SLOW BRAIN POTENTIALS PRECEDING TASK PERFORMANCE

Printed by Academische Pers B.V. – Amsterdam.

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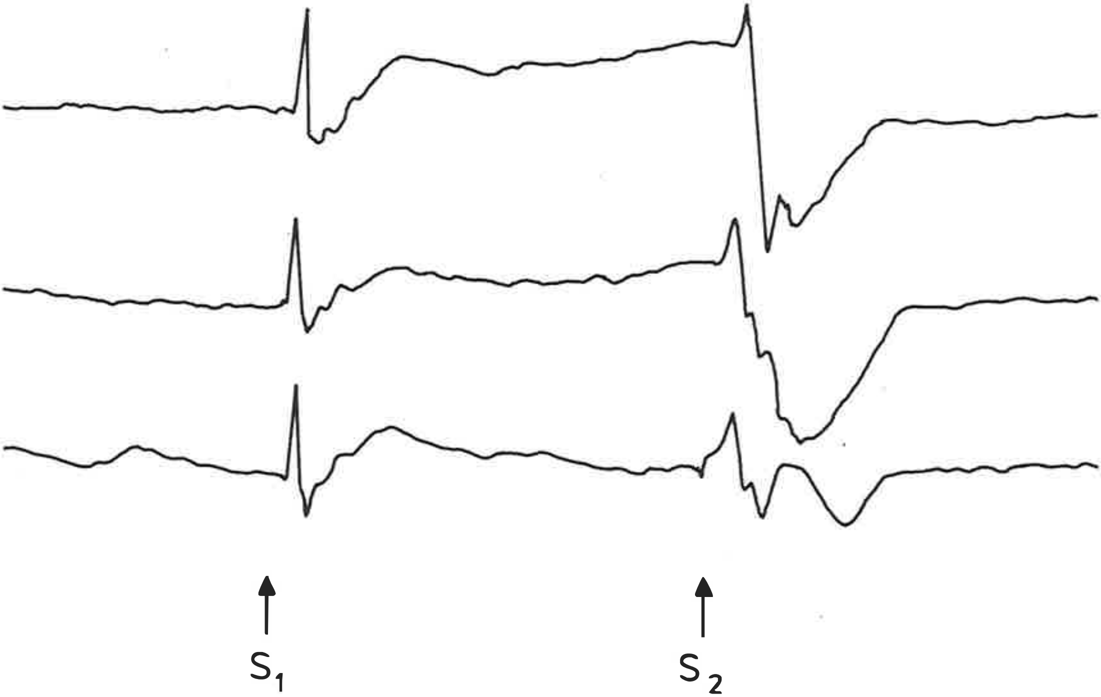

1978
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ACKNOWLEDGMENTS

The author wishes to express his thanks to C.H.M. Brunia, R. Näätänen, M.E. Noble, A.F. Sanders and C.A. Varey for their stimulating criticism on earlier versions of this report. Most of the studies were carried out together with J. Perdok. The technical and statistical assistance of J.Th. Eernst and A.J. Krul is gratefully acknowledged.

The problem of the relation between our bodies and our minds, and especially of the link between brain structures and processes on the one hand and mental dispositions on the other is an exceedingly difficult one. Without pretending to be able to foresee future developments, both authors of this book think it improbable that the problem will ever be solved, in the sense that we shall really understand this relation. We think that no more can be expected than to make a little progress here or there.

Popper and Eccles (1977),
The self and its brain.

CONTENTS

CHAPTER 1

INTRODUCTION

In 1964 Grey Walter and his colleagues (Walter, 1964a; Walter et al., 1964) discovered that slow negative potentials develop in the human brain in the interval between two stimuli if the first stimulus (S_1) serves as a warning and the second stimulus (S_2) requires a motor response. Fig. 1 shows a typical example of the development of this potential in the inter-stimulus interval (ISI): After the evoked potential to S_1 a gradual negative shift is seen which reaches its maximum just before S_2. This negative shift was called contingent negative variation (CNV) because it was thought that the occurrence of the CNV was dependent on the association (contingency) of two successive stimuli.

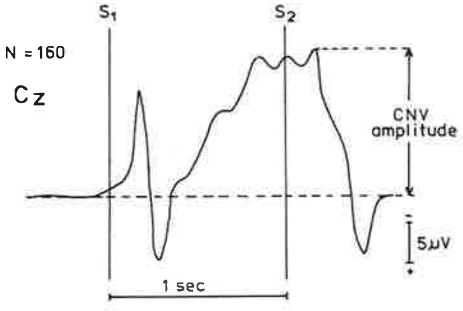

Fig. 1. The vertex (C_z) CNV from a typical subject, averaged across 160 trials.

The discovery of the CNV led to numerous experiments which attempted to specify the psychological significance of this negative shift by investigating it in all sorts of experimental situations. The results of these early studies were summarized by Cohen (1969) and Tecce (1972). Later studies were more concerned with the improvement of technology (e.g., electrode resistance, eye movement artifacts, cephalic skin potentials), the investigation of the CNV under extreme conditions (drugs, sleep deprivation, oxygen failure, etc.) or the relationship of the CNV with other physiological measures (heart rate, skin resistance, pupil diameter, background EEG, evoked potentials) (see for example the proceedings of the 2nd and 3rd congresses on the event related slow potentials of the brain; McCallum and Knott, 1973, 1976).

It is evident from the above mentioned reviews and also from more recent ones (Cohen, 1974; Hillyard, 1974 and McAdam, 1974) that there is considerable disagreement with regard to the functional meaning of the CNV. Although it has been shown that it can be obtained in many task situations and is affected by many task variables, it remains unclear which psychological processes are associated with the development of this brain potential.

Although the CNV has been most pronounced in reaction-time (RT) tasks where S_2 requires a fast motor response (e.g., Walter, 1964a; Low et al., 1966; Peters et al., 1970). it has also been found in signal-detection tasks which only involve the perception of stimuli at threshold level (e.g., Cohen, 1973; Hillyard, 1969b; Hillyard et al., 1971; Järvilehto and Fruhstorfer, 1970). Moreover, CNVs are found to precede complex or novel stimuli, even when there is no specified task at all (Walter, 1965a,b).

Since the CNV is also present in sensory tasks which do not require a fast motor response, Grey Walter thought that the expectancy of the subject for the arrival of S_2 was sufficient to produce the CNV; therefore the CNV was also called "expectancy wave" (e.g. Cohen, 1969; Walter et al., 1964, 1967).

Other investigators (Low et al., 1966; Hillyard, 1969a) preferred response readiness, motor preparation or conation (i.e., intention to act) as the mechanism underlying the CNV. The CNV has also been related to more general processes, like motivation (Irwin et al., 1966) or attention (Tecce, 1972).

Thus, the CNV has been associated with many psychological constructs, several of which are rather broadly defined. As long as the functional role of the CNV is unclear, its theoretical and applied value will be limited since possible effects (for example, individual differences or cerebral dysfunctions) cannot be interpreted in terms of psychological constructs. It is somewhat surprising that after 10 years of investigation the functional meaning of the CNV is still unclear. Of course, it is possible that the CNV is a general phenomenon, which accompanies many types of behavior. Another possibility, however, is that the CNV consists of more than one slow potential shift (SPS). If these shifts differ in their functional meaning, they might confound each other, since they will be affected differentially by experimental manipulations.

To shed more light on these issues a series of experiments was carried out; these experiments are described in detail in a separate section (Appendix: Experiments 1-6). Although the results of each experiment are preceded by an introduction and a description of the method, the next chapter will present the general methods which were used, then the behavioral background will be outlined and in Chapter 4 the research issues will be formulated which guided these studies. Following that the topographical results will be summarized. Finally, on the basis of the present experiments, and studies of other investigators, the psychological meaning of the SPSs occurring during the ISI will be discussed in separate sections.

CHAPTER 2

GENERAL METHODS

Although the method is described separately for each study, a general outline will be given here.

2.1. SUBJECTS

The subjects were students from the University of Utrecht who were paid for their participation. Only male subjects were used because too few females could be found who would allow the attachment of electrodes with collodion.

2.2. ELECTRODES

The EEG was recorded from the scalp with Ag-AgCl disk-electrodes. To keep the electrode resistance as low as possible electrodes were chlorided each time before their use. Before applying the electrodes the skin was thoroughly cleansed of oil and dead epidermis with alcohol. After filling the cup of the electrode with a conductive paste the electrode was attached to the scalp with collodion; care was taken that the contact between electrode and the scalp was very tight. The interelectrode impedance was measured using a 10 c/sec sinewave. An electrode was removed if the impedance was more than 5 kΩ or when it showed large baseline drifts or 50 c/sec "hum". If this happened during the experimental session, the subject was asked to return to the laboratory on a different occasion. The electrodes were placed along the midline of the scalp (F_z, C_z, P_z and sometimes O_z; see Fig. 2), according to the international 10-20 system (Jasper, 1958). These electrodes were referred to linked ears, because here the artifacts of electrodermal origin (cephalic skin potentials, see Picton and Hillyard, 1972) are minimal. In addition, Beckman miniature electrodes were taped on the forehead 2 cm above the nose-bridge (ground) and to the supra- and infra-orbital ridge to record the vertical EOG.

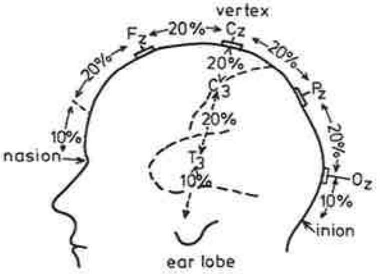

Fig. 2. The placements of the elctrodes according to the 10-20 system (Jasper, 1958). Letters refer to the general area of the cortex: F = frontal, C = central, P = parietal, O = occipital and T = temporal. Odd numbers indicate the left side (e.g. C_3), even numbers indicate the right (e.g. C_4) and z indicates the midline position. The distance between the electrode locations is always 10% or 20% of the distance between nasion (nose bridge) and inion (occipital bone) and the distance between the two ear lobes.

2.3. EYE MOVEMENT ARTIFACTS

The most serious and well-documented contamination of slow potential shifts results from slow eye movements, which often synchronize with the behavioral task. It has been shown (Hillyard and Galambos, 1970; Weerts and Lang, 1974) that the CNV is especially vulnerable to vertical eye movements and to eye blinks.

To prevent the intrusion of eye movement artifacts in the EEG several precautions were taken:

1) Subjects were trained to suppress their eye movements and blinks; during the training session the EOG was monitored and large eye movements were reported to the subject.
2) The subject was always given a fixation point (a light or a cross). In one experiment (Experiment 4) a fixation stimulus was given 3 sec before S_1. In this way very few eye movements occurred, those triggered by the presentation of S_1 especially were suppressed.
3) The computer skipped a trial when the EOG amplitude exceeded $\pm$ 200 μV relative to a pre-S_1-baseline. In general, a subject was discarded if more than 20% of the trials had to be rejected.

4) EEG averages per subject per condition were rejected also when the EOG amplitude, measured in the same way as the EEG amplitude, exceeded ± 50 µV relative to the pre-S_1-baseline. A subject was discarded if more than one of the conditions had to be rejected.
5) In general, it was attempted to design the stimulus configuration such that the task requirements did not induce eye movements. For example, in Experiment 3 the subject was asked to judge whether a circle was concentric or eccentric positioned around the fixation point; in this way the fixation point was an integral part of the stimulus configuration.

Procedures 3 and 4 for the rejection of eye movements were evaluated as to whether they influenced the experimental data. In general, it was found that although CNV amplitudes were reduced with stricter criteria, the effects of the experimental conditions remained proportionally the same. Thus when a lax (± 500 µV) and a strict (± 100 µV) criterion were compared, no interactions were found between the criterion level and task variables (see also Experiment 4). In Experiment 1 the effects of the other rejection criterion (4) were evaluated. Fig. 3 shows that with a less strict criterion the SNW amplitude increases, especially in the frontal derivation. However, the modality effect (visual vs. auditory S_1) remains proportionally the same. The largest reduction in EOG artifact was obtained when a rejection criterion of 25 µV was compared with no rejection at all. With an auditory S_1 this amplitude was reduced by 37%, while only 11% of 144 averages were rejected.

The above results suggest that a moderate amount of eye-movement artifacts does not confound the data as long as no systematic differences in vertical EOG are found between experimental conditions. Therefore it is recommended that EOG amplitudes measured in the same way as the EEG amplitudes should be reported.

2.4. APPARATUS

The experiment was conducted in a soundproof and electrically-shielded cubicle (Amplifon). The subject was seated in a comfortable chair which included neck- and arm-rests; response buttons were mounted on the right and left arm of the chair. Auditory stimuli were usually delivered via earphones (Sennheiser). Visual stimuli were usually presented on slides, which were projected (Kodak-Carousel-S) through the window of the cubicle onto a screen at a distance of ca. 1 m from subject's eyes. The stimuli were reasonably intense (luminance of 35 cd/m^2), while the cubicle was only dimly illuminated (background of 3,5 cd/m^2 The timing of the stimuli (including the trigger) and the measurement of RT (1

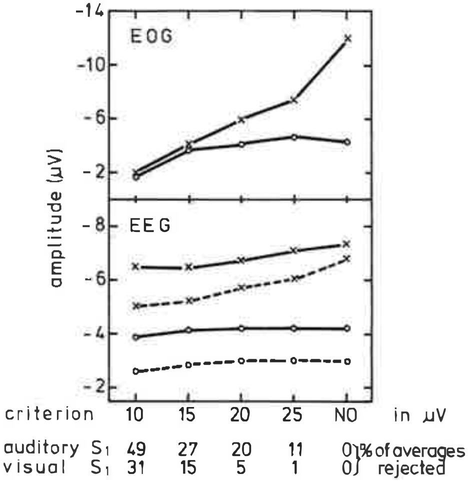

Fig. 3. The vertex (solid line), frontal (broken line) and EOG amplitudes (the average activity 600-800 msec after S_1, referred to a pre-S_1-baseline), for different criteria and when "no" criterion is used. The values underneath give the percentage of averages rejected. The data are given separately for an auditory (crosses) or visual S_1 (circles). The data were derived from Experiment 1 (see Appendix).

msec) was done by the PSARP equipment (van Doorne and Sanders, 1968). This equipment also produced a BCD code, which indicated the experimental condition: the trial number, the type of stimulus and response (e.g., left or right button) and the corresponding RT. This code was also recorded on tape and accompanied the EEG signals.

