

## WHILE A MONKEY WAITS: ELECTROCORTICAL EVENTS RECORDED DURING THE FOREPERIOD OF A REACTION TIME STUDY<sup>1,2</sup>

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In a typical reaction time study, a stimulus is presented to the subject, and he is instructed to respond to that stimulus "as fast as he can". It has been well established that if this "imperative" stimulus is preceded by another whose function is to alert the subject that the imperative stimulus is about to arrive, his reaction time is considerably reduced. This reduction of the reaction time in forewarned subjects is not surprising, and yet until recently there were few data on the events that occur during the "foreperiod", as the interval between the warning and the imperative stimulus is called. We report here a study of the electrocortical events recorded in rhesus monkeys during the foreperiod.

Our interest in the electrophysiology of the foreperiod has been triggered by the voluminous literature generated by Walter's report (Walter *et al.* 1964) that a slow negative wave can be recorded from certain areas of the scalp of human subjects during the foreperiod. This wave has been called by Walter the Contingent Negative Variation (CNV). Similar phenomena have been reported earlier by Kohler *et al.* (1952) and by

Rusinov (1960). However, Walter's report, coming at the period when the study of event-related components of the EEG has been advanced by the use of the signal averager aroused much interest. The current consensus (see discussion of Cohen's (1964) review) is that indeed such a pattern can be recorded from human subjects in circumstances closely resembling those described by Walter, although much caution must be exercised to eliminate artifacts (see for example Hillyard and Galambos 1970).

Although the CNV is accepted as a *bona-fide* phenomenon, there is very little agreement regarding its source and its functional significance and the degree to which various psychological variables affect its amplitude and time course. There is, for example, no definitive information on the distribution of the CNV over the cortex. Although in his early reports Walter stated that CNVs are recorded from the frontal areas, systematic surveys have not been published. (See also Cohen 1969.) Even more controversial is the nature of the psychological circumstances under which the CNV is recorded. Walter (1967) underlined the fact that during the foreperiod, the subject "expects" the second stimulus. He therefore sometimes calls the CNV the "expectancy" wave (E wave). Others have stressed the fact that during the foreperiod the subject is *preparing to respond* to the imperative stimulus and have suggested that the CNV is associated with conation rather than with expectancy (Low *et al.* 1966a). This debate is reminiscent of an earlier controversy about the nature of "set" during the foreperiod, where some investigators tended to emphasize "motor" sets, whereas others stressed

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sensory sets (see Woodworth 1938 for a review of this controversy).

The issue has been complicated by Kornhuber and Deecke's (1965) description of a "readiness potential", a slow negative wave that precedes a voluntary motor response. This wave has been studied in detail by Vaughan *et al.* (1968), who called this wave a motor potential and pointed out that the time course of the CNV and the motor potential are very similar. This would support the suggestion of Low *et al.* (1966b) that the CNV is a *conative* negative variation rather than an expectancy wave. Deecke *et al.* (1969), however, have distinguished, on the basis of spatial distribution of the potentials, between the "readiness" and the "motor" potentials, reserving the first term for the slow, CNV-like, negative swing beginning some 800 msec before the response. They use the term "motor potential" to label a short negative spurt which is superimposed on the readiness potential just before the response. It is, of course, possible that the readiness potential is, in fact, a CNV, for which the warning stimulus is generated internally by the subject. However, the fact that Deecke *et al.* (1969) report that the readiness potential is *positive-going* in the frontal area is not consistent with this suggestion. The issue stands unresolved.

It appeared to us that a detailed study of the electrophysiological events that can be recorded directly from the cortex of a rhesus monkey would provide important information about the locus of the generator mechanism of the CNV and thereby help to solve some of these issues and illuminate the functional significance of the CNV. Clearly such a strategy presupposes that a CNV can be recorded in the rhesus. Low *et al.* (1966a) and Borda (1970) have reported that this can be done. Using an experimental paradigm closely resembling Walter's, they have recorded what appears to be a CNV-like wave in monkeys. We therefore proceeded to investigate in detail, using a transcortical recording technique, the electrocortical potentials that appear over the monkey's brain while the monkey waits.

## METHODS

### Subjects

The data reported here were obtained from

seven *Maccaca mulatta*. The monkeys were purchased from a commercial supplier and on their arrival at the laboratory weighed 5–7 lb.

### Apparatus

During experimental sessions, monkeys were placed in the training chamber shown in Fig. 1. Visual stimuli were presented on a circular ground glass screen occasionally enclosed in a viewing tube. Stimuli were generated by a xenon arc lamp driven by a special purpose power supply and driving mechanism<sup>1</sup>. Lamp onset and offset times were a few microseconds. The lamp could be kept on for any desired duration without loss of brightness. The intensity of this source was reduced by neutral density filters. The brightness of the light patch at the screen measured by a Zoomar S. E. I. exposure meter was 2.18 log foot lamberts. The patch subtended a visual angle of 2.5°. A 1000 c/sec tone of moderate intensity generated by a Hewlett-Packard Oscillator (no. 241A) could be presented via a small speaker mounted in the chamber as shown in Fig. 1. A speaker, mounted outside the chamber, delivered white noise at an intensity sufficient to mask out the sounds of the experimental apparatus and of nearby offices.

The monkey's head position was continually monitored via closed circuit television. A red lamp mounted outside the chamber provided continuous illumination. A response key was available within access of the animal's right hand. To depress the key the monkey had to extend his hand fully, grasp the handle and depress the key over a distance of 2 in. (A force equivalent to 365 g was required to depress the key fully.) The reinforcements, 1 g pellets of non-nutritive mixture, were delivered by a Foringer feeder down a chute into a pellet dispenser. The monkeys could not reach the pellets with their hands. They had to scoop the pellet out of the receptacle with their tongue and lips. Given a bit of training, the monkeys were quite adept at this task.

