtained over the right. As previously noted, perhaps this frontal asymmetry is a manifestation of parallel processing of motor information by visuo-motor neurons preliminary to making the appropriate response to the trigger stimulus. In humans, sequencing of motor acts, including speech, is thought to be organized by the left hemisphere (Kimura, 1976). Since the present study employed tasks with both visuo-spatial and motor requirements, perhaps the first was processed primarily by the right hemisphere and the second primarily by the left frontal hemisphere.

The interactions observed for the late positive component (P-355) involving hemispheres, tasks, attention, and recording region have previously been discussed (pp. 94-97).

Time-locked Alpha Activity and Attention

Further examination of the averaged waveforms of Fig. 1 and the difference potentials of Figs. 2 and 12 reveals that the deflections have a sinusoidal characteristic. These sinusoidal-like oscillations are more pronounced at the parietal than frontal region and under the attend than under the unattend condition. They are present for all task conditions and to about the same degree. The oscillations are highly visible in the difference potentials, particularly for the parietal region.

Occipitally recorded sinusoidal oscillations of this type have been extensively described by Eason, Oden, and White (1967). Four to six such oscillations occurred within 500 msec poststimulus. The onset, peak amplitude, and duration of the oscillations were found to depend on the retinal area stimulated (fovea out to 50 degrees) and the color of the stimulus used (red or blue 1-degree circular flashes). Foveally-elicited oscillations began sooner and terminated earlier than peripherally-elicited ones. Those elicited by a 50-degree peripheral stimulus had the longest onset and termination times. Once initiated, the oscillations progressively built to a maximum amplitude (at 180 to 200 msec, depending on experimental conditions), then gradually attenuated. The duration of a single oscillation was approximately 100 msec; in terms of frequency, about 10 cycles per second. In the present study, oscillations of this type are most evident in the difference potentials obtained at the parietal region (Figs. 2 and 12).

Because of the alpha-like properties of these waves, Eason, et al (1967) postulated that the evoked response obtained over occipital cortex was time-locked alpha-like activity which was momentarily brought under the control of an "external trigger" or "extrinsic pacemaker". The incoming thalamocortical volley elicited by the stimulus was deemed to be the immediate "neural trigger" responsible for the synchronized discharge of a neural ensemble of cortical cells normally under the influence of the brain's intrinsic alpa rhythm pacemaker. The sequential increases in amplitude was considered due to the recruitment of additional units on subsequent reverberations, and the decay function was considered due to elements gradually being brought back under the influence of the internal pacemaker.

This model, which was based on earlier writings by Lindsley (1960; 1961), was developed further by Eason and Dudley (1971). A very brief, but potent, envelope of incoming impulses with a sharp leading edge was assumed optimal for setting off an alpha-like discharge in a given ensemble of cells. Such a crisp burst of incoming neural activity may be elicited by a small, punctate stimulus of extremely short duration (e.g., 10 microseconds) with a virtually instantaneous rise and decay time (Lindsley, 1969). Relatively long-duration stimuli with substantial rise and decay times (e.g., a 50 msec flash with 20 msec rise and decay times) may elicit a less crisp neural stimulus of longer duration. Such activity would serve as an imprecise, "fuzzy" pacemaker signal. One consequence of this might be that the oscillatory activity becomes less pronounced, and the initial oscillation which is always relatively small, may even be indiscernible.

The oscillatory activity observed in the present study between 100-300 msec may be accounted for in terms of this model, particularly that recorded at the parietal region. Except for one large deflection which peaked out at about 170 msec (N1), the sinusoidal oscillations were not as clearcut at the frontal region. Neural ensembles in frontal cortex seem less subject to alpha-like reverberatory activity than those in parietal cortex; thus, the time-locked discharge attenuates sooner. This is consistent with the fact that the spontaneous alpha rhythm is larger over occipital and parietal regions than over frontal regions of the scalp. Even though the frontal area may be less subject to reverberatory activity, low-amplitude secondary oscillations are discernible in the difference potentials obtained over this frontal region (see Fig. 12).

If the oscillations occurring during the 100-300 msec interval were in fact due to the momentary time-locked, alpha-like activity occurring in subpopulations of cells, then more units must have been recruited by the extrinsic pacemaker to participate in such activity under the attend than under the unattend condition and for the eye task than for the counting task. The greater recruitment was presumably brought about by a more potent incoming neural trigger signal influencing the participating elements. In order for a more potent signal to influence the neural elements, differential transmission must have occurred at one or more levels prior to the level of impact. Based on the C-55 data, such differential transission must have occurred at subcortical levels.

Viewed solely from the perspective of the external trigger, alpha-recruitment hypothesis, the effect of spatial attention on early cortical components of the VER (i.e., P1 and N1) should be as predicted by Hillyard, et al (Hillyard et al., 1985; Hillyard & Mangun, 1986). That is, the effect should be analogous to adjusting the volume on a radio, causing the exogenously driven components to be altered in amplitude but without any bias imposed with respect to baseline. But since the potentials were negatively biased throughout most of the 100-300 msec interval under the attend condition, some other type of electrophysiological activity (manifested as a negative slow wave) must have occurred during the alpha recruitment period, the amplitude of which tended to parallel the amplitude envelope of the alpha recruitment cycle. That is, the latency of the peak deviation of the negative slow wave from baseline was approximately the same (perhaps slightly later) as that at which the peak amplitude of the externally triggered sinusoidal oscillations occurred. It appears, therefore, that the magnitude and duration of the "endogenously" driven, negative slow-wave response was yoked to the "exogenously" driven alpha-recruitment response. If true, then the two types of activity could not be a manifestation of truely independent generators. That is, even if independent generators were involved, there must have been at least one generator source that was common to both types of activity.

The mechanisms whereby slow potentials may be generated during the phasic discharge of neurons have been reviewed by Rockstroh, Elbert, Birbaumer, & Lutzenberger (1982). It has been shown that negative slow potentials may be generated by neurons, glial cells, and by the transmission of nutrients across the blood-brain barrier. Slow waves generated by all three types of activity have been shown to be event related.

Within neurons, the occurrence of excitatory postsynaptic potentials (EPSPs) in apical dendrites give rise to negative slow waves recorded at the scalp.

According to Rockstroh et al (1982), slow potentials are probably a combination of field potentials generated by neuronal activity and concomitant glial cell activity produced by the flow of potassium ions from active neurons into the glial cells. Neurons release potassium ions into the extracellular space when activated. The potassium ions depolarize the glial membranes which are selectively permeable to these ions. A graded potential develops which can reach its peak in 100-300 milliseconds (or even later) depending on stimulating conditions. Since glial cells can draw currents from unaffected cells over relatively large distances, potassium ions entering the glial cell system from firing neurons spread out, and an equivalent number of ions leaves the glial system at distant regions in which neuronal activity is low. This flow of potassium ions gives rise to a potential difference in the external fluid which can be recorded at the scalp. The greater the neuronal activity, the greater the glial cell potassium ion current flow. This process is equivalent to the flow of potassium ions in Muller cells of the retina which is believed to be the basis of the b-wave of the ERG (Eason, et al., 1983; Miller and Dowling, 1970). The flow of substances from the blood to the brain and *vice versa* also gives rise to slow wave potentials, but these are too slow to be related to the negative shifts seen in the VERs recorded in the present study 100-300 msec poststimulus.

It is plausible, however, that the slow-wave shifts may reflect the increased flow of potassium ions into glial cells during the period in which ensembles of neurons were brought under the influence of an extrinsic pacemaker following the presentation of the trigger stimulus. At least two observations are consistent with this interpretation. At the frontal region the sinusoidal oscillations reached a peak sooner and attenuated sooner than at the parietal region. So did the slow potentials. At both regions the slow potential peak lagged slightly the peak amplitude of the sinusoidal oscillations. This would be expected if the slow-wave activity was occurring as a *consequence of* the neuronal activity.

Even though the negative bias manifested in the difference potentials of Fig. 12 may have been due in part to glial cell activity associated with the greater neural discharge under the attend condition, it would be premature to conclude that the observed bias was entirely due to such activity. It should be recognized, however, that a portion of the negative bias contained in VERs in experiments designed to factor out when and at what level the brain processes various types of information could be due to a glial cell-generated correlate of the magnitude of the response of a given neural generator; and that not all or even most of the negative (or positive) slow-wave bias registered in difference potentials ("processing negativity") is due to experimentally induced, endogenously activated generators as cognitive neuroscientists assume.

CHAPTER X

SUMMARY

Purpose

The primary purpose of this investigation was to establish whether motor set, along with perceptual set, produces short-latency poststimulus effects in the visuomotor system, and if so, whether such effects occur precortically. Another major purpose was to determine whether earlier demonstrations from our laboratory that spatial selective attention results in the precortical gating of incoming sensory information could be replicated. A third purpose was to examine the effects of perceptual and motor set on later components of the VERs within the context of the existing literature. It was hypothesized that if both perceptual and motor set influence poststimulus activity precortically, then VER-components occurring as early as 40-70 msec should be influenced by spatial attention and the type of response the subject was set to make. It was further hypothesized that set-related activity should be manifested in later components associated with processing at a cortical level.

Method

Eighteen subjects participated in three two-hour sessions each for a total of 12 trials. Two replications of data were obtained for each of six experimental conditions generated by which of two visual fields (right or left) to which the subject was instructed to attend, and which of three types of response he/she was set to make to trigger stimuli appearing in the attended visual field (eye movement vs foot vs counting).

The stimuli consisted of small (35' visual angle) circular spots of blue light of 10 microseconds duration presented on a red background with a luminance of approximately one millilambert. The stimuli were approximately 2.7 log units brighter than the background, and were presented 30 degrees peripherally in each visual field slightly above the horizontal meridian. The majority of the stimuli appearing in each visual field consisted of single flashes. Interspersed among the single flashes were double flashes separated by 200 msec. The subject was required to make one of the three types of responses to the doublets ("target stimuli") but to withold making a response to the single flashes ("nontargets") appearing in the relevant (i.e., attended) visual field. Evoked responses were obtained only to the single flashes.

Scalp-recorded EPs were obtained from four locations, two frontal (f3 and F4) and two parietal (P3 and P4). Each recording site was referenced to the ipsilateral earlobe. During data collection eye movements and blinks were continuously monitored, and if the eyes moved more than three degrees from the fixation point or if the subject blinked, the recording system was instantaneously deactivated. The subjects sat in an electrically shielded room during data collection. White noise was channeled into the room to prevent extraneous sounds from affecting the VERs.

Results and Discussion

VER deflections in the 40-70 msec latency range (C-55) were found to be dependent on the relevancy of the visual field from within which evoking stimuli were presented; the type of response subjects were set to make; and the region (frontal or parietal) from which recordings were obtained when subjects were set to count target stimuli, C-55 was relatively more positive under the relevant field (i.e., the attend) condition. When set to make an eye movement, C-55 was more negative under the attend condition. No significant effect was obtained for the foot-lift task. The absolute magnitude of C-55 was very small, compared to later components, and tended to have a shallow gradient across the four recording locations. C-55 was more negative over the right than over the left hemisphere.