2.5. AMPLIFIERS

Except for the last two studies (Experiments 5 and 6), EEG signals were amplified with Ahrend van Gogh equipment, using a time constant of 6 sec. It could be argued that this is not long enough for the intervals of 4 sec which were used in Experiments 2 and 5. However, it can be shown that a DC shift measured at the end of a 4 sec ISI is attenuated by 14%, starting from a ramp wave, which is most similar to the gradual development of the CNV. Moreover, this attenuation would be generally the same for all experimental conditions. In addition the experimental results would not have been changed essentially if a baseline midway in the ISI (e.g. 2 sec before S_2) had been taken instead of before S_1 (see for example, Fig. 1 of Experiment 6). Finally, the results obtained in Experiments 3 and 6, which did use longer time constants (20 and 10 sec, respectively) did not deviate substantially from the other results, nor did the results of the Experiments 1 and 4, which used a shorter ISI (3 sec).

2.6. DATA ANALYSIS

The EEG and EOG signals were recorded on magnetic tape (Philips, Analog 7 to 14), so that various off-line analyses could be performed. At least two programs were used for these analyses, which were done on a LAB 8 system (DEC).

A. The CNV-program

In this program a maximum of 8 channels can be sampled at a certain rate (mostly 25 samples/sec). The analysis period started 1 sec before S_1 and ended at the onset of S_2. Per channel and per trial data reduction was accomplished by averaging successive groups of samples. Fig. 4 gives the results of such an analysis carried out on recordings obtained in the speed

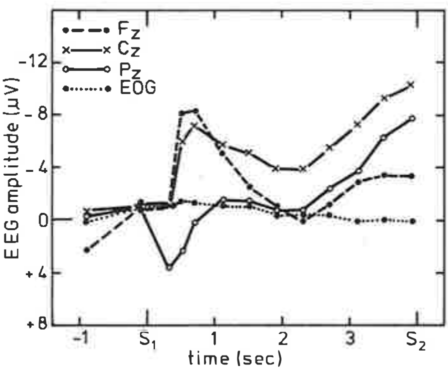

Fig. 4. The slow potential changes, separately for the frontal (F_z), vertex (C_z) and parietal (P_z) derivation and for the EOG. Each curve consists of 13 data points, i.e. the average of 5 successive samples (sample interval 40 msec). The data were obtained in experiment 5 under speed instruction varied within a block of trials.
The figure also shows the three slow potential shifts occurring in the S_1-S_2 interval: the slow negative wave (SNW), the slow positive wave (SPW) and the terminal CNV.

(within blocks) condition of Experiment 5. The figure shows curves of 13 data points for the frontal (F_z), vertex (C_z) and parietal (P_z) derivation and the EOG. Each data point consists of 5 successive samples (sample interval of 40 msec), yielding an average data point every 200 msec. Due to space limitations only every second data point was retained for further analysis, i.e. the periods 200-400 msec after S_1, 600-800 msec, 1000-1200 msec, etc. after S_1, except that in the 1 sec before S_1, only the first and the last data point (1000-800 msec and 200-0 msec before S_1) were reserved and in the early phase of the interval one data point more was taken (400-600 msec after S_1).

On the basis of these data points the following slow potential measures are generally obtained (see also Fig. 6):

- Slow Positive Wave (SPW): the average EEG activity during the 200-400 msec period after S_1. This wave could be regarded as a measure for the P_{300}, which is commonly observed, for example, in selective listening tasks.
- Slow Negative Wave (SNW): the average EEG activity during the 600-800 msec period after S_1. This wave has also been called "orientation wave" (O-wave) or "early CNV" (Loveless and Sanford, 1974b).
- Terminal CNV: the average EEG activity during the 200 msec period preceding S_2. This wave has alternatively been called "expectancy-wave" or "late CNV".
- The above measures were with reference to a baseline, viz. the average EEG activity during the 200 msec period before S_1;

Note on nomenclature: The above mentioned terminology was preferred to orientation or expectancy wave, because the latter refers to a functional significance which is yet unproven and therefore should be avoided. The terms "early" and "late" CNV are also misleading because they suggest that there are two components of a common process. In fact, the available data indicate that the SNW is dependent upon the characteristics of S_1 (largely in the same way as the SPW), and that the terminal CNV is dependent upon the task requirements at S_2.

Successive averaging has the following advantages:

1) For slow potential changes, the average EEG over a certain period will provide a better measure than when one sample is taken.
2) This on-line data reduction saves much space in computer memory, so that the data of single trials of several channels and experimental conditions can be stored on disk. This enables the rejection of eye-movement and

other artifacts on single-trial basis. Moreover, it is then also possible to correlate single CNV amplitudes with behavioral measures and to average the CNV amplitudes selectively for behavioral or other measures (e.g. hits, quick RTs),

3) Since the EOG is also averaged "successively", eye blinks are attenuated relative to the eye movements. Consequently, the detection of eye-movement artifacts is favored as compared to eye blinks. This is in line with the observation (e.g., Weerts and Lang, 1973) that the ratio between EOG amplitude and EEG artifact is larger for eye movements than for eye blinks.

B. Advanced averager

To obtain the evoked potentials to either S_1 or S_2 the "Advanced averager" of DEC was used. The program was modified so that for triggering and selection of the trials the BCD code of the PSARP-equipment could be used. In this way it was possible to obtain not only averages time-locked to the S_1-S_2 paradigm (S-related), but also to the response to S_2 (R-related). In the latter case a "negative delay" was used to obtain the activity preceding the response. This analysis was done in Experiments 5 and 6 (see for example, Fig. 3 and 4 of Experiment 5).

CHAPTER 3

TASK VARIABLES AND PREPARATORY PROCESSES

Some of the psychological processes which have been proposed to underlie the CNV are thought to be associated with perceiving S_2 (e.g., expectancy, perceptual sensitivity) and others with the execution of a motor response (motor preparation or readiness to respond). The CNV has also been related to task difficulty (see Tecce, 1970); however, this concept has two meanings which should be clearly distinguished: in some studies it refers to the difficulty of discriminating S_2 and in others to the complexity of the relationship between stimulus and response. This relationship may be manipulated by varying the information processing demands. For example, Poon et al. (1976) compared a simple RT task with a "same-different" task. In the latter task, S_2 consisted of two letters and the subject had to press one of two keys when the letters were both consonants or both vowels (same) and the other key when the letter pair contained a vowel and a consonant (different).

The development of the CNV in advance of S_2 suggests that the CNV is a cortical correlate of a preparatory process, which is triggered by a warning (S_1). To discover the functional meaning of the CNV we should pose a question as to the nature of the preparation during the ISI. At the moment this question is far from settled (see Posner et al., 1973; Näätänen and Merisalo, 1977). In the S_1-S_2 paradigm preparation could be defined as <u>performing in advance what can be performed before the arrival of S_2</u>. One can, for example, assume "the appropriate posture and make the necessary peripheral sensory adjustments, such as the fixation of the gaze on the display on which the stimulus will appear. But preparation is more than that; it appears to include the facilitation of relevant sensory, motor, and central, integrative functions" (Näätänen and Merisalo, 1977, p. 133).

In the present context it is assumed that the presentation of a warning (S_1) enables the subject to prepare for 1) the perception of S_2, 2) the execution of a motor response, or, 3) the decision linking S_2 to an overt or covert response. These three preparatory processes could be labelled stimulus anticipation, decision anticipation, or motor preparation.

To examine the functional role of the CNV, the experimental paradigms used should be classified into general categories (c.f. Hillyard, 1973). One possible classification is in terms of the type of task variables used in these paradigms. In the present study three types of task variables will be distinguished, stimulus and response variables, and variables which affect the relationship between stimulus and response (SR-variables); these variables are assumed to affect stimulus anticipation, motor preparation and decision anticipation, respectively. Thus, if a physiological change occurring during the ISI is affected by stimulus variables, such as the physical characteristics (intensity, duration, etc.) or the discriminability of S_2, this change is assumed to be related to stimulus anticipation. If the change is instead selectively affected by the amount of information processing required to translate a stimulus into a response, it shall be said to refer to decision anticipation. Similarly, if physiological phenomena are affected by variables which are related to the execution of a motor response to S_2, it is assumed that they reflect motor preparation.

A similar methodology is used in RT-research in an attempt to identify the psychological mechanisms involved in the processing of information. This so-called "additive factor" method assumes that stimulus information is processed in successive stages. Since processing in a particular stage is assumed not to start until processing in an earlier stages is finished, the mean RT is regarded as the sum of the processing times in the individual stages ($\overline{RT} = t_1 + t_2 + t_3 \ldots$). When the processing time of a stage increases, (for example, because stimulus discrimination is made more difficult) mean RT will increase to the same extent. The additive factor method assumes that two task variables refer to the same processing stage if their effects on mean RT are found to interact, and that they refer to different stages if their effects are additive (Sternberg, 1969).

On the basis of a number of consistent results obtained in choice RT tasks, Sanders (1977) concluded that there are at least three successive stages, namely "encoding", "choice" and "motor adjustment". Fig. 5 gives these stages and the task variables by which they are identified. Thus, the "encoding" stage is mainly affected by signal degradation, which involves the "degrading" of the stimulus configuration by making it less discriminable (for example, by putting visual noise across letters). The typical variable of the choice stage is

SR-compatibility, which refers to the relationship between stimulus and response: for instance, if two lights are beside one another, and the right hand and left hand are used to respond to the right and left lights, respectively, then the relationship is said to be compatible. However, if these relationships are reversed, so that the right hand is used to respond to the left light, and vice versa, the relationship is said to be incompatible. The third stage, "motor adjustment", is affected by time uncertainty, which refers to the duration of the ISI or the irregularity of the ISI.

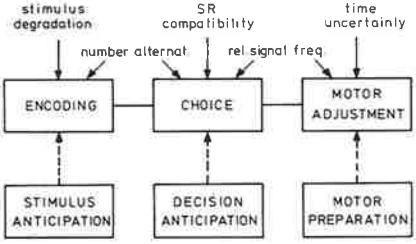

Fig. 5. The three processing stages in the reaction process, with corresponding preparatory processes.

The above stages have been postulated on the basis of the following evidence (see also Sanders, 1977): SR-compatibility shows additive effects with stimulus degradation (Frowein and Sanders, 1978; Sternberg, 1969) and with time uncertainty (Frowein and Sanders, 1978; Posner et al., 1973; Sanders, 1977). Moreover, time uncertainty has additive effects, not only with stimulus degradation (Frowein, 1978), but also with other stimulus variables, such as stimulus duration (Posner and Boies, 1971) and visual stimulus intensity (Raab et al., 1961; Sanders, 1977).

Although the relationship between these processing stages and the preparatory processes under discussion is still unclear, it appears that they have similar characteristics in the sense that they relate either to stimulus-input, response-output or to more central processing. As is illustrated in Fig. 5 it is assumed that the three processing stages are preceded by corresponding preparatory processes; of course, this is only possible when the task situation enables the subject to predict to some extent the moment when the imperative stimulus will arrive (for example, by introducing a warning signal).

For the moment it is assumed that the three preparatory processes are affected by the same task variables as the processing stages. This has the advantage that the task variables which have been shown to affect a certain stage can now be used to investigate which of the three preparatory processes are related to certain phasic changes in physiological variables. Evidence for the existence of these preparatory processes can be obtained either from physiological variables (such as slow cortical shifts, phasic changes in background EEG and heart rate) or from behavioral experiments (for example, by investigating the effects of time uncertainty in RT-tasks, or by using S_1 to provide advance information with regard to the task requirements or to the stimulus configuration at S_2).

In RT-research it has been generally found that RT increases either with longer or with more irregular ISIs. In the latter situation, the duration of the ISI varies in a pseudo-random fashion from trial-to-trial (e.g., Klemmer, 1956; Trumbo and Gaillard, 1975). These effects have mostly been interpreted in terms of expectancy and motor preparation. Generally, the stronger the expectancy for S_2, the more intensely the subject prepares for the response. In this view expectancy is regarded as a higher ordered process, which regulates motor preparation (see Näätänen, 1971, for a further discussion of these concepts). Although different definitions are possible (Sanders, 1966), expectancy may be described in the present context as "the subjective probability of the immediate delivery of the imperative stimulus" (Näätänen and Merisalo, 1977).

Näätänen and Merisalo showed that, with some exceptions (Op. cit., p.134), expectancy reflects rather well the objective probability of the immediate arrival of S_2. As the interval between S_1 and S_2 elapses this probability, and thus the expectancy for S_2, increases. With increased time uncertainty this process is hindered by increased difficulty in predicting the exact moment S_2 will arrive. Expectancy is affected not only by time uncertainty but also by event uncertainty: expectancy for a given signal will be greater the larger the chance that this particular signal will be presented. Thus, motor preparation appears to be directly related to the degree of certainty about both the likilihood of occurrence and the time of occurrence.

Another source of variation in motor preparation is the extent to which the subject can control his response system. Näätänen and Merisalo (1977) have pointed out that the organism has no direct way of "perceiving" the moment-to-moment distance between the level of motor preparation at a given moment and the level where an actual response is initiated. It appears that there is no clear limit between increasing motor preparation and the initiation of the motor response, but apparently when the increasing motor preparation reaches a certain limit it "flows over", as it were, into a motor response (see Meyer, 1953). According to Näätänen and Merisalo (1977) the organism needs to stay in the vicinity of this "motor-action" limit to maintain a high level of motor preparation. The distance between the level of motor preparation and the motor-action limit where a response is initiated is largely determined by the amount of training and the instructions given by the experimenter. During training subjects will learn to what extent they can increase their motor preparation without making too many errors. Under accuracy instructions subjects will keep a larger safety margin, which results in a lower probability of errors but also in long RT's. If the importance of speed is stressed subjects will prepare intensively and the distance between their preparation level and the limit where a response is initiated will be low. In this situation almost any stimulus will trigger a response, and consequently they run the risk of making many errors.