Stimulus scheduling was controlled by an Iconix system 136, an assortment of digital timing and logic equipment. Each of the critical events in the experiment generated amplitude-

<sup>1</sup>We are indebted to Mr. Donald Humphreys, Radiation Branch, Ames Research Center, for designing and building this light source.

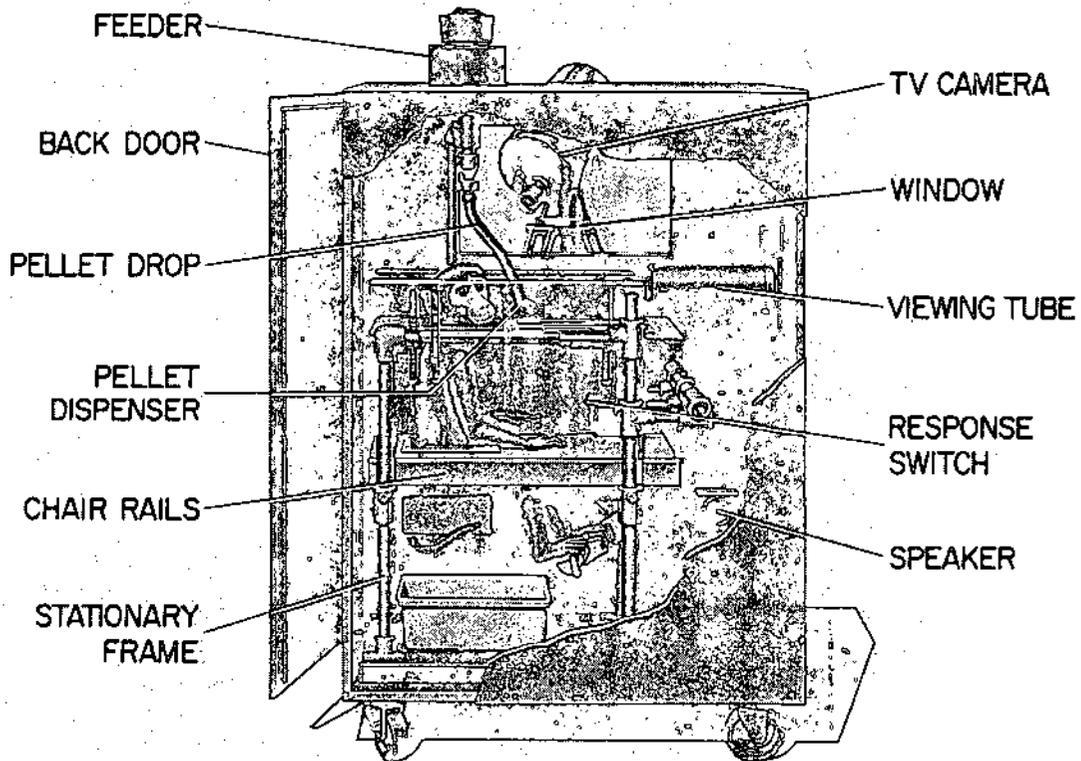


Fig. 1. Metal chamber in which monkeys were trained and tested. Behavior was monitored continuously via closed circuit television.

coded event markers using an event coder described elsewhere (Donchin and Pappas 1970). These were recorded on one channel of a magnetic tape recorder (Ampex FRI300). Electro-physiological data from the monkey were amplified using Brush EEG amplifiers with a band width of 0.1–30 c/sec (roll off slope 20 dB/octave), and also recorded on tape. The data were subsequently analyzed with an IBM 1800 computer.

#### *Behavioral techniques*

The sequence of events in one trial in each of the three experimental paradigms used is shown in Fig. 2. The first paradigm can be described as follows. The warning stimulus (S1) (a tone for task A and a flash for task B) would be turned on. If the monkey failed to depress the key within T1 msec, S1 would be turned off, and a new inter-trial interval (ITI) of 10 sec would ensue. Manipulation of the response key during the ITI would then restart the ITI. Thus, before the presentation of S1, a 10 sec interval during which

the key was not manipulated must have passed. If the monkey did depress the response key within the allotted interval after S1, S1 would not be turned off, and the foreperiod (ISI) would commence. During that period the monkey was not allowed to release the key. If the monkey released the key during the ISI, the trial would again abort, S1 would be turned off and a new ITI would ensue. The foreperiod terminated with the presentation of the "imperative" stimulus (S2). Following S2 (a flash for task A and a tone for task B), the monkey had to release the key within a specified interval, T2. A key release within that interval terminated both S1 and S2 and produced a pellet. A failure to release in time caused both stimuli to terminate and a new 10 sec ITI commenced. Thus to obtain a pellet the monkey had to press the key in response to S1 within T1 msec, hold it down for ISI msec (until the presentation of S2), then release the key within T2 msec. Any deviation from this sequence aborted the trial and commenced a

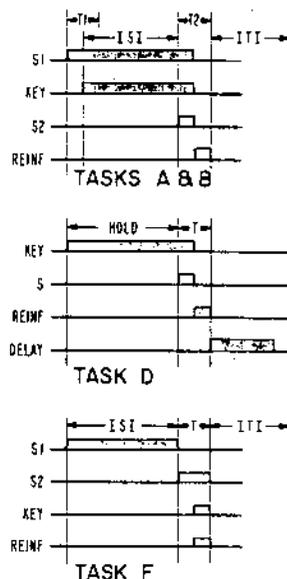


Fig. 2. Diagram of three basic training tasks. S1 and S2: first and second stimuli; T1 and T2: time intervals during which key press and release has to be made; ISI: inter-stimulus interval; ITI: inter-trial interval. In task A ("signalled key press"), S1 was a tone and S2 a light. The order of stimuli was reversed in task B. Note in tasks A and B that the ISI was initiated by key pressing, not by S1 onset. Task D is the "unsignalled key press" task, whereas task F is referred to as the "delayed key press" task.

10 sec time-out period.

