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ELECTROCORTICAL CORRELATES OF DECISION TASKS

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DECISION TASKS

Two experiments were designed to define the behavioral functions that might correlate with human cortical DC responses. These responses, negative in polarity and 500 to 5000 msec. in duration, were referred to as Contingent Negative Variation (CNV) to provide continuity with existing literature. In preliminary observations it was established that CNV occurs during a variety of tasks all of which could be said to involve "time-locked concentration." In the first formal experiment, in which a selective reaction time task was used, it was shown that CNV duration and the timing of the task stimulus are independent of one another. In the second experiment it was shown that the late components of the cortical response to sensory stimulation were not altered during CNV. The results of these experiments support the theory that CNV is a correlate of the response selection process, but is independent of sensory processing. The neural substrate of CNV is thought to be widespread cortical inhibition; this could subserve concentration on response-relevant associations by filtering out associations not crucially related to the task.

ELECTROCORTICAL CORRELATES OF FIXED-FOREPERIOD
DECISION TASKS

by

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
Measurement of Electrocortical Potentials	3
Origin and Distribution of Cortical Potentials	6
Behavioral Correlates of Electrocortical DC Responses in Rats, Rabbits, and Cats	9
Behavioral Correlates of Electrocortical DC Responses in Man	12
The Present Study	17
THE INVESTIGATION	19
General Method	19
Exploratory Studies	23
Experiment I	32
Experiment II	39
GENERAL DISCUSSION	50
SUMMARY	57
REFERENCES	60
APPENDIX 1	
APPENDIX 2	

INTRODUCTION

On the basis of comparative-anatomical and clinical evidence the cerebral cortex has long been regarded as the probable locus of many of the higher-order synthetic functions of the human brain. Particular importance has been given to the role of cortical control over subcortical structures in such aspects of behavior as set, expectancy, and the sequential programming of action and thought. Yet early recordings of cortical electrical potentials did not reveal any distinctive electrical correlates of such higher-order psychological functions. In fact, microelectrode recordings served primarily to elaborate anatomical evidence for the existence of specific afferent systems and convergent cortical neurons, while gross electroencephalography revealed only rough correlations between electrocortical rhythms and very general aspects of behavior such as arousal level or orienting reactions.

Computer-averaging techniques now permit the measurement of electrocortical activity that is responsive to subtle and meaningful psychological variables. The electrocortical potential changes generated by these variables are too small to be detectable in a raw electroencephalographic record, but can be isolated from electrocortical "noise" by average-response computers; they are often referred to as averaged evoked potentials. They consist of complex and remarkably reliable spatio-temporal patterns of potential change distributed over most of the surface of the cerebral cortex. They have been studied recently in a variety of paradigms similar to those employed in the experimental psychological literature on human attention, perception, and decision processes.

One outstanding contribution of these recent studies has been the demonstration of systematic relations between averaged evoked potentials and selective attention. Two types of averaged evoked potentials have been found to be related to selective attention. First, brief (usually less than 500 msec. in duration), cortical responses to sensory stimuli are modifiable by varying the relevance, importance, or predictability of those stimuli (e.g., Sutton et al., 1965). This finding is congruent with numerous empirical formulations of cortical functional organisation, especially that of Milner (1957). Second, slow potential changes, 500 to 5000 msec. in duration, have been shown to occur during particular phases of decision task performance (e.g., Walter, 1964). These slow potentials constitute a unique electrocortical phenomenon that has yet to be integrated into any overall theory of cortical function. The present paper is concerned primarily with the functional significance of the latter slow potentials, especially in relation to performance on simple human decision tasks. The large literature on the relation of the brief sensory evoked potentials to selective attention (e.g., Donchin & Lindsley, 1966; Morrell & Morrell, 1966; Harter & White, 1967) is not directly relevant and will not be reviewed in detail.

The remainder of this chapter is a review of the literature on the nature and origin of DC potentials recorded from the human scalp, and on the animal and human studies relevant to understanding their relation to behavior. This review is designed to define the theoretical and methodological issues to which my experiments are addressed.

Measurement of Electro cortical Potentials

It is well known that electrical potential differences may exist between any two points on the cerebral cortex. These potential differences may be measured by placing conductive electrodes on the cortical surface. An oscillographic study of such potentials on a time axis reveals two types of potential changes: oscillatory or periodic potential changes, and aperiodic slow potential changes. The former may be "high" frequency (3-15 cycles per second) or "low" frequency (0.1-2 cycles per second). Low-frequency oscillations and slow aperiodic changes are normally filtered out of the electroencephalogram (EEG), and in order to record them a DC amplifier and non-polarisable electrodes are required. The slow aperiodic changes which are the primary concern of this study require such DC amplification of electrocortical activity and are therefore referred to as DC potentials.

A difficulty encountered in studying electrocortical potential changes in response to specific stimuli, is that they are often obscured by spontaneous ongoing fluctuations in electrocortical potentials. When this is the case, it is possible to "average" the obscured responses to the experimental stimulus. This is achieved by taking samples of the total electrocortical activity immediately following each stimulus presentation and summing the samples in a computer so that the sum of irrelevant potential changes not related to the time of stimulation is approximately the same for any given point in time after the stimulus. Thus if there is no electrical response to the stimulus, the averaged activity during

the period following the stimulus will form a straight line. If there is an electrical response to the stimulus, it will consist of potential changes occurring regularly at a constant latency after the stimulus. The average of these changes will produce a waveform called the averaged evoked potential. The waveform of the averaged evoked potential will approach an ideal waveform as the number of samples is increased.

For the purposes of the present investigation it is useful to distinguish three kinds of averaged evoked potentials: the slow or DC response, the early components of sensory evoked potentials (SEP), and the late components of SEP. The first is a non-cyclic potential change which is usually 500 to 5000 msec. in duration. The early SEP is a complex high-frequency waveform which terminates within approximately 100 msec. of stimulation. The late SEP follows the early, but is regarded as a separate response. It consists of a brief complex waveform whose major components usually terminate within 500 msec. of the stimulus. The DC response tends to be correlated with longer-lasting organismic states and complex stimulations; the early and late SEPs are brief transients caused by sudden, momentary changes in the pattern of exteroceptive stimulation, such as a flash of light.

With the advent of computer-averaging techniques it has become feasible to measure human evoked potentials from the intact scalp. Such potentials are slightly attenuated but generally resemble potentials recorded from epidural electrodes (Walter, 1964). Although scalp electrodes integrate activity from more widely

dispersed regions than do epidural electrodes, early SEPs from scalp and cortex resemble each other over sensory-specific regions, and late SEPs resemble each other over non-specific regions of the cortex (Calvet, 1962; Domino et al., 1964; Cooper et al., 1965; Heath & Galbraith, 1966). Scalp-recorded DC potentials also show close agreement with epidural records (Walter, 1964).

There are various sources of artifact which may disrupt the correlation between scalp and epidural recordings. Muscle artifacts may contaminate a scalp record, particularly when the recording electrodes are placed in the mastoid region, on the temporalis muscle, or at the base of the inion, near the neck musculature (Bickford, 1964; Davis et al., 1964). These artifacts are usually controlled, first by placing the reference electrodes at loci which are relatively free from muscular potentials, such as the earlobe or the nasion; and, second, by assuring that the subject (S) is comfortably seated with his neck in a relaxed position.

Skin artifacts caused by the chemical action of the electrode jelly or the tension of the drying collodion holding the electrode in place are generally confined to the early minutes of the recording session. They can be avoided by waiting until the electrode contacts have reached a stable chemical state. Emotional sweating may be controlled by encouraging the S to relax; (unusually anxious Ss are usually rejected if it is impossible to obtain an artifact-free record from them).

Eye movements, if correlated with stimulus onset or task performance, may be a source of artifact. The effect of eye movement may be reduced by presenting visual stimuli with a fixation point, and instructing the S to avoid correlating his blinks with any stimulus. As a further precaution, eye movements are usually recorded on a separate polygraph channel to check for any unwanted correlation with stimulus events.

Other artifacts, from line voltages and other electrical installations, may be greatly reduced by attaching a ground lead from the S to the recording apparatus. When these procedures are followed, scalp-recorded averaged evoked potentials are cortical in origin and closely resemble potentials recorded from epidural electrodes (Walter, 1964; Geisler, 1964; Low et al., 1966).

Origin and Distribution of Cortical Potentials

The direct anatomical origins of surface-recorded electrocortical potentials are believed to lie in the neurons of the upper four cortical layers. The recorded potentials represent the activity of hundreds of thousands of neurons, of which many are pyramidal cells whose apical dendrites spread out in the uppermost layer, and whose somas lie in layers III and IV (Allison, 1962; Goff et al., 1962; Walter, 1964; Morrell, 1967). Such radially oriented pyramidal cells have large numbers of axon terminals on their dendritic formations and somas; many of these terminals originate in excitatory and inhibitory systems mediated by the polysynaptic reticular formations of the mesencephalon and thalamus.

These systems induce inhibitory (hyperpolarising) and excitatory (depolarising) post-synaptic potentials (PSPs) in the pyramidal cells, changing the end-to-end polarisation of the cells, making the dendritic aborisations at the surface either positive or negative with regard to the deeper cell somas. A sustained change in the end-to-end polarisation of large pools of neurons is measured at the cortical surface as a positive or negative shift in the standing DC potential. Other projection systems which may contribute to surface DC shifts originate in the exteroceptive afferent systems, which project from the sensory cortex to the anterior regions of the cortex. Cell unit firing is not thought to be the basis of sustained DC shifts, but synchronous cell firing does contribute to high frequency sensory evoked potentials (Morrell, 1967).

Morrell (1967) has recently reported correlations between specific patterns of PSPs, unit discharges, and surface potentials in human SS. The most important source of surface activity appears to be the PSPs; the role of cellular unit discharges declines as the surface waveform approaches the lower frequency ranges. On the basis of this evidence, and in agreement with Walter (1964), DC responses are herein regarded as sustained post-synaptic potentials mediated largely by non-specific excitatory and inhibitory systems, and possibly by anterior projections of exteroceptive afferents. The early components of sensory evoked responses, on the other hand, probably involve significant unit firing components as well as post-synaptic potentials (Morrell, 1967).

The spatial distribution of DC responses to experimental stimuli may vary greatly. The anterior DC responses studied in this thesis are widely distributed, with greatest amplitude in the prefrontal areas, as measured by Walter (1964) with implanted electrodes in human Ss. Although SEPs are also widely distributed across the cortical surface, the waveform of these responses changes from one locus to another, indicating more complex spatio-temporal patterns of neural activity than those apparently present in DC responses (Goff et al., 1962; Clynes et al., 1964; Walter, 1964). Studies of stimulus parameters of averaged visual SEPs have shown that the spatio-temporal patterns of responses vary according to the intensity, color, complexity and shape of the stimulus (Clynes et al., 1964; Cavonius, 1965; Shipley et al., 1965; Spehlmann, 1965; John et al., 1967; White & Eason, 1967). These stimulus-specific patterns of response are replicable within Ss from session to session despite the low amplitude of the responses relative to the ongoing EEG.

The details of the anatomical substrates and distribution of human DC responses have yet to be described. Nevertheless the interpretation given above is reasonably well-founded in fact. While the anatomical and physiological basis of electrocortical activity may lead one to speculate about its functional significance, such speculation must be supplemented by a consideration of the behavioral correlates of electrocortical responses.

Behavioral Correlates of Electrocortical

DC Responses in Rats, Rabbits and Cats

Much of the basic exploration of the DC response has been conducted on species other than man. This work, mainly on rats, rabbits and cats, is briefly reviewed here before discussing the human experimental literature.

Cortical DC shifts in response to unconditioned stimuli in rats, rabbits and cats have been correlated with brain electrical stimulation, onset of sleep, arousal from sleep, satiation of hunger, spontaneous locomotion, and sensory stimulation. DC shifts in response to conditioned stimuli have been produced with both classical and operant conditioning of rats and cats. The DC responses correlated with these different phenomena vary in frequency, amplitude, and locus of the maximum shift.

Unconditioned surface-negative shifts of short duration (1-5 sec.) may be induced by electrical stimulation of the cortex, the peripheral sensory nerves, or the mesencephalic reticular formation of the cat (Goldring et al., 1954; Arduini et al., 1956; Goldring & O'Leary, 1957; Brookhart et al., 1958; Vanasupa et al., 1959; Caspers, 1961). These responses can be measured in the upper cortical layer, in the specific sensory areas of the cortex, as well as in the nonspecific cortex. The responses of the nonspecific cortex are not blocked by topectomy of specific sensory areas of the cortex, implying that nonspecific DC responses must be mediated by a separate subcortical system such as the reticular formation of the mesencephalon (Arduini, 1961).

Stimulation of the exteroceptors has been found to be accompanied by DC shifts in the cat cortex, corresponding in duration to the duration of the stimulus (Gumnit, 1960, 1961; Caspers, 1961). These shifts are localised in specific sensory areas of the cortex, but a response of lower amplitude may be detected in cortical areas adjacent to the main focus of activity. In cats, Caspers (1961) also observed a DC shift of variable polarity correlated with spontaneous locomotion.

Gradual, much longer DC shifts occur during the transition from wakefulness to sleep, and following arousal from sleep, in both the rat and the cat (Caspers, 1961; Wurtz, 1965, 1966; Norton & Jewett, 1965; Pirch & Norton, 1967). Similarly, very slow DC shifts occur during and after ingestion of food in the rat and cat (Rowland, 1964; Norton & Jewett, 1965; Cowen & McDonald, 1965). These slow shifts are highest in amplitude in the anterior cortex. The polarity of DC shifts during onset of and arousal from sleep varies with individual animals and preparations, but is constant within any single case. DC shifts associated with eating are somewhat less variable from animal to animal; the majority show a negative shift during eating, followed by a positive shift after eating to satiation (Rowland, 1964).

Conditioned DC shifts have been demonstrated in numerous studies of the rat and cat. Shvets (1958), Rusinov (1960), and Wurtz (1966) have shown the gradual development of a brief surface-negative DC shift to the CS during acquisition of an avoidance response. Morrell (1960) conditioned a negative DC shift to a tone stimulus using electrical stimulation of the centre median nucleus as the US. Rowland (1961) showed a similar DC response in cats to classically

conditioned visual and auditory stimuli. Rowland and Goldstone (1963) reported longer conditioned shifts, both positive and negative, to trains of flash and click stimuli which had been reinforced with food after 10 sec.; these responses increased in amplitude as food deprivation was increased, and extinguished as a function of the volume of food ingested rather than of the number of trials. Finally, Pirch and Norton (1967) reported a biphasic conditioned DC shift: during approach towards a food reward a negative shift occurred, and during eating a positive shift was observed.

In summary, two kinds of unconditioned short-duration DC shifts have been reported in animals: nonspecific responses to stimulation of the reticular formation and cortex, and sense-specific responses to stimulation of the peripheral sensory nerves and exteroceptors. Conditioned DC shifts have also been reported, and are most similar in duration and locus to the nonspecific responses to stimulation of the reticular formation.

The longer unconditioned DC shifts described above, which are correlated with sleeping, waking, and eating behavior are quite different in duration, amplitude and locus from other DC responses: they tend to be greater in amplitude, and endure for periods as long as 30 minutes. Often the response takes the form of a constant drift in one direction, with no immediate return to the previous baseline. Because of these differences they will not be included in my interpretation of the shorter human DC responses which have been related to complex behavior.

The most common interpretation of the above findings with the shorter duration DC shifts is that a change in the DC potential is an indication of sustained central activation at a given cortical locus (Arduini, 1961; Rowland, 1964). With the exception of the slow unconditioned shifts during sleeping and eating which vary widely in polarity and amplitude, surface-negative DC shifts correlate with sustained cortical excitation and behavioral activation, and surface-positive DC shifts correlate, in several experiments, with reduced behavioral activation. However, Motokizawa and Fujimori (1964) have shown the independence of the cat's DC response from frequency changes during the EEG arousal response, thus refuting any simple relation between activation and DC shifts. One investigator (Cowen, 1967) has offered an alternative interpretation, based on the different cortical projections of exteroceptors and interoceptors. Negative anterior DC responses might occur with attention to the external world, that is, specific facilitation of the exteroceptive afferent systems. Positive responses at the same locus might indicate attention directed towards internal sensations, such as the visceral sensations following satiation of hunger. The two hypotheses, the activation hypothesis and the direction-of-attention hypothesis, have been further studied with human subjects and will be referred to in the following section.

Behavioral Correlates of Electro cortical

DC Responses in Man

Unconditioned DC responses in human Ss have been correlated with sensory stimulation, some aspects of visual perception, and with voluntary movements. Conditioned DC responses have been

produced in both classical and operant conditioning paradigms.

Stimulation of visual or auditory receptors produces unconditioned DC shifts in the specific sensory areas of the human cortex. Köhler (1955) and Köhler et al., (1957) found both positive and negative shifts in the occipital cortex with visual stimuli, and in the temporal cortex with auditory stimuli. Although some controversy followed the publication of these results, they were reinforced to some extent by Gumnit's (1960) similar findings with cats. The responses reported by Köhler were highly localised and specific and thus quite different from the non-specific anterior responses with which the present investigation is concerned; therefore, they are not discussed further in this thesis.

Kornhuber and Deecke (1965) reported anterior negative DC shifts preceding spontaneous voluntary movement of hand and foot, and positive DC shifts following each movement. The former, which they called the "readiness potential" resembles the negative DC shifts accompanying acquisition of a CR in cats; the latter, the authors pointed out, resembles the late bilateral components of the responses evoked by electrical stimulation of the peripheral nerves.

Walter (1965) and Cohen and Walter (1966) observed a positive wave of 1-2 sec. duration following a brief exposure of a complex visual stimulus requiring S to keep track of correct solutions to a perceptual problem. This positive DC shift, reaching its highest amplitude in cortical prefrontal regions was independent of stimulus duration, and was maintained even after the S was bored and drowsy.

Cowen (1967) reported a number of unconditioned DC shifts in human Ss. He measured the response of the anterior cortex, using the inion as reference, in contrast to most other studies in the literature, which reported using more inactive reference points such as the earlobe or mastoid. His results provided some support of his thesis that brief stimulation of exteroceptors (tactile, auditory, olfactory, gustatory, visual, or proprioceptive) is followed by negative anterior cortical DC shifts of several seconds duration, whereas stimulation of the interoceptors (visceral organs, carotid body, or vestibular organs) is followed by positive shifts. Evaluation of his results is made difficult by his failure to report his data in sufficient detail.

Conditioned DC shifts have been widely studied in human Ss during the past three years. Walter (1964) observed that when two stimuli are paired sequentially so that the first serves to signal the occurrence of the second, a negative shift reliably occurs at the surface of the anterior cortex immediately following the first stimulus and endures until the occurrence of the second stimulus. Since the negative shift is independent of the intensity or modality of the stimuli, it appears to correlate with a state of expectancy within the S. Thus the author called it the Expectancy Wave, or Contingent Negative Variation (CNV). When induced by simple pairing of stimuli, CNV has a relatively low amplitude and habituates rapidly. However, when a response is required to the second stimulus, CNV is very slow to habituate and is sensitive to instructional and social influences. The CNV has been observed to persist even when the onset of the second stimulus occurs as long as 4 seconds after the

first stimulus, but as the interstimulus interval is prolonged past this point the DC shift becomes less well timed, lower in amplitude, and thus more difficult to observe in an averaged record.

The significance of CNV is not yet clear. Walter (1964) suggested that CNV is a sort of fronto-cortical priming which regulates the time relations of the voluntary motor discharge related to the task, and corresponds to the enhanced orientation of the S. McAdam (1966) demonstrated that trained Ss can increase the amplitude of CNV by increasing the amount of "effort" or "concentration" they devote to the response to the second stimulus, and also that CNV increases in amplitude with more difficult tasks. The same author showed that CNV is most prominent as the S learns a temporal interval, and that after learning has taken place CNV habituates even though time estimation remains at its previous optimal level. Thus CNV does not appear to be a necessary feature of either expectancy or temporal set. It is more likely that CNV is a correlate of the enhanced concentration that is necessary during response acquisition, but which is unnecessary once learning has reached its asymptotic level or once the performance of the task is automated and less concentration is needed.

In summary, there is considerable agreement among studies of human Ss concerning the conditions that elicit a negative DC shift. Kornhuber and Deecke's "Readiness Potential" and Walter's CNV appear to be essentially the same phenomenon: in both cases a negative DC shift occurs during the period immediately preceding a response on the part of S, and in neither case is the DC shift a

function of stimulus parameters per se. Positive DC shifts have also been observed by Kornhuber and Deecke (1965) following voluntary movements by S, and by Walter (1964) following a complex perceptual identification task.

The results of these human studies confirm in many ways the results of experiments on other species. Negative DC shifts reported during conditioning of cats and rats apparently resemble the CNV observed in human experiments. Responses preceding and following voluntary movements in cats (Caspers, 1959) resemble to some extent those reported by Kornhuber and Deecke with human voluntary movements.

Despite these few similarities between studies of man and studies of other species, I interpret the data from human Ss as evidence against applying to man the explanations of the DC response generated from studies of infrahuman species. The activation hypothesis, reported in the previous section, is weakened by Walter's (1965) finding that positive DC shifts occur following visual stimulation when S is required to keep track of complex aspects of the stimulus; this result implies that the type of behavioral activation demanded by the task used in Walter's study is neurophysiologically distinct from those kinds of activation which produce a negative DC shift. A unitary activation interpretation could not account for both positive and negative DC responses. Similarly, Cowen's (1967) direction-of-attention hypothesis cannot be applied to the data from human Ss. First, most available evidence indicates that surface-negative DC shifts (of which CNV is the prototype) occur not following exteroceptive stimulation, but during periods of anticipation of exteroceptive stimulation and preparation for response. Second,

exteroceptive stimulation may be followed by either a positive or a negative DC response or none at all, depending upon the task demanded of S. Finally, CNV can occur in the absence of any clearly defined external task stimulus; it has been elicited in time estimation tasks in which the signal to respond was generated within S himself (McAdam, 1966).

Thus neither of the hypotheses which were based upon studies of infrahuman species appears to account for the data on the human DC response. Whether this is due to differences between the species, differences in experimental design, or differences in recording techniques cannot yet be ascertained.

The Present Study

The present study is concerned with the functional significance of DC responses in the human cortex which, like CNV, are of negative polarity and fall within a duration range of approximately 500 to 5000 msec. In my experiments, the electrocortical DC potentials of human Ss are studied in a variety of paradigms which have the common characteristic of being fixed-foreperiod decision tasks.

As reviewed in the previous section, available evidence shows that the processes underlying CNV are not part of the primary sensory or motor systems, and should be considered central or associative in nature. These central processes are not correlated with a specific pattern of stimulation or a particular kind of response. They are rather related to an internal state which existing studies define as "timed expectancy in a motivated S." This definition could lead one to hypothesize that the substrates of CNV serve to facilitate cor-

tical processing of anticipated sensory input. But it could equally well indicate another hypothesis; that CNV is related to sequential cortical association systems which determine the rules and programmes for response--in short, the response selection process. Or finally, it could mean both or neither of these possibilities. In other words, the definition of the behavioral correlates of CNV is not yet clear enough to provide evidence for or against any of these hypotheses. An understanding of the functional significance of CNV must await such evidence.

In my studies I attempt to construct a clearer definition of the behavioral correlates of CNV. My working hypothesis about the behavioral correlates of CNV places emphasis upon cortical control of performance, rather than upon sensory processing or general activation. My tentative view is that CNV is related to the process of response selection--whether the task requires a perceptual, cognitive or overt motor response. Thus the termination of CNV would be considered as a correlate of the termination of the response selection process.

In the context of my hypothesis I conducted a pilot study in which CNV and similar cortical DC responses were explored within a broader range of performance than was used in earlier studies. Following the exploratory studies I conducted two experiments. The first experiment concerned the relation of CNV to the response selection processes which follow the presentation of the task stimulus in a selective reaction time paradigm. The second experiment asked whether a sustained negative DC response influences the late components of the SEP, in the manner of a central attentional system.

THE INVESTIGATION

Throughout the following investigation cortical DC responses were elicited by having human Ss perform various tasks in response to task stimuli (TS), with a fixed foreperiod preceding either the TS, or S's response, or both. The S's DC electrocortical activity was averaged on a computer during and following the fixed foreperiods, and the resulting averaged responses were studied as a function of S's performance. The relevant averaged responses were always negative in polarity. Since the term "CNV" has been used recently (McAdam, 1966) in a broader context than that originally used by Walter (1964), the averaged responses reported below are always referred to as CNV, to provide as much continuity as possible with the existing literature.