Posner and his colleagues (Posner and Boies, 1971; Posner et al., 1973) attempted to separate stimulus anticipation (encoding, in his terms) and motor preparation by giving advance information to S_1 in a "same-different" RT task, where S_1 either served as a warning only, or it also gave a letter with which another letter had to be matched at S_2. He concluded that advance information and ISI duration have additive effects on the RT, as long as the ISI is long enough to enable the build-up of a template with which S_2 could be matched. According to Posner (see also Thomas, 1974) the anticipatory processes for stimulus processing are independent of ISI duration and also of motor preparation, and the introduction of a warning signal does not affect the rate at which information builds up in the early stages of processing (in our terms, the encoding and choice stages). As well as the additivity between advance information and ISI duration mentioned above, he gives two further arguments. Shortening of RT as a function of ISI is not accompanied by a decline in errors, and sometimes there is even an increase in errors. This indicates that stimulus processing is of no higher quality when the subject is highly prepared. With short ISI's errors are faster than correct RT's, which suggests that responses were given before the evaluation of the stimulus was completed (see also the Ollman-model, discussed below).

There are still other methods for investigating the processes of stimulus and decision anticipation, for example, by comparing "between" and "mixed" conditions. In the latter situation, two or more types of stimuli are presented randomly from trial-to-trial, whereas in the former situation the type of stimulus is varied between blocks of trials. In Experiment 2 the level of discrimination difficulty was varied in these two ways. When the subject did not know in advance whether S_2 involved a difficult or an easy discrimination the RT was enhanced on average by 56 msec, as compared to the between-condition. However, if S_1 indicated the type of discrimination to be presented at S_2 the RT was almost the same as in the between-condition.(see also Fig. 1 of Experiment 2). In general, not more than 500 msec is required to process the information provided by S_1 (Leonard, 1958; Posner et al., 1973; Sanders, 1971). Thus, with longer ISIs the average RT obtained in conditions where S_1 provides advance information will not be longer than the RT obtained in the comparable between-conditions.

Although the issue certainly needs further research, it appears that preparatory processes associated with perceiving and processing of information are of a different character to those associated with preparing for a motor response. Motor preparation is most probably a gradual process which is optimal (i.e., close to motor-action limit, see above) towards the end of the ISI. Stimulus and decision anticipation seem instead to be more an all-or-none phenomenon, in the sense that S_1 only enables the build-up or reactivation of a template or the pre-setting for a particular decision, which appears to be independent of ISI duration. This view is supported by the results obtained in choice RT tasks where it was found that time uncertainty shows additive effects with stimulus and decision factors which affect the "encoding" and the "decision" stages, and consequently might influence stimulus and decision anticipation. That perceptual sensitivity is affected by time uncertainty in signal-detection tasks (Egan et al., 1961a, b; Leavitt, 1970; Loveless, 1975; Lowe, 1967; Klein and Kerr, 1974) does not necessarily contradict this view. Even in signal-detection tasks the preparation for detecting a signal may consist largely of motor adjustments, such as suppression of eye movements and blinks, and fixation on the stimulus location.

Apart from preparatory processes already discussed there may be additional psychological processes associated with the CNV, such as motivation, attention, etc., which cannot easily be related to them. Motivation and attention have been defined differently by different investigators and they are complex concepts. Thus, motivation may or may not intensify selectively one of the three preparatory processes. Attention is sometimes defined as the selection of relevant stimuli to the exclusion of other stimuli and sometimes it refers to the task in general (e.g., Tecce, 1972, p. 101). In the former definition, attention refers to almost the same processes as stimulus anticipation since it will be influenced by the same types of task variables. Taking the second meaning the concept not only includes sensory, but also motor and decisional aspects of the task. In this sense attention is very similar to other non-specific concepts, such as motivation or effort. Thus, when a subject is distracted he will pay less attention to the task, but it cannot be specified which preparatory process is affected.

The relationships between non-specific task variables, such as distraction, knowledge of results or incentives, and the structural variables which define the processing stages have been investigated on a limited scale only. With one exception, the effects of these non-specific variables will therefore not be investigated here, since the aim of the present studies is to find out whether the CNV is specifically related to one of the three preparatory processes.

The only non-specific variable which will be studied is the instruction governing the trade-off between speed and accuracy although its relationship to the three preparatory processes is still unclear. Originally the terms accuracy (sensory set) and speed (motor set) referred to the distinction between either concentrating on the perception of S_2, or upon muscular preparation for the response (e.g., Lange, 1888). Thus, larger CNV amplitudes will be obtained under accuracy instructions if the CNV is related to stimulus anticipation, and under speed instructions if it is related to motor preparation. However, it could be argued that under speed instructions, stimulus and decision anticipation are enhanced also, which might accelerate the processing times of the encoding and the choice stages of information processing.

Recent models for the speed-accuracy trade-off generally do not specify its relationship to the processing stages or to preparatory processes (see Ollman, 1977; Pachella, 1974; Wickelgren, 1977). In his review, however, Pachella shows that speed-accuracy instructions may have interactions with both stimulus factors and decision factors. Moreover, it was shown in an item-recognition task that subjects may change the strategy by which they perform the task. The effect (a reduction in RT of ca. 200 msec) of stressing speed appeared to be located in the "encoding" and/or "motor adjustment" stage. However, more extreme speed emphasis seems to affect the way in which memory is scanned (self-terminating search instead of the usual exhaustive search). Thus, speed-accuracy instructions seem to affect all three processing stages.

According to most recent models, discussed by Ollman (1977), the preparation for and the execution of a motor response are seen as independent processes which run parallel to the processing of stimulus information. Another common property of these models is the idea that at least a proportion of the responses are guesses, which are given independently of the ongoing evaluation of the stimulus information and which are correct only by chance. One model (deadline model) supposes that there is a time limit (deadline), which is set by the subject or by the experimenter. A response is made when processing is terminated or when the deadline expires, whichever comes first. If processing finishes before the deadline, the response time is representative of the time needed to process the stimulus information. If the deadline elapses before processing is complete, the response is a guess and less likely to be accurate.

According to Ollman (1977), speed instructions do not enhance the quality of information processing or the rate at which information builds up, (although subjects may change their strategy as was shown by Pachella). A similar view is taken by Posner et al. (1973, 1976) in discussing the effect of a warning signal. Rather than increasing perceptual sensitivity, low time uncertainty (short constant ISI) was said to increase the level of motor preparation, to invite the subject to react sooner, but less accurately.

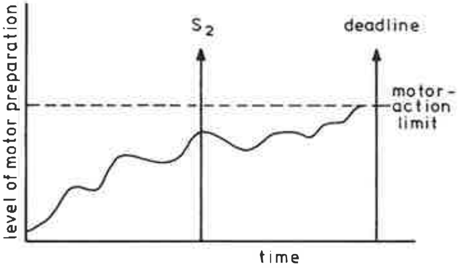

Fig. 6. Schematic representation of the time-course of motor preparation when speed is stressed by using a deadline within which the subject has to respond. It is assumed that motor preparation is increased to a level close to the "motor-action limit", where a response is initiated and that this limit is reached just before the deadline or earlier. In the latter case a response may be given either because the stimulus evaluation was terminated or because this limit is reached "spontaneously" (see also text).

The relationship between speed-accuracy instructions and motor preparation can be described elegantly, when the models of Ollman ("deadline") and, Näätänen and Merisalo (motor-action limit) are combined. Thus, when speed is stressed the level of motor preparation will be increased in such a way that it will come closer and closer to the motor-action limit, and this limit will be reached just before the deadline expires. This is illustrated in Fig. 6. This combined model is taken as a basis for the present studies (Experiments 4 and 5).

CHAPTER 4

RESEARCH ISSUES

In the previous section it was argued that RT-studies can provide a basis for investigating the psychological significance of physiological phenomena. In particular the postulate of preparatory processes connected to stages of information processing may provide a foothold for the evaluation of phasic changes in physiological variables occurring during the ISI. Of course the experiments to be reported here were not only prompted by the RT literature, but also by the CNV literature.

In this section an outline will be given of the ideas and expectations which guided the present experiments; in general the following research issues were investigated in one or more experiments:

A. Is the CNV a unitary phenomenon?

It has been suggested that the CNV is not a unitary potential but consists of several slow potential shifts (e.g. Hillyard, 1974; Tecce, 1972). This possibility is based both upon the finding that in experiments with animals more than one component was found which differed in neurophysiological generator (Borda, 1970; Cant and Bickford, 1967; Donchin et al., 1971; Hablitz, 1973; Low, 1969) and upon differences in waveform which seems to depend both on the type of subject and on the experimental condition (Cohen, 1969; Donchin et al., 1972; Tecces, 1972). The waveform of the CNV has been investigated by obtaining measurements at different times during the ISI: e.g. the "early CNV", the potential about midway between the interval, and the "late CNV" at the end of the interval. It was found that the modality of S_1 (Gaillard and Näätänen, 1976) and the intake of amphetamine (Tecce and Cole, 1974) have effects on the early CNV only. The two components of the CNV seem also to differ in midline distribution: the early CNV is frontal dominant, whereas the late CNV is located more posteriorly (Low *et al.*, 1966; Näätänen and Gaillard, 1974b; Walter, 1964b). Moreover, shifts in midline distribution were observed between experimental conditions, which also have been interpreted as suggesting that the CNV consists of more than one slow potential shift (Donald, 1973; Järvilehto and Fruhstorfer, 1970; Syndulko and Lindsley, 1977).

Early investigations which used long ISIs found two negative potentials, (e.g. Connor and Lang, 1969; Weerts and Lang, 1973). Therefore in Experiment 1 (see Appendix) the issue of the components was investigated by using a short (1 sec) and a long ISI (3 sec). In addition, the modality of S_1 was varied between blocks: S_1 was either a click or a flash. On the basis of an earlier experiment (Gaillard and Näätänen, 1976), it was expected that the modality of S_1 would have a differential effect on the two potentials, and indeed two negative potentials were found and only the first was enhanced by the auditory S_1. During the preparation of the manuscript of experiment 1 the publications of Loveless and Sanford (1974a, b) appeared which showed essentially the same results: the first potential reaches its peak within 1 sec after S_1 and thereafter declines; the second potential gradually develops during the ISI, and reaches its maximum towards the end of this interval. Because of its occurrence towards the end of the ISI and its contingency to S_2 (or to the response to S_2) the second potential seems to resemble more closely the "classical CNV" obtained with short ISIs; therefore, it will be called terminal CNV. The term CNV will be used in its original meaning, to denote the negative shift preceding S_2 in studies with short ISIs, which generally did not discriminate between the two negative potentials described here. The first potential will be called slow negative wave (SNW) because of its similarity to the "slow wave" observed in selective listening tasks (N. Squires et al., 1975). Consistently the slow positivity following S_1 will be called slow positive waves (SPW). This notation is preferred because often a clear peak cannot be detected in these slow waves following S_1. It is still open to question whether the SPW is the same as the P_3; in the present context P_3 will denote the peak amplitude of the positivity occuring 200-400 msec after S_1, while the SPW refers to the continued positivity after this peak. Similarly a distinction may be made between the negative peak (N_3) and the continued negativity (i.e., the SNW). It is to be noted that the continued positivity (labelled SPW here) is often called P_3 in the literature. The present studies will concentrate on the separation of the slow potential shifts (SPSs), i.e. SPW, SNW, and terminal CNV, occurring during the ISI. This separation was attained by using ISIs of relatively long duration in all experiments. Of course there may be other methods for the separation of these components, for example Donchin et al. (1977) found evidence for these SPSs, using factor analysis on data collected with a 1 sec ISI.

B. Topography

In experiment 1 it was found that the three SPSs differ in their anterior/posterior distribution. Therefore in all experiments the EEG was derived from frontal (F_z), vertex (C_z) and parietal (P_z) location. Moreover, in two recent experiments (Experiment 6 and Perdok and Gaillard, in preparation) the lateral distribution was also investigated by comparing the SPSs obtained from the right (C_4) and left (C_3) hemisphere. The topographical results are summarized in Chapter 5.

C. Sensory versus motor requirements

Most theoretical issues reduce to the question "On what is the contingent negative variation (CNV) contingent?" (see also Näätänen, 1973). This question may be reformulated as "Is the CNV related to S_2 or to the motor response to S_2?". One way to answer this question is to compare sensory and motor tasks. In the latter the subject has to respond as quickly as possible (RT-instruction) and in the former the subject is instructed to delay his response (detection-instruction). In general smaller amplitudes have been found under detection instruction (e.g., Näätänen et al., 1977; Syndulko and Lindsley, 1977). Since all these studies used short ISIs (ca. 1 sec), this reduction in CNV-amplitude could be accounted for by the absence of the second SPS, the terminal CNV, when no speeded motor response is required to S_2. It was also hypothesized on the basis of the results of experiment 1 and the study of Loveless and Sanford (1974) that there would be no negativity preceding S_2 in a sensory task.

In three experiments (3, 4, 5) an RT-instruction was compared with a detection instruction where the subject had to delay his response by 1 sec.

D. Stimulus anticipation versus motor preparation

The question as to whether the CNV is related to stimulus or to response factors could be approached also in a different way. In the previous chapter it was argued that the psychological significance of CNV could be investigated as a function of task variables which refer to certain preparatory processes. Thus, it could be asked whether the SPSs occurring during the ISI reflect stimulus anticipation or motor preparation. For the latter hypothesis there is already some evidence, since the CNV was found to be affected by anticipated muscle effort (Irwin et al., 1966; Low and McSherry, 1968; Rebert et al., 1967) and time uncertainty (Blowers et al., 1973; Gaillard and Näätänen, 1973; Loveless, 1973; McAdam et al., 1969; Posner and Wilkinson, 1969). In general, the CNV increased the larger the muscle effort and the smaller the time uncertainty. With regard to stimulus anticipation the reviews show considerable disagreement as to whether the CNV is related to perceptual processes or not. For example, Cohen (1974) maintains that the amplitude of the CNV is positively correlated with perceptual efficiency, while Hillyard (1973) regards the evidence as too meagre for this conclusion.

The hypothesis that the SPSs preceding S_2 reflect stimulus anticipation was tested by varying the discriminability of S_2. Two levels of difficulty (easy/difficult) were used for the following task variables: relative line length (Experiment 2), absolute position of circles (Experiment 3) and exposure duration (Experiment 3). One can expect that if an SPS is related to stimulus anticipation, then larger amplitudes will occur when S_2 is more difficult to discriminate. Moreover, this should be the case not only under RT-instruction, but also under detection instruction. Therefore in experiment 3 the effects of S_2-discriminability are investigated under both instructions.

CNV research has been mainly concerned with the issue of whether the CNV is related to stimulus or response variables. Of course, the controversy between these types of variables holds the most promise of giving clear results. While the present experiments were carried out, several studies appeared, which had decision anticipation, mostly called task difficulty or task complexity, as the subject of investigation (e.g. Poon et al., 1974; Roth et al., 1975, 1977, 1978). Since in all such studies the CNV was not increased with higher task demands (see Chapter 8.3), no experiments were done here on decision anticipation.