Monkeys were trained to perform this task according to schedules described by Stebbins and Lanson (1961). Relatively young monkeys could be easily trained in 4 weeks to respond with T1 and T2 reduced to 400 msec and ISI increased up to 2500 msec. Older monkeys were more difficult to train. All trials in the paradigm described above were initiated by the presentation of a stimulus to which the monkey was expected to make a motor response. In order to tease apart the effects of the stimulus and the effects of the response on the ensuing slow cortical potentials, two additional tasks were devised. Task D (Fig. 2) was designed to assess the effects of the key press, and the sustained motor activity following it, in the absence of a signal to respond. We shall refer to this as the "unsignalled key press" paradigm. Three monkeys (A-76, A-77 and A-81) were trained to initiate trials voluntarily by pressing and holding a lever down without any external sensory cue. After a fixed holding interval, corresponding to the length of the ISI in task A, a stimulus was presented signal-

ling the monkey to release the key. Animals were required to release the key within T msec in order to obtain reinforcement. A forced delay of 1–4 sec was interposed between successive trials to provide an inter-trial interval. With the exception of removing the first stimulus, task D was identical to task A.

Task F (Fig. 2) was designed to elicit cortical evoked potentials to a tone or a light presented without an associated motor response. Three monkeys (A-77, A-80 and A-85) were trained to perform task F. Two stimuli paired in the same temporal sequence as the original task were presented, but monkeys were trained to delay the response until the onset of S2. Reinforcement was contingent upon pressing the key within T msec after S2. Response within the ISI aborted the trial. Task F is comparable to the paradigms used in most human CNV experiments in which no overt response to the warning stimulus (S1) is required, but a definitive response or decision following the imperative stimulus (S2) must be made. Borda (1970) used an equivalent task in his study of CNV-like cortical activity in rhesus monkeys.

#### Transcortical electrodes

To obtain a mapping of the distribution of electrocortical events associated with the fore-period, we used transcortical electrodes<sup>1</sup> (Fig. 3). The electrode consisted of a coil of "platinized" platinum mesh (a), placed inside a plastic receptacle. A 5.5 mm shaft of platinum-iridium wire (b) protruded through the core of this coil. The shaft was insulated along its length except for an exposed tip of 1.5 mm. When implanted successfully the coil was placed epidurally and the tip was placed in the subjacent white matter or in the lower cortical layers. The lead wire from the surface (f) and the subcortical (b) electrode were brought to Amphenol miniature connectors embedded in the plastic capsule (c). This arrangement of the electrode was quite helpful during surgery. The wires connecting the electrode to the head plug were pre-cut to the proper length and soldered to the plug and to an Amphenol connector. During surgery the connectors

<sup>1</sup> The electrodes were manufactured by Mr. Dale Shute at the Mechanical Instrument Branch at Ames Research Center.

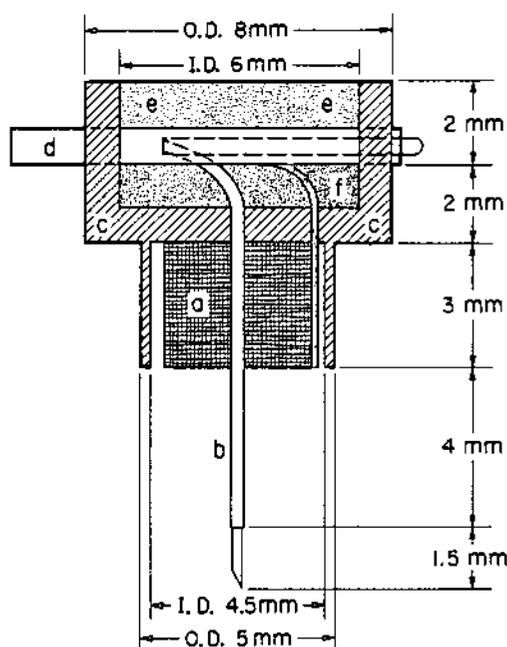


Fig. 3. Schematic diagram of platinized platinum transcortical electrode used to record electrocortical events. *a*, epidural Pt mesh coil; *b*, Teflon-insulated subcortical Pt probe; *c*, plastic (polyvinyl chloride) capsule; *d*, Amphenol connector; *e*, Epoxy resin used to seal crown of electrode; *f*, lead from epidural coil to connector.

on the wire were inserted into the electrode receptacles, thus eliminating the need for crimping or soldering.

#### Surgical procedure

Surgery was performed under Diabulal anesthesia (35 mg/kg) after aseptic procedures with the monkey's head immobilized in a stereotaxic instrument. A 5 mm hole was drilled in the skull to accommodate each electrode capsule, and a cataract knife was used to make a small slit in the dura through which the subcortical shaft was inserted. Electrodes were secured to the skull with dental cement and a cap fashioned from the same dental acrylic. A recovery period of one week was allowed before resumption of training.

A total of 43 transcortical electrodes was implanted in seven animals as indicated in Fig. 4. Electrodes were implanted in the left hemisphere of all animals with the exception of Buber (A-79), who had three electrodes placed symmetrically in the right parietal lobe in addition to those shown in Fig. 4.

- △ BAT (A-76)
- CINDY (A-77)
- ⊙ BUBER (A-79)
- SONJA (A-80)
- MILHOUSE (A-81)
- △ SPIRO (A-85)
- DIABLO (131)

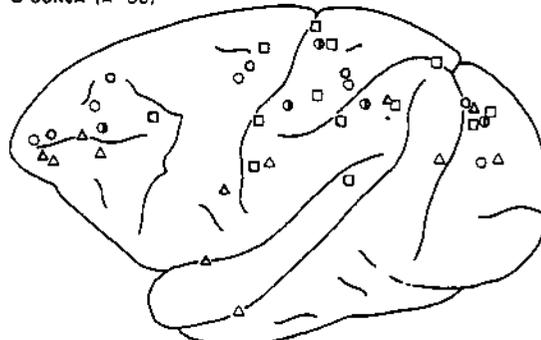


Fig. 4. Composite drawing of electrode placements in all monkeys used in this study.