General Method

The apparatus and procedures common to all experiments are described below. The apparatus subsection includes recording, stimulation, programming, and data processing techniques, all of which are illustrated schematically in Figure 1. The procedure subsection includes details of electrode placement and seating of S, general instructions, and the testing procedure.

Apparatus

Recording. All electrocortical potential changes reported in this study were obtained from the scalps of adult human Ss. Non-polarisable silver-silver chloride DC electrodes (Tursky type) filled with a conducting jelly (Sanborn Redux) were attached to the scalp

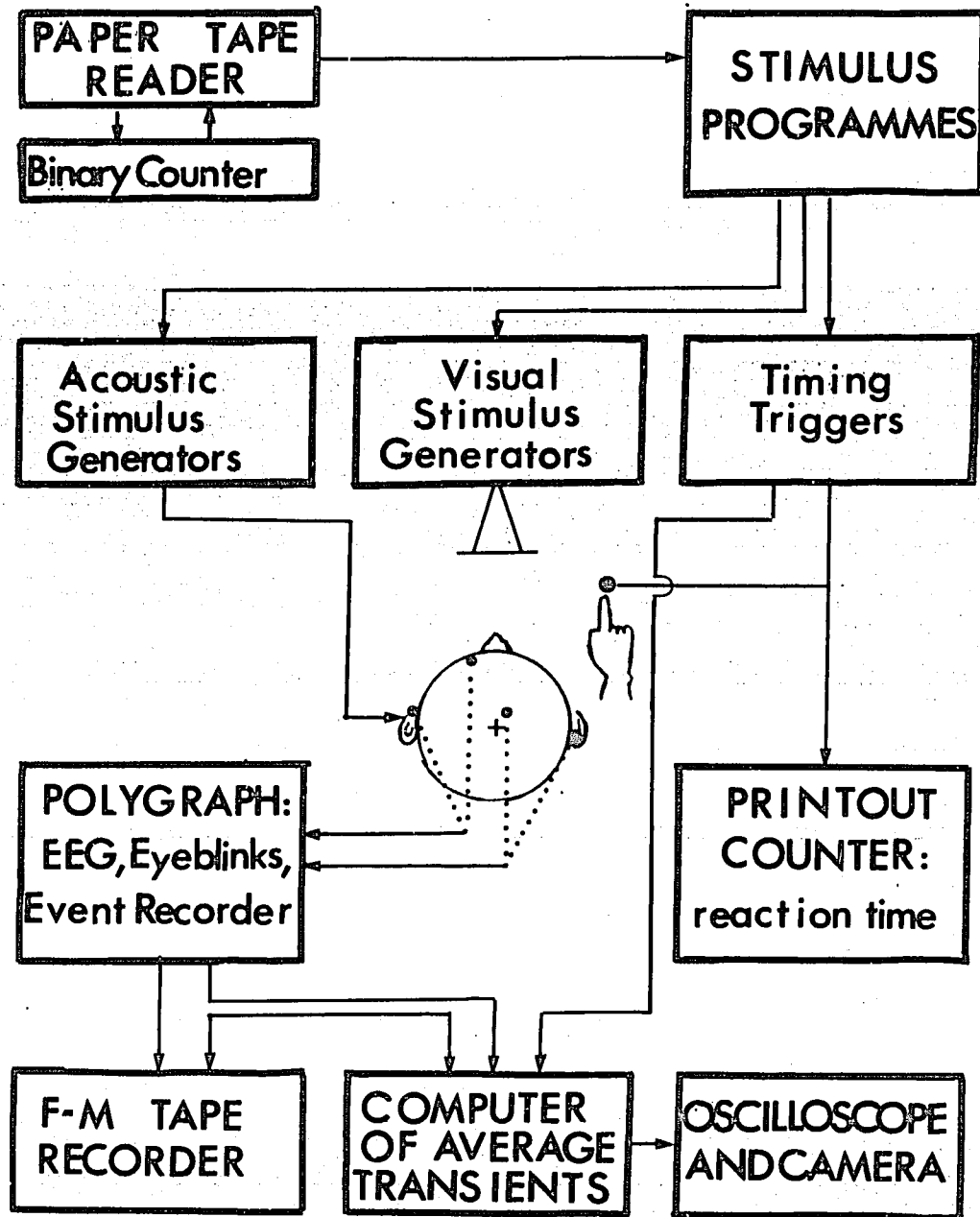


Figure 1. Schematic diagram of recording, stimulation, programming, and data processing apparatus.

with flexible collodion. The S was grounded to the recording system. A low-level DC preamplifier (Grass, model 5Pl) and a DC driver amplifier (Grass, model 5D) were used to amplify the electroencephalogram. An ink-writing oscillograph (Grass, model 5D) provided a permanent record of the raw data. The DC signal was also taken from the driver amplifier via a reverter (Grass, model R5) to an oscilloscope (Tektronix, model 502 A) and to an average-response computer (Mnemotron Computer of Average Transients, or CAT 1000), which was triggered by a 3-volt pulse synchronised with the appropriate stimulus event. When necessary the data were stored on an FM tape recorder and later played back into the CAT computer; the CAT trigger pulse was also recorded on a separate channel of the tape recorder. A potentiometer provided on the preamplifier was used to balance the voltage on the oscillograph several seconds before each stimulus. Behavioral reaction times (RT) were measured from a microswitch set into an armrest adjusted so that S's right index finger rested comfortably beside it; thus a minimum of motor movement was required for S's response. The RT was recorded on a printout counter (Hewlett-Packard, model 562 A).

Stimulation. Visual stimuli were generated from two sources. First, brief 10 microsec. flashes, used in the exploratory studies, were produced by a photostimulator (Grass, model PS-2) masked to 5 cm. in diameter and set at intensity level 3. Second, pictorial stimuli used in the exploratory studies were flashed from a tachistoscopic projector onto a small screen 130 cm. in front of S, subtending a retinal angle of 3 degrees. Third, the flash and digit

stimuli for all other experiments were produced by in-line stimulus projectors (Grason-Stadler, model 10052-44-B) whose brightness was approximately 29 foot-lamberts. The photostimulator tube and the stimulus projectors were placed at eye level about 70 cm. in front of S. All stimuli except the second subtended a retinal angle of 2 degrees and were centred on a fixation point. Ambient light level in the testing chamber was kept to a minimum so that distractions were minimized. A white-noise generator, an oscillator, and a microphone were connected to an audio mixer and an amplifier so that the experimenter (E) could deliver a variety of auditory stimuli to S via a set of padded earphones (Koss, model SP-3X).

Programming. Timing and ordering of stimuli were achieved with logic modules (BRS solid-state Digibit components) programmed from a paper tape reader (Omnitronix, model 119). Signals punched on a paper tape served to control both stimulus events and intertrial intervals. The CAT computer trigger pulse and the operate pulse for the printout counter were synchronized with stimulus events by means of logic modules.

Data Processing. Data were stored in two forms. Ink-written oscillograph records of each recording session were kept, and in addition the CAT-averaged EEG responses were projected onto the oscilloscope screen and photographed with an oscilloscope camera (Tektronix, model C-12). The oscillograph records contained the DC electroencephalograph, a record of eye movements, a record of S's reaction times, and two channels of stimulus event markers.

Procedure

Electrode placement and seating of S. The active DC electrode was attached to the scalp approximately 2 cm. anterior and to the right of the vertex (the point at which the nasion-inion and interaural lines intersect), and the reference DC electrode to the inside face of the right or left earlobe. The placement of the active electrode was over premotor cortex (Brodmann area 6), according to a method for calculating the relative skull position of the Fissure of Rolando described by Chusid and McDonald (1960), and illustrated in Figure 2. An eye-movement electrode was placed with adhesive tape over the left eye orbit, with its reference on the right or left earlobe. A ground lead was attached to the earlobe other than that used as the EEG reference. S was seated in a comfortable chair, and the earphones were placed on his head. White noise at 73 db. SPL was fed through the earphones to mask distracting sounds. Although the masking was not complete, there was no stimulus-locked noise reaching S. The armrest containing the RT microswitch was adjusted to a comfortable position, and the stimulus generator was set about 70 cm. in front of S's eyes.

General instructions, calibration, artifacts. The S was told to relax completely, to close his eyes, while the amplifiers were calibrated, the balance voltage was adjusted, and the standing DC voltage recorded. At this point electrode contacts were checked, and the electrodes reapplied if electrical noise (especially 60 cycle) was not at a minimum. S was then told the nature of the task he was to perform, and to react "as fast as possible without making any errors." He was then given a series of practice trials until E

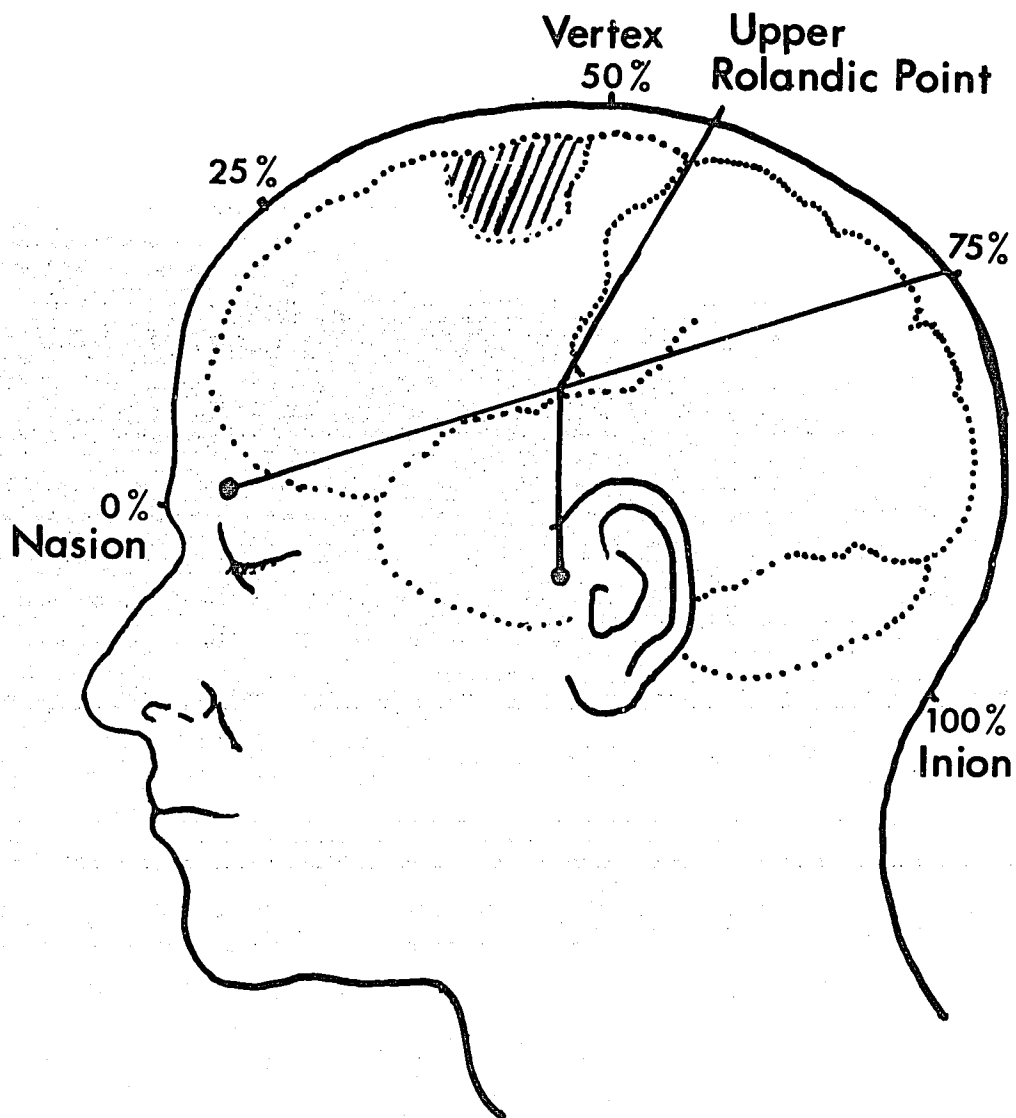


Figure 2. Estimation of position of Rolandic Fissure relative to Vertex. Hatched area represents approximate range of active electrode placements during all experiments. Adopted from Chusid & McDonald, 1960, p. 223.

judged that S had mastered the task. At this point the actual programmed trials were begun. S was also told to avoid blinking or moving his eyes in any systematic way during the trials, and during the practice session his performance and EEG record were carefully scrutinized for evidence of artifacts such as frowning, blinking, clenching of the jaw, etc., any of which might contribute non-cortical electrical activity to a record. Throughout all experiments particular attention was given to control of artifact, and any records which were suspected of containing serious distortions of the relevant cortical response were discarded and the trial repeated.

General testing procedure. Individual testing trials lasted between 10 and 20 minutes, and the overall session from 2 to 3 hours. Regular 2 min. breaks were given after every block of trials, and longer breaks were given approximately every half hour. Ss were instructed to stop the session for a further break if they felt drowsy or fatigued. Specific aspects of the testing procedure are described in each study.

Exploratory Studies

In several exploratory studies I examined CNV with a wide variety of procedures, including the simple "expectancy" paradigm used in previous investigations, in order to further specify the nature of its behavioral correlates. The general characteristics of CNV were determined with four different tasks: simple visual and auditory reaction time; short-term storage and recall of digit sequences; short-term storage and recall of pictorial stimuli; and the multiplication of acoustically presented digits by a constant.

Procedure. The Ss were three male and two female undergraduate students, aged between 19 and 24 years. Of these, two were tested on several occasions during a period of six weeks; the remaining three were tested on four sessions each, usually within a period of one week. There was no strictly determined design for any specific recording session; the duration of the tasks, the modality of stimulation, and the duration of the averaged responses were varied from one session to another, according to each S's performance.

Four kinds of stimuli were used: brief flashes of light delivered from the PS-2 stimulator; digits presented visually via the stimulus projectors mounted in front of S; pictorial stimuli (cartoons) projected from behind S onto a screen 130 cm. in front of S; and digits spoken by E into a microphone connected to the S's earphones.

The four tasks employed in the study may be described as follows: (a) SIMPLE REACTION TIME. The S was required to press the reaction key as fast as possible after every stimulus. Both visual and acoustic stimuli were used. For visual RT, a flash from the PS-2 stimulator served as the TS; it was preceded by a 30 msec. warning tone (900 cps., 80 db SPL) presented between 1 and 4 sec. before the TS. For auditory RT, a 30 msec. tone (900 cps, 80 db SPL) served as the TS; the TS was preceded by the word "ready" spoken by E into the earphones between 1 and 4 sec. before TS.

(b) SHORT-TERM STORAGE OF DIGIT SEQUENCES. The S was required to memorize a series of five to eight digits presented at regular intervals of .8 sec., and to repeat the series upon the instruction

"report" spoken by E into the earphones about 5 sec. after the end of the series. S was given practice trials until E had determined the maximum number of digits S could memorize without error, and without undue frowning or tensing of artifact-causing muscles.

(c) SHORT-TERM STORAGE OF PICTORIAL STIMULI. The S was required to remember as many details as possible of a complex pictorial stimulus presented for a 4 sec. exposure, and to report what he remembered upon the instruction "report" from E, about 5 sec. after the TS. Care was taken to eliminate eye movement artifacts on these trials.

(d) MULTIPLICATION OF DIGITS BY A CONSTANT. The S was required to multiply an auditory digit stimulus, spoken by E into the earphones, by a two-digit constant previously given to him by E, and to state the product upon the instruction "report" from E, spoken into the earphones about 5 sec. after the stimulus.

The experimental sessions were not all uniform; a good deal of the time was spent learning how to control and detect artifacts due to eye movements, frowning, blinking, etc., and trying various ways to record the data. Also, much attention was given to background DC activity which affected the waveform of CNV.

The DC potentials were recorded on polygraph paper, along with a record of eye movements. The evoked DC responses during the various tasks were averaged on the CAT computer. At first an epoch (sweep time) of 2000 msec. was used, but for the greater part of the experiment an epoch of 16000 msec. was employed because of the added information it provided. Use of the 16000 msec.

epoch provided considerable technical difficulties, because (1) such long averaging periods are much more susceptible to artifact than shorter periods, and (2) the interstimulus intervals had to be so long that recording sessions became dull and arduous for the S. Nevertheless, the added information proved invaluable in understanding CNV and planning further experiments.

Results. A typical polygraph writeout of the DC record is presented in Figure 3, top. It will be noticed that no correlation is present between eye blinks or eye movements and the presentation of the stimulus. The record is 150 mm. in length; the paper speed, 2.5 mm./sec.; therefore, this record represents about one minute of recording time. There is a slight but insignificant drift negative; at the end of the record the baseline is about 40 microvolts more negative than at the beginning.

(a) SIMPLE REACTION TIME. Given a relatively stable baseline, and freedom from other sources of artifact, the typical waveform and amplitude of CNV during simple RT tasks is given in Figure 4. The two top traces show how the CNV develops following the presentation of the acoustic WS, and terminates after the presentation of the auditory or visual TS. This is the "classic" CNV during a period of "expectancy," and resembles closely the data reported by Walter (1964). The two lower traces show control averages taken during the same sessions, with no WS preceding the TS; they show no CNV. The waveforms of the responses following the TS need not be taken as typical; these waveforms vary greatly from task to task and subject to subject, as will become evident in later figures.

Channel

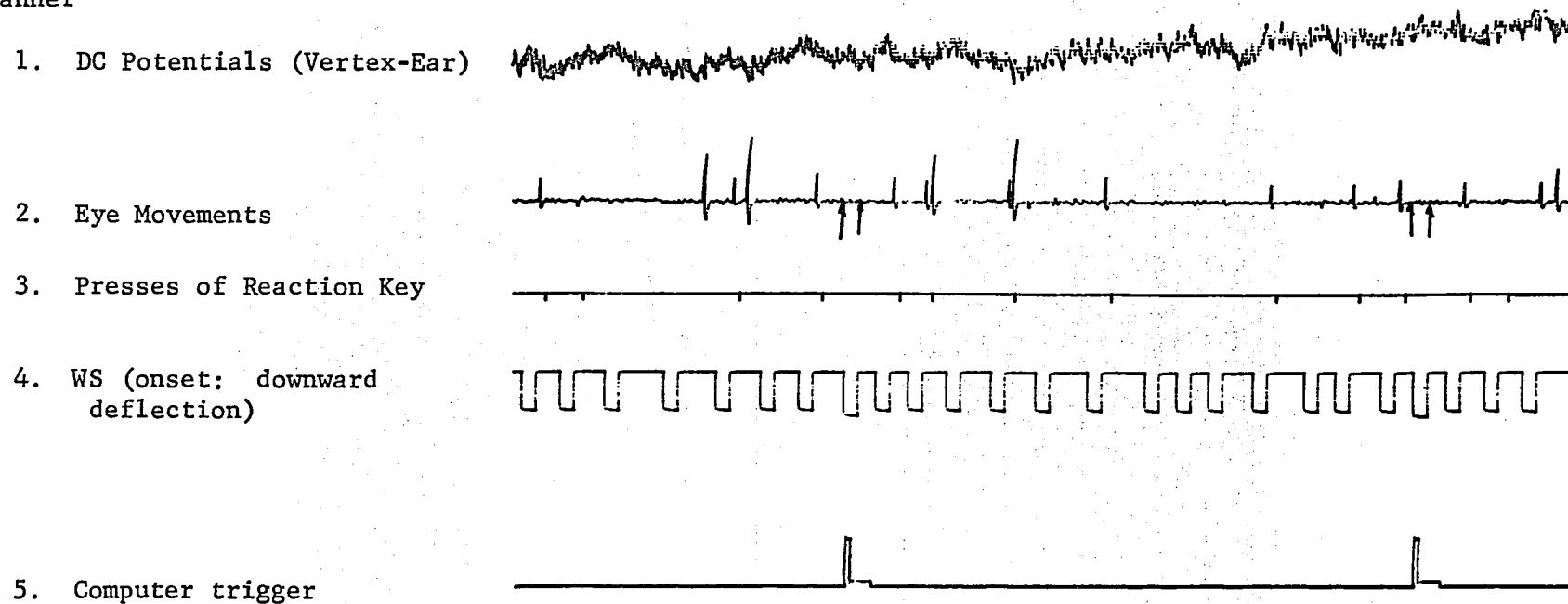
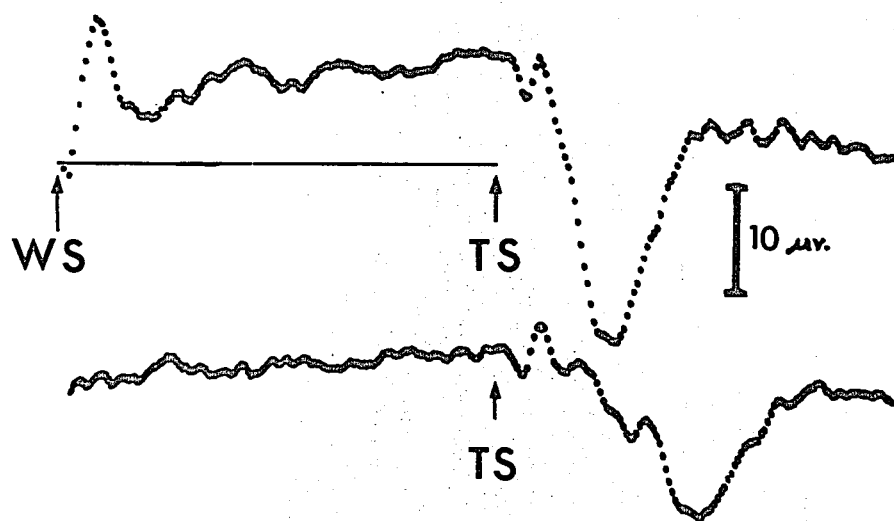


Figure 3. Polygraph writeout of (1) DC potentials, (2) eye movements, (3) RT key presses, (4) onset and offset of WS, and (5) computer sweeps. Subject: P.M. Arrows on channel 2 indicate computer sweep epochs are free of gross eye movements.

VISUAL



AUDITORY

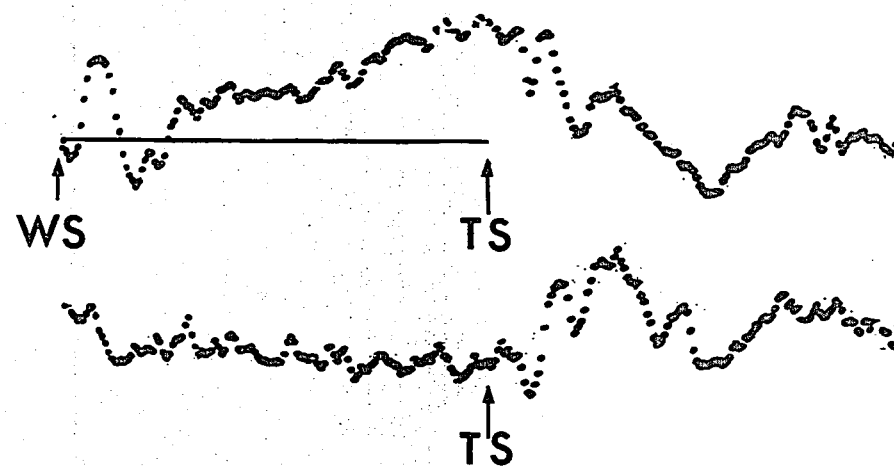


Figure 4. Form of CNV during simple visual and auditory RT tasks with fixed foreperiods (upper traces) and without fixed foreperiods (lower traces). Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: 1000 msec. N: 20. Subject: P.A. An upward deflection indicates a negative potential change at the vertex.