E. Expectancy versus motor preparation

Originally the CNV was regarded as a correlate of expectancy and therefore was called "Expectancy Wave" (Walter et al., 1964). Most studies which investigated this issue manipulated the expectancy of the subject by varying in a RT-task the probability that S_2 would occur (e.g. Järvilehto and Mäntysalo, 1976; Karrer et al., 1973). The results of these studies are difficult to evaluate since the effects of expectancy and motor preparation are confounded: both increase with the probability of S_2. In an earlier study (Näätänen et al., 1977) an attempt was made to separate the effects of these psychological processes by investigating the effects of S_2 probability under both RT-instruction and detection instruction. Under both instructions S_2 was an auditory signal which was difficult to detect. The probability of

S_2 had a significant effect on the "late" CNV but only under the RT-instruction, suggesting that the terminal CNV is related to motor preparation rather than to expectancy. Since a short ISI (1 sec) was used the amplitude of the terminal CNV was possibly contaminated by the SNW; therefore this issue was studied again with a longer ISI (3 sec) in experiment 4.

F. Speed-accuracy trade-off

Since it has been shown (Loveless and Sanford, 1974b) that instructions governing the trade-off between speed and accuracy have an effect on the terminal CNV, (but not on the SNW) this variable is investigated in two experiments (Experiments 4 and 5). As was outlined in the previous chapter the relationship between these instructions and the three preparatory processes is still unclear. Although under speed instructions stimulus and decision anticipation may increase also, it seems that this instruction in any event increases the level of motor preparation (see previous chapter).

G. Characteristics of S_1

Early investigations (Gaillard and Näätänen, 1976; Experiment 1) showed that the SNW is enhanced after an auditory S_1 as compared to a visual S_1. Thus, the SNW appears to depend on the physical characteristics of S_1 (see also Chapter 6). Therefore, it is quite possible that this wave is also affected by other psychological properties of this stimulus. This was investigated by varying the information content: S_1 was either non-informative, i.e. it only warned the subject that S_2 would arrive soon, or it was informative. In the latter case it provided information about the task to be performed at S_2. In experiment 2, S_1 consisted of two tones of different frequency which indicated whether S_2 would involve a difficult or an easy discrimination. S_1 incicated in Experiment 4 the probability that S_2 would occur, and in Experiment 5 the instructions (speed, accuracy or detection) to be followed at S_2.

One can expect that the SNW will be enhanced when S_1 is made informative and that the extent of this enhancement depends on the psychological significance of the information provided.

H. Comparison of CNV and RP

It has often been noted (e.g. McAdam, 1974) that the readiness potential (RP) and the CNV have much in common. The RP, which is also a negative SPS, precedes the initiation of any voluntary movement. According to Deecke et al., (1976) CNV and RP differ depending on the following aspects:

(1) the experimental situation, i.e., S_1-S_2 paradigm vs. voluntary movements;
(2) the form: the RP is linear, whereas the CNV has more an inverted U-shape;

(3) topography: the CNV is located more anteriorly than the RP; moreover, the CNV is bilaterally symmetrical and the RP asymmetrical;
(4) in contrast to the RP, the CNV seems to be independent of a motor act; the CNV may also be found in sensory tasks or even when no task is required at S_2 (see Chapter 1).

On the basis of Experiment 1 it will be argued that the terminal CNV and the RP are largely the same phenomenon, and that they only differ in the way they are averaged, i.e. time locked to the stimulus or to the response. Since the enumerated differences were based on CNV studies with short ISIs (e.g. 1 sec), it is further hypothesized that these differences, and in particular 2, 3 and 4, are produced by the SNW. Thus, both form and topography will change when the SNW and the terminal CNV are mixed, as occurs with a 1 sec ISI. Moreover, the negativity present in sensory tasks may only consist of the SNW.

This issue is investigated in Experiments 5 and 6 by comparing stimulus related averages with response related ones and by comparing RT-instruction with a synchronization instruction. Under the latter instruction a subject is asked to synchronize his response with S_2 rather than responding to S_2. This task situation resembles both the S_1-S_2 paradigm and the voluntary movement situation. This instruction could be regarded as a "time-locked" voluntary movement. Finally, the readiness potential (RP) preceding voluntary movements is compared not only with the negativity time-locked to the RT under the RT-instruction but also with the negativity preceding the delayed response under the detection instruction.

In summary, it is expected that the classical CNV in fact consists of two negative SPSs (the SNW and the terminal CNV) which differ in form and topograpy. It is hypothesized that the SNW is affected by the physical and psychological properties of S_1, whereas the terminal CNV is dependent on the task variables related to S_2. One may expect that the terminal CNV is response related and produced by the same neurophysiological generator as the RP. Moreover, its amplitude is expected to reflect the level of motor preparation.

CHAPTER 5

TOPOGRAPHICAL RESULTS

In all experiments presented in the Appendix large differences were found between the waveforms of the midline positions (F_z, C_z, P_z). Fig. 7 gives a typical example of the time course of these SPSs during an ISI of 3 sec: The frontal SPS shows an initial rise which peaks ca. 700 msec after S_1 and declines thereafter. This peak is also present at the vertex, although to a lesser extent. However, this SPS is clearly biphasic and shows a further but more gradual rise towards the end of the interval. Although less prominent this negativity is also present at P_z. In addition the parietal derivation shows a positive wave at the beginning of the interval.

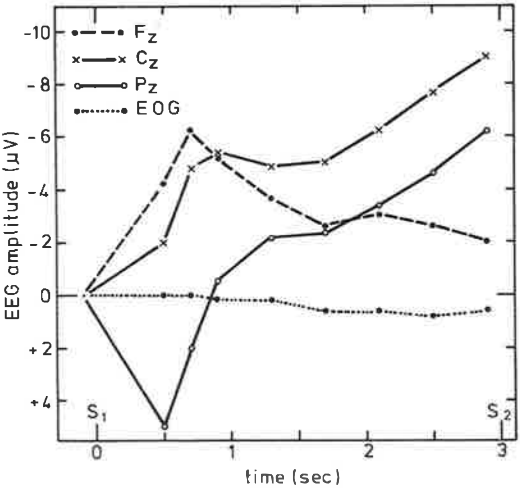

Fig. 7. The slow potential changes, separately for the frontal (F_z), vertex (C_z) and parietal (P_z) and for the EOG. The data were obtained in experiment 4 under speed instruction and in the high probability condition. These data obtained with a 3 sec ISI are very similar to the curves shown in Fig. 4, where a 4 sec ISI was used.

These differences in waveform strongly suggest the existence of three SPSs occurring during the ISI: a "slow positive wave" (SPW) which is most prominent parietally, a "slow negative wave" (SNW) which has a fronto-central distribution and a "terminal CNV" which has parieto-central distribution.

Table 1 summarizes the frontal, vertex and parietal amplitudes of the SNW and the terminal CNV for those experimental conditions which were run under RT-instructions. Table 2 shows that in 9 out of 17 conditions the SNW was largest at F_z and in 8 conditions at C_z; in the latter case F_z was always larger than P_z, thus the anterior gradient was less steep than the posterior gradient. For the terminal CNV the amplitudes of 6 conditions were largest at P_z and of 15 conditions at C_z; in the latter case, the amplitudes at F_z were larger than at P_z in 5 conditions; this was the reverse in 8 conditions, while in 2 conditions the amplitudes at F_z and P_z were equal. Fig. 8 gives the midline distribution of the terminal CNV, SNW and SPW, when the amplitudes are averaged across all the experimental conditions involving a RT-instruction.

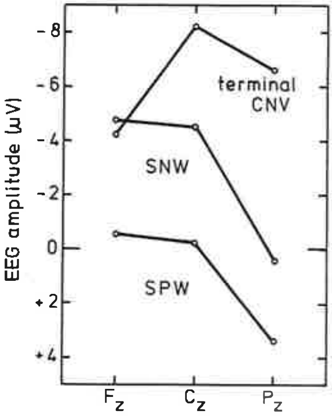

Fig. 8. The midline distribution (F_z, C_z, P_z) of terminal CNV (200 msec before S_2), the SNW (600-800 msec after S_1) and the SPW (200-400 msec after S_1); amplitudes are averaged across subjects and all experimental conditions involving a RT-instruction (see also Tables 1 and 2).

Table 1. The amplitudes of the SNW and the terminal CNV in the conditions involving a RT-instruction, separately for the frontal (F_z) and vertex (C_z) derivation.

Experiment no.	Condition	SNW F_z	SNW C_z	SNW P_z	terminal CNV F_z	terminal CNV C_z	terminal CNV P_z
1	auditory S_1-3 sec	-6.0	-7.1	-3.2	-1.0	- 3.3	- 1.5
	visual S_1-3 sec	-3.0	-4.2	-0.8	-1.7	- 4.5	- 2.6
2	simple	-3.8	-4.4	-0.2	-7.6	-12.6	-12.8
	between - easy	-1.2	-3.0	+0.8	-5.8	-10.4	-14.0
	- difficult	-5.0	-4.4	-0.8	-6.8	- 8.0	-12.8
	within - easy	-4.2	-3.4	+0.8	-5.0	-10.2	-14.4
	- difficult	-4.2	-4.0	+1.0	-6.8	- 9.6	-13.6
	mixed	-2.4	-3.2	+0.4	-6.4	- 8.4	-11.0
3	difficult - short	-*	-	-	-3.2	- 7.2	- 0.4
	- long	-	-	-	-4.0	- 7.2	0.0
	easy - short	-	-	-	-5.2	-10.8	- 5.2
	long	-	-	-	-6.0	- 9.6	- 3.2
4	speed - high	-5.6	-5.8	-1.2	-2.4	- 8.8	- 6.8
	- medium	-6.6	-5.4	-0.4	-4.8	- 7.8	- 4.8
	accuracy - high	-5.2	-3.6	0.0	-2.2	- 5.0	- 3.6
	- medium	-4.8	-3.4	+1.0	-2.6	- 4.0	- 1.8
5	between - speed	-2.4	-3.0	0.0	-4.2	-12.0	- 7.2
	- accuracy	-2.6	-3.8	-2.2	-1.6	- 5.6	- 4.0
	within - speed	-7.4	-6.2	+1.2	-2.4	- 9.4	- 6.6
	- accuracy	-6.4	-4.2	+0.8	-5.2	- 7.4	- 4.6
	speed (detection)	-9.8	-8.0	-2.2	-4.0	-10.0	- 7.2
	average	-4.74	-4.54	+ .37	-4.23	- 8.18	- 6.58

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* In experiment 3 no clear SNW was observed.

Table 2. Number of experimental conditions where the amplitudes of the SNW, terminal CNV or SPW were largest at either F_z, C_z or P_z. Moreover, for the amplitudes which were largest at C_z, a distinction is made as to whether the posterior ($F_z > P_z$) or the anterior ($F_z < P_z$) gradient was steeper. The summary involves the 21 experimental conditions of the present 5 experiments with RT-instruction; except that data of experiment 3 are omitted for SNW and SPW because here these waves could not be clearly observed. Moreover, amplitudes of the SPW of experiment 1 were not available.

	F_z	C_z		P_z	Total
		$F_z > P_z$	$F_z < P_z$		
SNW	9	8	-	-	17
terminal CNV	-	5	10[1])	6	21
SPW	-	-	-	15	15

Of course, no definite statements can be made over the exact location of the generator fields of the three slow potentials. However, if it is assumed that these fields have symmetrical distributions the data suggest that the SNW is located closer to F_z than to C_z, while the terminal CNV seems to be located over the motor cortex, i.e., posterior to C_z before the sulcus centralis (see also Fig. 2). Finally, the SPW is located in the association cortex, i.e. anterior to P_z and behind the sulcus centralis.

In general, these results corroborate those of other topographical studies which used ISIs of longer duration (Klorman and Bentsen, 1975; Rohrbaugh et al., 1976); except that, compared with the present study, the midline distribution of both the SNW and the terminal CNV were located more anteriorly in the Rohrbaugh et al. study and more posteriorly in the study of Klorman and Bentsen. An explanation for these shifts in midline distribution, which also occurred in the present experiments (for example, Experiment 2), is not readily available. Also considerable differences in midline distribution were found among individual subjects. More research is necessary on the relationship between the topography on the one hand and individual differences and task requirements on the other hand.

In the present experiments the distribution of the terminal CNV tended to shift posteriorly under more "difficult" task conditions. For example, in Experiment 2 the difference between the simple-RT task and the condition involving the difficult discrimination was much larger at C_z than at P_z (see Table 1). Similarly, the reduction in terminal CNV under accuracy as compared to speed instructions was larger at C_z than at P_z in both Experiments 4 and 5. However, these results suggest that the type of task may influence not only the amplitude of the CNV but also its midline distribution, i.e. the ratio between the vertex and parietal amplitudes. A comparable shift posteriorly has been reported also by Cohen (1973) in a pattern recognition task and by Poon et al. (1976) in a "same-different" task; in both studies these task conditions were compared with a simple-RT task. Such a shift in a posterior direction was also observed in an earlier study by Poon et al.,(1974), where a "guessing task" was compared to a choice RT-task. Since short ISIs (between 1 and 1.5 sec) were used in the latter studies, no distinction could be made between the two components (SNW and terminal CNV) and their relative contribution to the CNV. However, the results cannot be easily explained by the confusion of the components. If it is assumed that the terminal CNV is mainly affected by motor preparation (see Chapter 8), a change from motor to sensory requirements would increase the relative amplitude of the SNW and would produce a shift anteriorly, rather than posteriorly.

Since in all of the above mentioned studies an increase in RT was accompanied by a shift in the ratio between vertex and parietal amplitudes, the results suggest that the terminal CNV consists of two SPSs: a "motor CNV", which is largest over the motor region (C_z) and is connected with motor preparation, and a "sensory CNV", which is largest over the association cortex (P_z) and connected to stimulus- and/or decision-anticipation. In a simple RT-task stimulus processing will be minimal and motor preparation maximal, consequently the motor CNV will be larger than the sensory CNV. This will be the reverse in tasks involving difficult discriminations or complex information processing (see also Chapter 8.3.1.