#### Histology

Histology was completed at 37 of the 43 electrode sites<sup>1</sup> in order to determine tip positions and the effect on brain tissue of prolonged contact with platinized platinum. Of the placements examined, 12 tips were located unequivocally in subjacent white matter, 5 tips straddled grey and white, and 21 tips were in various cortical layers. Electrodes were designed such that the 5.5 mm shaft would penetrate through the cortex and lodge in subjacent white matter, thus providing a convenient indifferent reference for each epidural coil. Due to the highly convoluted structure of the macaque brain, the majority of tips did not terminate in white matter as intended. The morphology of averaged responses recorded at similar sites in different animals, however, appeared to be very consistent as long as the tips were located in deep cortical layers (4, 5 or 6) or subjacent white matter. Inconsistencies were noted when the tip crossed a sulcus or underlying white matter and lodged in the cortex of a different convolution. Ten placements were excluded from analysis because the reference tips were located in superficial cortex, a different convolution or a fissure.

Limited atrophy of superficial cortical layers occurred beneath the surface coils of some early implants. This resulted from the use of plastic

<sup>1</sup> Six occipital electrodes were not examined histologically because occipital averaged responses showed little correlation with activity occurring in other regions in the tasks used in this study.

electrode capsules which were too long, causing depression of the cortical surface beneath the electrode. Shortening the capsule length eliminated this problem in later implants. No irritation or degeneration of brain tissue due specifically to contact with the platinized electrode surface was discernible in any animal. Location of electrode tips was facilitated by the fact that small particles of platinum black remain in the brain after removal of the electrode.

Table I summarizes the distribution of electrodes in cortical areas and indicates how many have been used in the following analysis.

TABLE I  
Distribution of transcortical electrodes

Electrode position	Total implanted	Used in analysis
Anterior frontal	10	6
Precentral	4	4
Postcentral	11	8
Posterior parietal	6	4
Temporal	3	1
Occipital	9	2

## RESULTS

### *The transcortical negative variation (TNV)*

In the data recorded transcortically during paradigms A and B, the most prominent and reliable wave form occurred in the postcentral parietal region. As can be seen in Fig. 5, there are three major peaks in this wave form—surface negative peaks at 200 and 800–1000 msec (N200 and N1000) and a surface positive peak with a latency of from 300–400 msec (P400). A definite notch appears approximately half-way from P400 to N1000. This notch appears near the time of the key press. The N1000 peak occurs after the response key is pressed. After N1000, a slow positive-going shift occurs. No prominent potential changes associated with S2 could be discerned in most recordings from paradigms A and B. The temporal “jitter” associated with variable reaction times after S1 and S2 probably attenuated the potentials which appear at these delays. Data presented in Fig. 6 and 7 represent the remarkable degree of intra- and inter-subject consistency of the TNV. When performance stabilized on tasks A or B, the wave forms were remark-

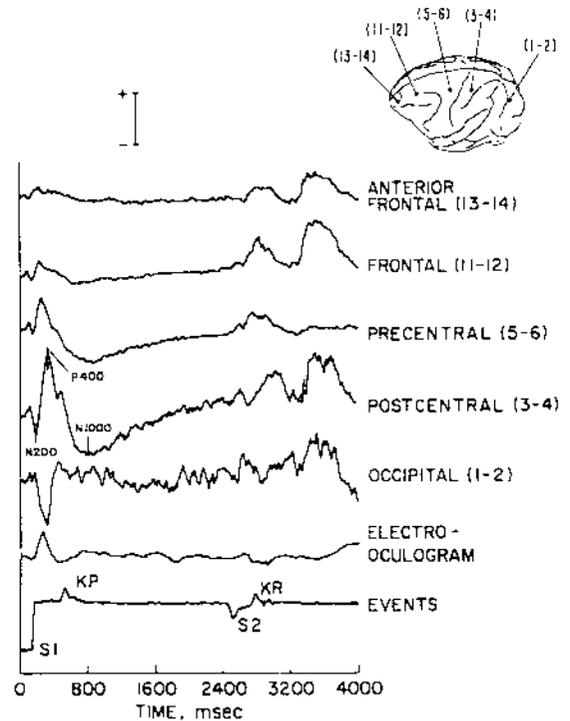


Fig. 5. Averaged transcortical records obtained during task A. Onset of stimuli (S1 and S2), key press (KP), and key release (KR) are depicted in lowest channel. Positivity of the surface electrode in this and subsequent figures is upward. Averages of 25 trials.

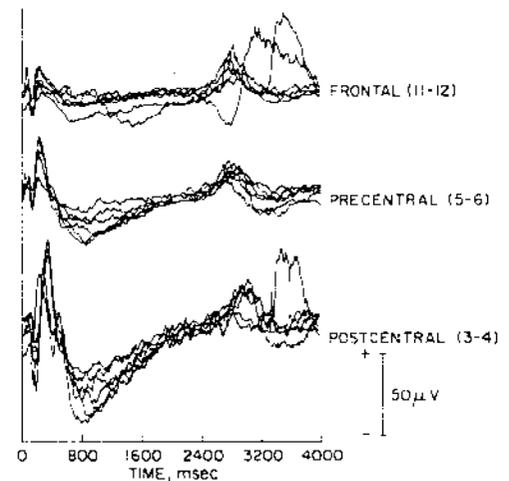


Fig. 6. Superimposed records from three cortical sites in one monkey illustrate a high degree of within-subject consistency across six training sessions spanning a 45 day period. Each trace represents an average of 25–50 trials. Task A: 2000 msec inter-stimulus interval.