These findings were interpreted as evidence that both perceptual and motor set can influence the responsivity of visuo-motor neurons very early following the presentation of a trigger stimulus, such influence being manifested precortically. The findings are consistent with results obtained in previous experiments conducted in our laboratory, and provide confirmation of the reliability of the earlier observations. Anatomical and physiological data derived from the animal literature indicate that likely sources for the occurrence of set-related activity observed in this study are the LGNd, the SC, and the pulvinar.

A component which peaked at 100-130 msec (C-115) was of positive polarity over parietal cortex for all subjects and of negative polarity over frontal cortex in 12 out of 18 subjects. Based on analysis of all subjects the deflection was influenced by the attention manipulation at the parietal but not at the frontal region. An analysis based on the 12 subjects showing a negative-going potential at frontal cortex in the 100-130 msec range revealed a significant attention effect for the eye task. At the parietal region the response was greater to contralateral than to ipsilateral field stimulation. This was the case at the frontal region for the right hemisphere only. The results suggest that at least two dipole sources contributed to the field potentials registered at the frontal and parietal regions.

A negative component with a peak latency of 160-170 msec (N-165) was much greater under the attend than under the unattend condition for all tasks at both frontal and parietal regions. The component also varied as a function of tasks, being greatest for the eye and smallest for the counting task. The responses obtained over each hemisphere were larger to contralateral than to ipsilateral stimulation. The attention effects are consistent with those obtained in numerous studies, and serve as prima facie evidence that selective attention was in fact varied in the present study. The task-related findings suggest that general activation varied somewhat across tasks, perhaps as a function of difficulty.

A late positive component which peaked at 350-360 msec (P-355) was significantly affected by the attention manipulation as a main effect at the parietal region only. A hemisphere by attention interaction was obtained at the frontal region for the foot task, the left hemisphere yielding a larger attention effect than the right. P-355 was found to interact with hemispheres, recording region, tasks, and visual field relevancy at first, second, and third order levels. Thus, the changes registered at this latency were quite situation specific.

The set-related findings, integrated across all of the components, indicate that the effects of prestimulus set (whether perceptual or motor) were manifested within 40 msec upon presentation of a trigger stimulus to the peripheral retina and continued for at least 300 msec. The oscillatory components observed in the VERs were found to "ride" on a slow wave which was of negative polarity from 100-300 msec. The significance of the slow wave was discussed in terms of "endogenous" vs "exogenous" potentials and in terms of glial cell activity associated with stimulus evoked alpha-like neural discharges.

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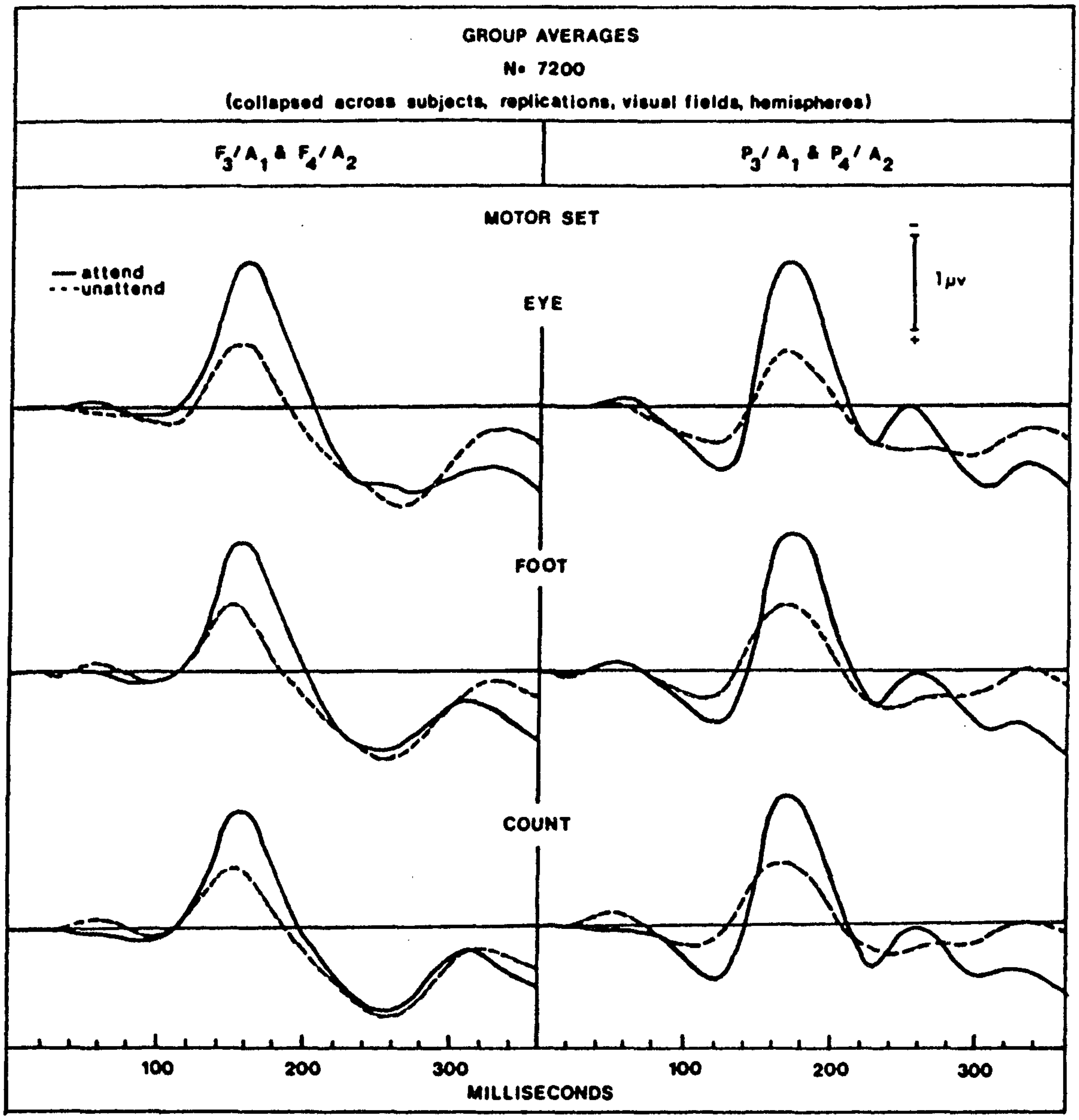
APPENDIX A

Figure 1. Group analog VERs plotted as a function of visual field relevancy (attend vs unattend), Tasks (eye, foot, and count), and location (frontal and parietal). The tracings have been collapsed across replications, visual fields, and hemispheres.


GROUP AVERAGES

N= 7200

(collapsed across subjects, replications, visual fields, hemispheres)

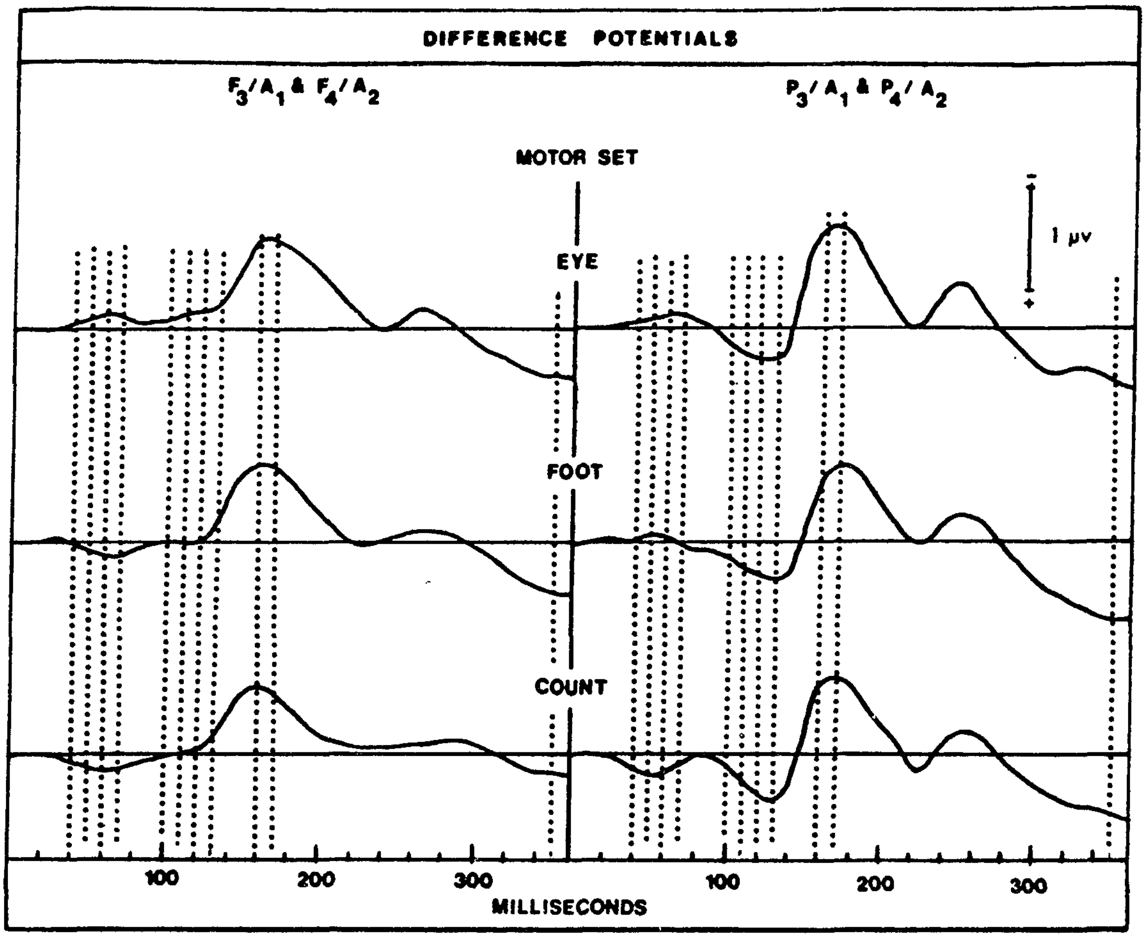
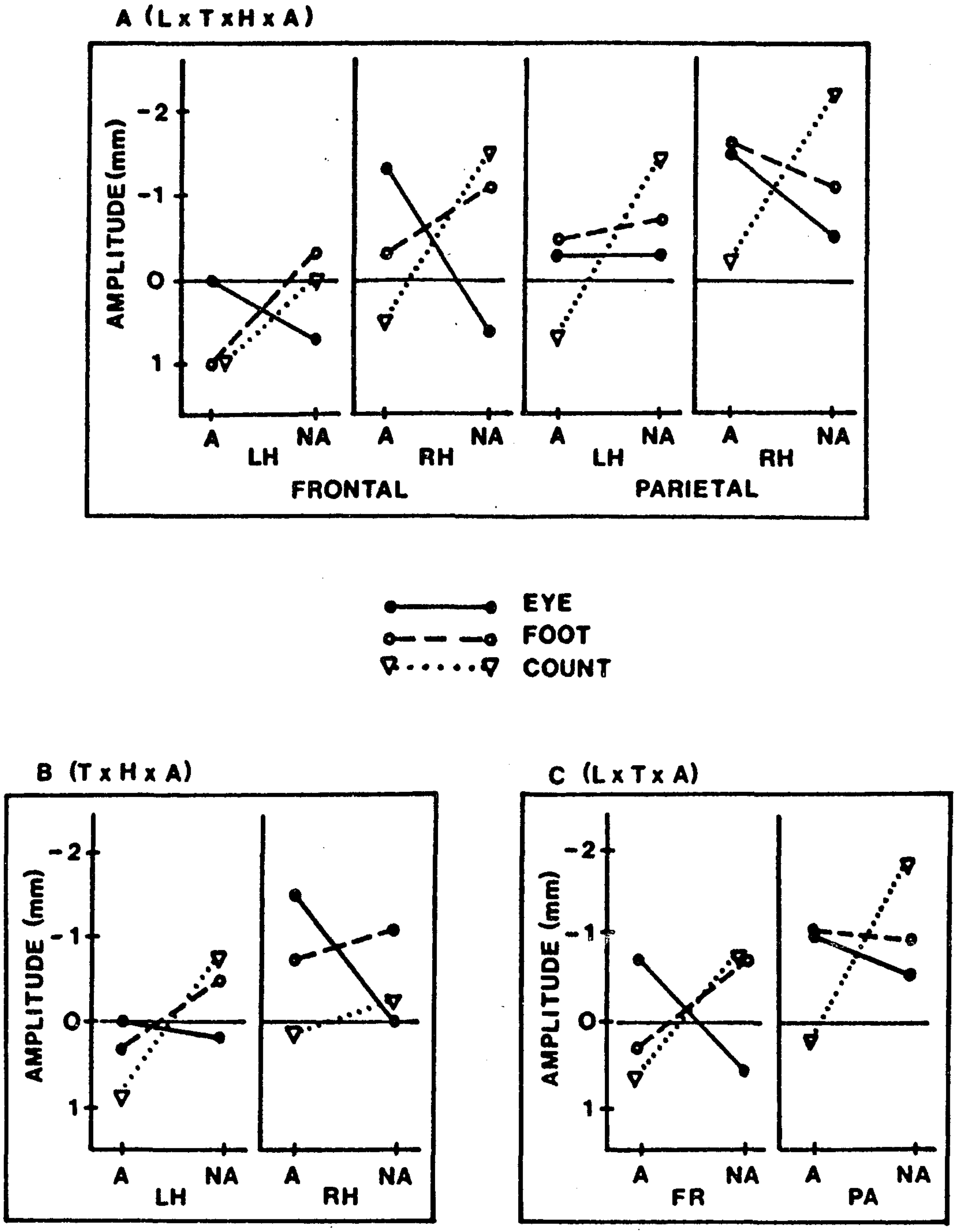