Since all studies where a change was noted in the vertex/parietal ratio used a visual S_2 (except Experiment 4), it is quite possible that this sensory CNV is limited to the visual modality only. In line with this view are the recent results by Simson et al., (1977): In a detection task (ISI 1 sec) a late negative shift with a parieto-occipital dominance was found when S_2 was visual but not when it was auditory (Op.cit. p. 872). Also in Experiment 3 evidence was found for a visual CNV. In this experiment the terminal CNV tended to be larger when S_2 had a short exposure duration (80 msec) as compared to a long one (500 msec); as is shown in Fig. 9 this effect is present in the occipital derivation only. Also Syndulko and Lindsley (1977) and Gaillard and Näätänen (1976) provide evidence for an occipital CNV preceding the detection of visual sti-

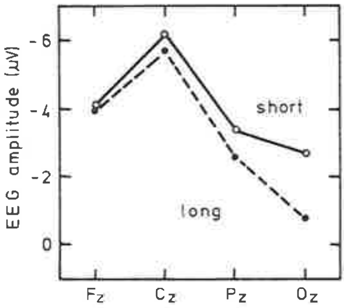

Fig. 9. The midline distribution (F_z, C_z, P_z, O_z) of the terminal CNV as a function of exposure duration (short, 80 msec; long, 500 msec). The amplitudes, obtained from experiment 3, were averaged across subjects and experimental conditions (easy/difficult, SD vs. RT instructions).

muli. Moreover, similar SPSs localized over occipital regions have been recorded in animals (Köhler and O'Connell, 1957; Rosen, 1969).

The laterality of the present SPSs have been investigated less frequently than the midline distribution. The data reported by Rohrbaugh et al. (1976) suggest that the lateral distribution of the SNW and the SPW is symmetrical, whereas the terminal CNV is asymmetrical. These results were replicated in two recent experiments (Experiment 6; Perdok and Gaillard, in preparation). In Experiment 6 a laterality effect of 3.5 µV (across left and right hand responses) was found in a simple RT-task: the amplitude of the terminal CNV was larger at the contralateral side (C_3 vs. C_4).

This laterality effect has also been observed in studies using short ISIs (e.g. 1.5 sec) (Otto and Leifer, 1973; Syndulko and Lindsley, 1977), although it was not found by McCallum (1978). In addition, Syndulko and Lindsley showed that the laterality effect was concentrated in the motor region (C_3-C_4); that is, it was reduced at frontal sites (F_3-F_4) and absent parietally (P_3-P_4) and occipitally (O_1-O_2). Moreover, it was shown in this study that this effect was neither present during bimanual response preparation nor under a detection instruction, where the response to S_2 was delayed by one sec. However, the laterality was found in the negative shift which preceded this response. The dominance of the terminal CNV over the motor regions and its hemispheric laterality suggest that this electrocortical shift is connected with preparation for the execution of a motor response.

Topography, morphology and ISI duration

What is the relationship between the SNW and the terminal CNV, and the classical CNV obtained with a 1 sec ISI? The most simple explanation would be that the two negative potentials summate with shorter intervals, so that the classical CNV obtained with a 1 sec ISI is the sum of the terminal CNV and the amplitude of the decreasing limb of the SNW. This hypothesis was tested in Experiment 1, where the slow potentials occurring during a 1 sec and a 3 sec ISI were compared. In addition, the modality of S_1 was varied between blocks: S_1 was either a click or a flash. On the basis of an earlier experiment (Gaillard and Näätänen, 1976), where a differential effect of the S_1-modality was found on the early CNV, it was expected that an auditory S_1 would enhance the SNW, while the terminal CNV would remain unaffected. The results of this experiment are summarized in Fig. 10. It can be seen that although both potentials are most prominent at C_z, the anterior-posterior gradient (indicated by thin line) of these potentials is different. For the SNW the anterior gradient (F_z-C_z) is less steep than the posterior gradient (P_z-C_z), while this is the reverse for the terminal CNV. Moreover, the figure shows that an auditory S_1 enhances the SNW-amplitude, although the midline distribution is unaffected. In contrast, with a 1 sec ISI the distribution

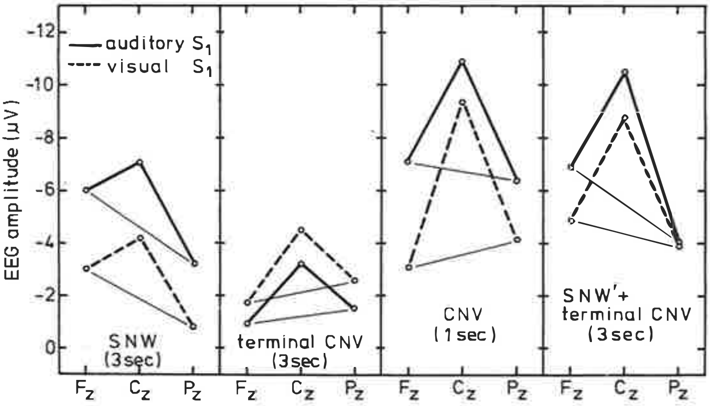

Fig. 10. The midline distribution (F_z, C_z, P_z, O_z) as a function of S_1-modality (visual/auditory); the SNW and the terminal CNV were obtained with a 3 sec ISI and the CNV with a 1 sec ISI. The fourth panel gives the sums of the SNW' amplitude, measured 800-1000 msec after S_1 and the terminal CNV. The data were obtained from experiment 1.

of the CNV is affected: the anterior gradient is less steep after an auditory S_1 than after a visual S_1 (see Fig. 10). This result suggests that the CNV is indeed the sum of the terminal CNV and the SNW, and that the shift anteriorly with an auditory S_1 is caused by a larger contribution of the SNW to the amplitude of the CNV. This view can be supported by summating the terminal CNV and the SNW measured 1 sec after S_1 (SNW'). This result is given in the 4th panel of Fig. 10 and shows that approximately the same amplitudes and the same midline distribution is obtained, as when the CNV is recorded with a 1 sec ISI.

There has been considerable debate (e.g. Cohen, 1969; Tecce, 1972) as to whether the neurophysiological generator of the CNV is located anteriorly or posteriorly relative to C_z. Although the CNV-amplitude is generally found to be maximal at the vertex (C_z), some studies reported an anterior-posterior gradient which is steeper posteriorly ($F_z > P_z$), while other studies found it to be steeper anteriorly ($F_z < P_z$); (see Cohen, 1969; Tecce, 1972, for review). Although the prominence of the CNV in frontal regions has been attributed to spurious enhancement of eye-movement potentials, these shifts can be explained more conveniently by changes in the ratio between the amplitude of the SNW and the terminal CNV. Any variable which affects the amplitude of the SNW (such as the modality of S_1) will also affect the midline distribution of the CNV, since it will change the relative contribution of the SNW to the amplitude of the CNV. Although in many instances detailed information regarding the experimental situation (e.g., intensity and modality of S_1) is lacking, it seems that the relative contribution of the SNW to the CNV is <u>not</u> taken into account when topographical effects are evaluated. For example, Järvilehto and Fruhstorfer (1970) and Syndulko and Lindsley (1977) compared task situations where both S_1 <u>and</u> S_2 were either visual or auditory. In both studies the CNV was located more anteriorly in the auditory task. In view of the present data this shift can be explained more conveniently as an S_1-modality effect in the SNW than by the interpretation provided by the authors in terms of functional differences.

The above reasoning also accounts for the form of the CNV: with shorter ISIs the gradual development of the terminal CNV will change into a quick rise to a peak. With an ISI of 1 sec the form of the CNV will largely depend on the ratio between the amplitudes of the SNW and the terminal CNV: the risetime of the CNV will be faster the larger the relative size of the SNW. Since the SNW is affected by the characteristics of S_1 (e.g. modality) the form of the CNV also will depend upon these variables. Several investigators have made a distinction between two CNV-forms: a quick (A-type) and a slow (B-type) rise to peak (Cohen, 1969; Donchin et al., 1972; Tecce, 1972). The figures of the CNVs shown by these authors suggest a larger SNW in the waveform with a quick risetime. Thus, subjects with an A-type CNV may have a more prominent SNW relative to their terminal CNV.

CHAPTER 6

SLOW NEGATIVE WAVE (SNW)

It has been demonstrated that the SNW is affected by the physical characteristics of S_1, such as intensity (Loveless and Sanford, 1975), modality (Experiment 1) and stimulus duration (Klorman and Bentsen, 1975). Larger SNW amplitudes have been found with louder tones, with auditory as compared to visual stimuli and with tones of longer duration.

Yet the SNW is not only influenced by the physical but also by the psychological properties of S_1. In the present studies the amplitude of the SNW was enhanced when S_1 contained information about the task requirements at S_2.

Thus, in Experiment 5 task instructions were varied either <u>between</u> blocks of trials or were varied from trial-to-trial <u>within</u> a block of trials. In the latter situation S_1 indicated the instruction to be followed at S_2 by using two tones of different pitch. As can be seen in Fig. 11 the frontal SNW is enhanced when S_1 contains information in addition to its warning function (between-vs. within-condition). This enhancement was most prominent when S_1 indicated the speed instruction in those tasks where speed and detection instructions were varied from trial-to-trial (see also Fig. 11). This further enhancement is explained by assuming that the larger discrepancy in task demand between speed and detection instruction made the information provided by S_1 more significant for the subject.

In Experiment 2 the SNW was affected when S_1 indicated whether the discrimination at S_2 would be easy or difficult (as compared to the SNW after a non-informative S_1). However, the effect here was not found in the amplitude, but in a prolongation of the SNW. This effect was interpreted as reflecting prolonged central processing associated with the discrimination to be made at S_2.

It also has been found (Kok, 1978; Experiment 4, this thesis) that the SNW is increased when S_1 indicates that a quick response has to be given to S_2, compared with the situation where no further overt or covert response is required (Go-NoGo situation). Kok also investigated the a-priori probability of S_1. His S_1 consisted of three tones differing in pitch: two of them were infrequent ($p = 0.1$) and one was frequent ($p = 0.8$). The SNW was larger after infrequent tones, in particular when it was relevant (i.e., indicated that a response had to be made).

These results show not only that the SNW is enhanced when S_1 is informative, but also that the amplitude of this wave is affected by the relevance of this information.

Since the SNW is affected by both the psychological and the physical characteristics of S_1 and occurs at a fixed latency after S_1 (independent of ISI duration), this wave has to be considered as a slow potential change evoked by S_1.

In line with this is the observation that the pairing of S_1 and S_2 is not necessary for the occurrence of the SNW. Thus the SNW follows non-signal stimuli also even when these are not paired with an imperative signal (Loveless, 1976; Rohrbaugh et al., 1976). Also, in selective listening tasks a frontal "slow wave" is observed (Näätänen et al., 1978; McCarthy and Donchin, 1976;

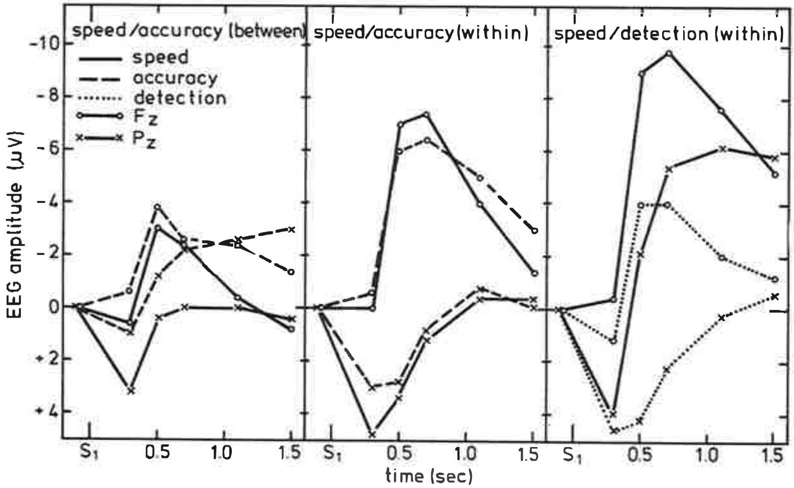

Fig. 11. The frontal (F_Z) and parietal (P_Z) potentials in six experimental conditions of Experiment 6. The speed and accuracy instructions were either varied between or within blocks of trials. In addition the speed and detection instruction were also varied within one block of trials. For clarity only the first 1.5 sec of 4 sec ISI is shown (see also Figs. 1 and 2 of Experiment 5 for comparison).

N. Squires et al., 1975; K. Squires et al., 1977). In this kind of task the subject is presented with series of tones in which unpredictable shifts occur either in frequency or in intensity. In general, these experiments show that a frontal "slow wave" is present after rare, but relevant, stimuli. Moreover, in a perceptual judgement task, Simons and Lang (1976) found enhanced slow negativity after the presentation of a difficult discrimination as compared to an easy one. In a detailed analysis it was found that this enhancement of the SNW to difficult stimuli was most prominent when the subject was insecure about the correctness of his judgement.

To sum up: the SNW appears to be affected by the following properties of S_1: 1) the physical characteristics (intensity, modality and duration of the stimulus), 2) frequency of occurrence, 3) informative vs. non-informative, 4) the immediate relevance of this information (speed vs. detection instruction; Go vs. No-Go situation). In addition, the SNW to unpaired stimuli is affected by 1) level of discrimination difficulty, 2) the confidence of this discrimination, 3) attended vs. non-attended stimuli, and 4) the frequency of occurrence.

It should be noted that the SNW is found to be unrelated to the task demands at S_2. Therefore, it is concluded that the SNW is not related to one of the three preparatory processes: stimulus and decision anticipation and motor preparation (see Chapter 3).

The combined results of the present studies and others support the idea that the SNW reflects a non-specific arousal response in the frontal cortex which is largely dependent on the psychological significance of S_1.

This response could be regarded as a cortical component of the orientation reaction. The discovery that the SNW does not habituate over trials is not necessarily in conflict with this notion. It can be argued that habituation is inhibited as long as the stimulus is significant for the subject (Lynn, 1967).

The nonspecific character of the SNW is in line with its frontal dominance. According to Luria (1973) the function of the frontal lobes is to organize behavior and to regulate arousal systems in accordance with the immediate task demands. This view is supported by the observation that the largest effects on the SNW were found when S_1 indicated task demands which considerably diverged (see also Experiment 5). On the other hand, when task demands are constant or very similar over a block of trials, the preparation for the execution of the task is very likely to take place before the arrival of S_1.