Although the 2000 msec. sweep time provided a convenient time base from which to study CNV, I became interested in longer-lasting DC shifts, and conducted the rest of this study with a 16000 msec. sweep time. Averaging such long time periods revealed two phenomena associated with CNV which have an important bearing on the way we regard shorter CNVs. Examples of these phenomena are given in Figure 5. On the left side of each trace a typical CNV is shown developing from the time of onset of the acoustic WS, and terminating shortly after the auditory TS. The remaining part of each trace represents the averaged DC potentials during a period of silent inactivity which followed the CNV. The uppermost trace shows no non-random DC activity following termination of CNV; the averaged potential following CNV is flat, and the activity associated with CNV is restricted within a 5 sec. period. The middle trace demonstrates a phenomenon which frequently follows CNV during task performance: a protracted positive "rebound." In this trace the positive going wave of activity starts about 1.5 sec. after the TS, and lasts for 5 sec. before the DC voltage returns to its previous level. The lower trace demonstrates a CNV followed by a long negative rebound after the TS; this phenomenon occurs frequently when intertrial intervals are long and fairly regular and the task overpracticed. Although the meaning of these rebound effects is not clear, it is important to note them because computer sweeps shorter than 16000 msec. might include only the early seconds of a rebound effect, thus producing the mistaken impression of a positive or negative voltage shift following CNV with no return to the previous voltage.

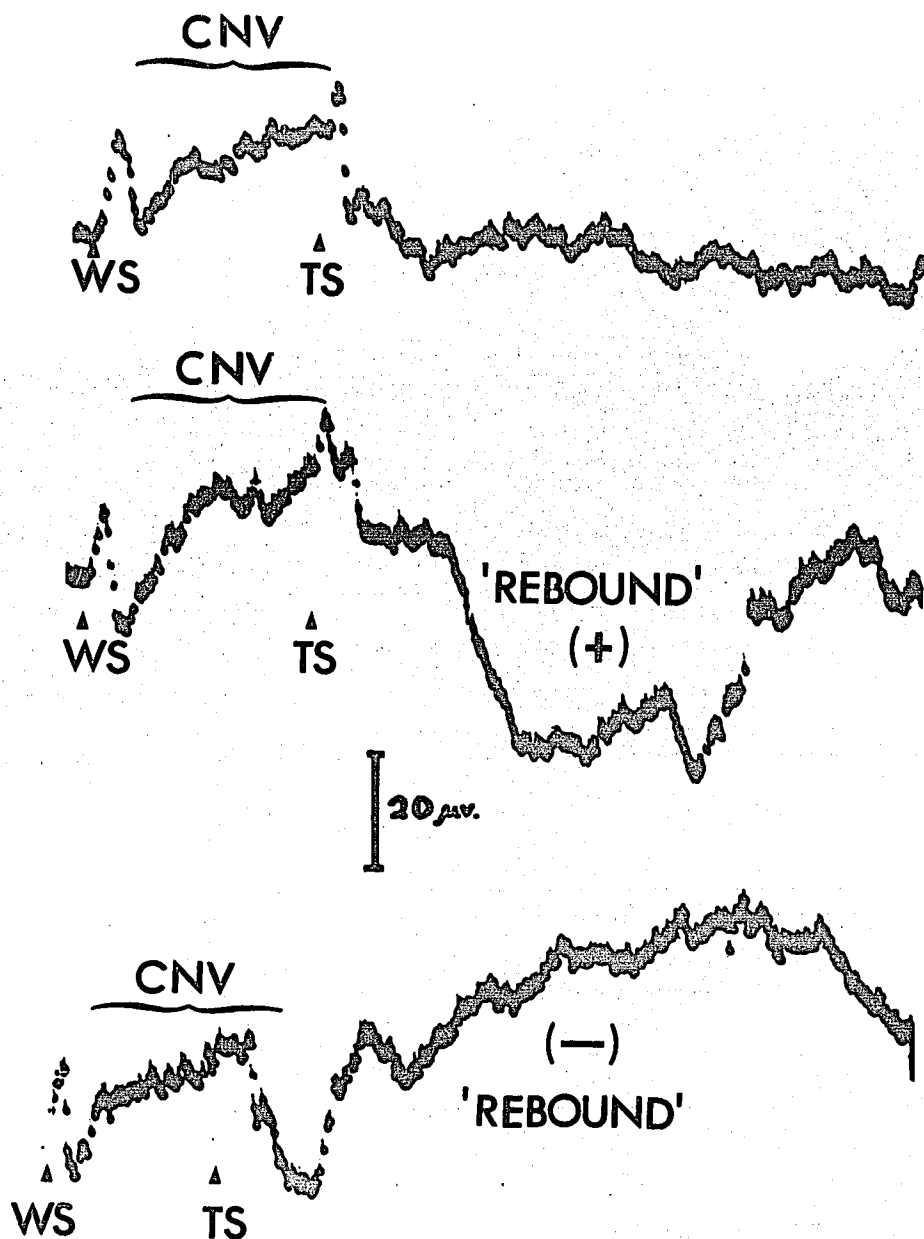


Figure 5. CNV during simple auditory RT task, illustrating two kinds of averaged DC activity which may follow CNV itself: positive rebound (middle trace) and negative rebound (lower trace). Sweep time: 16000 msec. WS: warning signal. TS: task signal. WS-TS interval: upper and middle traces, 3000 msec.; lower traces, 2500 msec. N: 15. Subjects: upper and middle traces, A.S.; lower trace, M.B. An upward deflection indicates a negative potential change at the vertex.

(b) SHORT-TERM STORAGE OF DIGIT SEQUENCES. During several trials with simple RT, I had observed negative DC shifts of much larger and longer amplitude than CNV on the raw EEG oscillographic record, which were apparently related to preparation for a trial by S on a verbal cue from E. In order to control these shifts so that averaging was possible, S was given a task which required sustained attention to a TS, followed by sustained rehearsal of a response until the response was demanded by E. The time from TS to E's instruction to respond was constant, and it was possible to average the DC response during this constant interval. One such task was the short-term storage of digits presented visually or acoustically. Typical records from these trials are shown in Figure 6. There was a slight negative drift during the presentation of the TS, which became steeper in slope as the stimuli were terminated, and which attained an amplitude several times that of previously observed CNV. Following the recall of the digits by S on the instruction "report," the DC voltage returned to its previous level. The negative DC shift was sustained throughout the rehearsal period, until the response was terminated by S. The phenomenon was the same for both visual (upper) and auditory (lower) TSs.

(c) SHORT-TERM STORAGE OF PICTORIAL STIMULI. A similar long-lasting, high amplitude response was observed during trials on which S was asked to store complex pictorial stimuli in memory. A period of rehearsal followed each 4 sec. stimulus presentation, and, as is shown in the upper trace in Figure 7, it is during the rehearsal period preceding recall rather than during the stimulation period

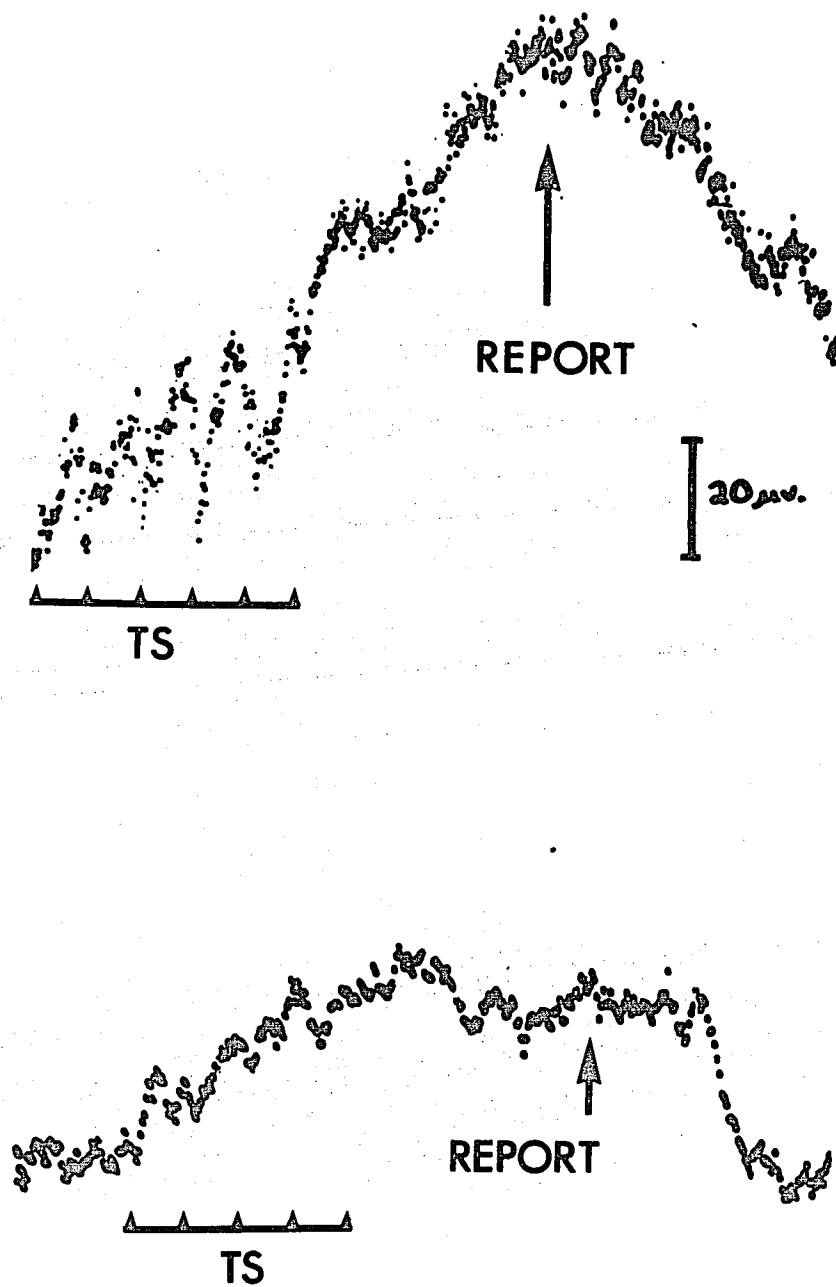


Figure 6. Averaged DC activity during short-term storage of digit sequences presented visually (upper trace) and acoustically (lower trace). Sweep time: 16000 msec. TS: task signal. N: 20. Subjects: upper trace, M.K.; lower trace, P.A. An upward deflection indicates a negative potential change at the vertex.

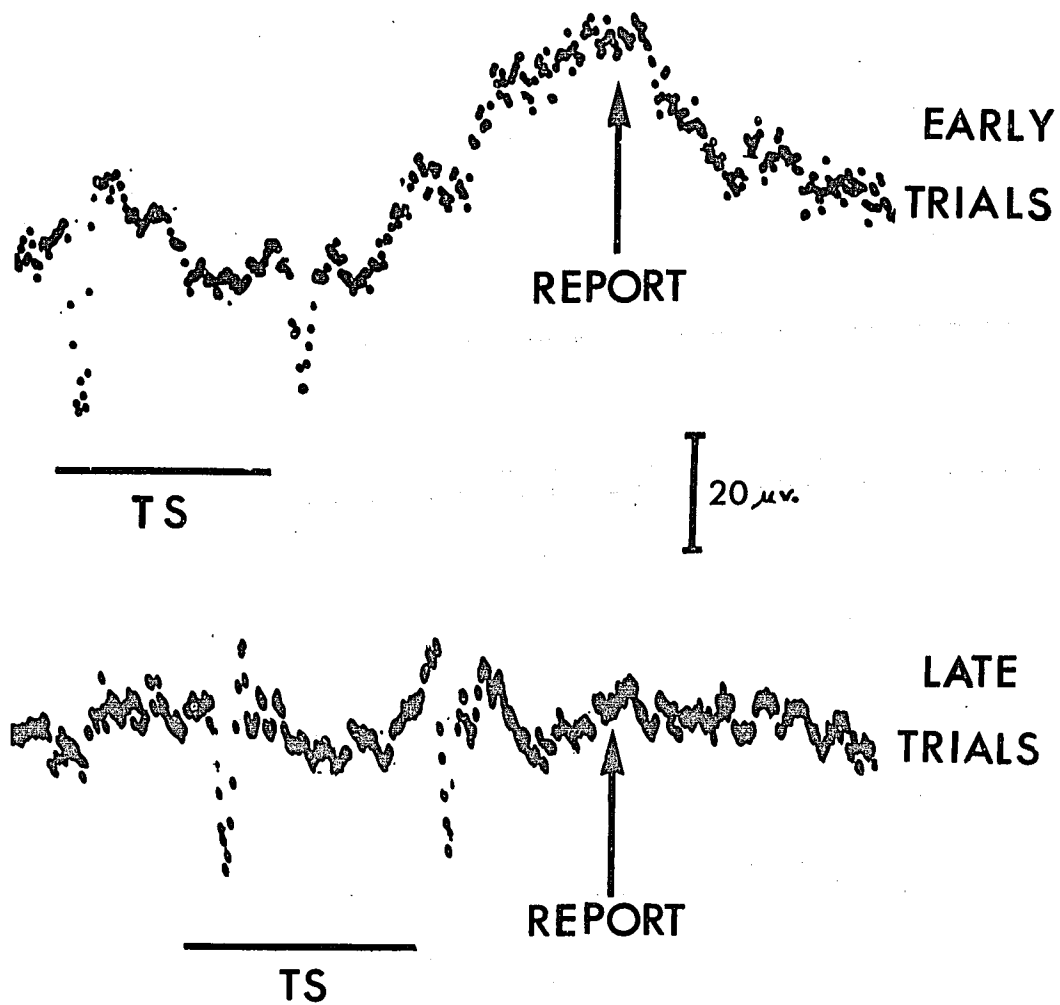


Figure 7. Averaged DC activity during short-term storage of pictorial stimuli: early (upper trace) and late (lower trace) trials. Sweep time: 16000 msec. TS: task signal. Duration of task signal: 4000 msec. N: 20. Subject: M.B. An upward deflection indicates a negative potential change at the vertex.

that large negative DC shifts were readily elicited. Note that the brief positive-negative waves to the left of Figure 7 are "onset" and "offset" SEPs to the TS. Following the TS, a negative DC shift develops and is sustained during rehearsal until S recalls the stimulus on the instruction "report." The lower trace shows the response of the same S after the task had been practised and the same stimuli were being repeated; the negative DC shift preceding recall habituated in the same manner as CNV habituates when interest or effort is reduced to a minimum (Walter, 1964; McAdam, 1967). This implies that a direct correlation exists between amount of "effort" and the amplitude of these long DC shifts, and is further evidence for considering them to be equivalent to CNV.

(d) MULTIPLICATION OF DIGITS BY A CONSTANT. An example of averaged DC responses during an auditory multiplication task (performed with the eyes closed) is given in Figure 8. In both upper and lower traces the stimuli were preceded by 3 sec. by a WS (the word "ready"), and followed by a request for report 4 sec. and 7 sec., respectively, after the TS. In the two traces the DC shift begins at the WS and continues until the report is given. The SEPs to the TS in these trials are almost non-existent because the spoken digits were physically rather imprecise stimuli producing SEPs of varied latency, not lending themselves to averaging; since the evoked potentials to the TS are not of primary interest here, I do not feel that this is an important drawback to the meaning of these results.

A more important drawback to these experiments in general is the slow, imprecise return to previous voltage level of these large responses,

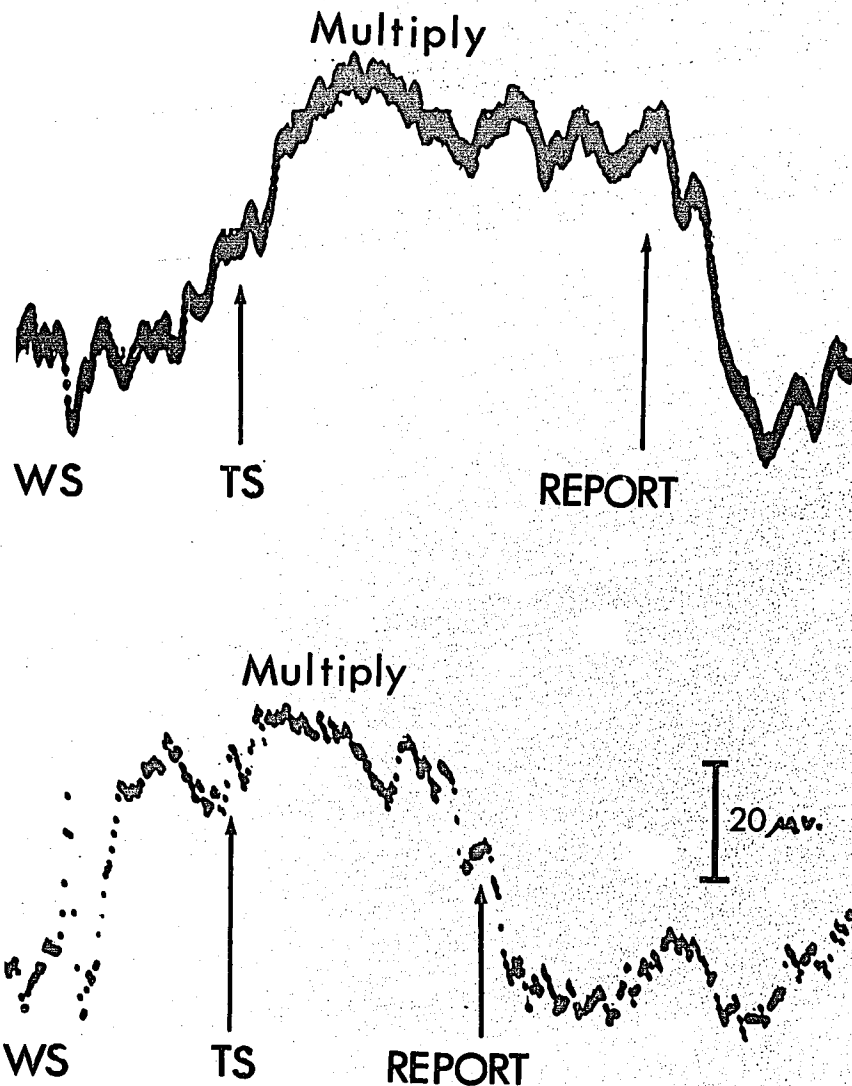


Figure 8. Averaged DC activity during silent multiplication of acoustically-presented digits by a constant. Sweep time: 16000 msec. WS: warning signal. TS: task signal. WS-TS interval: 3000 msec. N: 15. Subjects: upper trace, P.A.; lower trace, A.S. An upward deflection indicates a negative potential change at the vertex.

otherwise so like CNV. The reason for this undoubtedly lies in the wide variance in the latency of the Ss response following E's request of report. An attempt is made in experiment I to overcome this problem, by means of more precise control over RT, and use of a shorter averaging period.

Conclusion. The conclusion of this exploratory work is that CNV, or negative DC shifts which appear to share the characteristics of CNV, may be elicited with a wide variety of procedures other than the simple "expectancy" paradigm used in previous experiments. Expectancy was not the common correlate of CNV throughout the four different paradigms used in this study. In the simple RT tasks, the correlate of CNV could be termed "expectancy." But in the short-term storage tasks the correlate of CNV was rehearsal of the content of the stimulus, and in the multiplication tasks the correlate of CNV was the cognitive operation of multiplying two numbers. I hold that the common factor here is the limiting of attention to a small number of highly relevant associations for a brief period of time. Normally attention fluctuates and progresses in a continuous stream of associations more or less controlled; CNV appears to develop whenever S rigorously limits his associations, holding in immediate memory only what is immediately relevant to the task at hand. The particular task at hand does not matter--it may be simple reaction time, short-term storage or multiplication--except inasmuch as it determines the amount of effort required of S. Similarly the modality of stimulation whether visual or auditory does not bear upon the basic form of the response; (whether either of these factors affects the

cortical distribution of CNV cannot be ascertained from this study). Further interpretation of these data is reserved for the final chapter.

If CNV represents some cortical electrical correlate of the "holding of associations" involved in any kind of sustained concentration, the question remains: is the neural activity underlying CNV involved in the processing of sensory information relevant to the task, or is the CNV neural activity strictly a "central" event, that is, not involved in sensory processing? From the data of the exploratory studies CNV does not appear to be related to the TS, but, because of the long duration of the computer sweeps and the relatively imprecise timing of some of the stimuli, the SEPs to the TS are not clearly visible in these results. In the two experiments which follow, the question of the "central" nature of CNV is explored in more detail.

Experiment I

This experiment concerns the relation between decision time and the moment of termination of CNV following presentation of a task stimulus (TS) to which S is required to respond. If the function of CNV is to facilitate processing of the TS, it would be predicted that CNV would always return to baseline at some constant latency after presentation of the TS, so long as the stimulus properties were not changed. However, if CNV is not related to stimulus processing, but rather to some later associative stage of the response process--for instance, the stage at which the TS is related to a learned rule--it would be predicted that CNV would terminate at a constant latency after decision, and show no constant relation to the time of the TS.

These two alternatives were tested in a decision task paradigm which allowed E to change decision time without changing the stimulus parameters of the task. A visual RT task was employed, with an acoustic WS preceding each presentation of the TS. Variations in S's instructions regarding the rules for pressing the reaction key allowed E to manipulate task difficulty. By giving the appropriate instructions, E could control the RT distributions produced by S, while leaving the stimulus parameters unchanged. The CNV responses obtained under identical conditions of stimulation and differing only with regard to RT were then compared and any systematic changes in CNV that were a function of RT differences were noted.

Procedure. The Ss were two male and three female undergraduate students aged between 19 and 26 years.

The TS throughout this experiment consisted of a pair of digits presented simultaneously from two Grason-Stadler projectors mounted adjacent to one another at eye level 70 cm. in front of S. The digits subtended a visual angle of 4 degrees, and were exposed for a duration of 100 msec. at a brightness level of 27 foot-lamberts. On each trial a 30 msec. acoustic WS (900 cps at 80 db) preceded the TS by 1 sec. The two digits in the TS could be independently varied from 0 to 9, so that on any given trial they were either the same or different.

S's instructions, that is, the rules for pressing the reaction key, were varied from session to session. Four different sets of instructions were used:

(a) SIMPLE RT. S was instructed to press on every stimulus, regardless of the content. To assure that S was attending to the digits and not simply to changes in brightness, he was further instructed to count the number of times during each session that the stimulus array had been changed, and to report this number at the end of each session.

(b) SAME-DIFFERENT JUDGMENTS. S was instructed to press whenever the two digits in the TS were the same, and not to press if they were different.

(c) ODD-EVEN JUDGMENTS. S was instructed to press whenever the two digits in the TS were either both even or both odd, but not if one was odd and the other even.

(d) MULTIPLICATION. S was instructed to multiply the two digits in the TS, and to press only if the product of the two digits was equal to or greater than 15.

Trials were presented in blocks of 80, of which approximately half were "press" and half "no press" trials. Intertrial intervals were randomly ordered and ranged from 3 to 6 sec. in duration. At the beginning of every testing session S was given the instructions for the task and then put through a practice session until his performance was error-free.

The procedure for recording DC potentials, eye movements, and stimulus events was the same as reported in the previous section. In addition, S's reaction time (RT) was recorded. The RT distributions produced by S were examined periodically during the practice sessions, and when the variance of the responses was sufficiently low, an input channel of the average-response computer was opened for 20 successive "press" trials so that the CNV during these trials could be averaged and compared with the corresponding RTs. RT variance was judged to be sufficiently low when 90% of the RTs fell within 20% of the mean RT. In pilot work, I found that EPs averaged from stimuli with low-variance at RT distributions, were much more defined than EPs averaged from stimuli to which RTs had varied greatly. Thus I insisted upon low-variance at RT distributions for averaging.

The particular tasks used to demonstrate the relation between RT and CNV differed from one S to another, because of individual differences in performance. For each S, E selected two or three tasks whose RT distributions differed from one another, and whose RT variances were within the acceptable range described above, and used them in the actual averaging sessions when CNV was recorded.

Results. Selected averaged responses of the 5 Ss, along with the corresponding mean RTs, are presented in Figures 9, 10, 11, and 12, for detailed discussion. Supplementary data are presented in Appendix 1.

In Figure 9, three averaged responses are presented, photographed directly from the original Polaroid prints but reduced in size and inverted from white-on-black to black-on-white. The uppermost trace in Figure 9 is the averaged response taken during the performance of task D (Multiplication). CNV reaches a maximum of 30 μ v. at the time of the TS. Its return to the pretrial voltage level (indicated by the line emanating from the start of the averaged response) coincides approximately with the position of the RT histogram which ranges from 420 to 600 msec. The second trace is the same S's averaged response, in the same session, during performance of task B (Same-different Judgments). In this case CNV reaches a maximum amplitude of 48 μ v. at the time of the TS, and its return to pretrial voltage level coincides again with the RT distribution, which ranges from 400 to 500 msec. Finally, the lowest trace represents the averaged response of the same S in the same session during performance of task A (Simple RT). The CNV amplitude in this trace is 34 μ v. at the TS, and the slope of its return to the previous voltage level is much sharper than in the previous two averaged responses, coinciding approximately with the RT distribution, which ranges from 200 to 300 msec.