Figure 2. Group difference potentials (attend minus unattend) plotted as a function of recording location (frontal vs parietal) and tasks.

Figure 3. Mean deviation from baseline for C-55 plotted as a function of: (A) location by tasks by hemispheres by attention; (B) tasks by hemispheres by attention; and (C) location by tasks by attention. Code: A= attend; NA=not attend; L=location; T=tasks; V=visual field; H=hemispheres; LVF=left visual field; RVF=right visual field; LH=left hemisphere, RH=right hemisphere; FR=frontal location; PA=parietal location; 1 microvolt = 20 millimeters.

C-55



A (L x T x H x A)

B (T x H x A)

C (L x T x A)

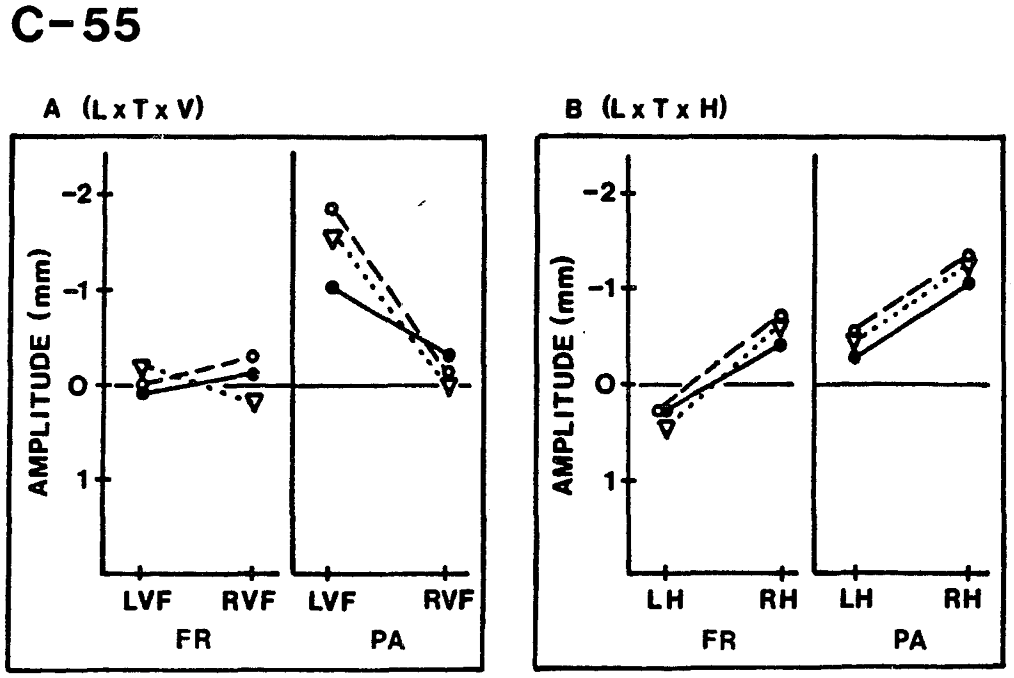
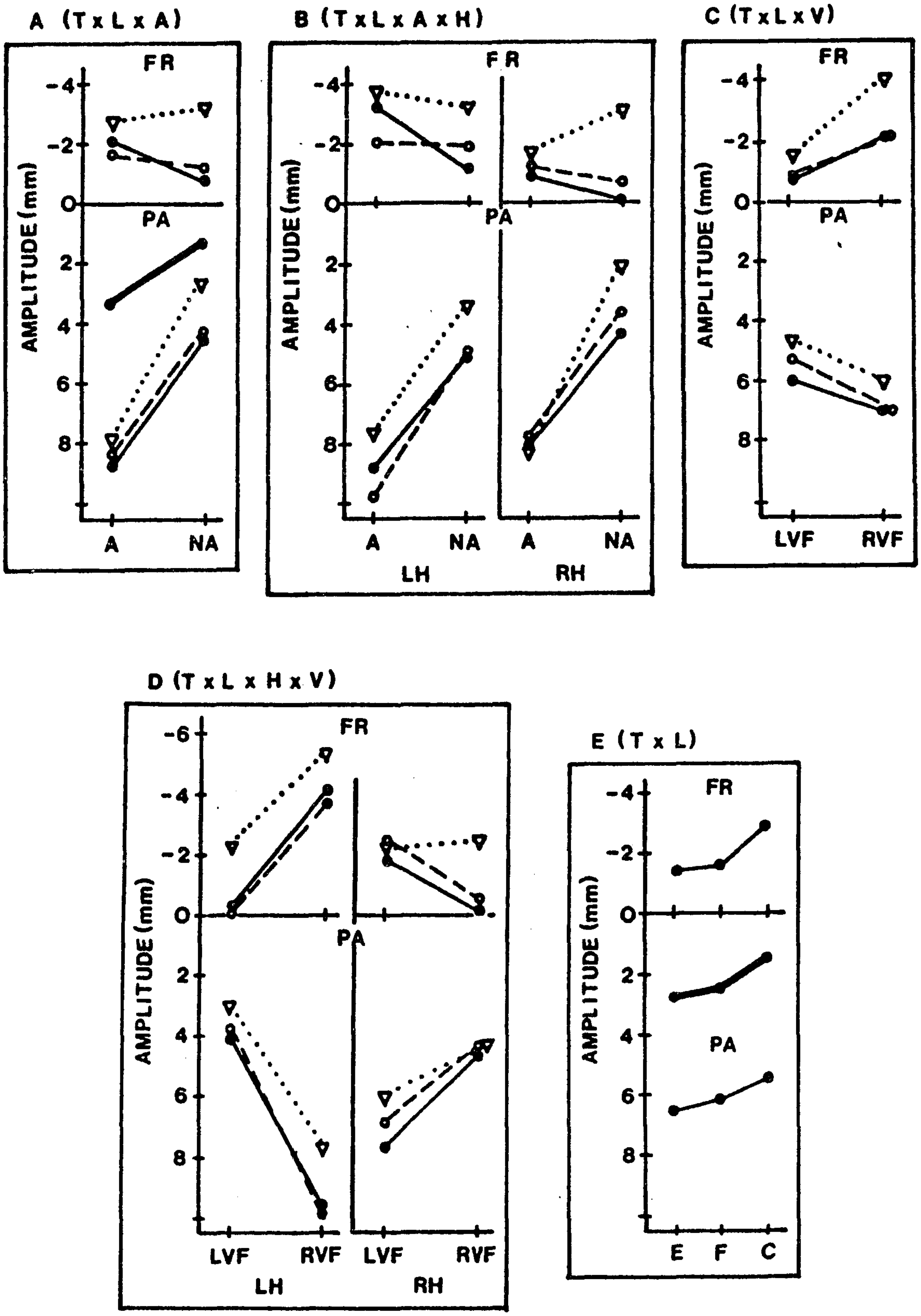


Figure 4. Mean deviation from baseline for C-55 plotted as a function of: (A) location by tasks by visual field; (B) location by tasks by hemispheres. Code for all symbols as in Figure 3.

Figure 5. Mean deviation from baseline for C-115 plotted as a function of: (A) tasks by location by attention; (B) tasks by location by attention by hemispheres; (C) tasks by location by visual field; (D) tasks by location by hemispheres by visual field; and (E) tasks by location. Code: E = eye task; F = foot task; C = counting task; all other symbols same as in Figure 3.

C-115



A (T x L x A)

B (T x L x A x H)

C (T x L x V)

D (T x L x H x V)

E (T x L)

Figure 6. Mean deviation from baseline for N-165 plotted as a function of location by tasks by attention by hemispheres by visual field. Code for all symbols as in Figure 3.