Evidence from animal experiments suggests that the SNW is produced by nonspecific activating systems (Borda, 1970; Donchin et al., 1971; Low, 1969; Skinner and Yingling, 1977; Yingling and Skinner, 1977). In the two last-named studies a negative frontal shift was found to accompany orienting responses and states of conditioned expectancy. Moreover, this shift could be elicated by novel stimuli and by electrical stimulation of the reticular formation.

CHAPTER 7

SLOW POSITIVE WAVE (SPW)

In general, the SPW has similar characteristics to the P_3. However, the P_3 is mostly obtained from unpaired stimuli in selective listening tasks (see Näätänen, 1975). In the S_1-S_2 paradigm the P_3 to S_2 has received much more attention than the slow positivity following S_1. In the present studies the SPW was always most prominent over the parietal area, a result also found by Hillyard et al. (1976) and Rohrbaugh et al. (1976). The P_3 evoked by S_2 (e.g. Poon et al., 1974, 1976) or by unpaired stimuli in a selective listening task (e.g. Näätänen et al., 1978; N. Squires et al., 1975; K. Squires et al., 1976) is also located in the parietal area.

In the present studies the SPW was generally affected in the same way as the SNW, although in some instances differential effects were found. As is shown in Fig. 11, for example, it was found in Experiment 6 that both the SNW and SPW are enhanced when S_1 contains information (within condition), but the SPW was also increased under speed as compared to accuracy instructions (both in the between and within condition). Moreover, in the condition where speed and detection instructions were varied within one block of trials, the amplitude of the SPW did not differ between these instructions while the amplitude of SNW was more than three times larger under speed than under detection instruction (see also Fig. 11).

When examining the differential effects of experimental conditions on the SNW and SPW, it should be noted that these waves could be instrumentally related. Although the SPW and SNW differ with regard to their spatial centres (parietal vs. frontal) and to their peak latency (300 msec and 700 msec after S_1), they will partially cancel each other because of their inverse polarity, and therefore contaminate each other (see also Experiment 4).

In any event it is clear that the two slow waves following S_1 reflect different but related mechanisms; this conclusion was also drawn by K. Squires et al. (1977), on the basis of a selective-listening study.

Although additional research is needed on the interrelationship between the SPW and the SNW, the available results suggest that the SPW reflects the outcome of an evaluation of the stimulus material, while the SNW reflects continued information processing in the frontal cortex, possibly related to subsequent output processes. This view fits very well into the model proposed by Luria (1973) of the functional organization of the brain. Luria distinguishes between three systems: a general arousal system (reticular formation), an input system and an output system. Within the two latter systems three zones are distinguished: primary, secondary and tertiary zones which differ in specificity with regard to incoming information or the response to be executed. Both slow waves are found in nonspecific zones: one in the input system (SPW) and one in the output system (SNW). It is assumed that in the association cortex, where the parietal SPW is found, stimulus information from different sensory channels is integrated and evaluated. The P_3 or SPW could be regarded as the outcome of this process, when a decision is made (see also Kutas and Donchin, 1977b). On the other hand, the SNW is found in the frontal lobes, which are assumed to organize behaviour and to regulate arousal systems.

CHAPTER 8

THE TERMINAL CNV

This chapter summarizes the available evidence regarding the functional role of the terminal CNV. This is done separately for the three categories of task variables distinguished in Chapter 3, i.e. stimulus and response variables, and variables which influence the relationship between stimulus and response (SR variables). Following that, the effects of two task variables are reviewed, whose relationship to these categories is unclear (distraction, speed-accuracy). Finally, the functional meaning of the terminal CNV is further illustrated by comparing it to the RP.

8.1. STIMULUS VARIABLES

From the reviews which attempt to relate the CNV to human behavior (Cohen, 1969, 1974; Hillyard, 1973, 1974; Tecce, 1972) it is evident that a large uncertainty prevails as to whether or not the CNV is related to perceptual processes. For example, Cohen (1974) maintains that the amplitude of the CNV is positively correlated with perceptual efficiency, while Hillyard (1973) believes that the results are too meagre for this conclusion.

Two major methods can be used to investigate this issue. The first method examines the SPS preceding S_2 in RT-tasks, as a function of two or more levels of discrimination difficulty; a larger negativity is expected when S_2 is harder to detect or when a more difficult discrimination has to be made. In other words, it is assumed that stimulus anticipation is more elaborate the harder the discrimination to be made.

The second method selectively averages the EEG preceding correct and incorrect responses in a detection task; or it divides the trials into the four stimulus-response categories of signal detection theory; viz. hits, correct rejections, misses and false alarms. Here it is expected that the negativity preceding S_2 is larger on correct (hits, correct rejections) than on incorrect trials (misses, false alarms). In most studies using this method, the subject

Table 3. Without delayed response. Authors (in chronological order), number of subjects, ISI duration in sec, task (det = detection of one stimulus, discr. = discrimination between two or more stimuli, vis. = visual, aud. = auditory), result and outcome (0 = no outcome because of artifacts, + = support, - = no support for relation with stimulus factor).

Authors	No. of subjects	ISI (sec)	Task	Result	Outcome
Low et al. (1967)	6	1	aud. signal det.	larger CNV with less audible tones	0[1]
Robert et al. (1967)	12	1.5	aud. signal det.	larger CNV with faint than with moderate tones	0[1]
Wilkinson and Haines (1970)	8	2	aud. intensity discr.	correlation between % detections and CNV	0[1] [2]
McAdam and Rubin (1971)	10	1	vis. position discr.	larger CNV on "correct and confident" vs. "no idea" trials	0[2]
Low and Swift (1971)	10	1	aud. frequency discr.	smaller CNV with difficult discr.	-
Picton and Low (1971)	12	1.5	aud. frequency discr.	no effect of discr. difficulty on CNV	-
Delse et al. (1972)	10	1	aud. frequency discr.	smaller CNV with difficult discr. (only females) smaller CNV on correct trials	-
Exp. 2 (this thesis)	8	4	vis. linelength discr.	no effect of discr. difficulty on terminal CNV	-
Exp. 3 (this thesis)	8	4	vis. position discr.	smaller terminal CNV with difficult discr.; no effect of exposure duration	

[1] no control of eye movements artifact

[2] possible contamination by motor activity

Table 4. Delayed response. Authors (in chronological order), number of subjects, ISI duration in sec, task (det = detection of one stimulus, discr. = discrimination between two or more stimuli, vis. = visual, aud. = auditory), result and outcome (+ = support, - = no support for relation with stimulus factors).

Authors	No. of subjects	ISI (sec)	Delay[1] (sec)	Task	Result	Outcome
Hillyard (1969b)	3	2.3	2	aud. signal det.	larger CNV on correct trials	+
Järvilehto and Fruhstorfer (1970)	6	1	1.5	aud. intensity discr.	no correlation between % correct on CNV	-
Hillyard et al. (1971)	3	1.5	1	aud. signal det.	larger CNV on correct trials	+
Paul & Sutton (1972)	8	1	2	aud. signal det.	no difference in CNV between hits and misses or between correct and incorrect trials	-
Jeness (1972)	4	1	1	aud. frequency discr.	no difference in CNV between correct and incorrect trials no correlation (across blocks) between correctness and CNV	-
Cohen (1973)	17	1	1	vis. pattern discr.	larger CNV on correct trials	+
Loveless (1975)	6	0.5, 1.3 and 6	?	aud. signal det.	no difference between correct and incorrect trials	-
Exp. 3 (this thesis)	8	4	1	vis. position discr.	smaller terminal CNV with difficult discr.; no effect of exposure duration; no difference between correct and incorrect trials	-

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[1] Delay between S_2 and response

has to report his observations one or more secs after S_2; another difference between RT tasks and detection tasks is that in the latter S_2 usually is at threshold level.

Tables 3 and 4 summarize the studies which have investigated the relationship between SPSs and perceptual sensitivity. A distinction is made between the studies which did not use a delayed response to S_2 and those which did, Tables 3 and 4, respectively. Several of the older studies had to be disregarded because eye-movement artifacts were not controlled (Low et al., 1967; Rebert et al., 1967; Wilkinson and Haines, 1970). Moreover, the interpretation of the studies of Wilkinson and Haines (1970) and of McAdam and Rubin (1971) is dubious because instead of using two levels of discrimination, the trials were selected for correct and incorrect detections. In both studies the observed relationship might be spurious in the sense that it may have been a manifestation of a general process. It is conceivable that performance (percentage correct) deteriorates and the amplitude of the CNV decreases with decreasing alertness or with a loss of motivation. The data of Wilkinson and Haines which were obtained in a 22 min vigilance task clearly suggest this relationship; their Figs. 3 and 4 show that during the test run both the CNV and percentage of detections decrease, while the RT was prolonged. The same results were found when "high and low signal rate" were compared. One interpretation is that a poorly motivated subject will not only discriminate S_2 less correctly, but will also prepare less intensively for the motor response to S_2. McAdam and Rubin report neither whether there was time-stress on the verbal responses the subject had to give, nor what the latency of the responses was. Since slow negativity also precedes the production of speech, these results can also be explained by increased motor preparation on "correct trials", as compared to trials where the subject had "no idea".

None of the other studies in Table 7.1 found an enhancement in CNV preceding the more difficult discrimination. However, several studies reported decreased amplitudes in this condition (Low and Swift, 1971; Delse et al., 1972; Experiment 3, this thesis). The latter results can be explained by assuming that the readiness to respond tends to be suppressed in the more difficult conditions (see also discussion in 8.3.). To sum up, the results obtained in RT-tasks involving different levels of discrimination difficulty do not support the hypothesis that the SPSs preceding S_2 are associated with perceptual processes.

From the nine detection studies where the response to S_2 was delayed (Table 4), only three studies obtained larger CNV amplitude on correct as opposed to incorrect trials (Hillyard, 1969b; Hillyard et al., 1971; Cohen, 1973), while the other studies found negative results. The studies showing positive results do not differ obviously from those where the results were negative, with regard to modality, type of task, detection vs. discrimination, etc. The method in the study of Paul and Sutton (1972) replicates many of the important features of the two studies by Hillyard but, instead of finding a larger CNV in correct trials, no differences were found. Other aspects which weaken the significance of the results are the use of 1) only few subjects and 2) rather short ISIs (1 sec or shorter). Since the CNV very possibly consists of two components (see Chapter 4), it is very likely that the positive relationships observed by Hillyard et al., (1971) and Cohen (1973) can be explained by an increased SNW. Thus, it could be argued that an enhanced level of arousal increases both the SNW and the percentage detections. This argument is less applicable to the study of Hillyard (1969), because a longer ISI (2.3 sec) was used.

Hence the available evidence is too meagre to decide whether the CNV reflects perceptual sensitivity. More studies are necessary, especially with longer ISI's. However, since only a small amount of negativity or none at all precedes S_2 in SD tasks (Loveless, 1976; Experiment 3, this thesis), the chances of finding clear effects have to be estimated as small. Finally, the co-variation of SPSs preceding S_2 and perceptual efficiency as a function of non-specific arousal or motivational factors should be ruled out, as much as possible. Even in the case of a delayed motor response to S_2 it is quite possible that motor activity is still present. For example, in Experiment 3 a terminal CNV of 6.2 μV was found under detection instruction, but only in the easy condition. Although no definitive arguments can be made, this could be explained by assuming that motor activity occurred incidentally during the $S_1 - S_2$ interval. Moreover, even with a delayed response it is possible that the SPSs are affected by motor activity connected with the control of eye movements, especially when S_2 is visual. In order to show that SPSs are an index of perceptual sensitivity independent measures, such as EMG and monosynaptic reflexes (see Brunia, 1978), should be used to control the involvement of motor systems in detection tasks. In Experiment 6 (this thesis) it was shown that under detection instruction EMG activity was present before S_2, but only in the flexor muscles of the arm involved in the delayed response.

Another type of experiment investigating the effects of stimulus factors centres around the concept of expectancy. Although expectancy can be defined in several ways (Hillyard, 1973; Sanders, 1966), most authors understand it as the subjective probability that S_2 will follow S_1; this is usually operationalized as the a priori probability that S_2 will occur. It has been shown by Walter et al. (1964) that the amplitude of the CNV reduces when S_2 is randomly omitted in 50 % of the trials; this result was confirmed in later studies by Walter (1965) and Low et al. (1966), but Hillyard and Galambos (1967) did not find a consistent effect. Moreover, with lower probabilities ($p = 0.2$) no further reduction in CNV was found (Walter, 1965a; Low et al., 1966). In general, wide individual differences were found which suggest that subjects react quite differently to this situation; for example, Hillyard and Galambos report that in some subjects the amplitude of the CNV increased by 50 %. If S_2 is omitted without warning some subjects may try harder, while others might wonder whether the apparatus had failed.

In some recent experiments, in which the subject was told the a priori probability beforehand, larger CNVs were obtained the larger the probability of S_2 (Järvilehto and Mäntysalo, 1976; Näätänen et al., 1973; see also Experiment 4); except that with complete certainty ($p = 1.0$) lower amplitudes are found (Karrer et al., 1973; Järvilehto and Mäntysalo, 1976). However, Loveless (1977) failed to find any difference between $p = 1.0$ and $p = 0.5$, using an ISI of long duration (4 sec).

These effects of S_2-probability have generally been interpreted in terms of expectancy and have been used as an argument for the hypothesis that the CNV is related to stimulus factors or to perceptual processes. However, in RT tasks not only expectancy but also motor preparation will increase the larger the probability that S_2 will arrive, i.e. the larger the probability that a motor response had to be made. Also the lower amplitudes found with complete certainty can be explained in terms of motor preparation. When there are no catch trials, quick RTs may even be produced without a high degree of motor preparation (see also Näätänen and Gaillard, 1974a). An explanation in terms of motor preparation is supported by the lack of effect of S_2-probability in sensory tasks: signal-detection task (Näätänen et al., 1975), guessing task (Friedman et al., 1973) and under detection instruction (delayed response) (Experiment 4, this thesis).

In summary, the studies reviewed above do not support the idea that the CNV, or more specifically the terminal CNV, is related to stimulus variables. Negative results were generally obtained in RT-tasks as a function of discrimination difficulty or in detection tasks where the SPSs on correct and incorrect trials were compared.

The major problem in investigating whether the SPSs in the S_1 - S_2 interval are connected to perceptual processes is the possible contamination by motor activity. In several experimental paradigms stimulus and response factors were confounded (e.g. S_2-probability), and an alternative explanation of the observed effects is in terms of motor preparation.