In Figure 10 the same juxtaposition of RT distributions with averaged responses is shown for another S, whose RTs were consistently

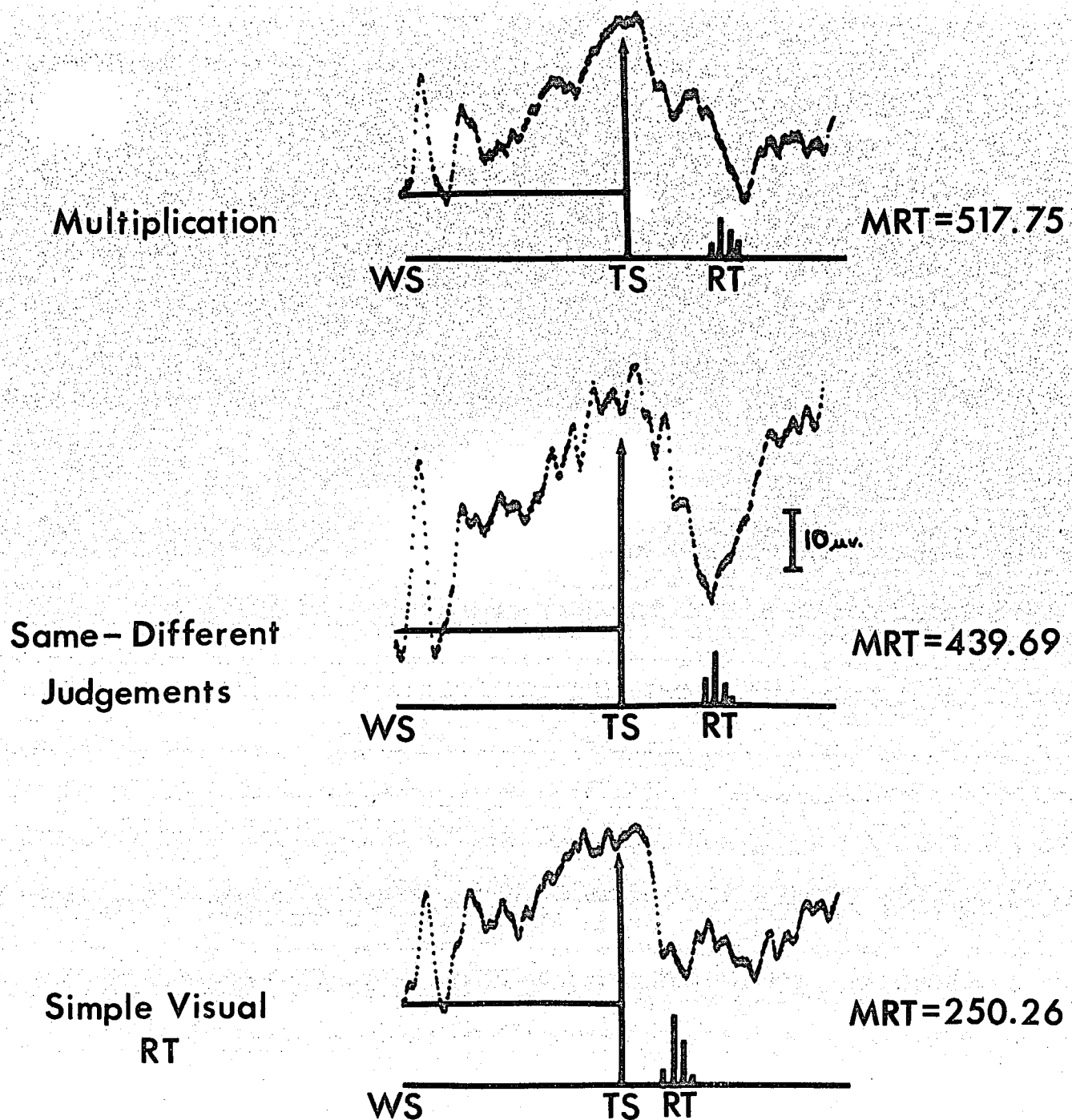


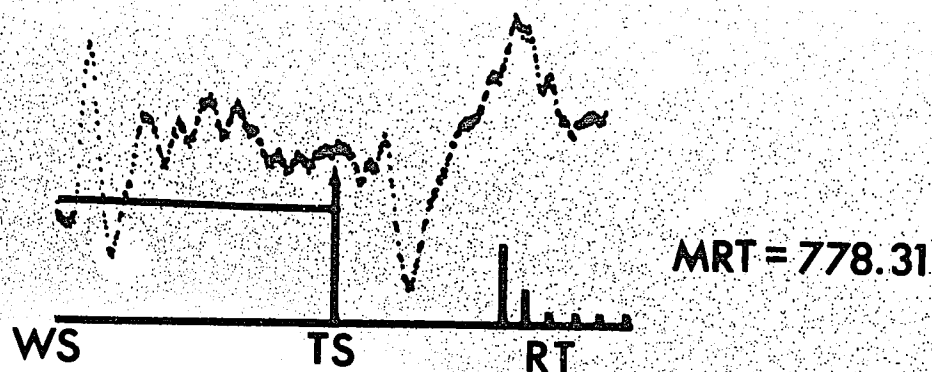
Figure 9. CNV during three different RT tasks using identical stimuli: multiplication of digits (upper trace), same-different judgements (middle trace), and simple visual RT (lower trace). Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: 1000 msec. RT: frequency histogram of distribution of RTs. MRT: mean reaction time, measured from TS onset. N: 20. Subject: T.D. An upward deflection indicates a negative potential change at the vertex.

longer and more varied than those of the S in Figure 9. The correlation between RT and CNV termination is in evidence in Figure 10, but the return of CNV to the previous voltage level occurs consistently after the RT distribution, instead of coinciding with it, as in Figure 9.

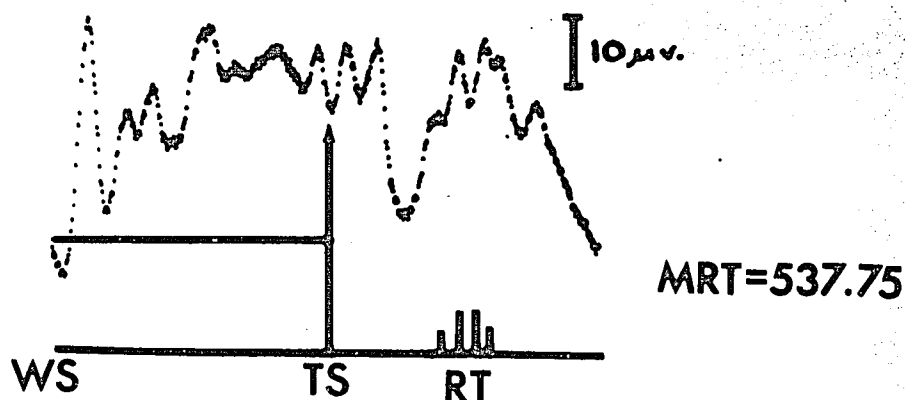
In the uppermost trace in Figure 10, RT variance was very high, with 30% of the RTs between 700 and 1000 msec. Nevertheless, when juxtaposed to the other two responses in Figure 10, the response is unambiguous, so it is used in the data analysis. CNV amplitude in this trace is relatively low--only 10 μ v. at the TS, and because of this the positive wave that is the SEP to the TS may be mistaken for the point of termination of CNV. In fact, CNV does not return to previous voltage level in this trace, because the time base is not long enough. However, the positive slope starting from the negative peak 680 msec. after the TS is presumably the start of the return to previous voltage level and it corresponds roughly to the RT distribution.

The second trace in Figure 10 helps to clarify the events in the first trace. CNV in this case is high enough in amplitude (30 μ v.) that the SEP in response to the TS cannot be confused with the return to previous voltage level of CNV, which occurs about 980 msec. after TS, or roughly 400 msec. after the RT distribution, which ranged from 400-600 msec. In the third trace, CNV amplitude is again about 30 μ v. and the return to previous voltage level of CNV occurs about 450 msec. after TS, or roughly 150 msec. after the RT distribution which ranged from 250 to 300 msec.

Multiplication



Odd-Even
Judgements



Simple Visual
RT

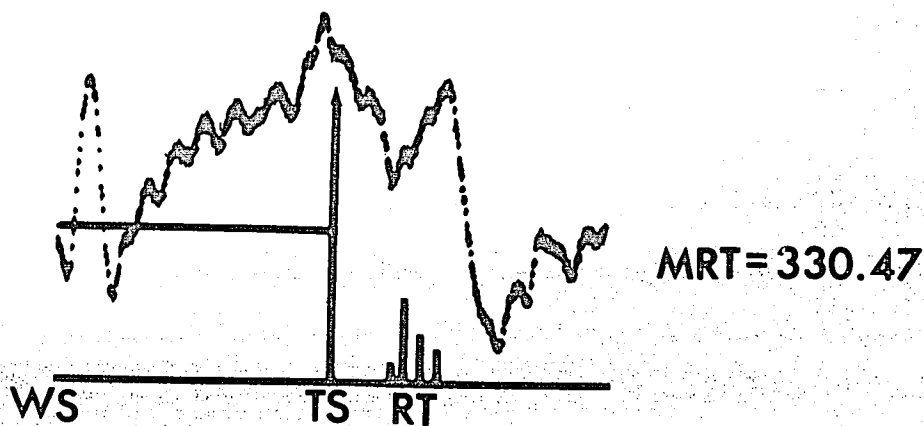


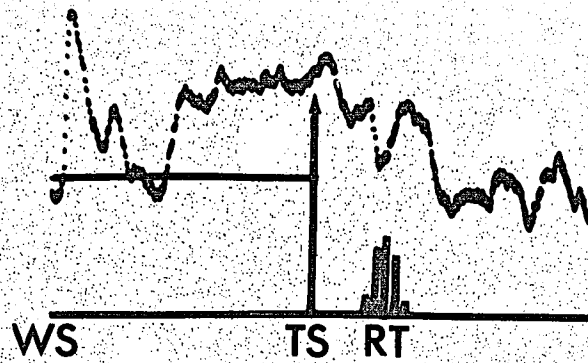
Figure 10. CNV during three different RT tasks using identical stimuli: multiplication of digits (upper trace), odd-even judgements (middle trace), and simple visual RT (lower trace). Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: 1000 msec. RT: frequency histogram of distribution of RTs. MRT: mean reaction time, measured from TS onset. N: 20. Subject: E.G.R. An upward deflection indicates a negative potential change at the vertex.

In Figure 11 similar data are presented for another S. CNV amplitudes from the two traces are, respectively, 17 uv. and 28 uv. Return of CNV to the previous voltage level in the two traces occurs, respectively, at 430 and 800 msec. after TS, or in each case about 50 msec. after the corresponding RT distribution.

From Figures 9, 10, and 11 it is clear that there is a correlation between RT and the time of return of CNV to the pretrial voltage level. Conversely, there is no evidence for a correlation between CNV amplitude and latency of the return of CNV to its previous voltage level. Further confirmation of the correlation between RT and CNV duration will be found in the Figures in Appendix I.

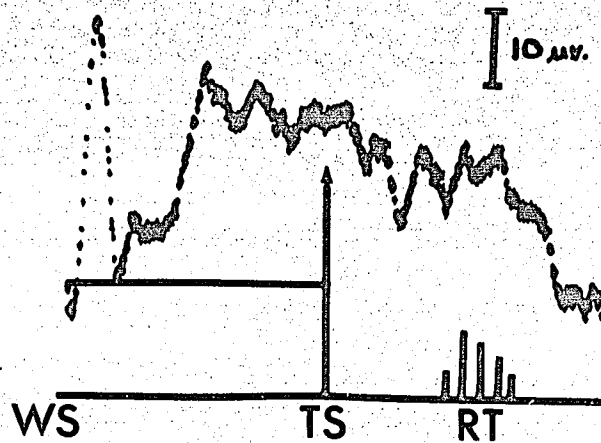
In Figure 12, two traces are presented which demonstrate the effect of practice on CNV. It is shown here that if S's motivational level is sustained CNV will not habituate completely, and the correlation between duration of CNV and RT will continue to be found in late as well as in early trials. The uppermost trace in Figure 12 is the same as the lower trace in Figure 11. The bottom trace in Figure 12 is a similar averaged response taken during S's performance of the same task but after a great deal more practice. Note that RT has shortened slightly but not significantly, and the time of return to the previous voltage level of CNV is unchanged, when compared to the uppermost trace. Interestingly the SEP to the TS is much larger in the later trials; the exact cause of this is not evident, but could possibly relate to a practice-related reduction of the variance of the late components of the SEP, sometimes called the Vertex wave. Such reduction in variance would enhance the signal-to-noise ratio of the signal, making it appear higher in amplitude.

Simple Visual
RT



MRT=329.84

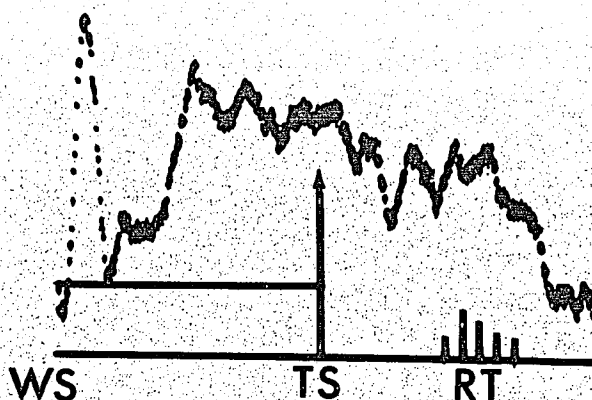
Same - Different
Judgements



MRT=625.78

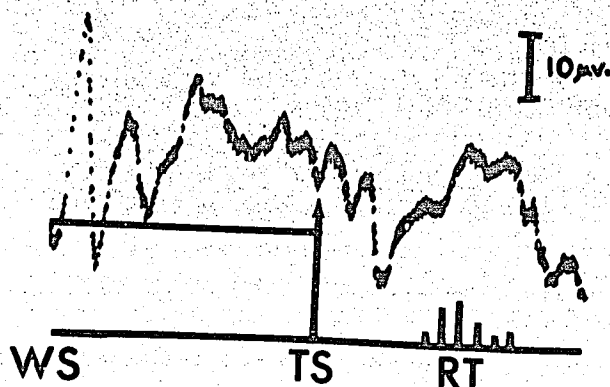
Figure 11. CNV during two different RT tasks using identical stimuli: simple visual RT (upper trace), and same-different judgements (lower trace). Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: 1000 msec. RT: frequency histogram of distribution of RTs. MRT: mean reaction time, measured from TS onset. N: 20. Subject: E. G.R. An upward deflection indicates a negative potential change at the vertex.

Early Trials
(#20-60)



MRT= 625.78

Late Trials
(#100-140)



MRT=594.66

Figure 12. CNV during early (upper trace) and late (lower trace) trials of a selective RT task requiring same-different judgements. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: 1000 msec. RT: frequency histogram of distribution of RTs. MRT: mean reaction time, measured from TS onset. N: 20. Subject: E.B. An upward deflection indicates a negative potential change at the vertex.

Conclusion. From the results of Experiment 1, it is evident that a correlation exists between the duration of CNV and decision time; and conversely that CNV duration and the timing of the TS are independent of one another. This confirms one of the general indications of the Exploratory Study--that CNV is related to some associative stage of the response process. That it is related to some very general aspect of cortical response is evident from the fact that in neither Study I nor the Exploratory Study did it matter what kind of behavioral response was being performed. It mattered only that some response was involved in the task, and consequently, that S had to momentarily limit his range of associations in order to concentrate on the task.

The independence of CNV duration from the timing of the TS is strong behavioral evidence that CNV is not concerned with the processing of stimuli per se, even in a task contingent upon a TS. However, corresponding electrophysiological evidence that CNV is distinguishable from the late "nonspecific" components of the cortical SEP to exteroceptive stimulation would enlarge our understanding of this independence. It is with such evidence that Experiment 2 was concerned.

Experiment II

In this experiment I attempted to determine the relation of CNV to the human "nonspecific" cortical response to exteroceptive stimulation, as measured by averaged sensory evoked potentials (SEP). Knowledge of this relation, whether it be one of interdependence or of independence, is of critical importance in assessing the functional significance of CNV. If the SEP and CNV are interdependent--that is, if SEP amplitude is clearly a function of CNV amplitude--it would follow that both phenomena are functions of a single underlying neural process. If they are independent of one another, then it would follow that the events underlying CNV are at least to some extent separate from whatever processes are responsible for SEPs.

In order to test the relation of CNV to the SEP it was necessary to measure the SEP during the course of CNV, rather than near the time of presentation of the TS, when CNV begins to slope sharply, as was seen in Experiment I. The reason for this is that the SEP in response to the TS can be distorted in the direction of the slope of CNV because the two responses summate. An example of such distortion is given in Figure 13. The lower trace shows a CNV during a simple RT task; note that the SEP in response to the TS is almost completely obscured because of the sudden positive wave caused by the termination of CNV. The middle trace shows a CNV to the same task from the same S, with a more gradual return of CNV to baseline, and hence a more gradual slope; the SEP to the TS here is less distorted, but still follows the slope of the DC activity. Finally, in the top trace, a similar SEP from the same

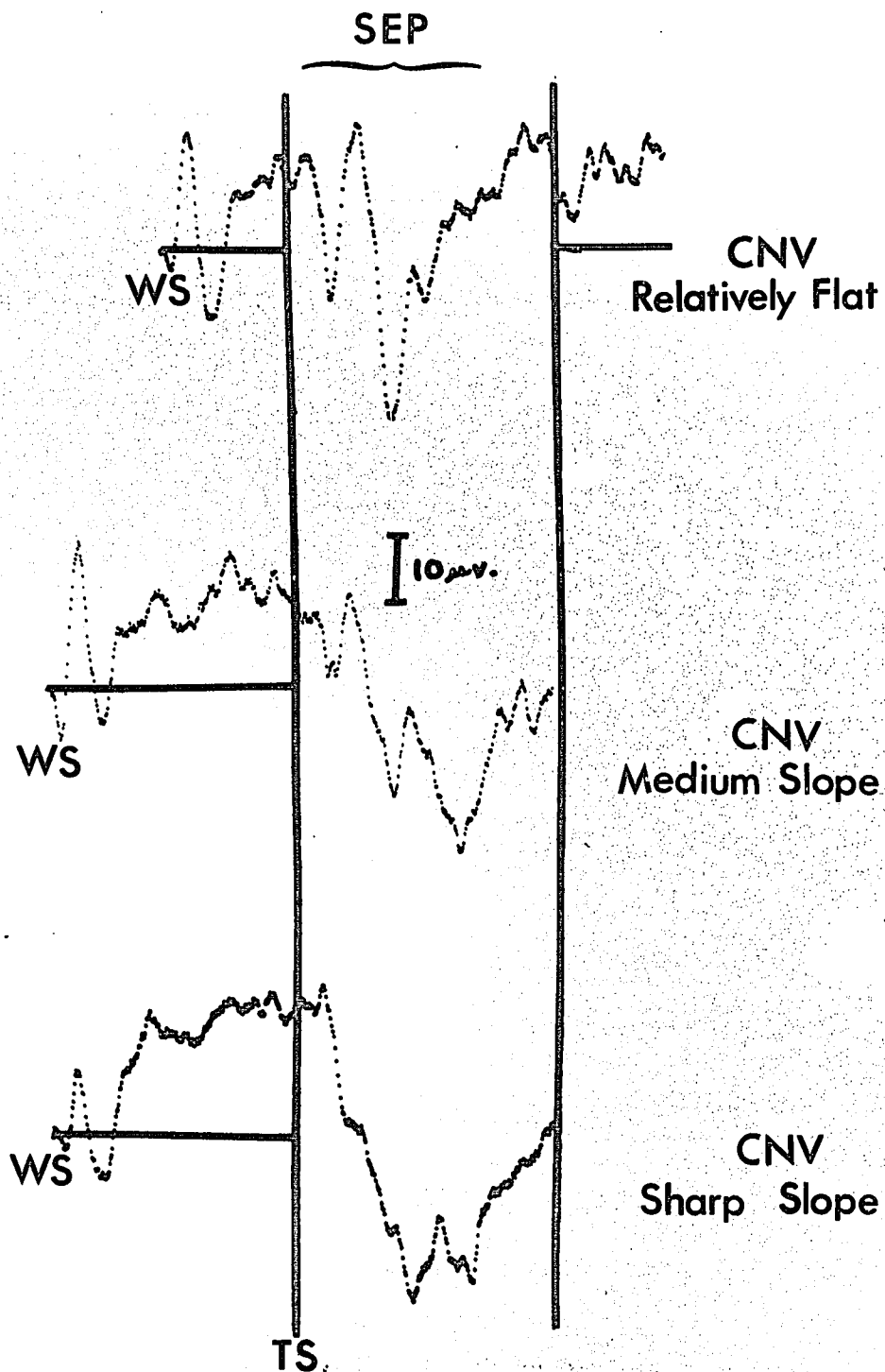


Figure 13. Distortion of the SEP by CNV. Upper trace: SEP superimposed on relatively flat CNV. Middle trace: SEP superimposed on CNV at time of gradual return to pretrial voltage level. Lower trace: SEP superimposed on CNV at time of abrupt return to pretrial voltage level. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: 1000 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: T.D. An upward deflection indicates a negative potential change at the vertex.

S is shown superimposed on a relatively flat CNV which is sustained for the whole duration of the trace. Note that the SEP here appears to be relatively undistorted.

In the two lower traces it is impossible to determine whether the amplitude of the SEP has been modified by CNV since the real waveform of the SEP has been obscured at least in part by summation with other time-locked neural activity. Any attempt to measure the interaction of CNV and the amplitude of the SEP must therefore avoid distortion of the SEP, as much as possible. This means that the slower activity which summates with the SEP should be as flat as possible during the period of the SEP to the stimulus. In addition to avoiding distortion of the SEP, a study of the interaction of the SEP and CNV should take into account variations in the SEP due to attentional factors which may be independent of CNV itself.

Both of these requirements, avoiding distortion of the SEP and controlling attentional factors, were met in the following experiment. S performed a selective RT task with a fixed foreperiod of 1500 msec. Once S had become accustomed to the foreperiod and his CNV was fully developed, sensory stimuli were presented during the occurrence of CNV. The SEPs to these stimuli, superimposed upon the corresponding CNVs, were averaged on the CAT computer.

The experiment is presented in two sections. The first part presents evidence that the presence or absence of CNV does not alter the late components of the SEP. The second part demonstrates that induced changes in the amplitude of SEPs due to changes in stimulus relevance are independent of CNV.

DC SEP During Sustained CNV

Procedure. The Ss were seven male and six female students aged between 20 and 27 years. Seating of Ss and electrode placements were as described in the General Method section. The Ss' DC potentials, eye movements and reaction times were recorded on a polygraph, along with a record of stimulus events. Throughout the experiment S performed a selective RT task. The TS was the same as in Experiment I, except that instead of two digits, it consisted of a single digit. S was instructed to press the reaction key as fast as possible whenever an even number appeared on the screen. S's DC potentials during performance of the task were averaged on the CAT computer in epochs of 2000 msec. Trials were presented in blocks of 200, of which half were "press" and half "no press" trials. Intertrial intervals were randomly ordered and ranged from 3 to 6 sec. in duration.

The RT task was performed under three conditions:

(a) NO WARNING SIGNAL. The TS was presented at irregular intervals. S had no precise timing signal by which to anticipate the TS.

(b) FIXED FOREPERIOD. In this condition the acoustic WS described in Experiment I was presented 1500 msec. before the TS on all trials.

(c) FIXED FOREPERIOD WITH OCCASIONAL SHORTER FOREPERIODS. In this condition the WS was presented, as above, with a fixed foreperiod of 1500 msec. before the TS, but only on 90% of the trials. On the remaining 10% of the trials, randomly distributed throughout the session, either the TS, or an irrelevant flash of white light of about the same area and luminance as the TS, was presented 500

or 1000 msec. after the WS. For any given session, the shorter foreperiod was either 500 or 1000 msec. in duration, never both. For any given session, the stimulus presented with the shorter foreperiod was either the flash or the digit, never both. The S was instructed to concentrate on producing the shortest possible RTs during the more frequent foreperiods. This was to force him to concentrate on the 1500 msec. foreperiod and to minimize any tendency to predict the occasional shorter foreperiods.