N-165

(L x T x A x H x V)

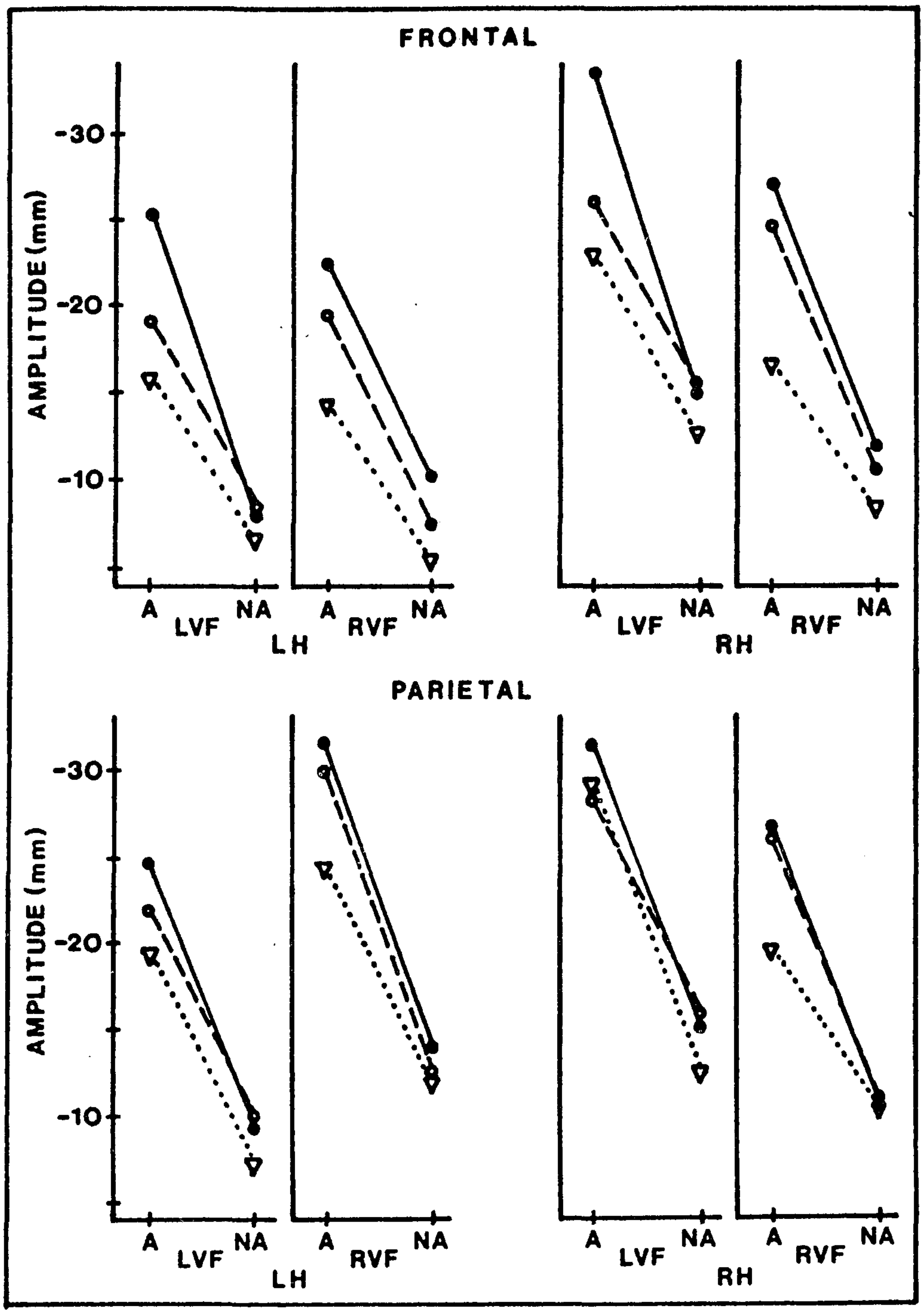
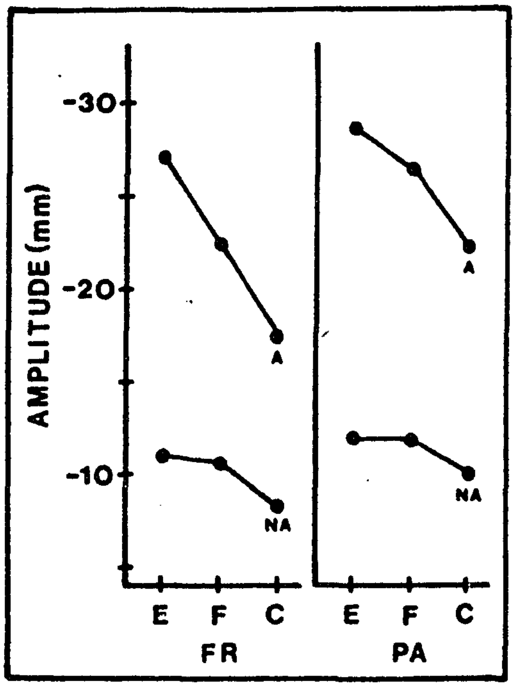


Figure 7. Mean deviation from baseline for N-165 plotted as a function of: (A) location by tasks by attention; and (B) location by tasks by hemispheres by visual field. Code for all symbols same as in Figure 3.

N-165

A (L x T x A)



B (L x T x H x V)

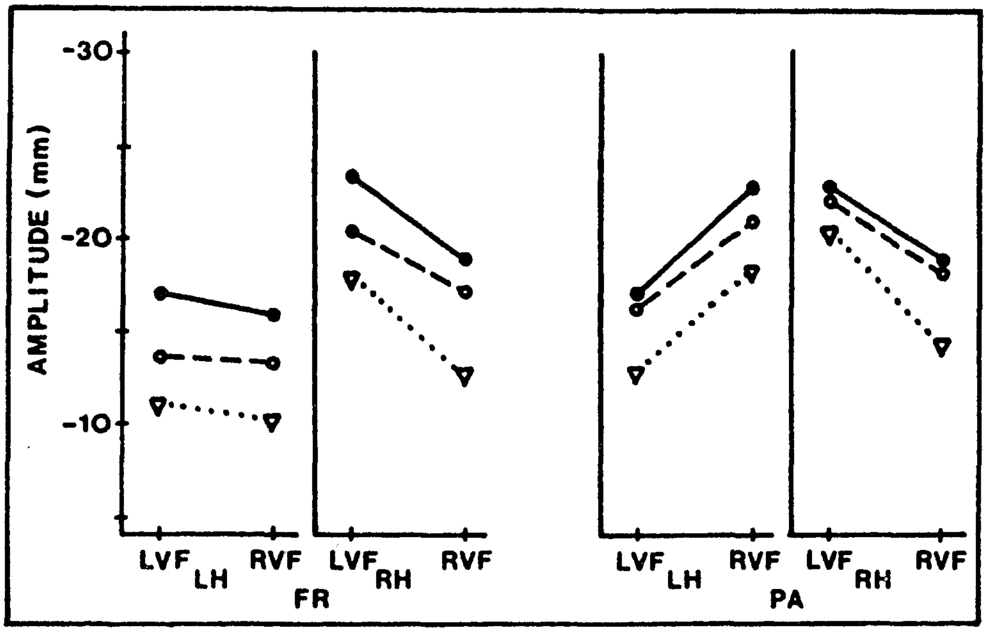
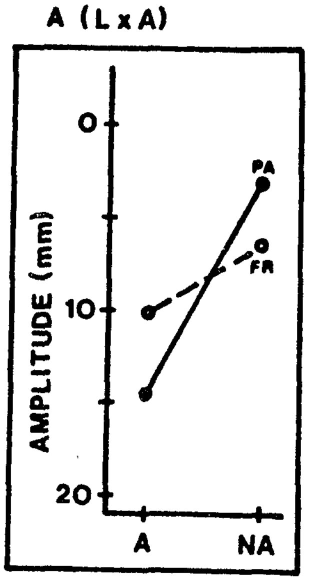
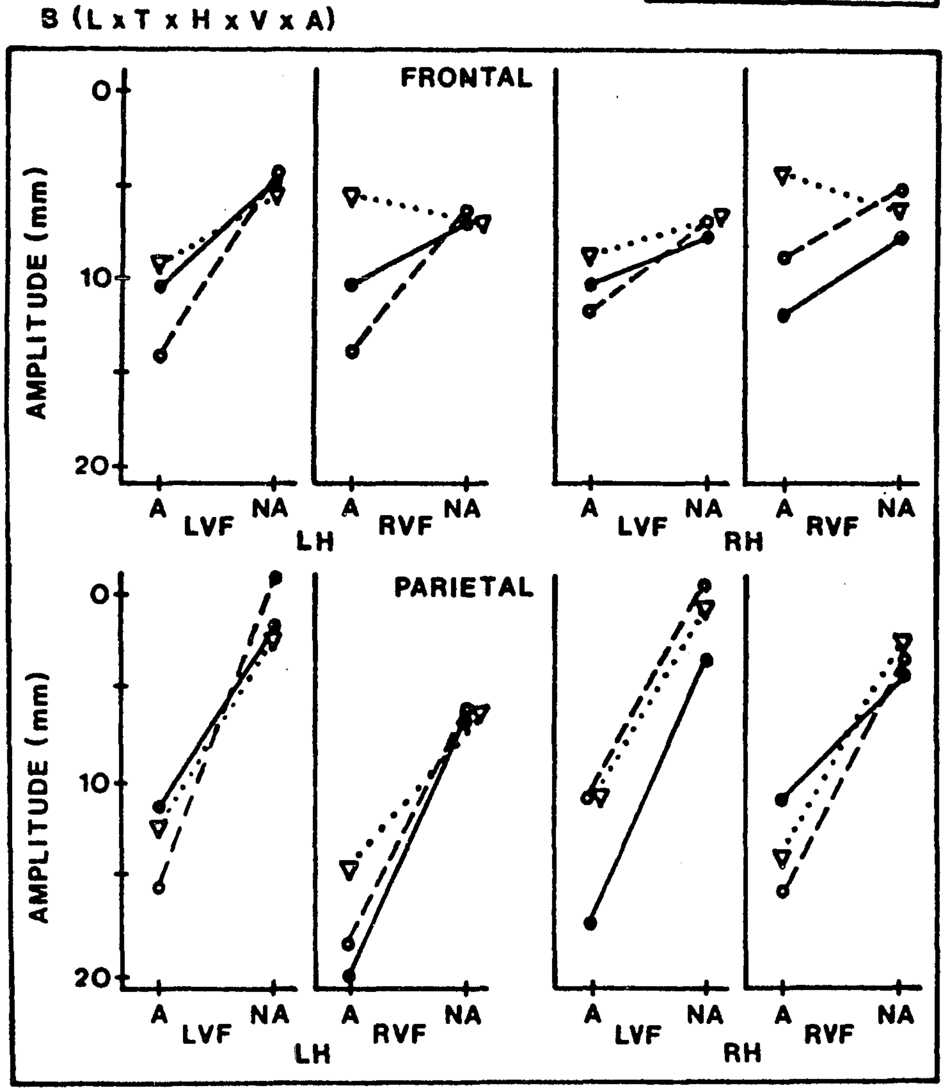


Figure 8. Mean deviation from baseline for P-355 plotted as a function of (A) location by attention; and (B) location by tasks by hemispheres by visual field by attention. Code for all symbols same as in Figure 3.