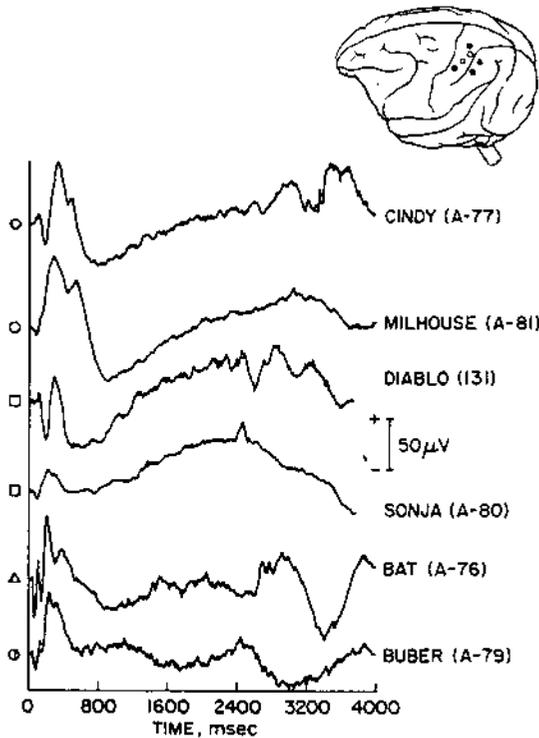


Fig. 7. Inter-subject consistency of the pattern recorded from the postcentral electrodes is apparent in records obtained from six monkeys performing tasks A or B; 2000 msec inter-stimulus interval. Averages of 25-50 trials.

ably consistent and virtually identical in shape for sessions distributed over several weeks (Fig. 6). The same general pattern appeared in five other monkeys (Fig. 7) trained to perform tasks A or B. The N200-P400-N1000 sequence is clearly apparent (although N1000 is somewhat attenuated for Sonja and Buber) and always of maximal amplitude in the postcentral parietal region.

A similar wave form appeared over the precentral motor cortex in three monkeys having electrodes in this region (Fig. 5 and 7). The amplitude of all components, however, was substantially smaller at pre-central than post-central sites in these monkeys. The notch between P400 and N1000 occurred consistently in the precentral records of monkey A-81 but was not always apparent in the precentral records of monkeys A-77 and A-80. The TNV is even more attenuated in the frontal area than it was in the precentral region. In proportion to the decrement in the P400 and N1000 waves, the positive-going slope after N1000 does not return to baseline so

rapidly frontally and precentrally as it does in the postcentral parietal area.

Three monkeys (A-81, A-85 and I31) were implanted before training in any tasks in order to observe the development of TNV configurations as a function of improvement in performance. Development of the TNV in monkey A-81 over a period of weeks is depicted in Fig. 8. This monkey's records can be seen at an even later stage of performance in Fig. 9. Monkey A-81 was trained to perform task B well in approximately 3 weeks. As reaction time and the proportion of aborted trials steadily decreased, the TNV gradually emerged. The negative-going portion of the TNV (P400 to N1000) shows the most striking changes as reaction time improves. The P400 to N1000 amplitude not only increases markedly, but it forms a steeper slope toward an earlier "N1000" peak. In turn, the positive-going portion after N1000 appears to return toward baseline more rapidly. With continued training it can be seen in Fig. 9 that the "N1000" peak now occurs as early as 800 msec after S1. In turn, a more rapid positive return to baseline is evident. Fig. 9 also illus-

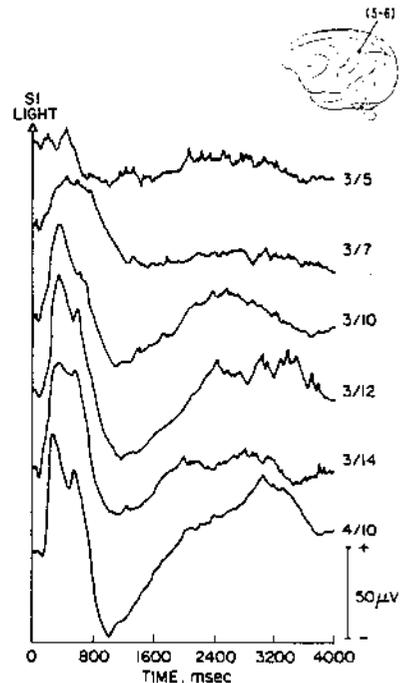


Fig. 8. Gradual emergence of the transcortical postcentral pattern during training. Monkey received approximately 100 trials daily, 6 days per week (task B). Averages of 25-50 trials.