The first two conditions were used only as controls. The outcome of the experiment hinged largely on the third condition, in which it was attempted to superimpose an SEP on an evenly sustained CNV. Under the third condition, the S's concentration was time-locked to the more frequent 1500 msec. foreperiod. Because of this, CNV was often successfully sustained for the full 1500 msec. even on the shorter foreperiods used on 10% of the trials, and thus it lasted throughout the time period of the SEP to the TS on those latter trials. By averaging the DC record for 2000 msec. after WS on the 10% of the trials with shorter foreperiods it was possible to observe both the CNV, and the SEP to the stimulus superimposed on the CNV. This technique was difficult inasmuch as S after several hundred trials often became aware of the relative frequency of the shorter foreperiods. When this happened, CNV usually did not remain time-locked to the 1500 msec. foreperiod, and thus was not sustained throughout the 1500 msec. period on the infrequent trials. This distorted the SEP and defeated the purpose of the experiment. However, S's concentration upon the more frequent foreperiod was sufficiently strong in over 50% of the sessions,

that CNV persisted 1500 msec. even on the infrequent shorter foreperiod trials. The Results section is based on the data of such sessions.

The criterion for judging the strength of S's concentration on the 1500 msec. foreperiod was the waveform of the averaged DC response during the corresponding block of trials. Typical waveforms are illustrated in Figure 14. Note that CNV in the upper trace is sustained until the point in time at which the more frequent TS would have been presented, despite the fact that the TS was presented at 500 msec. This is taken as indication that CNV was well time-conditioned. In the middle trace CNV was not sustained; note that CNV returns to the pretrial voltage immediately after the TS, just as in condition 3 shown in the lowest trace, thus distorting the SEP to the TS. The middle trace is typical of weak concentration, that is S was not producing a CNV for 1500 msec. on every trial. Only those traces which basically resembled the waveform of the uppermost trace were selected for use in the Results section. Because there is slightly less probability of movement artifact on "non-press" trials, all the traces in this analysis were averaged during "non-press" trials exclusively.

Results. The averaged DC responses obtained from the 13 Ss are presented in Appendix 2. Several selected traces are presented in Figures 15, 16, 17 and 18, for detailed discussion.

In Figure 15, four averaged responses obtained under conditions 1 and 3 are presented. The top two traces were obtained under identical conditions, with the TS presented at 1000 msec. on 10% of the trials. In both, CNV appears to have continued throughout

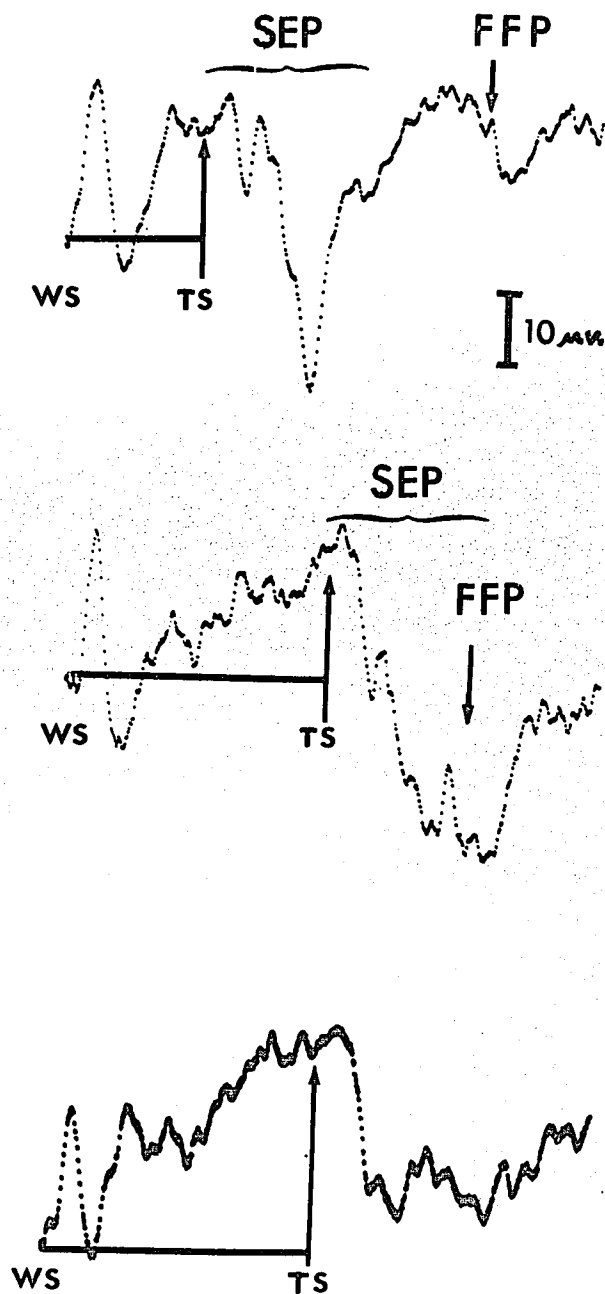


Figure 14. Illustration of a "sustained" CNV. Upper two traces: response averaged during occasional shorter foreperiods, under condition 3. Note that in the uppermost trace the DC voltage immediately after the SEP is the same as immediately before the TS: this is considered a "sustained" CNV, due to the fact that S was concentrating on the longer, more frequent 1500 msec. foreperiod. In the middle trace, the DC voltage immediately after the SEP returns to the pretrial level: thus CNV is not "sustained" in this case, and the SEP could not be seen clearly because of distortion. Lower trace: CNV obtained under condition 2; note that the DC level drops immediately after the TS, and remains at the pretrial level. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: upper trace, 500 msec.; middle and lower traces, 1000 msec. FFP: time of termination of 1500 msec. frequent foreperiod. SEP: sensory evoked potential in response to TS. N: 20. Subject: T.D. An upward deflection indicates a negative potential change.

the SEP in response to the TS. Although there are variations in the earlier components of the SEP, the basic form and amplitude of the large positive late waves in the two upper traces are virtually similar. Amplitude of the positive wave starting about 200 msec. after the stimulus is 30 uv. in both cases.

The third trace was also obtained under condition 3, but the TS was presented 500 msec. after the WS on 10% of the trials. CNV appears to have been sustained throughout the SEP to the displaced TS, since the SEP terminates at the same DC level as prevailed at the TS presentation. CNV then continues to go further negative, reaching a peak amplitude of about 40 uv. at the end of the more frequent 1500 msec. foreperiod, then slowly returning to baseline. The form and amplitude of the SEP are similar to those of traces 1 and 2.

The fourth trace, obtained under condition 1, provides a control for the upper three. There is no CNV during this trace; such fluctuations in the baseline as are present in this trace are not uncommon when the N is as small as 20. The overall amplitude of the large late wave is not significantly different from the upper three traces. The small negative peak superimposed on the large late positive wave is not present in the upper traces; the meaning of this peak is not clear. However, the important fact illustrated by this trace is that CNV does not appear to attenuate the late wave of the SEP. The fluctuations in the early SEP components are also clearly unrelated to CNV in these traces: the early components are large in traces 2 and 4, and small in traces 1 and 3.

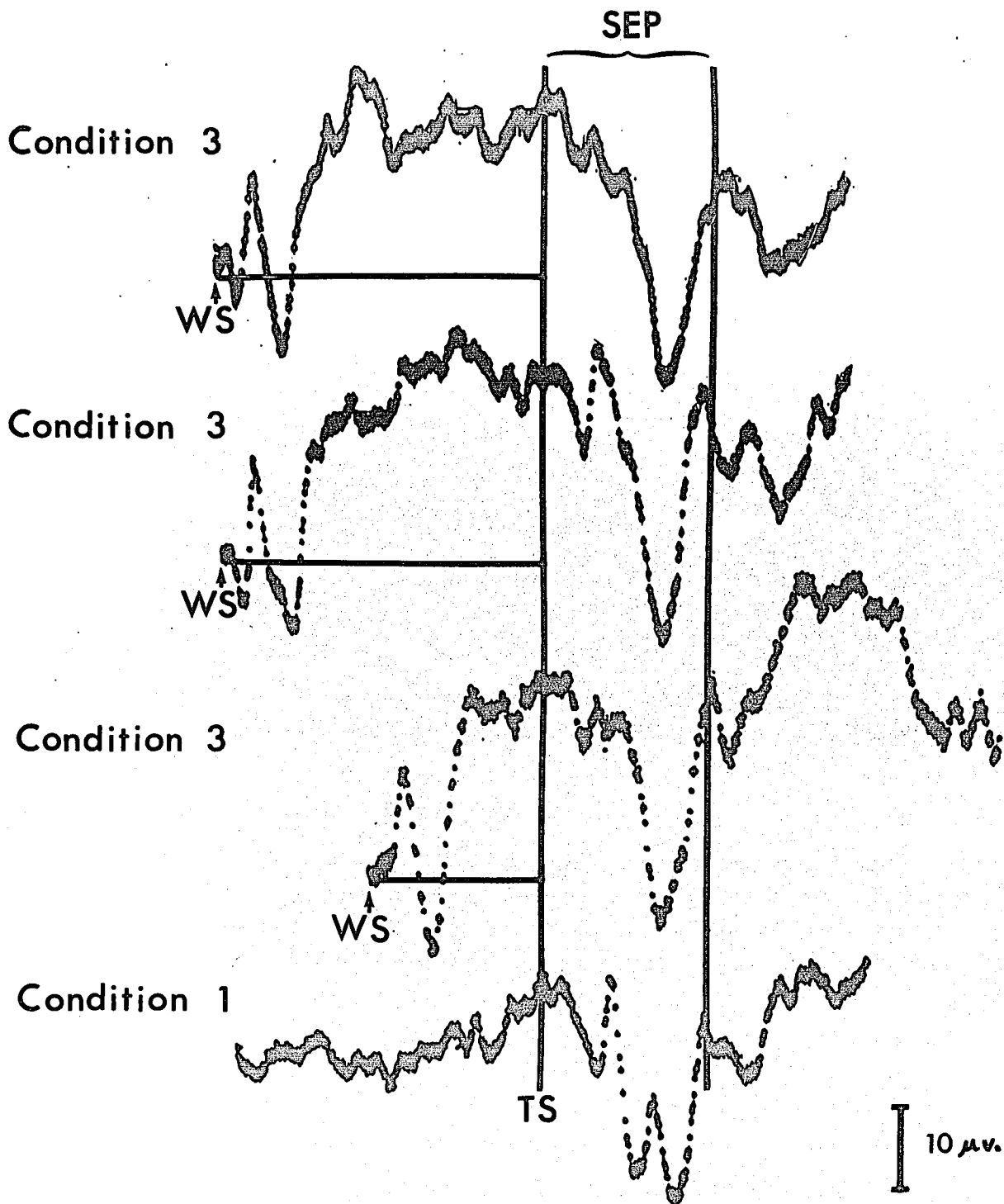


Figure 15. SEP to the TS, superimposed on sustained CNV. Upper three traces: responses were averaged only during occasional shorter foreperiods, under condition 3. Lower trace: response obtained under condition 1, with no WS. All traces were obtained during a single testing session. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: upper two traces, 1000 msec; third trace, 500 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: R.K. An upward deflection indicates a negative potential change at the vertex.

Thus two general findings emerge from Figure 15. First, slight fluctuations in waveform occur independently of the presence or absence of CNV. And second, the overall amplitude of the SEP is not affected in any consistent way when it is superimposed on a fairly flat CNV; these findings are reinforced by the remaining evidence presented in Appendix 2.

Although the SEPs of most Ss were predominantly positive in polarity, two Ss produced consistently negative SEPs; this provided an opportunity to study the relation of SEP polarity to CNV. In Figure 16 two predominantly negative SEPs are presented. In the upper trace, CNV is about 15 uv. in amplitude at the TS, and appears to have been sustained throughout the time of the SEP to the TS. The lower trace was obtained under condition 1. Note that the SEP is essentially the same as in the upper trace, despite the absence of CNV. These data, taken in conjunction with those of Figure 15 and Appendix 2, demonstrate that the polarity of the SEP does not affect the independence of the SEP from CNV.

In Figures 17 and 18, data similar to those in Figures 15 and 16 are presented, but for the flash stimulus, delivered earlier than the usual TS on 10% of the trials. In Figure 17 the uppermost trace is the averaged response under condition 3. CNV at time of stimulus reached an amplitude of about 30 uv. The second trace is a control trace, obtained without a WS, under condition 1. The third trace shows the averaged response to a stimulus presented again under condition 3. CNV at the time of the flash was 27 uv. and the SEP is similar to that of the first trace. The large positive wave of the SEP at 180 msec. after the flash stimulus is

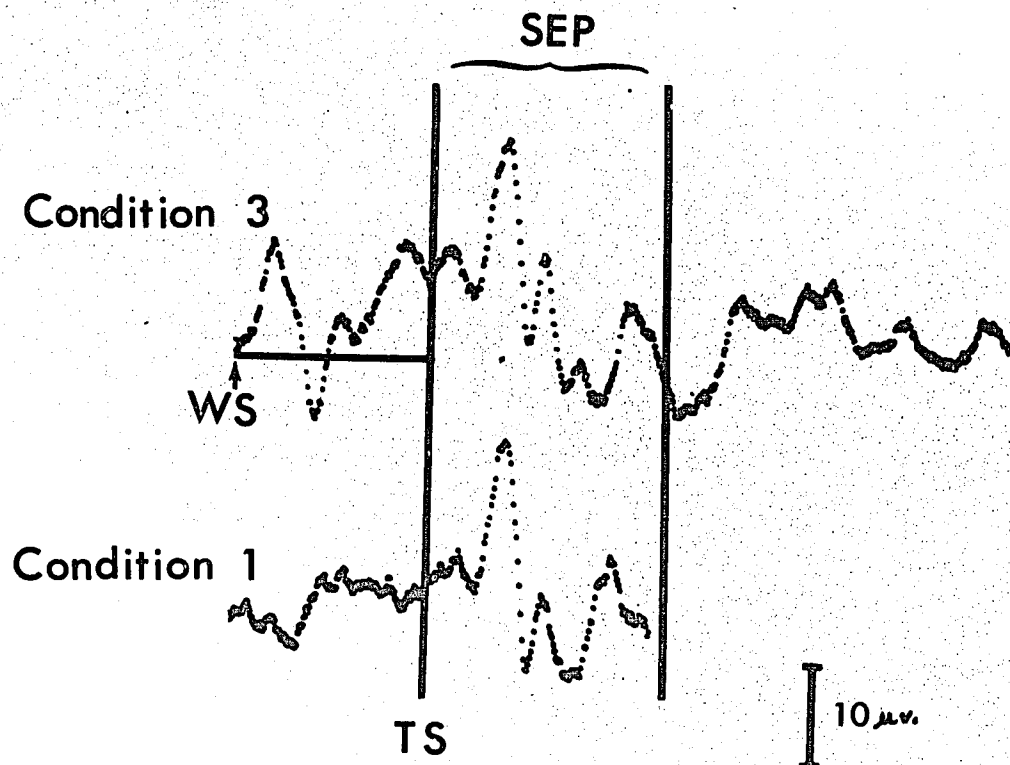


Figure 16. SEP to the TS, superimposed on sustained CNV. Upper trace: response was averaged only during occasional shorter foreperiods, under condition 3. Lower trace: response obtained under condition 1 with no WS. Both traces were obtained during a single testing session. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: upper trace, 500 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: G.T. An upward deflection indicates a negative potential change at the vertex.

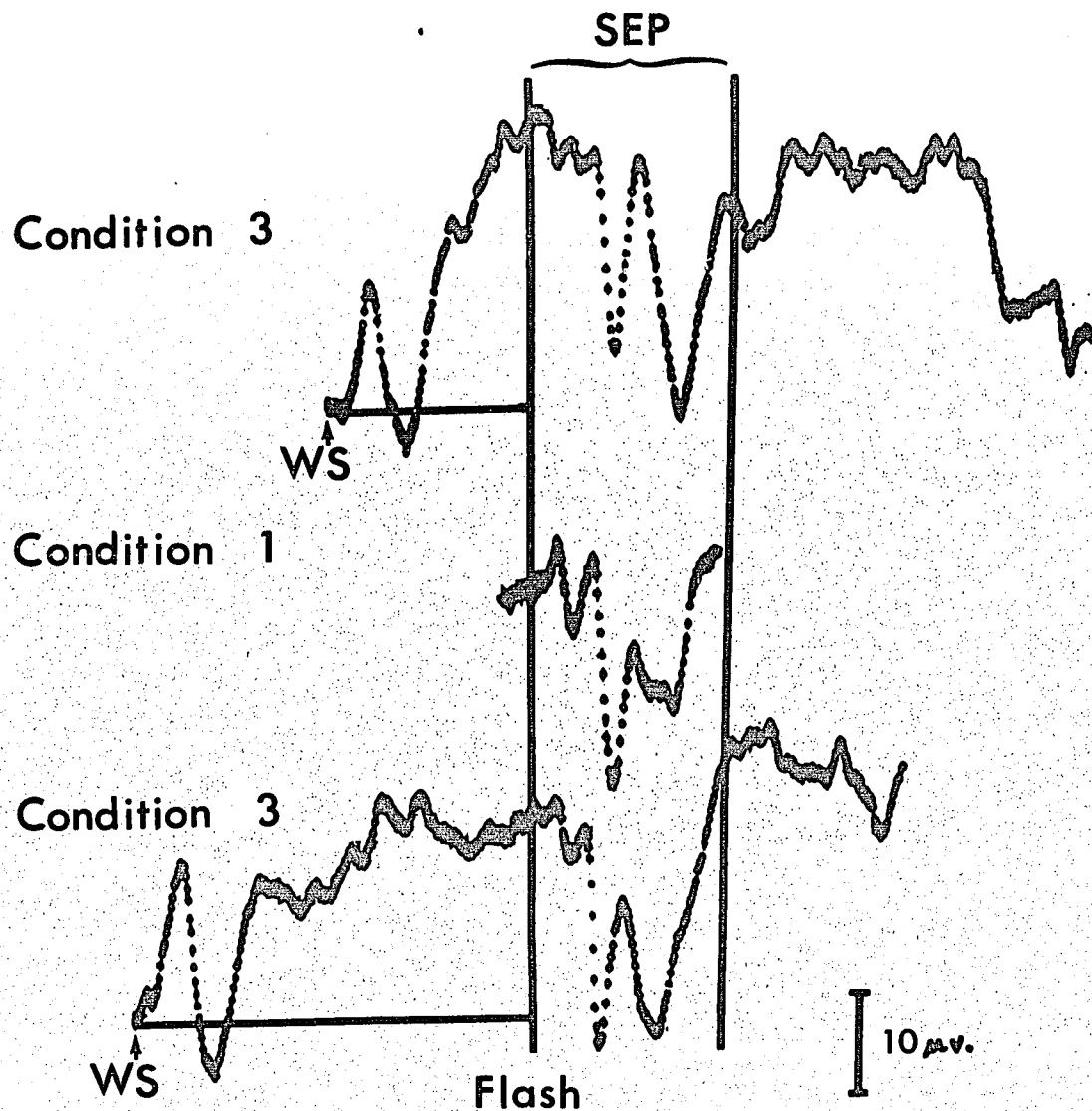


Figure 17. SEP to a flash, superimposed on sustained CNV. Upper trace: response was averaged only during occasional shorter foreperiods, under condition 3. Middle traces: response obtained under condition 1, with no WS. Lower trace: response was averaged only during occasional shorter foreperiods, under condition 3. All traces were obtained during a single testing session. Sweep time: 2000 msec. WS: warning signal. WS-Flash interval: upper trace, 500 msec.; lower trace, 1000 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: R.K. An upward deflection indicates a negative potential change at the vertex.

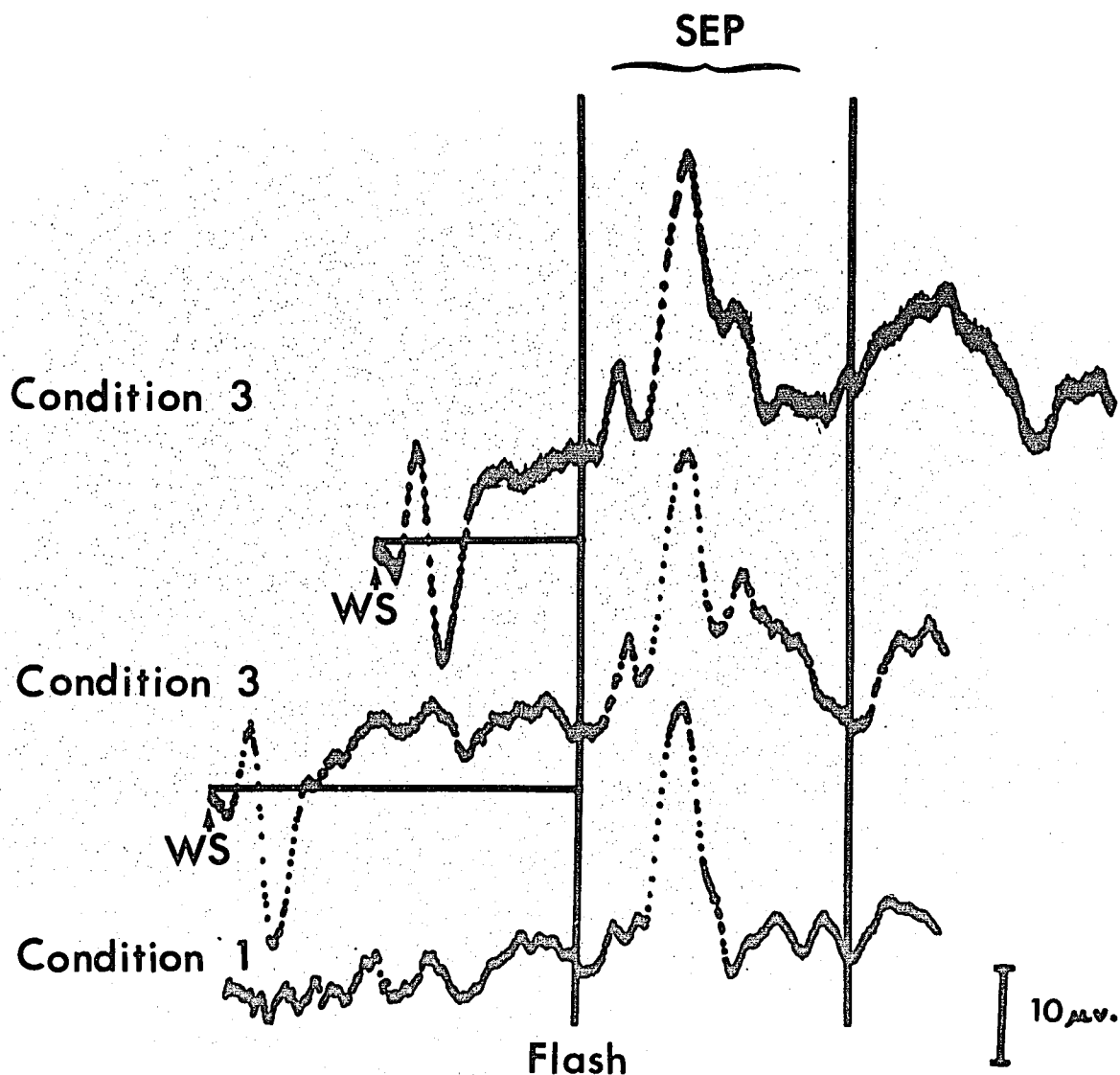


Figure 18. SEP to a flash, superimposed on sustained CNV. Upper two traces: response was averaged only during occasional shorter foreperiods, under condition 3. Lower trace: response obtained under condition 1, with no WS. All traces were obtained during a single testing session. Sweep time: 2000 msec. WS: warning signal. WS-Flash interval: upper trace, 1000 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: P.M. An upward deflection indicates a negative potential change at the vertex.

similar in all three traces. This constitutes evidence that the SEP in response to an irrelevant stimulus is also independent of CNV itself. This finding may be confirmed in Appendix 2.

In Figure 18 similar data are presented for an S whose SEP was predominantly negative in polarity. The results are again the same: the late components of the SEP do not change under varying conditions of CNV. No significant differences exist among the late components of the SEPs in Figure 18. There are differences between the three traces in the earlier negative wave at 100 msec., which are greatest in the upper trace; but, as mentioned above, variations in this earlier wave are common in these experiments and apparently not systematically related to CNV itself.