P-355


A (L x A)
AMPLITUDE (mm)
0
10
20
PA
FR
A
NA


B (L x T x H x V x A)
FRONTAL
PARIETAL
AMPLITUDE (mm)
0
10
20
A
NA
LVF
RVF
LH
RH

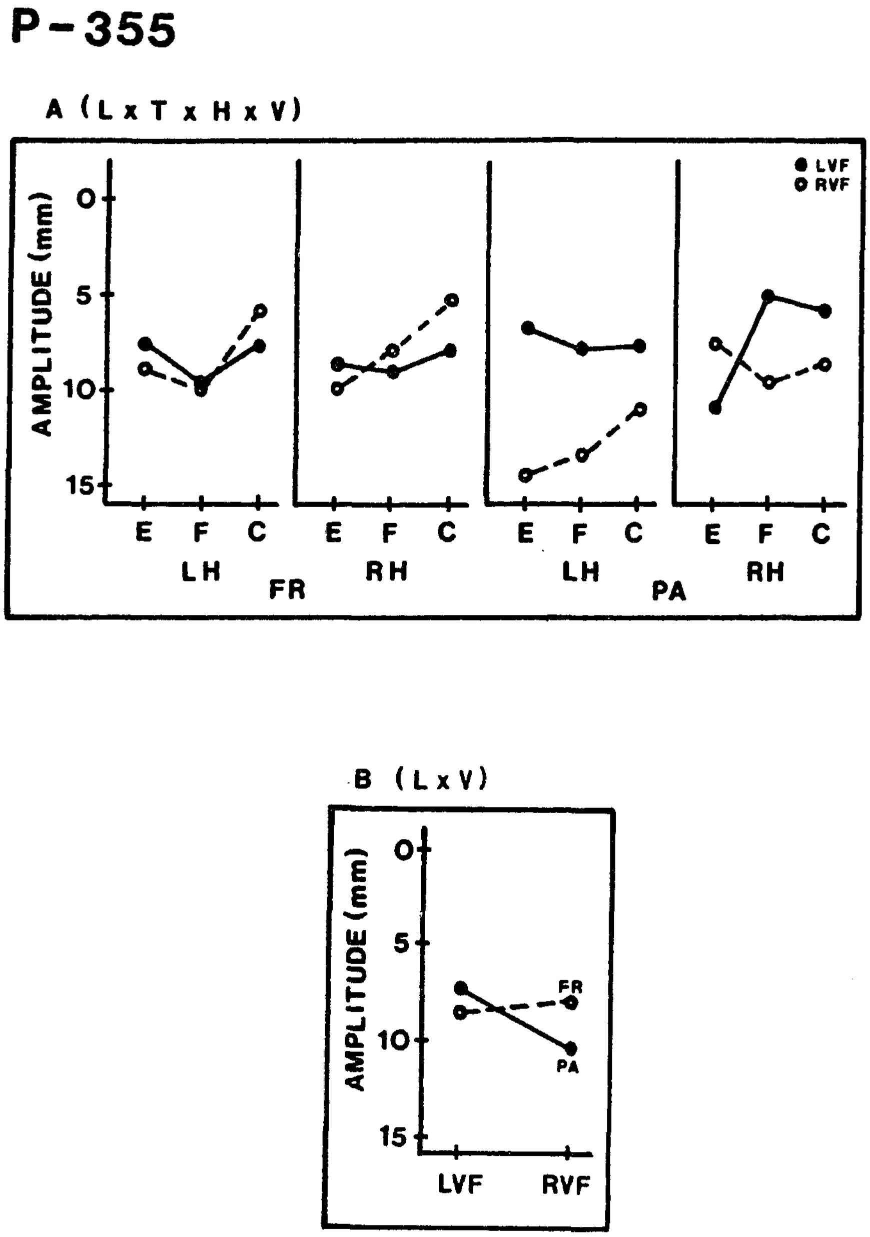
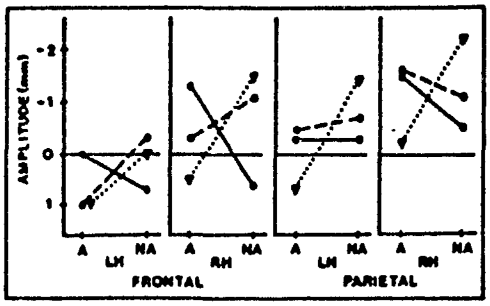


Figure 9. Mean deviation from baseline for P-355 plotted as a function of: (A) location by tasks by hemispheres by visual field; (b) location by hemispheres; and (C) location by visual field. Code for all symbols same as in Figure 3.

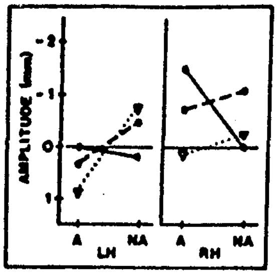
Figure 10. Reproduction of Figures 3, 5, 6, and 8 to facilitate visual comparison of attention effects across components c-55, C-115, N-165, and P-355.

C-55

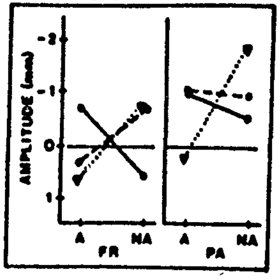
A (L x T x H x A)



B (T x H x A)

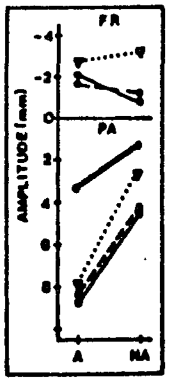


C (L x T x A)

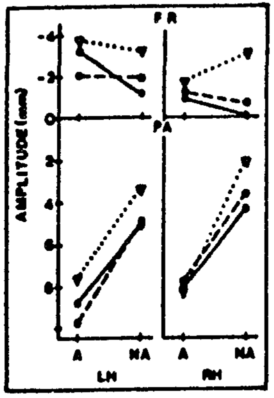


C-115

D (T x L x A)



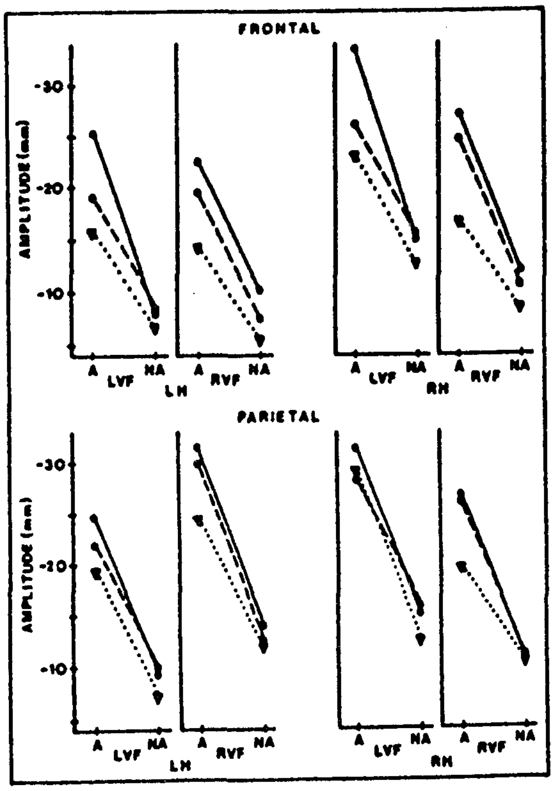
E (T x L x A x H)



EYE
FOOT
COUNT

N-165

F (L x T x A x H x V)



P-355

G (L x T x H x V x A)

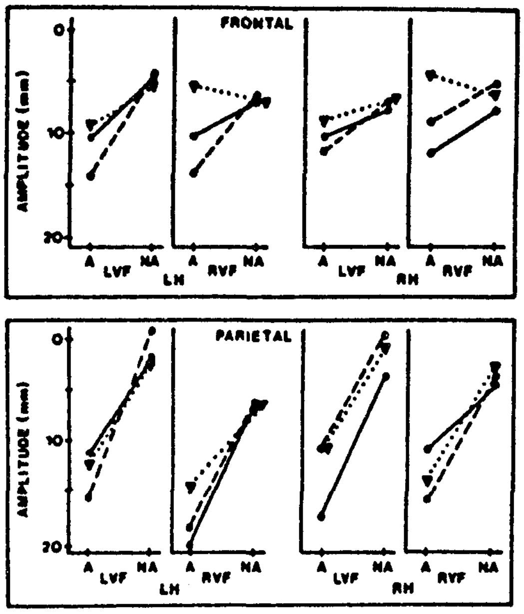
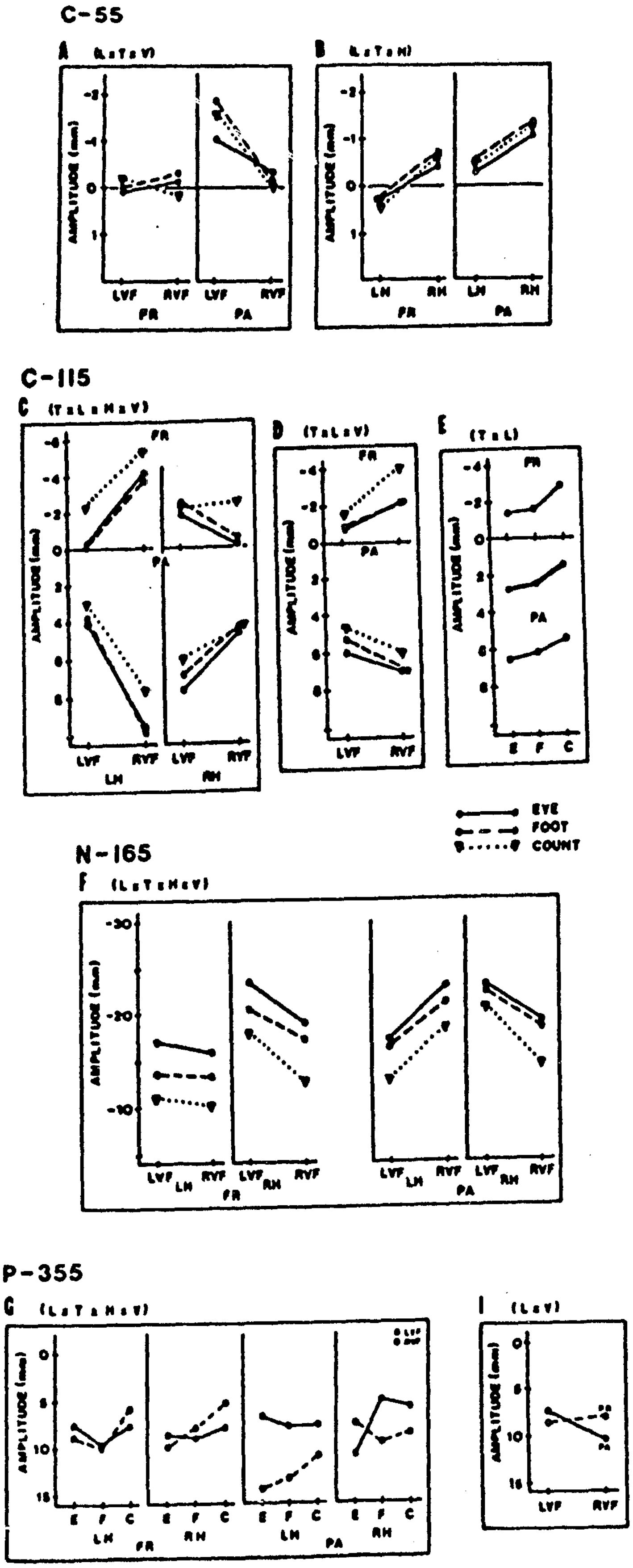


Figure 11. Reproduction of Figures 4, 7, and 9 to facilitate visual comparison of variables other than attention across components C-55, C-115, N-165, and P-355.