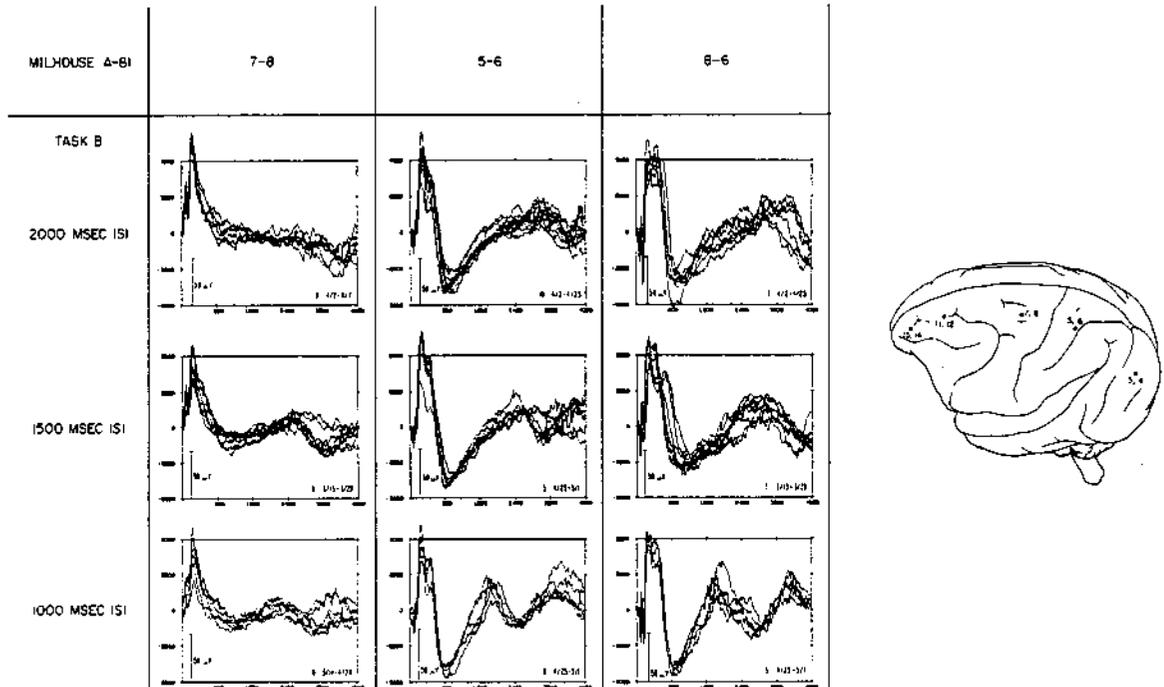


Fig. 9. Superimposed records from two cortical locations during performance of task B at varying inter-stimulus intervals. The first two columns show transcortical recordings. The third column (8-6) depicts bipolar surface-to-surface recordings between epidural coils of electrodes (7-8) and (5-6). Figures in the lower right corner of each box indicate the number of tracings superimposed in each record and inclusive dates of the recording periods. Each tracing is an average of 25-50 trials.

trates the fact that the positive return to the baseline is clearly affected by the interval between S1 and S2 (ISI). As the ISI is reduced, the positive return becomes more rapid. Similar data were obtained from all other monkeys.

#### Unsignalled key press (task D)

Data obtained during the unsignalled key press paradigm (task D) were averaged forward and backward in time from the key press. The transcortical patterns we have observed at postcentral, precentral and frontal electrode locations in the unsignalled key press task are shown in Fig. 10. Postcentrally, a negative wave begins at the time of the key press. This negativity is followed frequently by a positive drift during the latter part of the holding interval. Approximately 300 msec before complete depression of the response key, a more abrupt negativity occurs. Precentrally and frontally these same events can be seen at about half the amplitude that they are seen postcentrally.

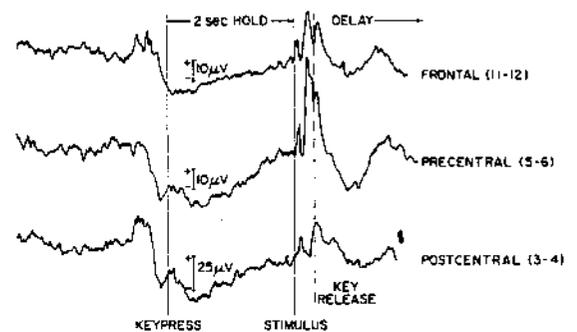


Fig. 10. Records obtained at three cortical locations when monkey voluntarily initiated a holding interval following a forced 2 sec delay (task D). Key press marker denotes point at which key was physically depressed. Averages of 50 trials.

The wave forms and topography shown in Fig. 10 resemble closely that part of the TNV which follows the peak of the P400 component in the signalled double reaction time tasks (tasks A and B). In comparing the signalled (Fig. 5 and 6) with the unsignalled key press (Fig. 10), notice the order of events which appear around the time of the key press. When the monkey presses the

key in response to a stimulus, the TNV following P400 is a negative-going wave with a superimposed notch, the negativity peaking at N1000. A positive-going wave follows N1000. When the key press is unsignalled, a positivity can be seen in some records before the key press. This positivity is followed by an abrupt negativity, a notch near the time of the key press, a subsequent negative peak after the key press, and a positive-going wave after the negative peak. As in the signalled key press task, the TNV's positive-negative-positive sequence of the unsignalled key press is largest in the postcentral parietal region. In evaluating the apparent differences in wave form between the signalled and unsignalled key press tasks, it is important to remember that the averages for the signalled key press are synchronized with the signal for key pressing (S1), whereas in the unsignalled task, they are synchronized with the key press. The complete loss of the N200 component and the great degree of attenuation of the possibly analogous P400 component could therefore be due either to the loss of the warning signal (S1) or to the loss of synchronization which the S1 stimulus provided. An analysis of the wave form which appears after an S1 which is not followed by a key press should be helpful in evaluating these alternatives.

#### Delayed key press (task F)

Some records obtained when monkeys performed this task, *i.e.*, when a key press was not required during the inter-stimulus interval, are presented in Fig. 11. When comparing these records to those obtained with the signalled key press task, it should be noted that the monkeys were not as overtrained in the delayed key press (task F) as in the immediate, signalled key press situation. Furthermore, all monkeys experienced task A training before training on task F commenced.

Several differences in wave form and topography are evident in Fig. 5, 9 and 11. First, the prominent inter-stimulus negativity and subsequent positive-going wave observed previously at the postcentral location in the signalled or the unsignalled key press tasks are virtually absent. The N200 component remains intact. The amplitude of the P400 component—approximately 75  $\mu\text{V}$ —is dramatically attenuated. Note, how-

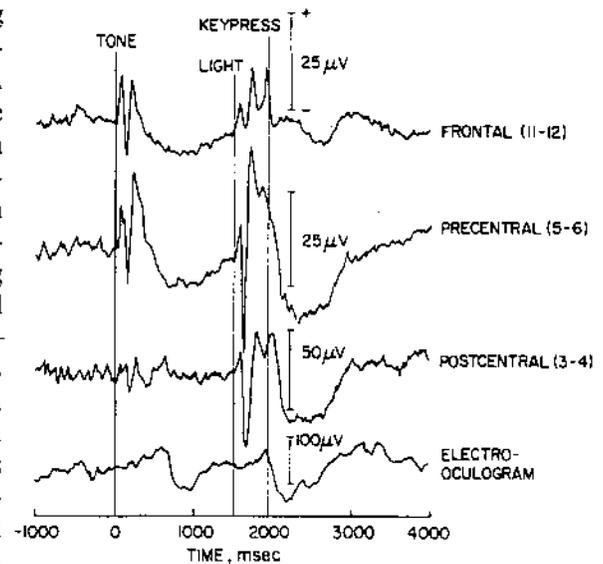


Fig. 11. Transcortical records obtained during task F in which monkey withheld response until S2. Sustained ISI negativity occurred at frontal and precentral sites, but not postcentrally. Averages of 40 trials.