This explanation is supported by studies with long ISI-duration, where a delayed response is required to S_2: in this situation the terminal CNV is largely reduced or virtually absent. This holds not only for sensory tasks using threshold level stimuli (Loveless, 1976; Experiment 3, this thesis), but also for stimuli within the normal range (Experiments 4 and 5, this thesis).

8.2. RESPONSE VARIABLES

In studies using a 1 sec ISI, it has been shown repeatedly that the amplitude of the CNV is attenuated when no response to S_2 is required (e.g. Donald, 1973; Järvilehto and Frühstorfer, 1970; Syndulko and Lindsley, 1976; Peters et al., 1970). Irwin et al. (1966) have pointed out that the enhancement of the CNV amplitude by a subsequent motor response is of the same magnitude as the RP, which precedes any voluntary movement. In Experiments 4, 5 and 6 (this thesis) it was shown on the one hand that the terminal CNV is largely attenuated or even virtually absent in sensory tasks; and, on the other hand, that the SNW is only marginally affected when RT-instructions are compared with detection instructions in which the response to S_2 is delayed. This result was also found by Loveless (1976) in a signal-detection task which involved auditory signals at threshold level. These results suggest that the terminal CNV is contingent on a motor response and that the negativity which is still present in sensory tasks with short ISIs, is produced by the SNW evoked by S_1.

The involvement of motor processes in the generation of the terminal CNV is also supported by the fact that this SPS is larger the larger the amount of force or muscular effort required for the response to S_2 (Low and McSherry, 1968; Rebert et al., 1967).

Several studies have investigated the effects of time uncertainty on the CNV. This can be done in two ways, either by varying the duration of the ISI or by comparing a regular condition in which the ISI is constant over a block of trials, with an irregular condition in which the ISI changes from trial-to-trial. In the former case the negativity preceding S_2 generally decreases with longer ISIs, except that for very short ISIs (less than 500 msec), the

CNV does not seem to have enough time to develop fully (Blowers et al., 1973; Gaillard and Näätänen, 1973; Loveless, 1973; Loveless and Sanford, 1974a, 1975; McAdam et al., 1969; Posner and Wilkinson, 1969; Experiment 1, this thesis). It appears that largest amplitudes are found with ISIs between 800 and 1000 msec, because with these ISI-durations the two components of the CNV are added; thus, the terminal CNV increases with smaller ISIs, while the SNW is largest at about 750 msec (see also Chapter 5).

Loveless and Sanford (1974a) compared a regular condition with an irregular condition and found that the SNW was present in both conditions, while the terminal CNV was only observed in the regular condition. In general, the above results run parallel to the behavioral effects, RT is shorter in the regular condition and increases with increasing ISI-duration (e.g. Klemmer, 1956; Trumbo and Gaillard, 1975).

As is outlined in Chapter 3, it has been demonstrated in choice RT-tasks that time uncertainty has additive effects with stimulus factors, such as stimulus degradation (Frowein and Sanders, 1978), exposure duration (Posner et al., 1973) and visual stimulus intensity (Raab et al., 1961; Sanders, 1977).

On the basis of those behavioral studies using choice RT-tasks, it was concluded in Chapter 3 that time uncertainty primarily affects motor preparation. On these grounds the effects of time uncertainty on the CNV can be most convincingly described in terms of motor preparation. The combined EEG and behavioral data show that with longer ISIs the subject has increased difficulty in predicting the moment S_2 will arrive, which leads to a suppression of the level of motor preparation at S_2, which is reflected in an attenuated terminal CNV and longer RTs.

To summarize, the terminal CNV seems to be contingent on a motor response and to be affected by task variables: muscular force, time uncertainty and S_2-probability. This suggests that the terminal CNV reflects the level of motor preparation in RT-tasks.

8.3. SR VARIABLES

In Chapter 3, SR variables were defined as those variables which manipulate the amount of information processing necessary to relate S_2 to a response. These task variables are assumed to influence decision anticipation. This category of experimental variables, of which the most important are the compatibility between stimulus and response, the number of alternatives and the memory-set size, has received little attention in CNV-research. In a study of Poon et al. (1976) a simple RT-task was compared with a "same-different" RT-task. In this task the subjects were instructed to press one of two keys to indicate whether two letters were both vowels or both consonants or whether the letter pair contained a vowel and a consonant. In the simple RT-task they only had to react to the letters, which were tachistoscopically presented; in both tasks they were instructed to react as quickly as possible, while still maintaining high accuracy. The CNV was found to be attenuated in the same-different RT-task as compared to the simple RT-task. The authors explain this result as a "ceiling" effect (see also Knott and Irwin, 1964); they assume that during the more demanding same-different RT-task the DC-level of the cortex is closer to the physiological maximum for negativity. However, the authors do not provide evidence for such an interpretation and it is questionable whether this task can be regarded as so demanding that the cortical DC-level reaches its maximum. A more simple explanation would be that the amount of motor preparation is lower in the more demanding task. For example, subjects might prepare less, because they are afraid of making errors. Although subjects may give anticipatory responses, errors of choice cannot be made in the simple RT-task. The interpretation in terms of motor preparation is supported by the fact that the reduction in CNV was specific to the motor region (C_z), and was not found at the parietal derivation (P_z).

Similar reductions in CNV in the more demanding condition were obtained in a memory retrieval task by Roth et al. (1975, 1977), although it was not found in a recent study (Roth et al., 1978). In these studies the processing demands at S_2 were varied by changing the size of the memory-set; this set consisted of 1 - 4 target stimuli (digits 0 - 9), which were presented on slides before S_1 (0.5 sec tone). One sec after the tone went off, a probe digit appeared to which the subject had to react as quickly as possible. He was instructed to press one of two keys if the probe stimulus was in the memory-set, and to press the other key (Roth et al., 1977) or to do nothing (Roth et al., 1975) when the probe was out-of-set. The authors found that the CNV was reduced as the size of the memory-set increased, and explained this by assuming that the subject is more distracted when he has to memorize more items (see also 8.4).

As with the same-different RT-task in the study of Poon et al., it is quite possible that this CNV reduction is caused by a suppression in motor preparation with increasing set-size. However, this interpretation would be in conflict with the RT-research, which shows that the two stages "choice" and "motor adjustment" operate independently and that the task variables related to these stages are additive. On these grounds one would expect motor preparation to be unaffected by task variables which relate to other processing stages (i.e., choice). Nor would an inverse relationship between processing demands (e.g. set-size) and terminal CNV be expected, on the grounds that, as argued in the previous section, this wave is primarily determined by motor preparation. A possible explanation for this controversy lies in the amount of training received by the subjects. It has been shown that interactions between task variables may be found, which disappear after practice (Sternberg, 1969). In the RT-studies reviewed in Chapter 3 subjects generally receive at least half a day of practice, mostly on a separate day. On the other hand, Roth et al. (1975) gave their subjects only 16 trials practice on each of the two experimental days. That practically no training was given was also clear from the mean RTs. For example, Poon et al. obtained an average RT of 1000 msec, while Posner and Boies (1971) report an average of 700 msec in a similar task. Similarly, the average RT in the study by Roth et al. (1977) was 200 msec longer than that reported by Sternberg (1969).

It is conceivable that unpracticed subjects will use a safer strategy on the speed-accuracy dimension, especially in more difficult conditions, because they are afraid of making errors, in particular when they are instructed to minimize errors. During practice, either before or during the experimental session, subjects will reach asymptotic performance earlier with the easier task than with the complex task. For example, in the simple RT-task of Poon and co-workers less practice will be necessary to reach an asymptotic level than in the more complex same-different RT-task.

Since it has been demonstrated that the terminal CNV is affected by speed-accuracy instructions (see 8.5), the inverse relationship between CNV and SR-factors might be explained by criterion shifts on the speed-accuracy trade-off between experimental conditions.

In any event the above results do not suggest that the CNV is positively related to the SR-variables; therefore the CNV seems to be unrelated to anticipatory processes connected with decisions linking S_2 to a response.

8.4. DISTRACTION

It has been shown that the amplitude of the CNV is reduced by the presentation of such extraneous stimulation as conversation and reading (Walter, 1964), irrelevant tones or pictures (McCallum and Walter, 1968), and also when a secondary task is given. In examples of the last instance subjects had to memorize four letters presented during the ISI (Tecce and Scheff, 1969; Tecce et al., 1976) or to perform mental arithmetic (adding sevens, Tecce and Hamilton, 1973). In these three experiments the CNV-reduction was accompanied by a substantial increase in RT. The evident interpretation of these results is that a subject confronted with a double task situation will divide his attention between the tasks, which will decrease his efficiency on the main task.

On the basis of the above-mentioned studies, Tecce (1972) formulated his "distraction-arousal" hypothesis, which says that the CNV is related to two separate, but related processes: attention and arousal. It was hypothesized that CNV amplitude bears a positive relationship to attention. Thus, it was expected that the CNV would be increased with moderate levels of arousal and decreased with higher levels of arousal. According to Tecce and Scheff (1969) the RT and the CNV are manifestations of a common process, which appears to be attention. This common process is not *motor-preparation* (conation, in their terminology) because subjects did not report that their intention to respond was lowered during distraction. At this point it should be seriously questioned whether subjective reports are sufficient evidence to conclude that motor-preparation was not decreased during distraction. For example, it might be that intention to react quickly was not affected, but that they in fact prepared less intensively. Moreover, it is quite possible that changes in the level of motor-preparation occur without subjects being aware of this (see also Broadbent, 1978).

In the studies of Tecce and co-workers, increases in heart-rate frequency were found during distraction, which lowers the likelihood that decreased *motivation* can account for the reduction in CNV. According to Tecce heightened automatic arousal is one of the processes which mediates the CNV disruption by distraction. Again, it could be seriously questioned whether this is necessarily true. From the observation that distraction reduces the CNV and increases automatic activity, it does not follow that there is a relationship between CNV and automatic arousal. One cannot exclude the possibility that distraction affects several processes which are mutually independent. It is possible that arousal shows a positive relationship with CNV, as a function of task variables which are *congruent* with the demands of the task, and which focus the attention of the subject on the task instead of distracting it. This might be the case when the subject's concentration on the task is increased with feedback, bonuses or speed instructions. To illustrate, in the present studies both the amplitude of the terminal CNV and the heart-rate frequency (obtained in the sec before S_1) were increased under speed instruction as compared to accuracy instruction (see Experiment 5), and under RT-instruction as compared to detection-instruction (see Experiment 4). Of course, it is difficult to disprove a U-curve relationship because it can account for both positive and negative correlations. This is also the weakness of such a hypothesis, in the sense that a post-hoc explanation can be found for practically every experimental finding. In general, it should be noted that a U-curve relationship can only be tested if the expected direction is hypothesized beforehand and when the expected level of general arousal (e.g. low, medium, high) is specified. Moreover, since the studies of Tecce and co-workers did not contain a control condition in which the secondary task (i.e. memorizing letters or adding sevens) was given alone, the increases in heart rate could be caused, at least partially, by the processing demands of the secondary task. The elevation in automatic activity therefore cannot be ascribed to distraction alone.

In general, the results on distraction have not sufficiently taken into account that introducing a secondary task or even extraneous stimulation might suppress the level of motor preparation, which in turn reduces the CNV and prolongs RT. To overcome this problem it is necessary to investigate the effects of distraction in sensory tasks where no quick response is required. However, given the negative results on stimulus variables, and also on SR variables, the chance of obtaining any effects of distraction in sensory tasks will be low.

Historically, the concept of attention has been used to represent "selective" or "steering" processes at several stages of information processing (see also Mostofsky, 1970; Tecce and Hamilton, 1973). Thus, attention could relate equally well to each of the three preparatory processes proposed in Chapter 3. Attention has also been related to the general level of activation (Hebb, 1955; Kahneman, 1973), which means that it may also refer to the motivation of the subject. If the CNV is to be regarded as an index of attention, it is necessary to specify exactly which sort of attention one has in mind and to obtain experimental data which give relatively unambiguous measures of that particular construction (see also Hillyard, 1973, p. 164). According to Tecce (1970, 1972) attention might be defined as a process which facilitates the selection of relevant stimuli to the exclusion of irrelevant stimuli in the environment. However, to explain the increased CNV preceding high muscular effort for the response to S_2, Tecce includes in his definition also attention to <u>motor</u> aspects of the task (Tecce, 1972, p. 101). In such a broad, nonspecific definition, which refers to the attention a subject pays to the task as a whole, it is not possible to specify to which type of preparatory processes (see also Chapter 3) attention refers. Consequently, defined in such a manner the concept approaches other nonspecific psychological constructs, such as motivation or effort.

If it is not stated beforehand how attention is defined and how different levels of attention are manipulated, almost all experimental results can be explained in terms of attention. For example, Roth and co-workers (1975, 1977) found that the CNV decreases with increasing memory-set size (see above under SR-variables). According to the authors, the greater memory load may cause a distraction of attention which attenuates the CNV. One wonders what the explanation would have been if larger amplitudes had accompanied the larger set-size: In that event it might again have been concluded that the CNV is related to attention, supposing that subjects paid more attention to the more demanding task.

In the present studies increased CNV, especially terminal CNV, was found under speed instruction as compared to accuracy instruction (Experiments 4 and 5), and RT-instruction as compared to detection-instruction. On the one hand, these results can be explained by assuming that subjects paid more attention in the case of the speed and the RT-instructions. On the other hand, no differences were found between two levels of discrimination difficulty (Experiment 2), or else even larger terminal CNVs were found with the more easy condition (Experiment 3). Therefore, these results and also the effects of distraction can be explained more convincingly in terms of motor preparation. Additional support for this view can be deduced from the topographical results of a recent experiment of Tecce et al. (1976). Distraction (i.e. memorizing four letters presented during the ISI) produced a significant CNV reduction at the vertex and parietal, but not at the frontal derivation. On the other hand, an <u>increase</u> in frontal and vertex CNV was found in the condition where letters were presented without the requirements to recall them. Although the study does not give separate measures for an early or a late CNV, the effects on the midline distribution suggest that distraction had a differential effect on the two components of the CNV. Thus, the secondary task (memorizing letters) attenuated the terminal CNV, while the presentation of extraneous stimuli (letters without recall) <u>increased</u> the SNW. According to the functional role given to these SPSs (see also Chapter 6 and 8.2) this would imply that a secondary task suppresses motor preparation and that extraneous stimuli increase the general level of arousal. The latter notion is supported by the fact that the presentation of letters (without recall) produced a small (one bpm), but significant, increase in heart rate.