C-55
A (L×T×V)
B (L×T×H)
AMPLITUDE (mm)
-2
-1
0
1
LVF
RVF
LVF
RVF
FR
PA
LH
RH
LH
RH
FR
PA
C-115
C (T×L×H×V)
D (T×L×V)
E (T×L)
AMPLITUDE (mm)
FR
PA
-6
-4
-2
0
2
4
6
8
LVF
RVF
LVF
RVF
LH
RH
E
F
C
EYE
FOOT
COUNT
N-165
F (L×T×H×V)
AMPLITUDE (mm)
-30
-20
-10
LVF
LH
RVF
LVF
RH
RVF
FR
LVF
LH
RVF
LVF
RH
RVF
PA
P-355
G (L×T×H×V)
I (L×V)
AMPLITUDE (mm)
0
5
10
15
E
F
C
LH
RH
FR
PA
LVF
RVF

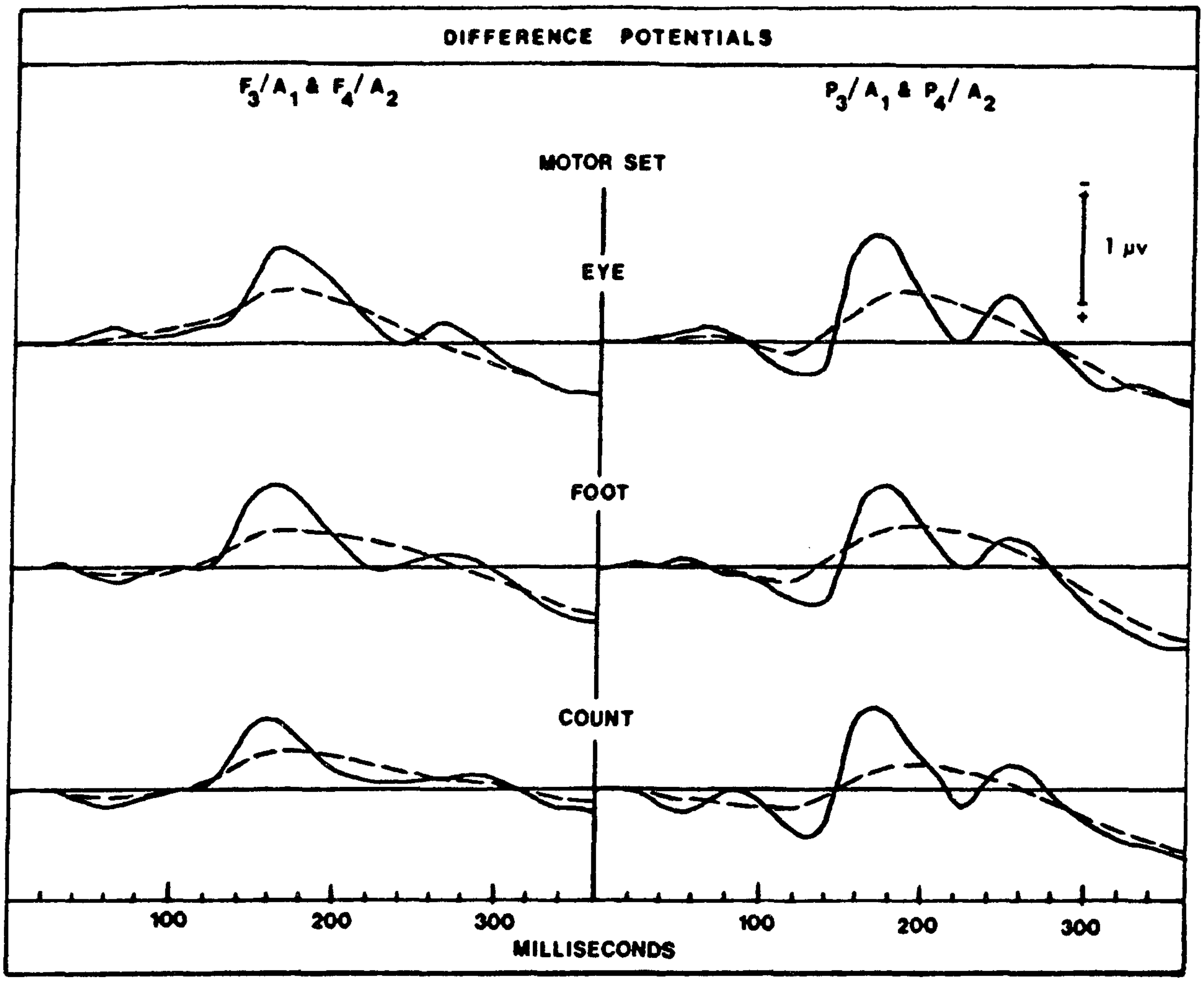


Figure 12. Reproduction of group difference potentials of Figure 2 with "best fit" curves (dashed lines) showing low wave changes.

Table 1. Summary of statistical analyses performed on C-55, C-115, N-165, and P-355. Significant results only.

Code: ●●●● = $p<.0001$
●●● = $p<.001$
●● = $p<.01$
● = $p<.05$
o = $.05<p<.10$

SOURCE OF VARIANCE	6 — WAY				5 — WAY								4 — WAY																							
					FRONTAL				PARIETAL				FRONTAL												PARIETAL											
													EYE				FOOT				COUNT				EYE				FOOT				COUNT			
	C-55	C-115	N-165	P-355	C-55	Fr-115	N-165	P-355	C-55	Pa-115	N-165	P-355	C-55	Fr-115	N-165	P-355	C-55	Fr-115	N-165	P-355	C-55	Fr-115	N-165	P-355	C-55	Pa-115	N-165	P-355	C-55	Pa-115	N-165	P-355	C-55	Pa-115	N-165	P-355
A		•	∷	••			∷			••	∷	∴	•		∷				∷	∴	••		∷			•	∷	••		••	∷	∴	••	••	∷	••
L x A		••		••																																
T x A	••		•		•		••		•																											
H x A								o					•							••	o	••										•		••		
V x A																																				
L x T x A																																				
L x H x A																																				
L x V x A																																				
T x H x A	o								•			o																								
T x V x A																																				
H x V x A											o																	o								
L x T x H x A																																				
T x H x V x A												••																								
L x T x V x A			o																																	
L x H x V x A			•																																	
L x T x H x V x A																																				
T		o	∷				∷				•																									
L x T																																				
H x T				•				o																												
V x T																																				
L x H x T																																				
L x V x T				•																																
H x V x T												••																								
L x H x V x T				••																																
H	∷				••	•	••		••			•	•	•	•		•		∴	••	••		∴									••	o			•
L x H																																				
V x H				•		••	•			∴	∷			o	•			•	o			••	o			∴	∷	•	•	••	∷			••	∷	
L x V x H		∷																																		
V									•			••																				∴				•
L x V	••	•		••																																
L	•	∴																																		

APPENDIX B

Table 2.

Summary of statistical analysis performed on C-55.
6-Way ANOVA.

Location x Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Location (L)	1,17	120.96	5.46	.03
Task (T)	2,34	8.92	.16	-
Attention (A)	1,17	47.52	2.14	-
Hemisphere (H)	1,17	155.50	26.20	.0001
Visual field (V)	1,17	92.15	2.87	-
L * T	2,34	.87	.03	-
L * A	1,17	.67	.01	-
L * H	1,17	1.07	.24	-
L * V	1,17	97.63	9.02	.008
T * A	2,34	261.88	5.45	.009
T * H	2,34	2.26	.28	-
T * V	2,34	14.90	.28	-
A * H	1,17	10.79	1.11	-
A * V	1,17	.00	.00	-
H * V	1,17	23.92	1.71	-
T * A * H	2,34	23.52	2.38	-
T * H * V	2,34	4.81	.41	-
T * A * V	2,34	25.55	.42	-
A * H * V	1,17	2.64	.49	-
L * T * A	2,34	43.40	2.49	.10
L * A * H	1,17	1.78	.56	-
L * H * V	1,17	.05	.01	-
L * T * H	2,34	.90	.06	-
L * T * V	2,34	8.30	.47	-
L * A * V	1,17	13.72	1.03	-
L * T * A * H	2,34	5.40	.80	-
L * T * A * V	2,34	9.32	.44	-
L * A * H * V	1,34	5.62	1.44	-
T * A * H * V	2,34	7.92	.55	-
L * T * H * V	2,34	1.43	.31	-
L * T * A * H * V	2,34	.60	.09	-

Table 3.

Summary of statistical analysis performed on C-55.
5-Way ANOVA.
Frontal recording sites.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Task (T)	2,34	3.34	.11	-
Attention (A)	1,17	22.01	1.94	-
Hemisphere (H)	1,17	91.15	15.13	.001
Visual field (V)	1,17	.04	0.00	.96
T * A	2,34	166.18	5.06	.01
T * H	2,34	2.98	0.40	.67
T * V	2,34	5.32	.22	-
A * H	1,17	1.90	.47	-
A * V	1,17	6.64	.31	-
H * V	1,17	10.85	1.02	-
T * A * H	2,34	25.34	3.97	-
T * H * V	2,34	2.72	.50	-
T * A * V	2,34	32.66	.89	-
A * H * V	1,17	.28	.06	-
T * A * H * V	2,34	4.94	.42	-

Table 4.