ever, that the typical transcortical pattern observed in the signalled key press task following S1 now appears in the pre- and postcentral electrodes following S2 and the delayed key press. In addition, a sustained inter-stimulus negativity, not unlike a human CNV, appears at the frontal site where it was practically unobserved when the monkeys performed task A or B. When an inter-stimulus interval of 1000 msec was used, practically all frontal recordings showed a sustained negativity peaking at the end of the inter-stimulus interval. Last, amplitude of the P400 component, which was found in the signalled, immediate key press task to be clearly maximal at the post-central electrode, now appears in the delayed key press situation (task F) to be maximal at the precentral site. Monkey A-80 showed a greater inter-stimulus negativity at the frontal than precentral electrode site, and A-77 showed about the same amount of negativity at frontal and precentral sites during the performance of the delayed key press task. The difference in amount of training between the signalled key press and the delayed key press tasks probably is not crucial in determining the differences which are apparent. Even when monkeys are not overtrained in the signalled key press situation (Fig. 8), the postcentral

negativity after S1 is obvious. In the delayed key press situation, on the other hand, the postcentral negativity is not present after S1, although it is present after S2 where the delayed key press occurs. The attenuation in the P400 component in the delayed key press situation (task F), compared to the immediate, signalled key press (task A), could be due either to the level of training, or to the fact that a positivity from the key press summates with the late positivity from the S1 stimulus. Future work will be needed in order to decide between these alternatives.

#### *Extracranial controls*

Electrodes for monitoring head and eye movements were implanted in all monkeys. Records obtained from these electrodes indicated that extracranial artifacts had minimal effect on the transcortical recordings. Samples of eye movement recordings are shown in Fig. 5 and 11. Although there are indications of eye movements which were synchronous with S1, for several reasons it is unlikely that these artifacts have contaminated the transcortical data. The transcortical recording technique is designed specifically to attenuate differentially potentials generated remotely; such potentials would affect ideally the two recording surfaces of the transcortical configuration equally. Furthermore, frontally generated artifacts would have affected precentral electrodes more dramatically than postcentral electrodes. The fact that maximal amplitudes were observed at postcentral parietal locations in the signalled and unsignalled key press tasks suggests that the source of electrical potentials monitored during these tasks was intracranial. Data obtained from monkey 131 (Diablo) further support this conclusion. Vertical restraining bolts were incorporated in a skull cap formed with epoxy on the head of this monkey. During training the head of this monkey was completely immobilized, precluding head movement artifact. The postcentral wave form recorded from this monkey (*cf.* Fig. 7) did not differ substantially from the wave form observed in the other monkeys.

#### DISCUSSION

This study was undertaken to clarify the source and functional significance of the CNV ob-

served by Walter *et al.* (1964). It is therefore important to determine if the events which have been observed in our experiments are homologous to the CNV recorded in humans, and if they are functionally similar to the wave form previously identified as a CNV in monkeys (Low *et al.* 1966a; Borda 1970). We shall examine three aspects of the data: wave form, topography and the dependence of wave form and topography on specific behavioral situations.

#### *Wave form and topography*

Walter *et al.* (1964) found that a gradually incrementing negativity (CNV) was recorded on the human scalp during the foreperiod (S1-S2 interval) of a reaction time task. Many investigators have since recorded this same event and are in general agreement about its wave form, providing that amplifiers with low-pass characteristics are used in their recordings (Cohen 1969). On the basis of limited intracerebral recordings in human patients, it was surmised (Walter *et al.* 1964) that the CNV originated in anterior frontal cortex and swept in an antero-posterior direction across the cerebral mantle. Low *et al.* (1966b) also report that CNV amplitude is maximum at midline frontal recording sites. Their records, however, were taken from the anterior portion of the motor cortex and show considerable CNV at the vertex. On the other hand, Cohen (1969) reports that the human CNV recorded from the scalp is maximal at the vertex. Hillyard (1968) has found that upward eye movements during the reaction time foreperiod can produce a frontally dominant distribution of eye movement artifact. These eye movement artifacts can account for as much as 25% of the negativity which appears at the vertex in a CNV situation. Vaughan *et al.* (1968) on the other hand, confirming Kornhuber and Deecke's (1965) report that a "readiness potential" appears in advance of an unsignalled voluntary movement, indicated that this potential is largest over the vertex. If these two sources of activity varied in the different studies of CNV topography, their summation could produce a maxima anywhere from over the rolandic fissure toward the frontal pole. Although there are considerable inconsistencies between these topographic studies, they do agree that the CNV is maximal precentrally. Other

studies of the CNV (Cant and Bickford 1967; Low 1969) also show that a CNV-like wave form is largest in front of the central fissure.

In contrast to the human and the monkey CNV topographies, the TNV during the waiting and key pressing period of the double reaction time task (task A) is clearly maximal behind the central fissure (postcentral amplitudes being approximately twice the precentral amplitudes). Little, if any, corresponding negativity was observed in the frontal electrodes. Furthermore, unlike the human CNV which shows a sustained or incrementing negativity that peaks just before the S2 stimulus, the postcentrally recorded transcortical pattern peaks approximately 800–1000 msec after the warning signal. This is so regardless of the interval between S1 and S2, although the positive-going return to baseline after N1000 is quite clearly affected by the S1–S2 interval. Similar results were obtained by Low *et al.* (1966a) who report wave forms peaking shortly after S1 in their preliminary CNV study with monkeys. Subsequent work from their laboratory, however (Low 1969; Borda 1970), indicates that the foreperiod negativity is clearly sustained for long intervals.