In summary, the data of Figures 15 to 18 support the hypothesis that CNV and the late components of the DC SEP in response to visual stimulation are functionally independent of one another. When experimental conditions are manipulated so that the SEP is superimposed upon a relatively flat CNV, it can be seen that the late DC SEP is virtually unchanged during CNV, whether or not the superimposed stimulus is similar to or different from the TS.

The Effect of Stimulus Relevance on the DC SEP

During Sustained CNV

Procedure. The Ss were two male and three female students aged from 19 to 26 years. The stimuli employed were the same as those used in condition 2 of the first part of this experiment. The TS consisted of two digits, instead of one, and S was required to press the reaction key whenever the two digits in the TS were the same,

and not to press when they were different. Trials were presented in blocks of 200 with the same timing as in the first part of this experiment. After the initial practice period of about 50 trials, a flash of white light was presented during the fixed foreperiod between WS and TS, 800 msec. after the WS, on 10% of the trials randomly interspersed. Since the TS was presented on all trials, including the 10% with a flash at 800 msec., S's concentration on the foreperiod was good and always served to sustain CNV until the TS at 1500 msec. By averaging for a 2000 msec. epoch after the WS, it was possible to observe the SEP to the infrequent flash superimposed on CNV. The reason the flash at 800 msec. was presented on only 10% of the trials was so that S would not use it, rather than the WS, as a timing signal.

The significance to S of the infrequent flash of light was varied in two ways. On half the sessions S was instructed to ignore the flash of light, and to concentrate only on the TS which always appeared 1500 msec. after the WS. On the other half of the sessions, the flash of light was made relevant. S was instructed to change the rule for pressing the reaction key whenever the flash occurred between the WS and TS: instead of pressing when the two digits in the TS were the same, he was to press when they were different. The DC record was averaged during the flash stimulus trials only.

The methods for recording the DC potentials and eye movements were the same as in the previous part of this experiment.

Results. The results are presented for discussion in Figures 19, 20, and 21.

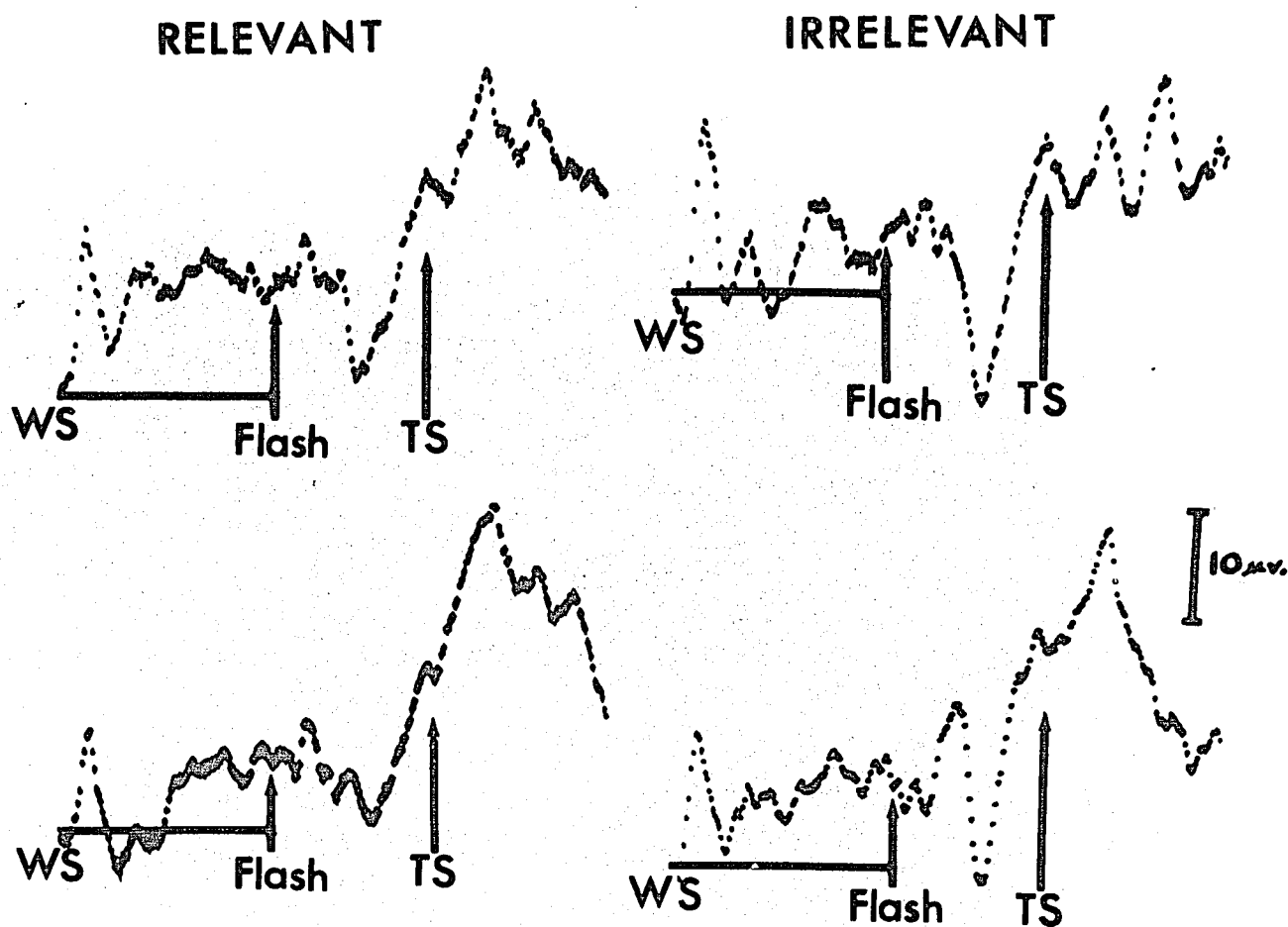


Figure 19. SEP to a flash during the fixed foreperiod of a selective RT task. The responses on the left were obtained under the Relevant condition: that is, when the flash of light appeared S was required to change the rule for pressing on that trial. Those on the right were obtained under the Irrelevant condition: that is, S was instructed to ignore any stimuli other than the TS. The upper two traces were from session 1; the lower two traces, from session 2, one day later. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: 1500 msec. WS-Flash interval: 500 msec. SEP: sensory evoked potential in response to flash. N: 20. Subject: E.B. An upward deflection indicates a negative potential change at the vertex.

Figure 19 presents four averaged responses obtained during the irrelevant and relevant sessions. Note that in all traces the amplitude of CNV was about 10 uv. at the time of the flash stimulus. Two findings emerge from Figure 19. First, the SEP in response to the flash was smaller during the relevant condition than during the irrelevant condition. Second, in both conditions, following the SEP to the flash and coinciding approximately with the time of the TS, there was a very large negative DC shift which peaked at about 30 uv. in each trace. The slope of this negative wave was so sharp that the SEP to the TS was obscured.

In Figure 20, the corresponding data are presented from two other Ss. Note that the SEPs in response to the flash for these two Ss are not smaller in the relevant condition: if anything, the opposite is true. Therefore, it cannot be claimed on the basis of these data that any consistent relation holds across subjects between the SEP and the relevance of the flash. However, the second finding in Figure 19 is corroborated in these two Ss: a negative wave follows the flash SEP. It is possibly a continuation, or amplification, of CNV preceding the flash. The slope of this negative wave is such that the SEP to the TS is obscured, as in Figure 19.

To see more clearly the timing characteristics of this negative wave, one averaged response was studied with the TS presented at 1000 msec. and the flash at 500 msec. after the WS. This allowed for a more complete record of the activity following the TS within the limits of the 2000 msec. computer sweep. These averaged responses are presented in Figure 21. The negative wave following the

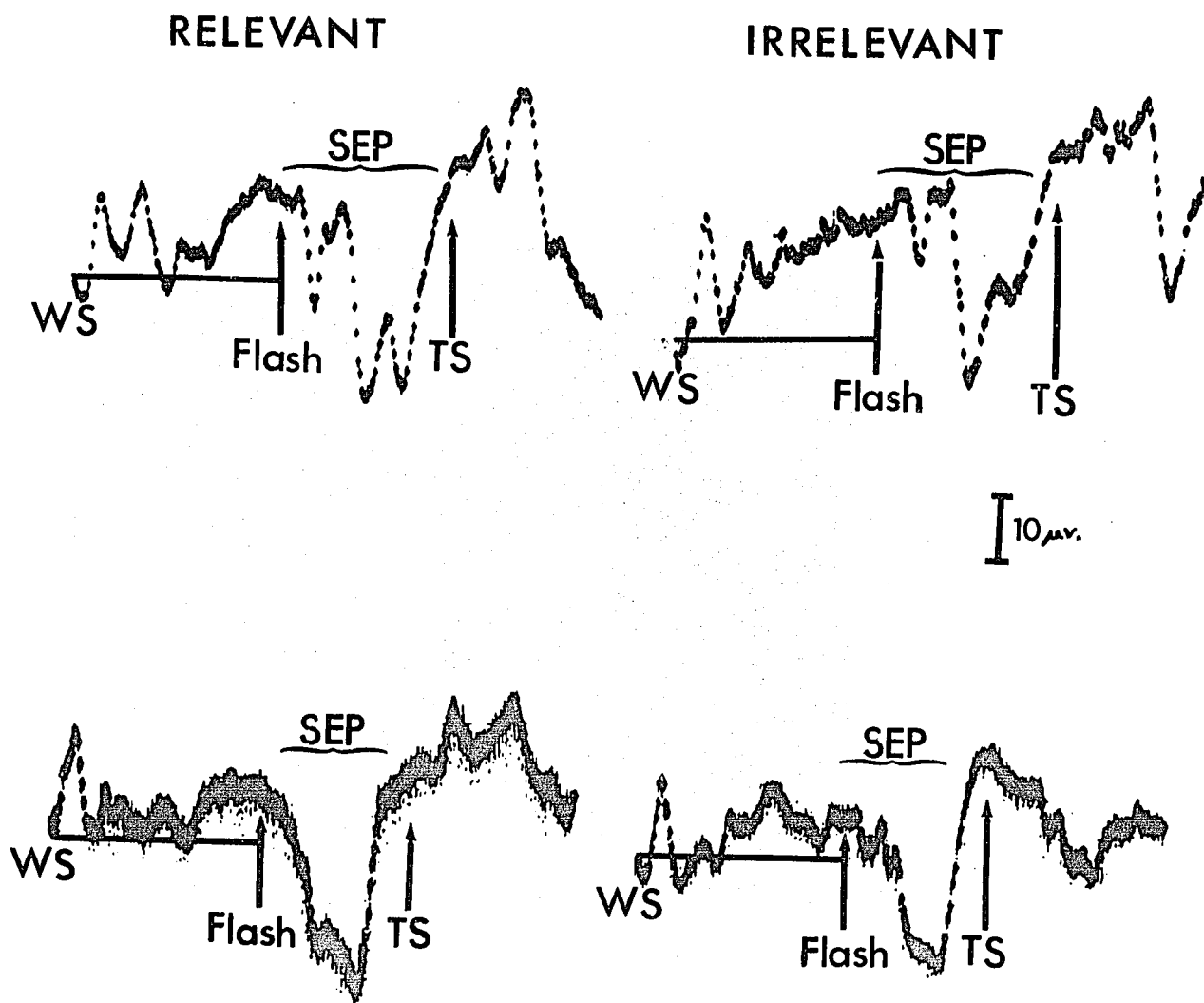


Figure 20. SEP to a flash during the fixed foreperiod of a selective RT task. The responses on the left were obtained under the Relevant condition: that is, when the flash of light appeared, S was required to change the rule for pressing on that trial. Those on the right were obtained under the Irrelevant condition: that is, S was instructed to ignore any stimuli other than the TS. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: 1500 msec. WS-Flash interval: 800 msec. SEP: sensory evoked potential in response to flash. N: 20. Subjects: upper two traces, R.D.; lower two traces, A.B. An upward deflection indicates a negative potential change at the vertex.

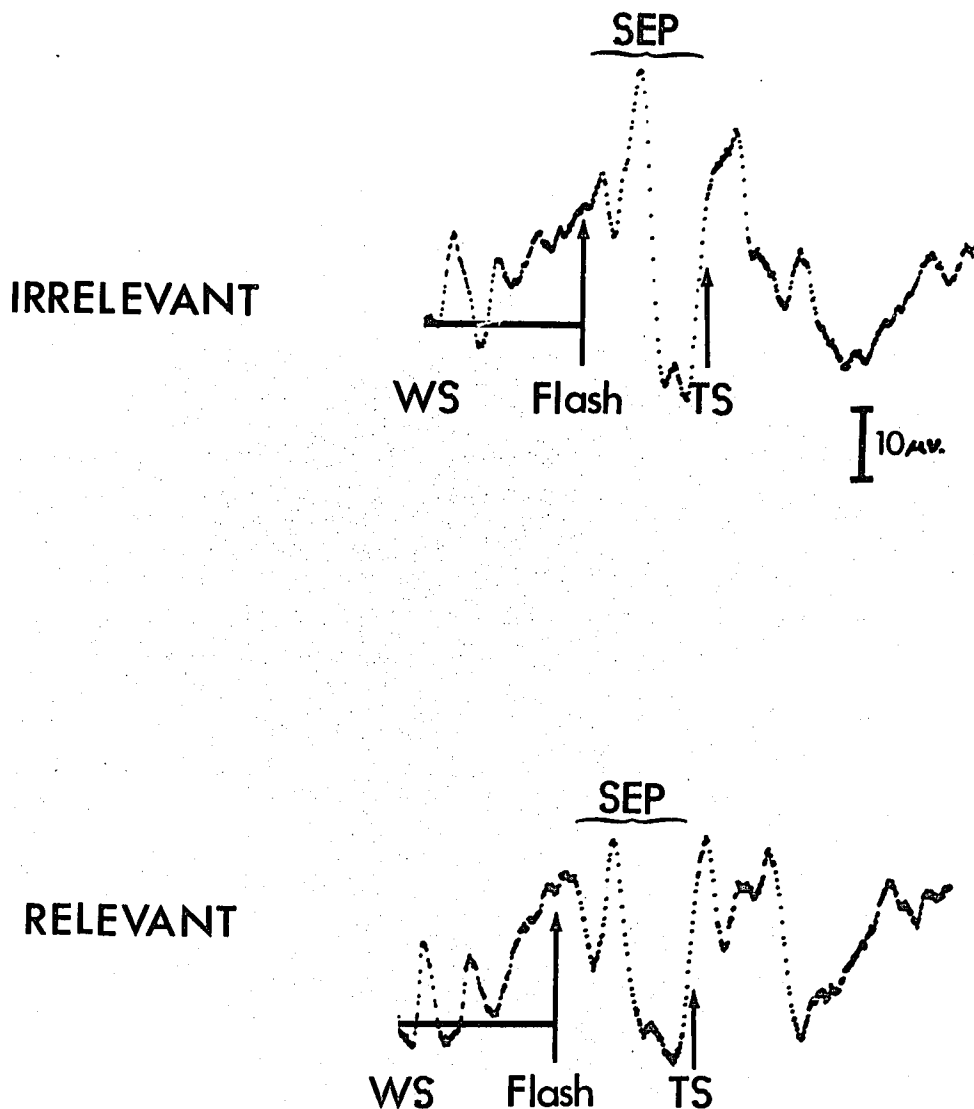


Figure 21. SEP to a flash during the fixed foreperiod of a selective RT task. Lower trace obtained under Relevant condition: that is, when the flash of light appeared, S was required to change the rule for pressing on that trial. Upper trace obtained under the Irrelevant condition: that is, S was instructed to ignore any stimuli other than the TS. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: 1000 msec. WS-Flash interval: 500 msec. SEP: sensory evoked potential in response to flash. N: 20. Subject: R.D. An upward deflection indicates a negative change at the vertex.

flash appears to be a continuation of the CNV starting after the WS. In both traces the amplitude of CNV at the flash is $15 \mu\text{v}$. The SEP to the flash is considerably higher in amplitude during the relevant flash condition. Despite this difference in amplitude, the timing of the SEP and the negative wave which appears to be a continuation of CNV are precisely the same under both conditions. The CNV returns to previous voltage level shortly after the TS, and there appears to be later "rebound" DC activity such as that described in the exploratory study.

In summary, the data of Figures 19 and 21 add further support to the hypothesis of the independence of CNV from the SEP. The amplitude of SEPs in response to relevant and irrelevant flashes of white light varied with changes in the significance of the flashes to S. The direction of these variations differed from one S to another, but the variations were not apparently related to CNV, since CNV amplitude and waveform were the same under the two conditions.

GENERAL DISCUSSION

Before discussing the functional significance of CNV, it is in order to review the available evidence on the behavioral correlates and neurophysiological substrates of CNV.

Behavioral Correlates

In Walter's original experiment (1964) the typical paradigm for eliciting CNV was a sequence of three events. The sequence consisted of, first, a WS, followed by a TS, and followed immediately by a response to the TS. CNV occurred during the WS-TS interval. Other experiments demonstrated that none of these three events was essential to the sequence. CNV or a DC response of the same polarity was elicited in the absence of an overt response by S (Walter, 1964), in the absence of an external WS (Kornhuber & Deecke, 1965), and in the absence of an external TS (McAdam, 1966). Therefore the behavioral correlates of CNV could not be described in terms of specific patterns of external stimuli or responses. Walter (1964) held that the behavioral correlate of CNV could best be described in terms of an internal state. The internal state corresponding to CNV he called "expectancy." However, Rebert et al., (1967) showed that a state of expectancy was not always accompanied by CNV; in addition to being in a state of expectancy, S had to be highly motivated regarding the expected event in order to sustain CNV.

The question remained whether CNV is a correlate solely of expectancy, or whether it also occurs during other types of behavior. My experiments were aimed at answering this question.

My exploratory studies were designed to determine the behavioral correlates of CNV within a broader range of performance than was used in earlier studies. My studies showed that CNV indeed occurs during performance of a variety of tasks which may not involve expectancy, but involve other cognitive functions, such as short-term storage and rehearsal, and cognitive operations, such as multiplication. A feature common to all these tasks was termed "time-locked concentration." Such concentration is characterized by a temporary stopping of the normal flux of what James (1890) called "the stream of consciousness." It is further characterized by a focusing of attention on a narrow range of associations for a prolonged period of time, that is, a holding of associations.

The question then remained whether concentration accompanied by CNV subserves the classification and channeling of sensory information, or whether it subserves primarily the response selection process. Experiments I and II dealt with this question.

In Experiment I it was demonstrated in selective reaction time tasks that a correlation exists between the duration of CNV and decision time, and conversely that CNV duration and the timing of the TS are independent of one another. This constitutes evidence that the processes underlying CNV are not concerned primarily with sensory information, even in a task contingent upon a TS.

In Experiment II it was demonstrated that the late components of the SEPs were not altered during CNV. Taken in conjunction with the results of Experiment I, this constitutes further evidence that CNV may be dissociated from sensory events and sensory processing. Taken

in conjunction with the results of the exploratory studies, Experiments I and II indicate that CNV is a correlate of the response selection process. Specifically, the response selection process may be described as sequential associative activity subserving rules and programmes for response, or more generally, the sequences of response-relevant ideas.

Therefore the behavioral correlate of CNV may now be described as timed concentration upon a specific set of associations relevant to the sequences of ideas.

Neurophysiological Substrates

What kinds of cortical activity that produce surface negative DC shifts might also serve to "hold" associations? The two most probable sources of sustained surface negative potentials with the timing characteristics of CNV are, first, excitatory PSPs in the apical dendritic arborizations of pyramidal cells, and inhibitory PSPs on the somas of pyramidal cells (O'Leary & Goldring, 1964; Morrell, 1967). DC shifts measured from the surface result from changes in the inhibitory-excitatory balance between the dendrites in the uppermost layer of the cortex and the cell somas in deeper layers, mostly in layer 3. Surface excitatory PSPs and inhibitory PSPs in deeper cortical layers both change this balance in the same direction, producing a surface-negative DC shift.

Fromm and Bond (1964) have demonstrated decreased firing rates in cortical neurons coincident with surface-negative DC shifts. This provides some support for the hypothesis that inhibitory mechanisms play a role in CNV. It is improbable that excitatory dendritic PSPs

play a dominant role in producing CNV, because in an alert S increased cortical activation might serve to disorganize neural firing patterns, rather than making firing patterns more circumscribed, as might be required for sustained concentration. On the other hand, inhibitory PSPs on the somas are a more likely source of CNV because a burst of massive inhibition might serve as a selector device by generally raising thresholds of pyramidal cells and thus reduce the number of cells any given cell could excite. This would improve the signal-to-noise ratio between task-related firing patterns and irrelevant background activity.

In contrast to the origin of CNV in cell somas, the origins of the late components of the SEP are probably in dendritic potentials. A recent review of the literature by Goff (1967) suggests that the late components of the SEP involve transmission in commissural structures, and particularly in the corpus callosum. A view of the late SEP as a product of changes in the inhibitory-excitatory balance in dendritic arborizations mediated by commissural structures, combined with a view of CNV as a product of sustained inhibition at the cell somas, might resolve a problem raised by the results of Experiment II. This experiment showed that CNV and the SEP summate rather than interact. This is consistent with the supposition that inhibition at cell somas in layer 3 would not interfere with changes in the inhibitory-excitatory balance within the dendritic arborizations, and thus the inhibition underlying CNV would summate in a surface recording with the waves of the late SEP.

This neural model for CNV and the SEP would be consistent with a fairly simple horizontal-vertical schema of cortical conduction circuits. Envisage the late SEP as representing a largely horizontal

transmission circuit involving commissural fibres and longitudinal association tracts; and CNV as representing a largely vertical (i.e., radial to the surface convolutions) transmission circuit affecting only the activity in pyramidal axones, which either climb to the surface arborizations to form small loops or descend into subcortical tissue to participate in larger circuits. In such a schema, obviously oversimplified, the processes responsible for CNV would allow "horizontal" patterns of neural firing to continue unaltered, while "vertical" patterns would be modified. This would account for the observed independence of the SEP and CNV.

Functional Significance

In the Introduction I argued that neither of the two theories of the functional significance of negative cortical DC responses which was developed on the basis of studies of infrahuman species was compatible with the existing literature on CNV. The activation hypothesis (Arduini, 1961; Rowland, 1964) cannot deal with the fact that both positive and negative responses may be elicited by behavioral activation. Similarly, the external attention hypothesis (Cowen, 1967), which is a more specific form of the activation hypothesis, does not receive support from the literature on CNV.

However, as discussed in the previous sections, both the behavioral and neurophysiological correlates of CNV would fit into an inhibition theory of CNV. If one makes the usual assumption that associations are in effect specific patterns of neural transmission, then the holding of task-relevant associations which characterizes concentration might well involve the kind of widespread cortical inhibition which could underlie CNV. The function of this inhibition would be to serve as a filter,

raising thresholds so that on a neural level only those patterns of firing activated by the task would remain above threshold, and on a behavioral level only task-relevant associations would remain active.

In conclusion, I am proposing that CNV is produced by widespread cortical inhibition subserving concentration on response selection. The first part of the proposal, that CNV is produced by cortical inhibition, is strongly suggested by my experiments, but cannot be said to be an established fact. However, the proposal might be directly verifiable with chronic intracellular recording techniques. The second part of the proposal, that CNV subserves concentration on response selection, is established in my experiments. Whether the latter part of the proposal exhaustively describes the behavioral correlates of CNV remains to be determined.

Indications for Future Research

Having completed the discussion of my experiments, I should like to make an observation on a parallel between recent neuropsychological and behavioral thinking about the higher-order synthetic activity of the brain.

It has been shown that the late components of the SEP are related to the relevance, importance, and predictability of stimuli (Chapman & Bragdon, 1964; Davis, 1964; Haider et al., 1964; Satterfield & Cheatum, 1964; Dustman & Beck, 1965; Morrell, L., 1965; Vaughan et al., 1965; Donchin & Lindsley, 1966; Wilkinson et al., 1966; Shevrin & Rennick, 1967; Wilkinson, 1967). Thus the late SEP is generally considered to be related to attention and the channeling of incoming information. On the other hand, my studies of CNV suggest

that CNV is to be considered as separate from the late SEP, both in its behavioral correlates and in its neurophysiological substrates. Rather than being concerned with information or attention to stimulation, CNV appears to be related to response selection, that is, to sequences of response-relevant associations.