Summary of statistical analysis performed on C-55.
5-Way ANOVA.
Parietal recording sites.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Task (T)	2,34	4.45	.12	-
Attention (A)	1,17	25.57	1.34	-
Hemisphere (H)	1,17	65.41	15.23	.001
Visual field (V)	1,17	189.74	7.61	.01
T * A	2,34	139.09	4.27	.02
T * H	2,34	.18	.01	-
T * V	2,34	17.87	.38	-
A * H	1,17	10.67	1.20	-
A * V	1,17	7.07	.30	-
H * V	1,17	13.13	1.28	-
T * A * H	2,34	3.58	.35	-
T * H * V	2,34	3.52	.32	-
T * A * V	2,34	2.2	.05	-
A * H * V	1,17	7.97	1.75	-
T * A * H * V	2,34	3.59	.38	-

Table 5.

Summary of statistical analysis performed on C-55.
4-way ANOVA.
Frontal recording sites. Eye task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	59.48	5.15	.036
Hemisphere (H)	1,17	16.84	5.80	.028
Visual field (V)	1,17	1.22	.09	-
A * H	1,17	14.79	4.88	.041
A * V	1,17	2.96	.16	-
H * V	1,17	8.78	1.80	-
A * H * V	1,17	4.18	.05	-

Table 6.

Summary of statistical analysis performed on C-55.
4-way ANOVA.
Parietal recording sites. Eye task.

Task x Attention x Hemisphere x Visual field x Subject

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>p<</u>
Attention (A)	1,17	8.95	.66	-
Hemisphere (H)	1,17	18.85	2.56	-
Visual field (V)	1,17	20.93	1.02	-
A * H	1,17	7.06	1.36	-
A * V	1,17	6.71	.54	-
H * V	1,17	12.54	2.84	-
A * H * V	1,17	.01	.00	-

Table 7.

Summary of statistical analysis performed on C-55.
4-way ANOVA.
Frontal recording sites. Foot task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	44.10	1.90	-
Hemisphere (H)	1,17	39.38	5.37	.033
Visual field (V)	1,17	1.01	.08	-
A * H	1,17	2.75	.61	-
A * V	1,17	. 2	.00	-
H * V	1,17	4.38	.86	-
A * H * V	1,17	1.01	.19	-

Table 8.

Summary of statistical analysis perfromed on C-55.
4-way ANOVA.
Parietal recording sites. Foot task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	$p<$
Attention (A)	1,17	.50	.02	-
Hemisphere (H)	1,17	22.33	4.11	.059
Visual field (V)	1,17	105.23	4.77	.043
A * H	1,17	7.06	1.11	-
A * V	1,17	2.32	.05	-
H * V	1,17	.89	.16	-
A * H * V	1,17	4.31	.98	-

Table 9.

Summary of statistical analysis performed on C-55.
4-way ANOVA.
Frontal recording sites. Count task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	84.61	8.95	.008
Hemisphere (H)	1,17	37.90	11.74	.003
Visual field (V)	1,17	3.13	.20	-
A * H	1,17	9.70	3.35	.085
A * V	1,17	36.32	2.44	-
H * V	1,17	.42	.07	-
A * H * V	1,17	.01	.01	-

Table 10.

Summary of statistical analysis performed on C-55.
4-way ANOVA.
Parietal recording sites. Count task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	155.21	10.33	.005
Hemisphere (H)	1,17	24.42	3.79	.068
Visual field (V)	1,17	81.45	2.73	-
A * H	1,17	.12	.02	-
A * V	1,17	.24	.03	-
H * V	1,17	3.21	.28	-
A * H * V	1,17	7.24	1.33	-

Table 11.

Summary of statistical analysis performed on C-115.
6-Way ANOVA.

Location x Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Location (L)	1,17	13724.90	29.43	.0001
Task (T)	2,34	264.91	3.10	.06
Attention (A)	1,17	844.73	6.51	.02
Hemisphere (H)	1,17	13.61	.16	-
Visual field (V)	1,17	7.25	.02	-
L * T	2,34	9.93	.20	-
L * A	1,17	1167.41	14.13	.002
L * H	1,17	233.93	3.32	.09
L * V	1,17	532.28	5.54	.03
T * A	2,34	105.09	1.12	-
T * H	2,34	18.63	.67	-
T * V	2,34	18.11	.19	-
A * H	1,17	33.38	1.42	-
A * V	1,17	174.39	1.58	-
H * V	1,17	155.76	1.85	-
T * A * H	2,34	39.39	1.44	-
T * H * V	2,34	11.23	.42	-
T * A * V	2,34	36.61	.38	-
A * H * V	1,17	.01	.00	-
L * T * A	2,34	6.94	.15	-
L * A * H	1,17	.08	.01	-
L * H * V	1,17	2034.70	26.29	.0001
L * T * H	2,34	8.57	.43	-
L * T * V	2,34	12.31	.17	-
L * A * V	1,17	12.19	.30	-
L * T * A * H	2,34	4.85	.45	-
L * T * A * V	2,34	59.30	.71	-
L * A * H * V	1,34	.08	.01	-
T * A * H * V	2,34	52.49	1.58	-
L * T * H * V	2,34	21.21	1.48	-
L * T * A * H * V	2,34	43.75	1.92	-

Table 12.

Summary of statistical analysis performed on C-115.
5-Way ANOVA.
Frontal recording sites.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Task (T)	2,34	178.68	2.15	-
Attention (A)	1,17	13.02	.17	-
Hemisphere (H)	1,17	180.19	4.64	.05
Visual field (V)	1,17	331.91	1.39	.25
T * A	2,34	70.46	.84	-
T * H	2,34	13.49	0.60	-
T * V	2,34	22.80	.32	-
A * H	1,17	18.36	1.14	-
A * V	1,17	139.40	1.66	-
H * V	1,17	532.27	8.77	.009
T * A * H	2,34	26.37	1.60	-
T * H * V	2,34	.90	.04	-
T * A * V	2,34	82.39	.89	-
A * H * V	1,17	.01	.00	-
T * A * H * V	2,34	13.76	.54	-

Table 13.

Summary of statistical analysis performed on C-115.
5-Way ANOVA.
Parietal recording sites.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Task (T)	2,34	96.15	1.85	-
Attention (A)	1,17	1199.11	14.60	.001
Hemisphere (H)	1,17	67.35	.57	-
Visual field (V)	1,17	207.63	.84	-
T * A	2,34	41.57	.74	.48
T * H	2,34	13.71	.54	-
T * V	2,34	7.61	.08	-
A * H	1,17	15.10	.81	-
A * V	1,17	47.18	.70	-
H * V	1,17	1658.20	16.44	.0008
T * A * H	2,34	17.86	.83	-
T * H * V	2,34	31.54	1.65	-
T * A * V	2,34	13.52	.15	-
A * H * V	1,17	.79	.00	-
T * A * H * V	2,34	82.48	2.68	-

Table 14.

Summary of statistical analysis performed on C-115.
4-way ANOVA.
Frontal recording sites. Eye task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	59.25	.98	–
Hemisphere (H)	1,17	122.64	4.95	.04
Visual field (V)	1,17	89.35	.82	-
A * H	1,17	8.04	.51	-
A * V	1,17	96.32	1.41	–
H * V	1,17	180.21	4.21	.06
A * H * V	1,17	2.17	.24	-

Table 15.

Summary of statistical analysis performed on C-115.
4-way ANOVA.
Parietal recording sites. Eye task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	508.92	8.09	.01
Hemisphere (H)	1,17	21.44	.26	-
Visual field (V)	1,17	40.21	.29	-
A * H	1,17	.16	.01	-
A * V	1,17	.93	.02	-
H * V	1,17	668.95	16.71	.001
A * H * V	1,17	46.21	2.96	.10

Table 16.

Summary of statistical analysis performed on C-115.
4-way ANOVA.
Frontal recording sites. Foot task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	2.92	.05	-
Hemisphere (H)	1,17	29.85	1.70	.21
Visual field (V)	1,17	60.89	.74	-
A * H	1,17	1.75	.14	-
A * V	1,17	.22	.00	-
H * V	1,17	180.54	7.78	.01
A * H * V	1,17	2.86	.20	-

Table 17.

Summary of statistical analysis performed on C-115.
4-way ANOVA.
Parietal recording sites. Foot task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	499.52	10.00	.006
Hemisphere (H)	1,17	34.81	1.40	-
Visual field (V)	1,17	138.06	1.13	-
A * H	1,17	4.62	.20	-
A * V	1,17	15.73	.22	-
H * V	1,17	742.56	14.48	.001
A * H * V	1,17	54.27	3.09	-

Table 18.

Summary of statistical analysis performed on C-115.
4-way ANOVA.
Frontal recording sites. Count task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	13.38	.35	-
Hemisphere (H)	1,17	51.97	2.90	.10
Visual field (V)	1,17	204.56	1.72	-
A * H	1,17	34.89	7.07	.02
A * V	1,17	134.89	2.45	-
H * V	1,17	158.82	9.10	.008
A * H * V	1,17	8.71	.81	-

Table 19.

Summary of statistical analysis performed on C-115.
4-way ANOVA.
Parietal recording sites. Count task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	962.40	13.65	.002
Hemisphere (H)	1,17	4.74	.14	-
Visual field (V)	1,17	70.18	.79	-
A * H	1,17	32.42	8.43	.01
A * V	1,17	29.82	.58	-
H * V	1,17	358.25	10.32	.01
A * H * V	1,17	2.02	0.09	-

Table 20.

Summary of statistical analysis performed on C-165.
6-Way ANOVA.

Location x Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Location (L)	1,17	1467.06	1.70	-
Task (T)	2,34	4037.21	14.60	.0001
Attention (A)	1,17	37883.75	85.25	.0001
Hemisphere (H)	1,17	2093.62	11.97	.003
Visual field (V)	1,17	266.83	.95	-
L * T	2,34	179.52	2.41	.11
L * A	1,17	201.01	.74	-
L * H	1,17	662.64	4.37	.05
L * V	1,17	415.90	2.19	-
T * A	2,34	958.97	3.83	.03
T * H	2,34	15.74	.48	-
T * V	2,34	69.70	.32	-
A * H	1,17	13.91	.27	-
A * V	1,17	.36	.00	-
H * V	1,17	2415.53	27.13	.0001
T * A * H	2,34	.76	.02	-
T * H * V	2,34	13.68	.45	-
T * A * V	2,34	320.02	1.68	-
A * H * V	1,17	22.02	.75	-
L * T * A	2,34	56.41	.71	-
L * A * H	1,17	10.65	.32	-
L * H * V	1,17	640.41	20.66	.0003
L * T * H	2,34	9.72	.42	-
L * T * V	2,34	5.87	.07	-
L * A * V	1,17	22.79	.34	-
L * T * A * H	2,34	15.77	.55	-
L * T * A * V	2,34	132.34	.06	-
L * A * H * V	1,34	95.70	9.68	.006
T * A * H * V	2,34	59.75	1.46	-
L * T * H * V	2,34	3.71	.25	-
L * T * A * H * V	2,34	3.85	.20	-

Table 21.