#### *Dependence of wave form on task*

The task which is used typically in human experiments on CNV is a simple delayed reaction time with a fixed foreperiod. Usually, 1 sec after a warning stimulus (S1) a command stimulus (S2) signals a response, such as pushing a button. In order to insure that the monkeys attend to the warning stimulus, we required them to depress a key upon presentation of S1. Release of the key was then required after S2 in order to obtain a reward. The task we chose to study the CNV in monkeys therefore differs from the human CNV paradigm by requiring a key press and maintaining pressure on the key until S2. Thus the wave forms which result and their topography may be affected by the key press required after S1. If the key press is critical for producing the patterns we have observed in the postcentral electrodes. (the TNV), a similar wave form should result when a monkey simply depresses a key to initiate a holding interval even without an S1. In fact, the work we have completed to date using this paradigm (unsignalled key press) indicates that a negativity

can be observed just before and soon after a key press which is not signalled. As in the signalled double reaction time situation, the negative wave begins before completion of the key press, continues after the key is pressed, and begins its return to baseline before the key is released. Furthermore, it is largest in the postcentral parietal area. In both the signalled and the unsignalled key press situations, a notch can be seen before this negativity reaches its peak. These parietal wave forms we observe in our key press tasks are remarkably similar to those found by Vaughan *et al.* (1970). In their work, monkeys also pressed and maintained pressing a lever. Unfortunately, they have implanted electrodes only over the motor cortex, where we see the same wave form but at half the amplitude that it is observed postcentrally. The data obtained during the unsignalled key press paradigm (D) can also be compared to the data obtained by Borda (1970) from one of his monkeys. In order to assess the effects of key pressing on the recorded potentials, Borda required one monkey to execute a series of unsignalled and unreinforced key presses and searched for event-related potentials during the 4 sec preceding the key press. In contrast to our data, no such potentials were observed. This discrepancy might be due to the fact that Borda's posterior electrode was placed anterior to the regions from which we recorded during paradigm D. It is also possible that the pre-key press potentials we observed are not just "motor" potentials, but rather appear in conjunction with a key press only when the key press is either reinforced directly or initiates a train of events leading to a reinforcement. Borda does not report how he induced the monkeys to execute unsignalled unreinforced key presses, and so it is difficult to compare the two studies. The issue however bears further careful study.

If the key press is crucial in determining the wave form and topography which we have found in the double reaction time paradigm, then the postcentral negativity and the positive-going return after N1000 should disappear when the key press is delayed until after S2. Since a delayed key press task is identical to the situation used in human CNV recording, the inter-stimulus negativity should now be largest pre-centrally or frontally rather than postcentrally (Walter *et al.*

1964; Borda 1970). Furthermore, since the key press is delayed until after S2, the postcentral negativity should now be found after S2 instead of after S1. The data we have gathered to date on the delayed key press paradigm (F) support these predictions. When a monkey waits for S2 and does not press the key during this period, there is virtually no postcentral negativity or positivity before S2. The postcentral negativity is seen, however, after S2, coinciding with key press.

### Conclusions

In order to clarify the source and functional significance of the CNV wave form of Walter *et al.* (1964), we have studied patterns of transcortical potentials which appear in the monkey's brain while the monkey waits in a reaction time task. A TNV was recorded with a topography which seemed to differ from the topographies of the CNV which have been obtained in other investigations whether made in humans or in monkeys. In lieu of concluding that the TNV represents a new kind of CNV, or that the subsequent positive-going wave is a "contingent positive variation", we have examined whether one task in which we observed the TNV differs functionally from the CNV paradigm more commonly used. The task we used differs from the usual CNV paradigm by requiring the monkey not only to wait for an imperative stimulus but also to press and continue pressing a response key immediately after S1. Such a motor response and its proprioceptive feedback may have yielded the wave forms which we have observed. Some secondary experiments were conducted in order to find whether the act of key pressing is crucial for producing a topography which differs from that observed when a monkey "waits" but does not press a key. The data from the experiments done to date indicate that waiting without key pressing indeed produces the classic frontal and precentral negativity (CNV) which has been observed during the waiting period by Borda (1970) in monkeys and by Walter *et al.* (1964) in humans.

### SUMMARY

Electrical potentials in frontal, motor and parietal cortex of young rhesus monkeys during three foreperiod reaction time tasks were studied using transcortical Pt-PtCl electrodes, long time-

constant amplifiers and computer-averaging techniques. A prominent positive-negative-positive wave form was observed maximally in postcentral cortex when monkeys held a key down during a fixed interval between two stimuli. When response was withheld until the second stimulus, sustained negativity occurred frontally but not postcentrally. The relationship of contingent negative variation, motor potentials and the observed electrocortical patterns is discussed.

### RESUME

QUAND UN SINGE ATTEND: EVENEMENTS ELECTRO-CORTICAUX ENREGISTRES AU COURS DE LA PERIODE PREALABLE A L'ETUDE DU TEMPS DE REACTION

Les potentiels électriques du cortex frontal, moteur et pariétal de jeunes singes rhésus ont été étudiés au cours de trois tâches préalables au temps de réaction à l'aide d'électrodes transcorticales Pt-PtCl, d'amplificateurs à longue constante de temps et de technique de calcul de moyenne. On observe une onde ample positive-négative-positive avec un maximum sur le cortex post-central quand les singes maintiennent en bas une clé pendant un intervalle de temps fixe entre deux stimuli. Quand la réponse n'est donnée qu'au second stimulus, une négativité prolongée survient sur la région frontale, mais non en post-central. La relation entre la variation contingente négative, les potentiels moteurs et les patterns électro-corticaux observés est discutée.

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