In short, by means of the averaged response technique two types of cortical potential changes have been described. Both are associative or central in nature--that is, they are not part of the peripheral sensory or motor systems. However, one response, the SEP, is a function of sensory information, the other, CNV, a function of response selection. I cannot avoid observing that this latter distinction parallels the distinction traditionally made in psychology between two different aspects of the central mediating process: the representative process, and the plans or sequences of ideas that determine the direction of thought and action, (Miller, Galanter, & Pribram, 1960; Hebb, 1963). Perhaps future research should be directed towards describing separate structural features of the cortex that could subserve these two fundamentally different kinds of psychological processes,

SUMMARY

The present study is concerned with the functional significance of DC responses in the human cortex which are of negative polarity and fall within a duration range of approximately 500 to 5000 msec. To provide continuity with the existing literature, these DC responses are referred to as Contingent Negative Variation, or CNV. In my experiments, as well as in most of those in the previous literature, CNV is studied in a variety of experimental paradigms which involve the use of fixed-foreperiod decision tasks.

A review of previous studies showed that the processes underlying CNV are not part of the primary sensory or motor systems, and should be considered associative in nature. Nor are the processes correlated with any specific pattern of stimulation or any particular kind of response. Rather, they appear to be related to an internal state which previous investigators describe as "timed expectancy in a motivated subject." This definition of the behavioral correlates of CNV is not clear enough to provide a basis for an understanding of the functional significance of CNV. In my studies I attempted to arrive at a clearer definition.

My exploratory study was designed to determine the behavioral correlates of CNV within a broader range of task performance than was used in earlier studies. The results showed that CNV indeed occurs during performance of a variety of tasks which may not involve expectancy, but involve other cognitive functions, such as short-term memory storage and rehearsal, and cognitive operations, such as multiplication. A feature common to all these tasks was termed "time-locked concentration." Such concentration may be characterized

as a temporary stopping of the normal fluctuation of attention, and a focussing of attention upon a narrow range of associations for a period of time.

The question was then asked whether the kind of concentration accompanied by CNV subserves the classification and channeling of sensory information, or whether it subserves primarily the process of response selection. Two experiments were designed to deal with this question.

In Experiment I it was demonstrated in selective reaction time tasks that a correlation exists between the duration of CNV and decision time, and conversely that CNV duration and the timing of the task stimulus are independent of one another. This constituted evidence that the processes underlying CNV are not concerned primarily with sensory information, even in a task contingent upon sensory information.

In Experiment II it was demonstrated that the late components of the cortical response to sensory stimulation were not altered during CNV. Taken in conjunction with the data of Experiment I, this constitutes further evidence that CNV may be dissociated from sensory processing. Taken in conjunction with the exploratory studies, Experiments I and II indicate that CNV is a correlate of the response selection process. The response selection process may be described as sequential associative activity subserving rules and programmes for response, or more generally, sequences of task-relevant associations. Therefore, the behavioral correlate of CNV may now be described as time-locked concentration upon a specific set of associations relevant to a required task.

The results of my experiments, taken together with other available evidence relating to the behavioral correlates and neurophysiological substrates of CNV, are best explained in terms of inhibition. Briefly, such a hypothesis holds that inhibitory post-synaptic potentials, concentrated largely upon the cell bodies of pyramidal cells in layer 3 of the cortex, constitute the principle neural substrate of CNV. If one makes the usual assumption that associations are in effect specific patterns of neural transmission, then the holding of task-relevant associations which characterize concentration might well involve the kind of widespread cortical inhibition which could underlie CNV. The function of this inhibition would be to serve as a filter, raising thresholds so that, at the neural level, only patterns of firing activated by the task would remain above threshold, and, at the behavioral level, only task-relevant associations would remain active.

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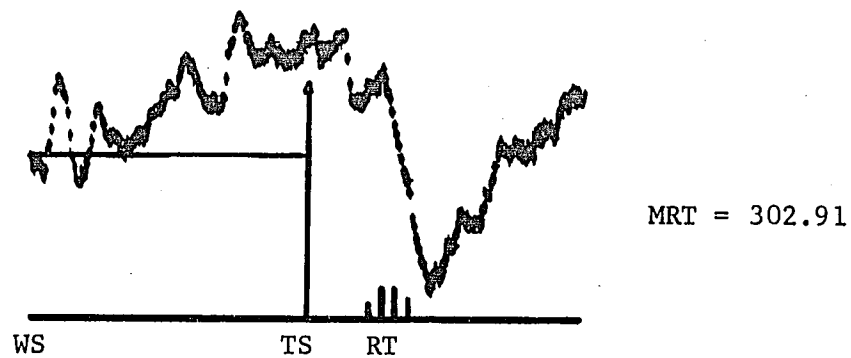
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APPENDIX 1

Supplementary Data, Experiment I



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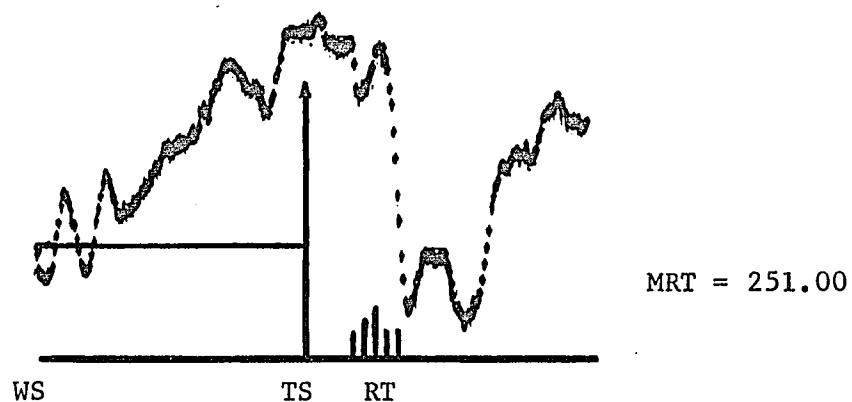


Figure A. CNV during two different RT tasks using identical stimuli: simple visual RT (lower trace), and same-different judgements (upper trace). Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: 1000 msec. RT: frequency histogram of distribution of RTs. MRT: mean reaction time, measured from TS onset. N: 20. Subject: R.D. An upward deflection indicates a negative potential change at the vertex.

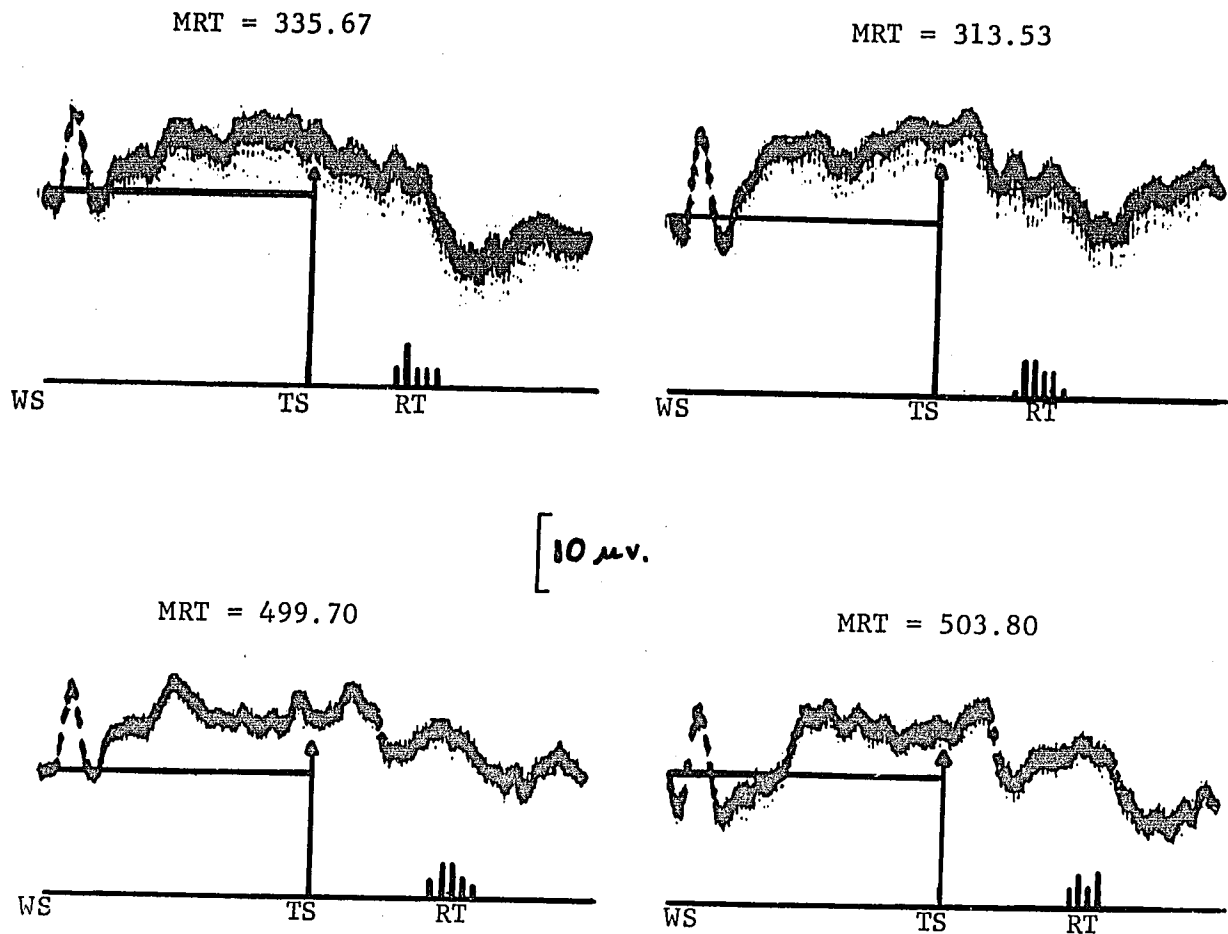


Figure B. CNV during two different RT tasks using identical stimuli: simple visual RT (upper two traces), and same-different judgements (lower two traces). The traces on the left were taken during the early part, those on the right during the later part, of a single testing session. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: 1000 msec. RT: frequency histogram of distribution of RTs. MRT: mean reaction time, measured from TS onset. N: 20. Subject: E.G.R. An upward deflection indicates a negative potential change at the vertex.

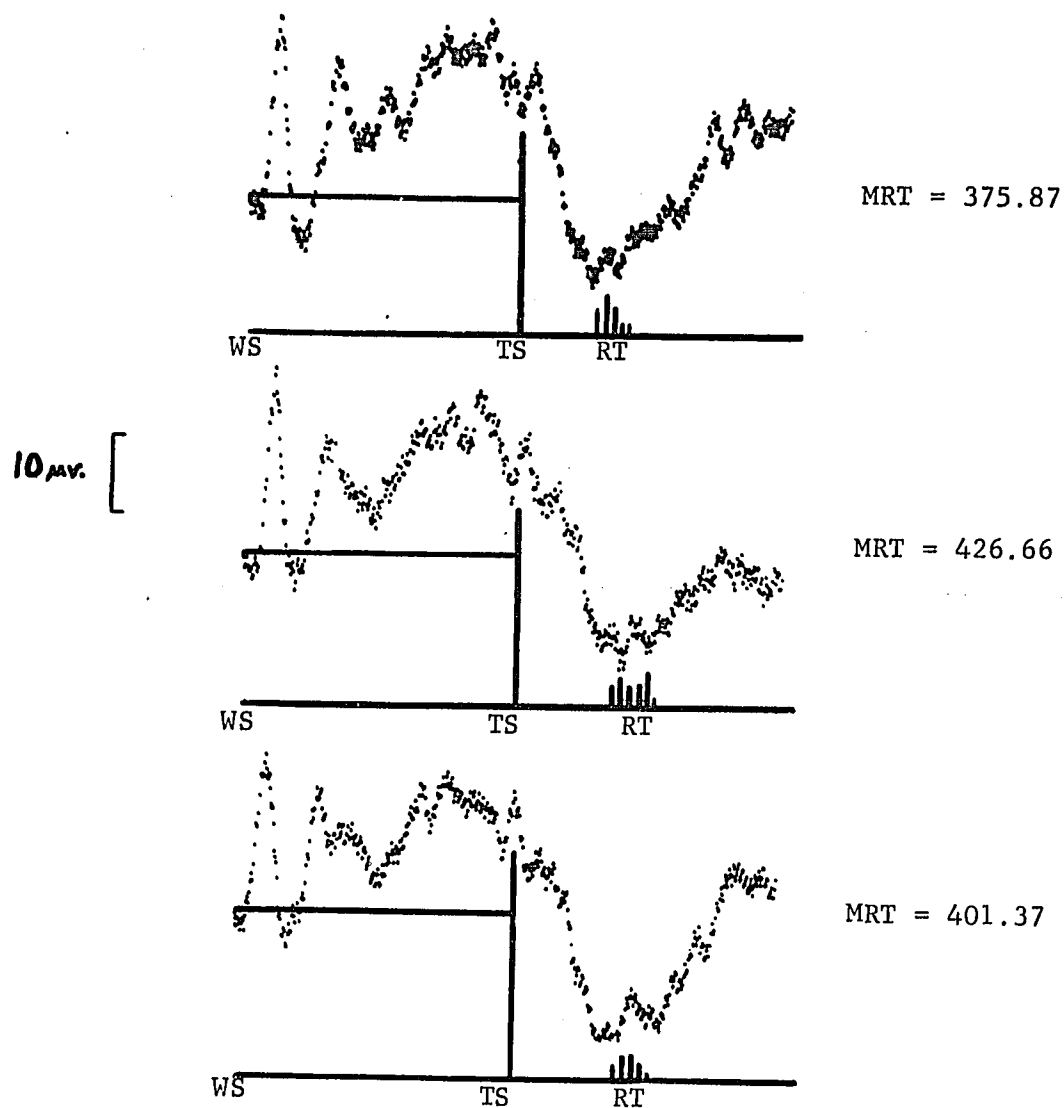


Figure C. CNV during two different RT tasks using identical stimuli: same-different judgements (upper trace) and odd-even judgements (lower two traces). Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: 1000 msec. RT: frequency histogram of distribution of RTs. MRT: mean reaction time, measured from TS onset. N: 20. Subject: T.D. An upward deflection indicates a negative potential change at the vertex.

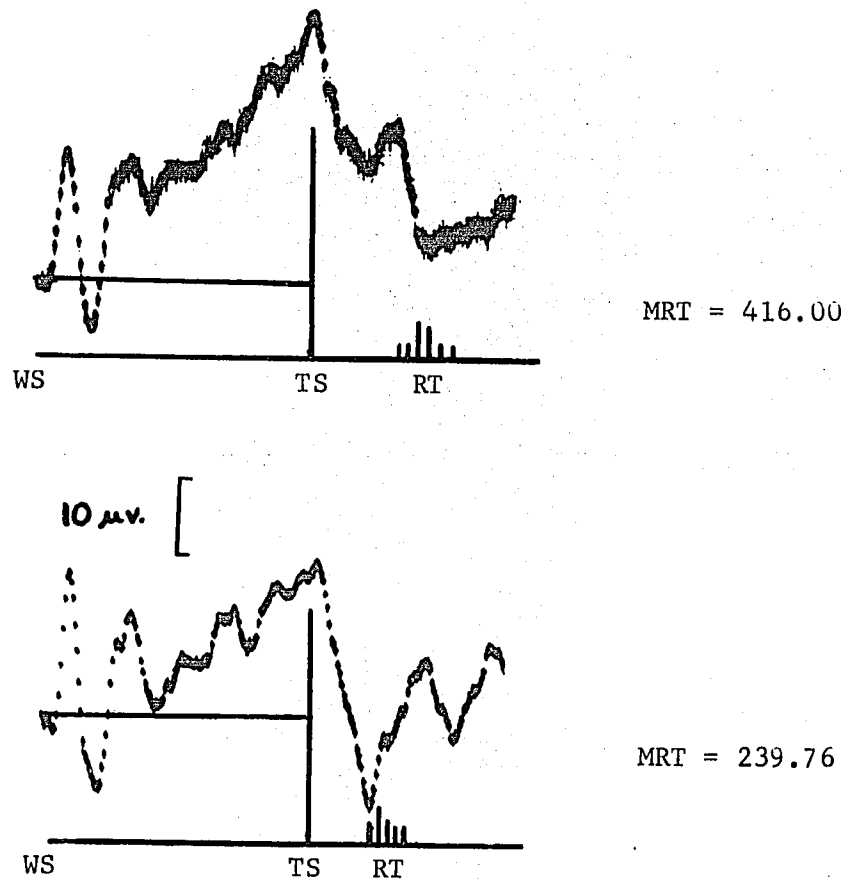


Figure D. CNV during two different RT tasks using identical stimuli: simple visual RT (lower trace), and same-different judgements (upper trace). Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: 1000 msec. RT: frequency histogram of distribution of RTs. MRT: mean reaction time, measured from TS onset. N: 20. Subject: T.D. An upward deflection indicates a negative potential change at the vertex.

APPENDIX 2.

Supplementary Data, Experiment II

Part 1.

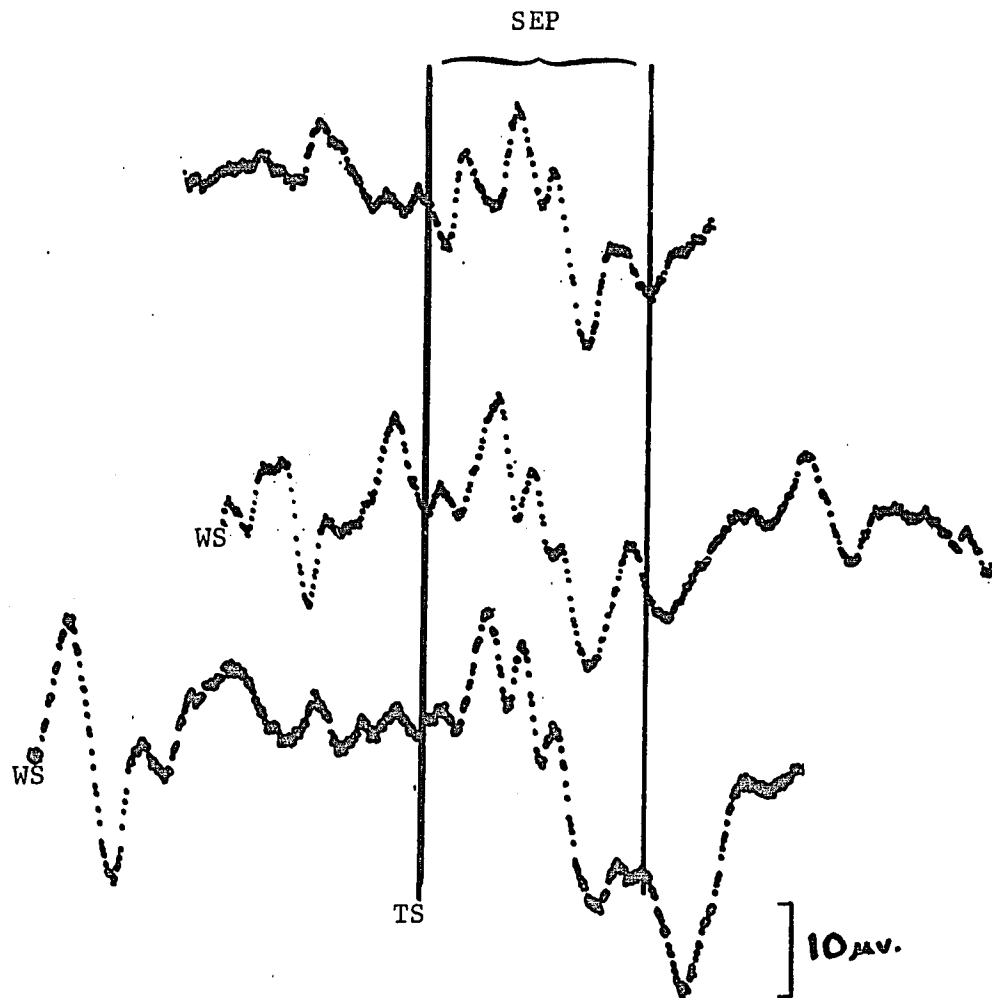


Figure A. SEP to the TS, superimposed on sustained CNV. Upper trace: response obtained under condition 1, with no WS. Lower two traces: responses were averaged only during occasional shorter foreperiods, under condition 3. All traces were obtained during a single testing session. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: middle trace, 500 msec.; lower trace, 1000 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: G.T. An upward deflection indicates a negative potential change at the vertex.

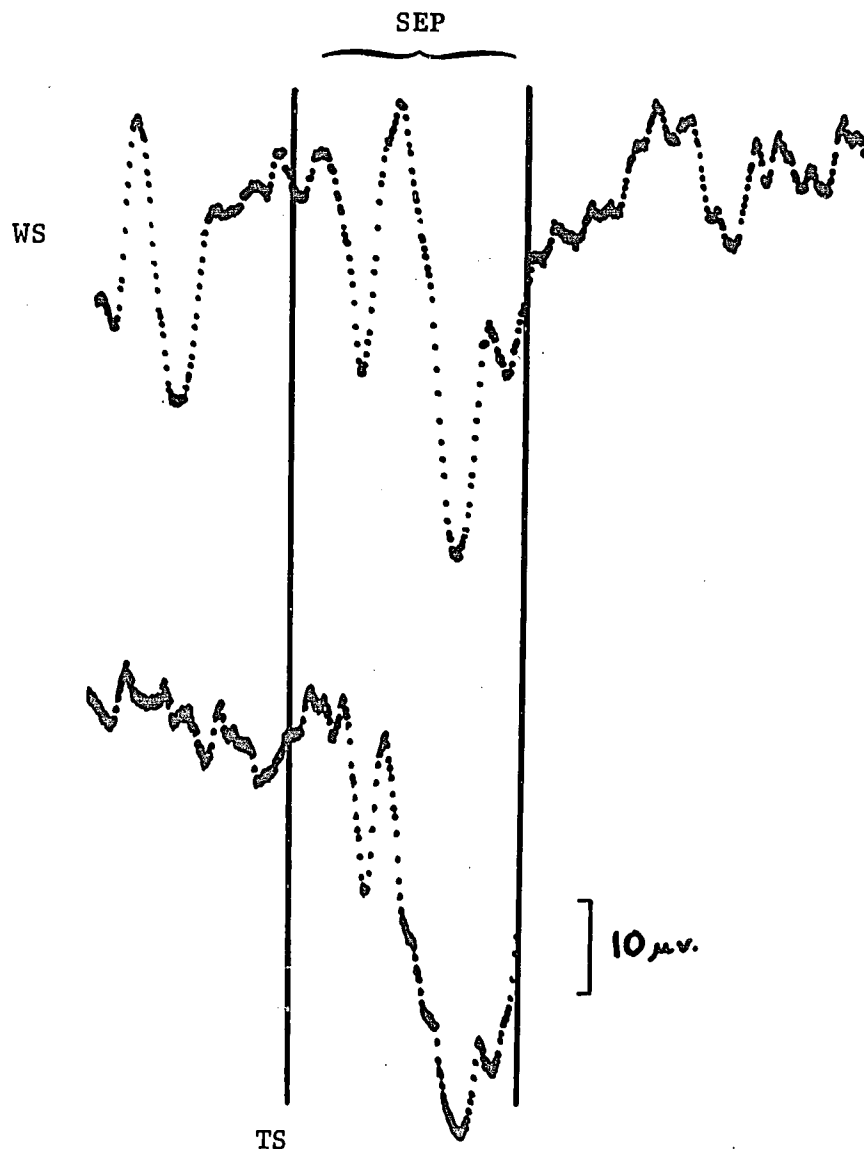


Figure B. SEP to the TS, superimposed on sustained CNV. Upper trace: responses were averaged only during occasional shorter foreperiods, under condition 3. Lower trace: response obtained under condition 1, with no WS. Both traces were obtained during a single testing session. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval: upper trace, 500 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: T.D. An upward deflection indicates a negative potential change at the vertex.