Summary of statistical analysis performed on C-165.
5-Way ANOVA.
Frontal recording sites.

Task x Attention x Hemisphere x Visual field x Subject

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>p<</u>
Task (T)	2,34	2877.98	16.10	.0001
Attention (A)	1,17	16282.79	49.71	.0001
Hemisphere (H)	1,17	2555.97	13.16	.002
Visual field (V)	1,17	674.50	3.00	-
T * A	2,34	736.51	5.01	.01
T * H	2,34	9.48	0.33	.72
T * V	2,34	43.14	.34	-
A * H	1,17	24.46	.59	-
A * V	1,17	14.45	.27	-
H * V	1,17	284.21	6.72	.02
T * A * H	2,34	6.03	.16	-
T * H * V	2,34	1.59	.06	-
T * A * V	2,34	190.17	1.74	-
A * H * V	1,17	12.95	1.16	-
T * A * H * V	2,34	18.38	.56	-

Table 22.

Summary of statistical analysis performed on C-165.
5-Way ANOVA.
Parietal recording sites.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Task (T)	2,34	1338.75	7.77	.002
Attention (A)	1,17	21801.98	55.90	.0001
Hemisphere (H)	1,17	200.29	1.51	-
Visual field (V)	1,17	8.23	.03	-
T * A	2,34	278.86	1.53	-
T * H	2,34	15.98	.59	-
T * V	2,34	32.44	.19	-
A * H	1,17	.11	.00	-
A * V	1,17	8.71	.09	-
H * V	1,17	2771.72	35.66	.0001
T * A * H	2,34	10.51	.26	-
T * H * V	2,34	15.80	.89	-
T * A * V	2,34	262.20	2.08	-
A * H * V	1,17	104.77	3.73	.07
T * A * H * V	2,34	45.23	1.66	-

Table 23.

Summary of statistical analysis performed on C-165.
4-way ANOVA.
Frontal recording sites. Eye task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	8828.16	41.19	.0001
Hemisphere (H)	1,17	753.96	6.57	.02
Visual field (V)	1,17	216.33	2.30	-
A * H	1,17	13.75	.56	-
A * V	1,17	147.02	2.92	.10
H * V	1,17	99.17	4.67	.04
A * H * V	1,17	21.39	1.76	-

Table 24.

Summary of statistical analysis performed on C-165.
4-way ANOVA.
Parietal recording sites. Eye task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	9475.40	47.93	.0001
Hemisphere (H)	1,17	30.16	.51	-
Visual field (V)	1,17	19.87	.11	-
A * H	1,17	.01	.00	-
A * V	1,17	6.89	.11	-
H * V	1,17	979.17	29.66	.0001
A * H * V	1,17	7.79	.38	-

Table 25.

Summary of statistical analysis performed on C-165.
4-way ANOVA.
Frontal recording sites. Foot task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	5076.56	25.21	.0001
Hemisphere (H)	1,17	1000.67	22.23	.0002
Visual field (V)	1,17	110.25	.96	-
A * H	1,17	16.00	.68	-
A * V	1,17	54.26	.79	-
H * V	1,17	76.56	3.68	.07
A * H * V	1,17	8.31	1.12	-

Table 26.

Summary of statistical analysis performed on C-165.
4-way ANOVA.
Parietal recording sites. Foot task.

Task x Attention x Hemisphere x Visual field x Subject

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>p<</u>
Attention (A)	1,17	7226.42	43.96	.0001
Hemisphere (H)	1,17	67.38	1.78	-
Visual field (V)	1,17	13.38	.16	-
A * H	1,17	3.83	.14	-
A * V	1,17	162.78	1.97	-
H * V	1,17	740.29	30.86	.0001
A * H * V	1,17	11.39	.78	-

Table 27.

Summary of statistical analysis performed on C-165.
4-way ANOVA.
Frontal recording sites. Count task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	3114.57	53.02	.0001
Hemisphere (H)	1,17	810.82	12.87	.002
Visual field (V)	1,17	391.05	2.72	.12
A * H	1,17	.74	.02	-
A * V	1,17	3.33	.08	-
H * V	1,17	110.08	3.90	.06
A * H * V	1,17	1.62	.07	-

Table 28.

Summary of statistical analysis performed on C-165.
4-way ANOVA.
Parietal recording sites. Count task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	5411.44	25.78	.0001
Hemisphere (H)	1,17	120.54	1.92	-
Visual field (V)	1,17	8.87	.06	-
A * H	1,17	6.78	.22	-
A * V	1,17	102.09	1.39	-
H * V	1,17	1057.60	27.63	.0001
A * H * V	1,17	129.87	6.60	.02

Table 29.

Summary of statistical analysis performed on P-355.
6-Way ANOVA.

Location x Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Location (L)	1,17	79.26	.13	-
Task (T)	2,34	433.91	.89	-
Attention (A)	1,17	12278.58	10.37	.005
Hemisphere (H)	1,17	326.22	3.14	-
Visual field (V)	1,17	378.82	3.20	-
L * T	2,34	104.72	.53	-
L * A	1,17	3062.68	7.98	.01
L * H	1,17	119.48	2.54	-
L * V	1,17	728.39	7.14	.01
T * A	2,34	754.03	1.61	-
T * H	2,34	199.68	4.22	.02
T * V	2,34	79.54	.65	-
A * H	1,17	104.10	2.29	-
A * V	1,17	123.38	.86	-
H * V	1,17	344.16	5.05	.03
T * A * H	2,34	110.22	2.72	.08
T * H * V	2,34	151.06	2.01	-
T * A * V	2,34	20.68	.11	-
A * H * V	1,17	.96	.01	-
L * T * A	2,34	48.37	.28	-
L * A * H	1,17	31.93	1.16	-
L * H * V	1,17	135.45	1.50	-
L * T * H	2,34	19.65	.41	-
L * T * V	2,34	202.40	3.33	.05
L * A * V	1,17	18.70	.25	-
L * T * A * H	2,34	27.37	.81	-
L * T * A * V	2,34	81.68	1.20	-
L * A * H * V	1,34	35.65	.73	-
T * A * H * V	2,34	145.49	2.13	-
L * T * H * V	2,34	335.14	5.79	.007
L * T * A * H * V	2,34	264.59	6.80	.003

Table 30.

Summary of statistical analysis performed on P-355.
5-Way ANOVA.
Frontal recording sites.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Task (T)	2,34	395.19	.80	-
Attention (A)	1,17	1538.31	2.11	-
Hemisphere (H)	1,17	25.42	.34	-
Visual field (V)	1,17	28.32	.21	-
T * A	2,34	564.57	1.13	-
T * H	2,34	169.94	2.94	.066
T * V	2,34	169.83	1.49	-
A * H	1,17	125.67	3.59	.075
A * V	1,17	119.07	.92	-
H * V	1,17	23.89	1.48	-
T * A * H	2,34	65.60	1.61	-
T * H * V	2,34	21.55	.46	-
T * A * V	2,34	91.78	.72	-
A * H * V	1,17	24.18	1.01	-
T * A * H * V	2,34	10.65	.26	-

Table 31.

Summary of statistical analysis performed on C-355.
5-Way ANOVA.
Parietal recording sites.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Task (T)	2,34	137.74	.69	-
Attention (A)	1,17	13628.28	16.38	.0008
Hemisphere (H)	1,17	390.26	5.16	.04
Visual field (V)	1,17	1128.43	12.45	.003
T * A	2,34	208.36	1.42	-
T * H	2,34	36.95	1.11	-
T * V	2,34	134.19	1.97	-
A * H	1,17	15.72	.40	-
A * V	1,17	30.72	.36	-
H * V	1,17	424.43	2.99	.10
T * A * H	2,34	85.31	2.70	.08
T * H * V	2,34	487.26	5.87	.006
T * A * V	2,34	14.22	.11	-
A * H * V	1,17	18.25	.20	-
T * A * H * V	2,34	374.19	5.69	.007

Table 32.

Summary of statistical analysis performed on C-355.
4-way ANOVA.
Frontal recording sites. Eye task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	602.29	1.17	-
Hemisphere (H)	1,17	45.00	.60	-
Visual field (V)	1,17	44.56	.41	-
A * H	1,17	6.71	.17	-
A * V	1,17	.09	.	-
H * V	1,17	.50	.02	-
A * H * V	1,17	29.25	.62	-

Table 33.

Summary of statistical analysis performed on C-355.
4-way ANOVA.
Parietal recording sites. Eye task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	4307.73	10.28	.005
Hemisphere (H)	1,17	51.84	.84	-
Visual field (V)	1,17	152.11	3.17	.09
A * H	1,17	15.08	.49	-
A * V	1,17	19.51	.20	-
H * V	1,17	895.01	6.61	.02
A * H * V	1,17	330.03	3.28	.09

Table 34.

Summary of statistical analysis perfromed on C-355.
4-way ANOVA.
Frontal recording sites. Foot task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	1475.84	2.69	.12
Hemisphere (H)	1,17	136.11	4.41	.05
Visual field (V)	1,17	18.06	.26	-
A * H	1,17	170.30	9.99	.006
A * V	1,17	24.66	.34	-
H * V	1,17	33.45	2.13	-
A * H * V	1,17	4.69	.56	-

Table 35.

Summary of statistical analysis perfromed on C-355.
4-way ANOVA.
Parietal recording sites. Foot task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	6142.64	21.82	.0002
Hemisphere (H)	1,17	249.38	11.56	.003
Visual field (V)	1,17	805.14	18.35	.0005
A * H	1,17	62.02	4.50	.05
A * V	1,17	25.41	.45	-
H * V	1,17	7.33	.28	-
A * H * V	1,17	47.26	2.02	-

Table 36.

Summary of statistical analysis performed on C-355.
4-way ANOVA.
Frontal recording sites. Count task.

Task x Attention x Hemisphere x Visual field x Subject

Source	df	SS	F	p<
Attention (A)	1,17	24.75	.15	-
Hemisphere (H)	1,17	14.25	.55	-
Visual field (V)	1,17	135.53	1.96	-
A * H	1,17	14.25	.72	-
A * V	1,17	186.09	1.31	-
H * V	1,17	11.50	.59	-
A * H * V	1,17	.89	.09	-

Table 37.

ummary of statistical analysis performed on C-355.
4-way ANOVA.
Parietal recording sites. Count task.

Task x Attention x Hemisphere x Visual field x Subject

<u>Source</u>	<u>df</u>	<u>SS</u>	<u>F</u>	<u>p<</u>
Attention (A)	1,17	3386.27	12.16	.003
Hemisphere (H)	1,17	126.00	4.83	.04
Visual field (V)	1,17	305.38	4.55	.05
A * H	1,17	23.93	.93	-
A * V	1,17	.02	.00	-
H * V	1,17	9.35	.15	-
A * H * V	1,17	15.14	.44	-