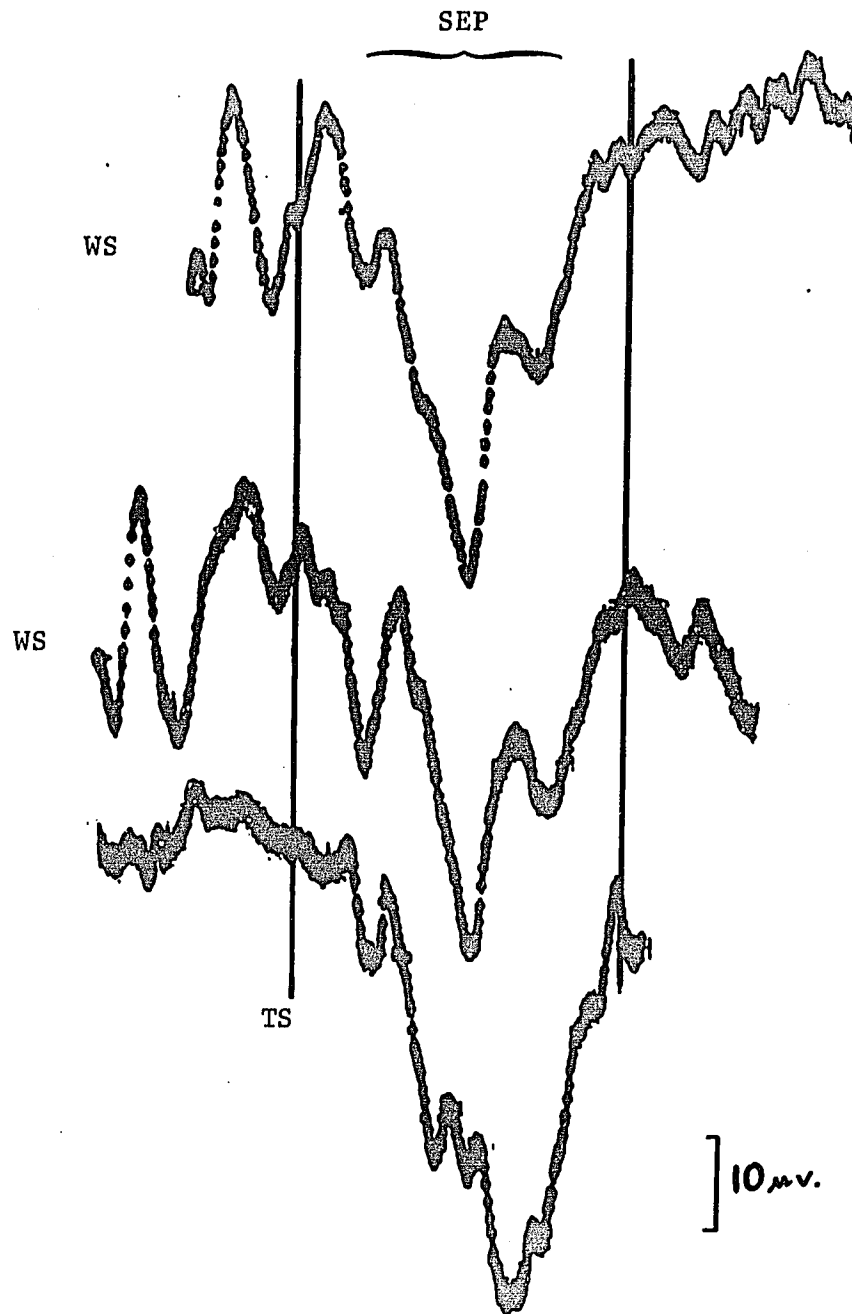


Figure C. SEP to the TS, superimposed on sustained CNV. Upper two traces: responses were averaged only during occasional shorter foreperiods, under condition 3. Lower trace: response obtained under condition 1, with no WS. All traces were obtained during a single testing session. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval; upper trace, 275 msec.; middle trace, 500 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: T.D. An upward deflection indicates a negative potential change at the vertex.

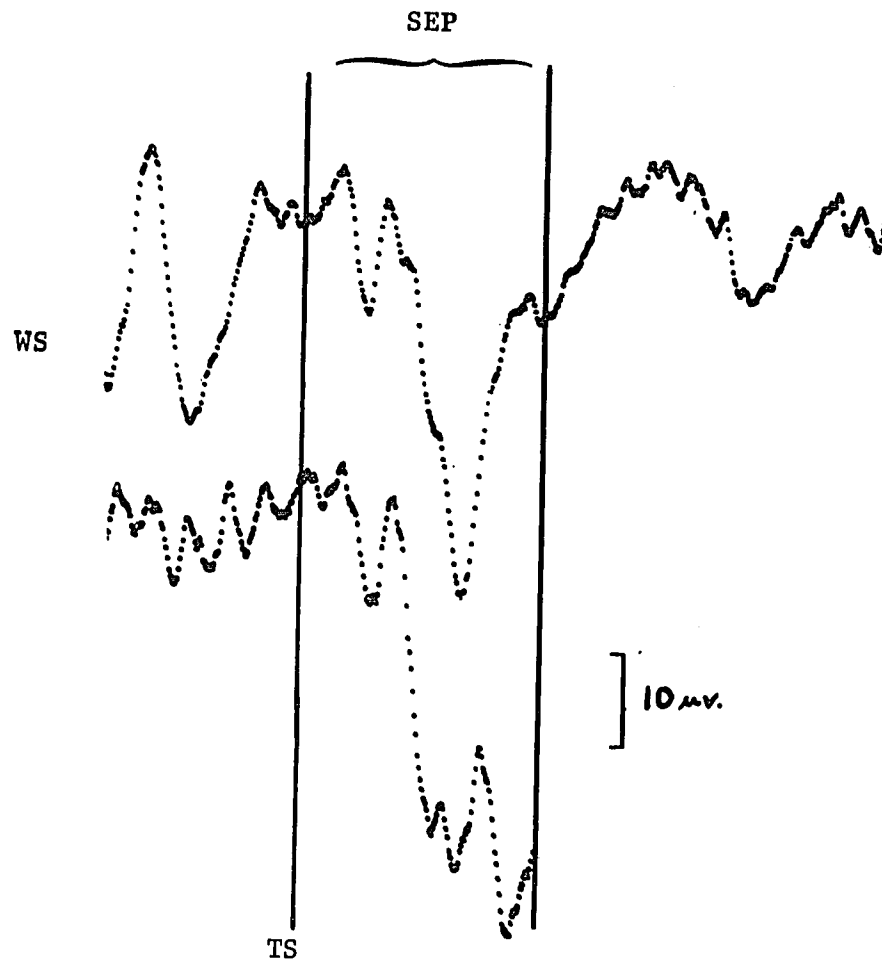


Figure D. SEP to the TS, superimposed on sustained CNV. Upper trace: responses were averaged only during occasional shorter foreperiods, under condition 3. Lower trace: response obtained under condition 1, with no WS. Both traces were obtained during a single testing session. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval; upper trace, 500 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: T.D. An upward deflection indicates a negative potential change at the vertex.

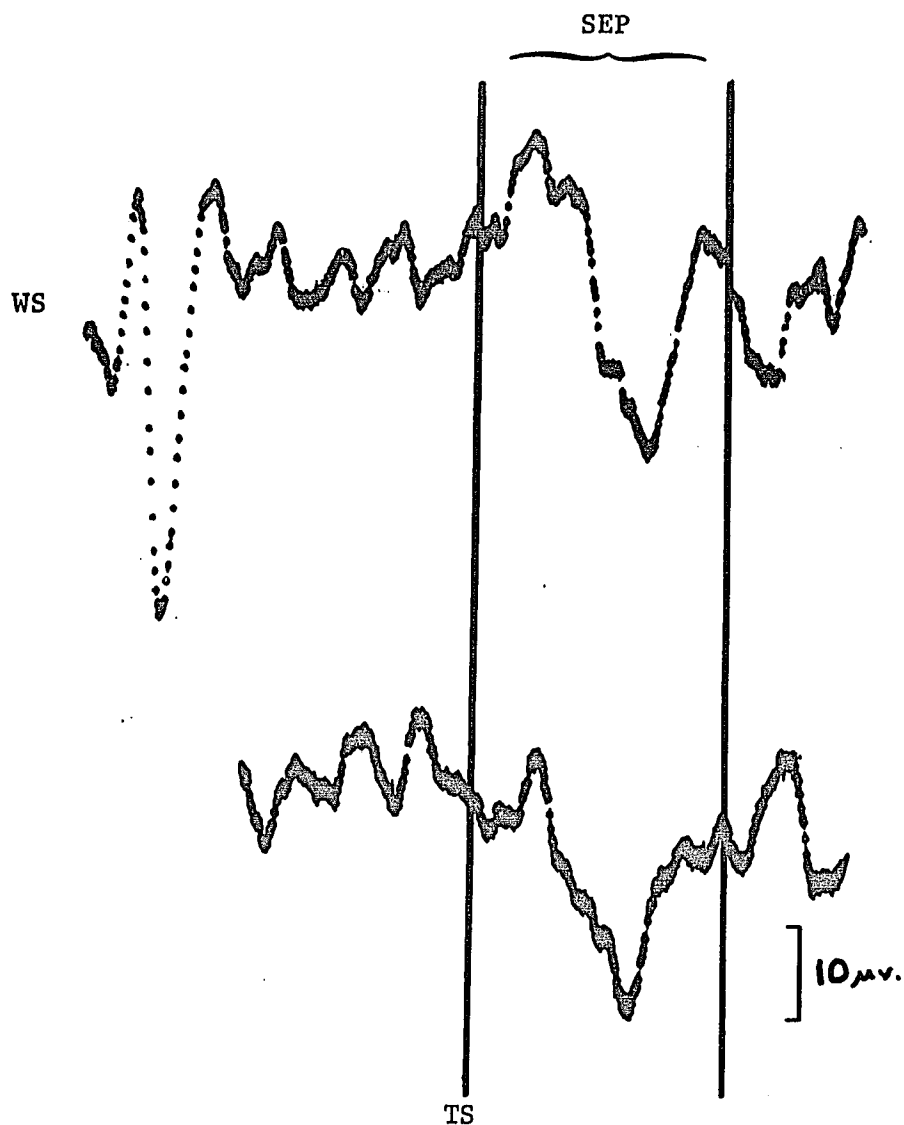


Figure E. SEP to the TS, superimposed on sustained CNV. Upper trace: responses were averaged only during occasional shorter foreperiods, under condition 3. Lower trace: response obtained under condition 1, with no WS. Both traces were obtained during a single testing session. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-TS interval; upper trace, 1000 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: J.D. An upward deflection indicates a negative potential change at the vertex.

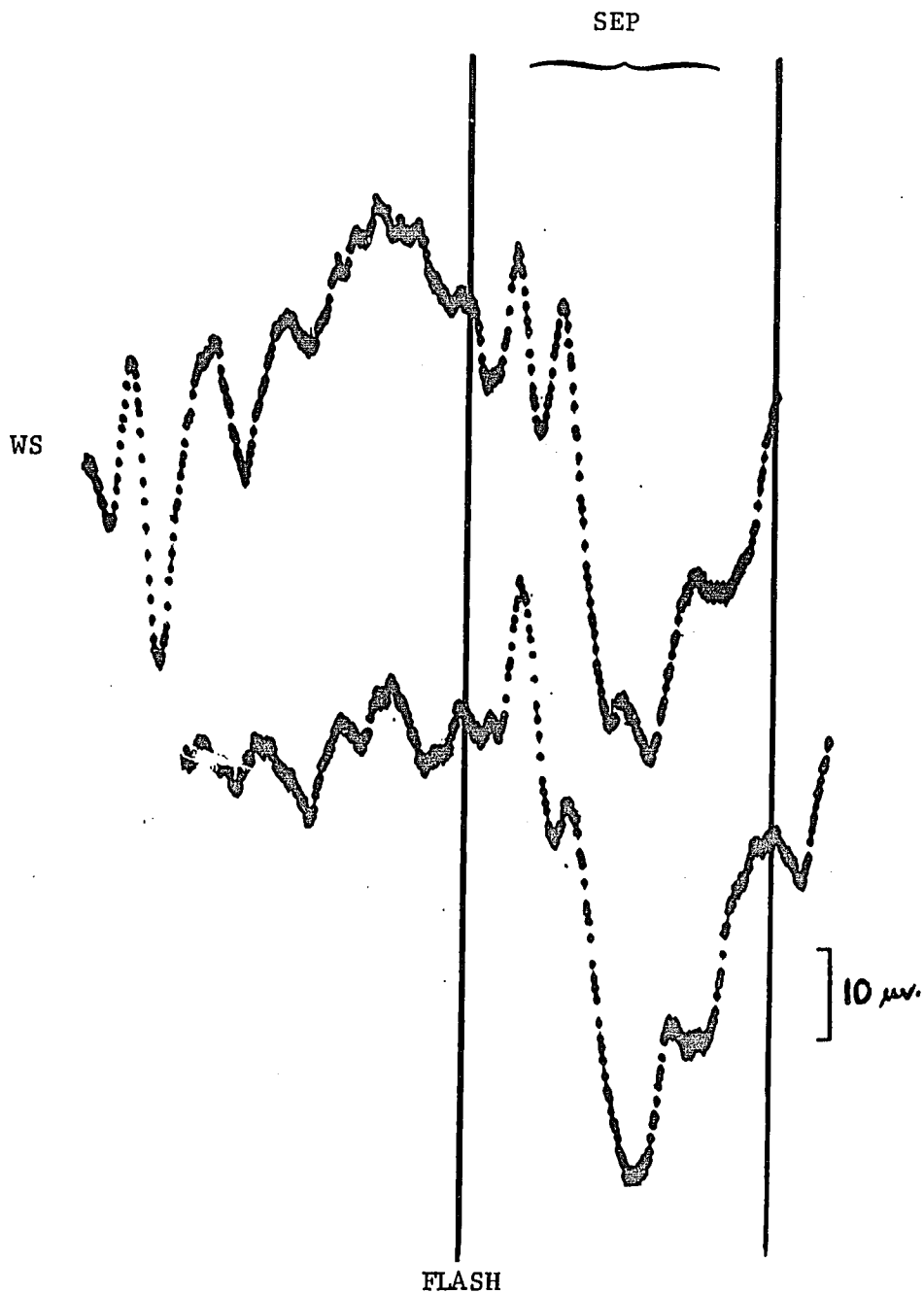


Figure F. SEP to a flash; superimposed on sustained CNV. Upper trace; responses were averaged only during occasional shorter foreperiods, under condition 3. Lower trace: response obtained under condition 1, with no WS. Both traces were obtained during a single testing session. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-Flash interval: upper trace, 1000 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: J.D. An upward deflection indicates a negative potential change at the vertex.

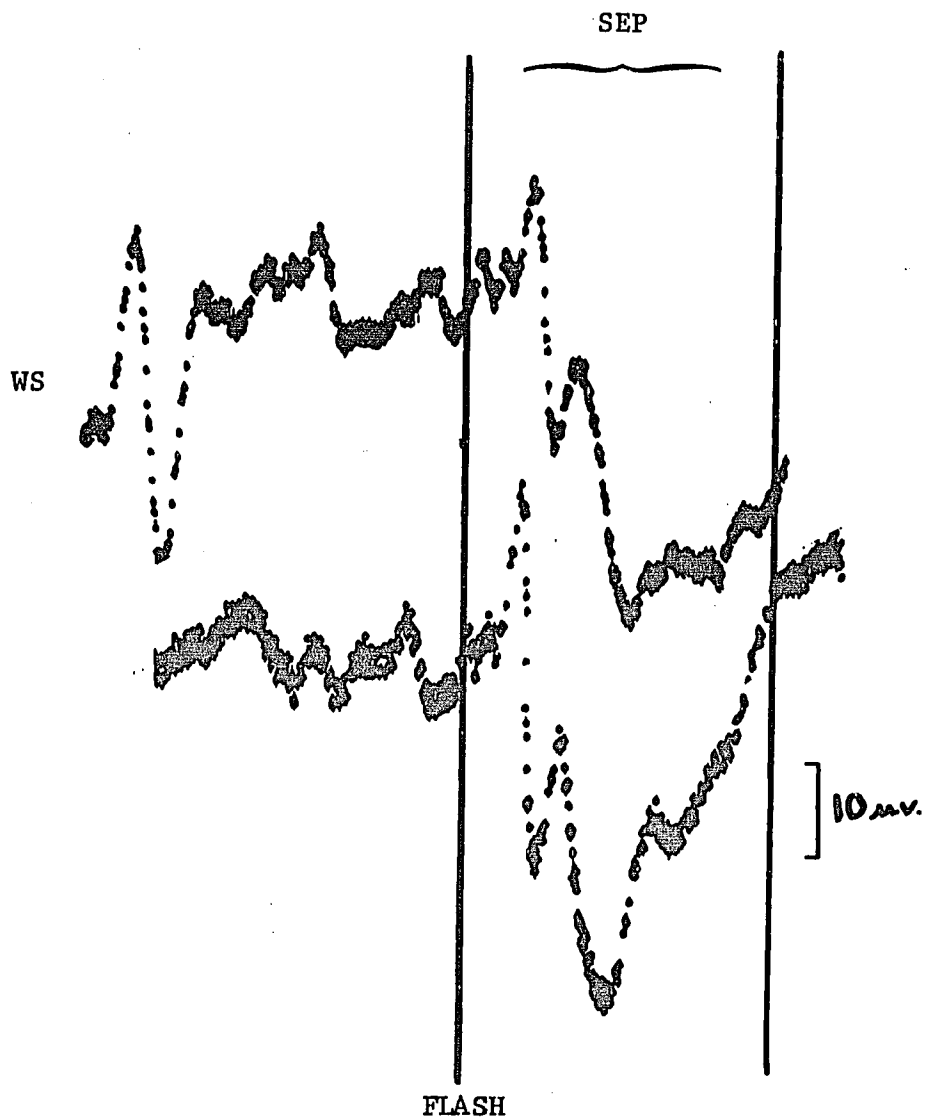


Figure G. SEP to a flash; superimposed on sustained CNV. Upper trace: responses were averaged only during occasional shorter foreperiods, under condition 3. Lower trace: response obtained under condition 1, with no WS. Both traces were obtained during a single testing session. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-Flash interval: upper trace, 1000 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: J.D. An upward deflection indicates a negative potential change at the vertex.

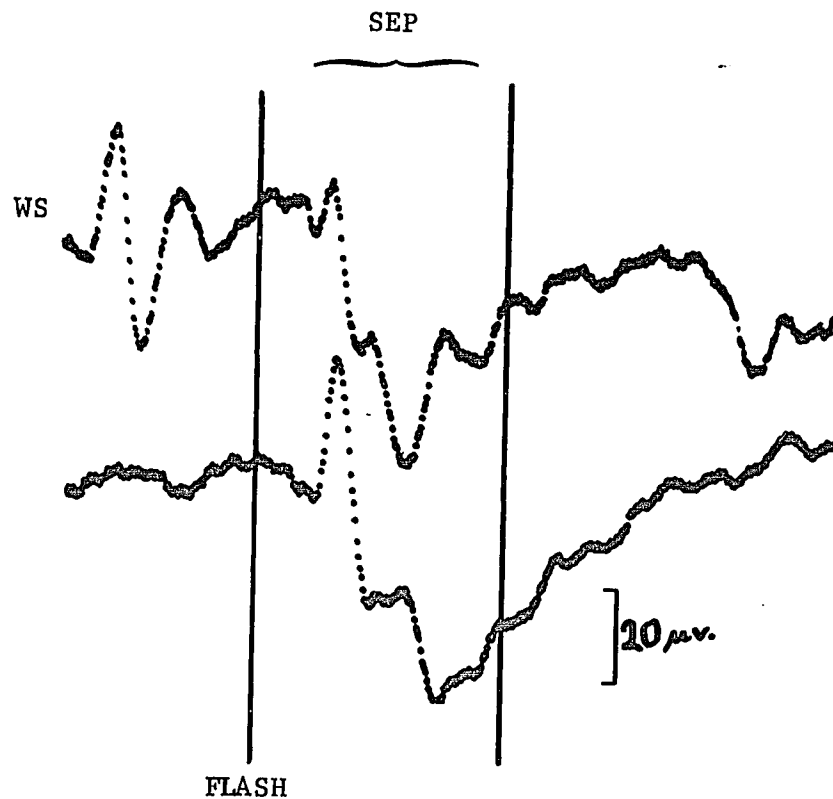


Figure H. SEP to a flash: superimposed on sustained CNV. Upper trace: responses were averaged only during occasional shorter foreperiods, under condition 3. Lower trace: response obtained under condition 1, with no WS. Both traces were obtained during a single testing session. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-Flash interval: upper trace, 500 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: J.D. An upward deflection indicates a negative potential change at the vertex.

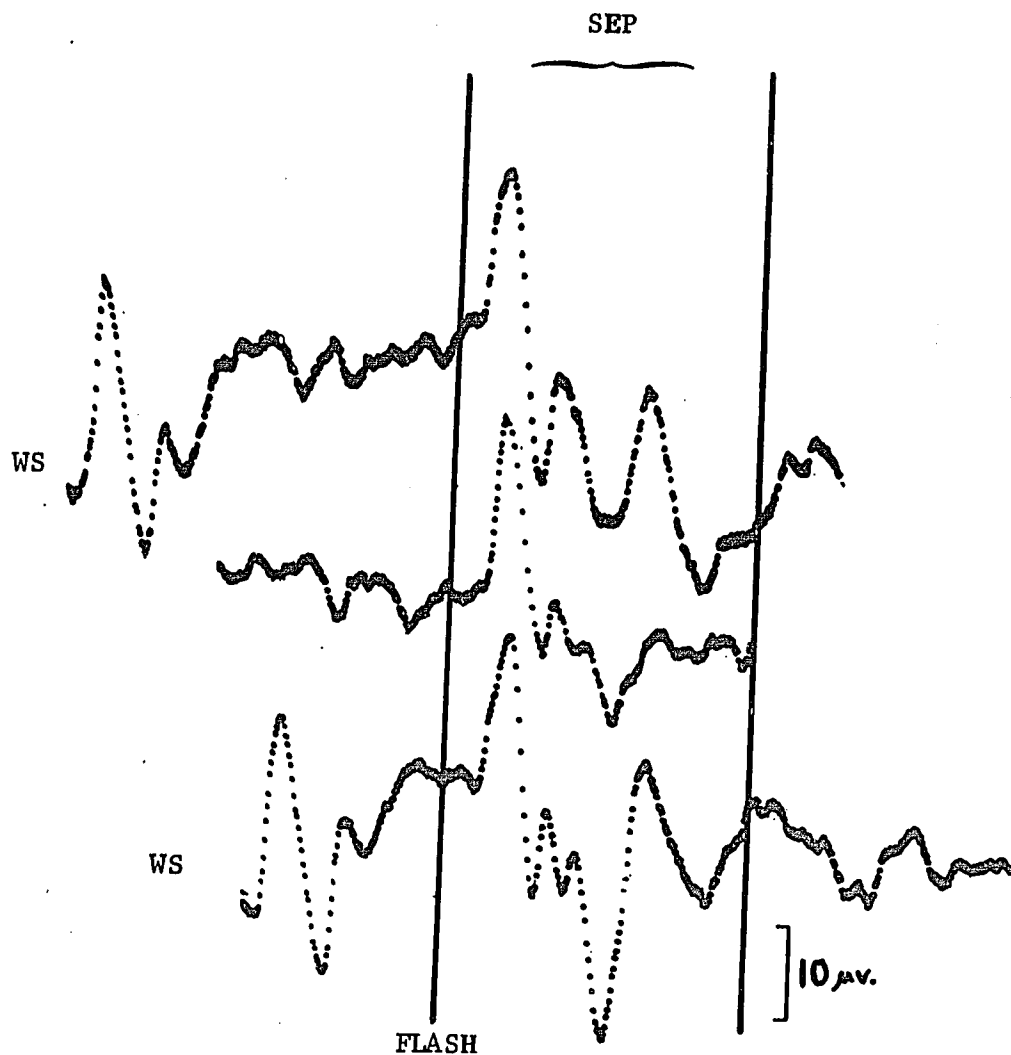


Figure I. SEP to a flash: superimposed on sustained CNV. Upper and lower traces: responses were averaged only during occasional shorter foreperiods. Middle trace: response obtained under condition 1, with no WS. All traces were obtained during a single testing session. Sweep time: 2000 msec. WS: warning signal. TS: task signal. WS-Flash interval: upper trace, 1000 msec., lower trace 500 msec. SEP: sensory evoked potential in response to TS. N: 20. Subject: G.T. An upward deflection indicates a negative potential change at the vertex.