8.5. SPEED-ACCURACY INSTRUCTIONS

In Experiments 4 and 5, it was shown that the terminal CNV is affected by instructions governing the trade-off between speed and accuracy, but that the SNW does not change. Under speed instructions subjects are instructed to respond as quickly as possible, even at the cost of some errors; under accuracy instructions, the subject is also required to produce quick RTs, but the necessity to avoid errors is emphasized. Both studies (Experiments 4 and 5) demonstrate that the terminal CNV increases under speed instruction, while the SNW remains unaffected. In general, these results replicate those of Loveless and Sanford (1974b).

The results of Waszak and Obrist (1969) could also be interpreted as a speed-accuracy effect. They compared a speed condition, in which subjects were motivated to react fast by telling then that their performance would be compared with that of other subjects, with a relax condition, in which the subject was told that the RTs would not be measured and that he should relax as much as possible, while continuing to respond appropriately. Larger CNVs were found in the speed condition than in the relax condition.

Also differences between "fast" and "slow" RTs (e.g. Connor and Lang, 1969; Lacey and Lacey, 1970; Tecce and Scheff, 1969; Waszak and Obrist, 1969) could be interpreted as reflecting shifts in criterion from trial-to-trial. Rohrbaugh et al. (1976) have shown that, when trials are selected on the basis of RT-performance, the terminal CNV increases with fast RTs, but the SNW is unaffected.

At the moment no studies are available which have systematically investigated the interaction between speed-accuracy instructions and task variables referring to these processing stages. Although recent theories (Ollman, 1977; Pachella, 1974) assume that speed-accuracy instructions influence mainly the level of motor preparation, the possibility that other preparatory processes are also involved is not excluded. It could be argued that speed instructions facilitate "encoding" or the "choice" stage and therefore the increased terminal CNV could be caused by increased stimulus- or decision-anticipation.

In any event the increase in errors does, on the one hand, make it unlikely that the perception of S_2 is facilitated. On the other hand, a more intensive motor preparation will produce shorter RTs and more errors. According to Ollman, errors are reactions which are given before the evaluation of the stimulus is terminated. Thus the subject reacts while the processes of encoding the stimulus and of choosing which response belongs to it have not yet finished. Under accuracy instruction response execution only takes place when these processes have been completed. In an experiment of Kutas et al. (1977) the RT was correlated with the latency of the P_3. Higher correlations between P_3-latency and RT were found under accuracy than under speed instructions. According to the authors the P_3 can be regarded as the outcome of the decision as to which response has to be made. Moreover, it was found that P_3-latency was unaffected by instructions, which suggests that the evaluation process (i.e. encoding and choice processes) were not shortened (see also Discussion of Experiment 5).

8.6. TERMINAL CNV AND READINESS POTENTIAL (RP)

It has often been noted that there is a remarkable similarity in form and topographical distribution between the terminal CNV and the RP. Both consist of a slow negative shift which develops in the one sec or so before the execution of a motor response.

Although some anterior-posterior shifts were found, which might be task related, the results presented in Chapter 5 generally show that the terminal CNV is maximum over centro-parietal areas. In simple RT-tasks, terminal CNV is largest over motor regions, where the RP is also found to be maximum. Only a few studies have investigated the RP and terminal CNV within the same experimental study. For example, Syndulko and Lindsley (1977) using an ISI of 1.5 sec compared an RT instruction with a detection instruction. In the latter case the subject had to make a discrimination at S_2 and to delay his response by one sec. It was found that the negativity preceding S_2 under RT instruction, and the negative shift preceding the delayed motor response, both had the same midline distribution. Both were centrally dominant. Similar results were obtained under speed and detection-instruction in Experiment 5.

Moreover, it was shown in the Syndulko-Lindsley study that the SPS over the motor region contralateral to the intended response was more negative than the SPS at the ipsilateral area. This asymmetry was not found in frontal, parietal and occipital regions. In addition, asymmetry was again not evident during bimanual response preparation, nor preceding S_2 under the detection-instruction. The similarity between terminal CNV and RP in both midline and lateral distribution was also observed by Rohrbaugh et al. (1976). They compared terminal CNV in a simple RT-task (ISI of 4 sec) with the RP preceding voluntary finger movements. In this study the difference between the contralateral-ipsilateral hemisphere in the RP correlated significantly ($r = .56$; $p < 0.05$, across 14 subjects) with this difference in the terminal CNV in the simple RT task.

In Experiment 6 it was found that the size of laterality effect of the SPS preceding the response in averages time-locked to the motor response was of the same magnitude in different task situations, i.e. under RT-, detection- and synchronization-instruction, and with voluntary movements.

Although it is difficult to prove that the terminal CNV and RP (both derived from the motor region (C_z)) are essentially the same phenomenon, there is at the moment little argument why they should not be produced by the same neurophysiological generator. Most arguments which have been raised to prove that they differ in their functional role can be accounted for by the contamination of the terminal CNV by the SNW (see also Chapter 5).

According to Deecke et al. (1976) the CNV differs from the RP 1) in the experimental situation producing it, 2) in the form of the potential, 3) in the topography, 4) in its higher bilateral symmetry and 5) in its possible independence of motor acts. Re 1): in Experiments 5 and 6 it has been shown that movement potentials can also be obtained in the CNV paradigm, either time-locked to the response to S_2 or to a delayed response with which the subject indicates his observation with a button press (see also Syndulko and Lindsley, 1977). As is shown in Figs. 5 and 6 of Experiment 6, the movement potentials obtained in this way have the same characteristics (form and topography) as those accompanying voluntary movements. Moreover, in Experiment 5 it was shown that the negativity preceding the motor response was generally larger in averages time-locked to the response to S_2 than in averages time-locked to S_2. This effect was largest in those conditions where the latency between S_2 and the response was very variable (synchronization-instruction) or when it was rather long (accuracy instruction). Thus, the looser the correspondence between stimulus and response, the larger the discrepancy. This result suggests that the negativity time-locked to the response might be a better measure for the level of motor preparation than the terminal CNV. Re 2): As was also noted by Deecke et al., the SPS preceding S_2 has the same form as the RP, with long ISIs, where the SNW and terminal CNV are separated. Re 3): The topography of the CNV has a more anterior distribution than the terminal CNV and the RP, because the SNW is located more frontally. Re 4): Although differences in terminal CNV between hemispheres were also found with short ISIs (Otto and Leifer, 1973; Syndulko and Lindsley, 1977), a large SNW may have disrupted eventual lateral asymmetries in some instances (McCallum, 1978). Re 5): In the present view the terminal CNV is response-related and the negativity observed in sensory tasks is produced by the SNW. However, it is not excluded that there is some sort of sensory CNV with a parieto-occipital distribution, although its amplitude would be very small compared to the terminal CNV (see Chapter 5).

Thus, there is no reason for regarding the vertex terminal CNV and the RP as reflections of different processes, whereas the notion that they are generated by the same neurophysiological mechanism is in line with the view that the terminal CNV reflects the level of motor preparation and is contingent on a motor response. Moreover, the RP is affected by task variables, such as muscle effort (e.g. Kutas and Donchin, 1977) and motivation (e.g. McAdam and Seales, 1969; McCallum, 1978), which also influences the terminal CNV (Low and McSherry, 1968; Rebert et al., 1967; Irwin et al., 1966; Waszak and Obrist, 1969).

Thus, the view expressed in this thesis is that both potentials refer to the same neurophysiological generator, but are obtained in different task situations and with different averaging techniques. In this view the terminal CNV is that part of the RP which precedes S_2. Of course, this idea is only true for single trials, because averaged potentials will diverge the larger the variability in RT. Since both the RP and the terminal CNV are slow phenomena, this effect will be negligible as long as the standard deviation of the RT is small (for example, < 50 msec). Thus, the amplitude of the terminal CNV can be predicted when the amplitudes and the waveform of the readiness potential and the RT are known. When the RP remains unchanged, the amplitude of the terminal CNV is determined by the RT. With shorter RTs the terminal amplitude increases, because a larger part of the RP precedes S_2.

In this view the reduction in terminal CNV under accuracy instructions is associated with the prolongation of the RT: the gradually increasing negative shift only precedes S_2 partially or not at all (for example, with detection-instructions). In the Rohrbaugh et al. study the attenuated terminal CNV preceding slow RTs (229 msec) as compared to fast RTs (140 msec) could also be interpreted in this way. Moreover, the bilateral asymmetry in the terminal CNV was larger preceding fast RTs (1.5 µV) than preceding slow RTs (0.4 µV). Since the asymmetry preceding voluntary movements was present only in the terminal phase of the RP, it suggests that with shorter RTs the RP intrudes more into the $S_1 - S_2$ interval and so produces the asymmetry of the terminal CNV. This result was confirmed in a recent study by Perdok and Gaillard (in preparation) where a larger asymmetry was found under speed (2 μV) than under accuracy instructions (0.5 μV).

As was also noted by Rohrbaugh and colleagues (1976), the above view enables the investigation of movement-related potentials within a much wider context. On the one hand, the study of the RP can be extended beyond the scope of repetitive stereotyped movements and the influence of psychological variables can be investigated. On the other hand, a strict pairing of stimuli is no longer necessary and new experimental paradigms can be used (for example, serial RT instead of warned RT tasks).

8.7. CONCLUSION

In the present chapter it has been shown that the terminal CNV is affected by muscle effort, time uncertainty, distraction, S_2-probability and speed-accuracy instructions. However, the terminal CNV is found to be unrelated to stimulus (and decision) anticipation. Several studies which investigated the SPSs before S_2 did not take into account possible contamination by response-related potentials. Studies in which the response to S_2 was delayed and in which long ISIs were used, found the terminal CNV to be attenuated or practically absent, which suggests that the terminal CNV is contingent on a motor response. This provides no comfort for theories such as attention and expectancy which relate the terminal CNV to stimulus variables. In contrast there is considerable evidence that the amplitude of this wave reflects the level of motor preparation. In fact, almost all experimental data can be explained in these terms. The motor character of the terminal CNV is further illustrated by its similarity in form and topography to the RP. Both potentials gradually develop in the one sec before the execution of a response, they are both most prominent over the precentral motor regions (C_z) and show an asymmetry to the contralateral side of the responding limb.

CHAPTER 9

CONCLUDING REMARKS

It is argued here that the classical CNV is not a unitary phenomenon but consists of at least two negative SPSs: the slow negative wave (SNW), which reaches its peak within one sec after S_1 and then declines gradually, and the terminal CNV, which gradually develops during the ISI and reaches its maximum towards the end of this interval.

These slow potentials differ in their topography (see Fig. 8); the midline distribution of the SNW is located more anteriorly than that of the terminal CNV. In most studies (see Chapter 5) largest SNW amplitudes are found at the frontal derivation, while the amplitudes of the terminal CNV are most prominent at the vertex. Since the anterior-posterior gradient is steeper between the vertex and frontal derivation than between vertex and parietal derivation, the terminal CNV seems to be located precentrally over the motor region. With regard to the lateral distribution of these SPSs the SNW appears to be symmetrical, whereas the terminal CNV shows a small, but significant asymmetry. Enhanced amplitudes were found contralateral to the responding limb.

In addition to their topography, the SNW and the terminal CNV also differ in their functional meaning. The SNW is affected by the physical and psychological properties of S_1, whereas the terminal CNV is dependent on the task demands of S_2. Another difference is that the pairing of S_1 and S_2 is not necessary for the occurrence of the SNW. This negative shift is even found after non-signal stimuli which are not followed by an imperative stimulus. Moreover, in selective listening tasks a frontal "slow wave" is also found, and this is most prominent after rare, but relevant (i.e., to be counted) stimuli. Since the slow positive wave (SPW) is also largest under these conditions, both the SNW and SPW seem to belong to a family of slow potential changes following S_1. It is in line with this view that both waves are enhanced when S_1 contains information in addition to its warning function. Although the SNW and the SPW are affected in the same way by several task variables they differ in other instances, which suggests that these waves reflect different but related processes. The involvement of different neurophysiological mechanisms is also suggested by the differences in midline distribution (parietal versus frontal). An explanation of the close inter-relationship between the SNW and the SPW might be found in the fact that both waves are most prominent in non-specific parts of the cortex: the SPW in the association cortex (input system) and the SNW in the frontal cortex (output system). These observations can be described rather well in terms of Luria's model of the functional organization of the brain.

In Chapter 8 it was argued that the terminal CNV is contingent upon a motor response because this negative shift is virtually absent in sensory tasks in which no quick response to S_2 is required. This result does not leave much room for theories, such as attention and expectancy, which relate the terminal CNV to perceptual or decisional processes. In contrast, there is considerable evidence that this negative shift reflects the level of motor preparation, because it is affected by such response variables as time uncertainty (ISI-duration, ISI-irregularity), the probability of S_2 and muscle effort. In fact, almost all experimental results, either from the present studies or from studies reported in literature, can be explained in this way. The effects of such task variables as distraction and speed-accuracy instructions can also be described conveniently in the same manner, although their relationship to motor preparation is less clear.

The motor character of the terminal CNV is further illustrated by its similarity in form and topography to the readiness potential (RP). Both gradually develop during the one to two secs before the execution of a response, they are both most prominent over the motor region (C_z) and they both show an asymmetry contralateral to the responding hand.

According to Syndulko and Lindsley (1977) the prominence of the CNV in motor tasks is so convincing that the occurrence of this SPS in so called sensory tasks, which do not involve specific, overt motor responses suggests that the latter tasks also involve at least some "motor" elements. Some support for this notion is provided by the EMG data of Experiment 6. Here the EMG activity recorded just before S_2 was larger in the forearm with which a delayed response had to be given. Thus, it cannot be assumed that motor systems are not involved at all in sensory tasks (see also Discussion of Experiment 6). Moreover, Sperry (1952) has suggested that regardless of the manifest behavioral situation, the primary end-product of the brain is motor output. Situations not involving specific, overt motor responses may nevertheless produce generalized effector readiness, receptor orientation (e.g. fixation of the eyes), and non-automatic postural adjustments, in addition to specific motor concomitants of mental processes.

With regard to the functional role of the terminal CNV, it should be noted that it is quite possible that the above statements about the motor character of this SPS are limited to the vertex derivation. As is outlined in Chapter 5, there is evidence that in addition to a motor CNV at the vertex there is a sensory CNV with a parieto-occipital distribution which is related to the perception of S_2. In that case it is assumed that the vertex terminal CNV only differs from the RP in the way of averaging (stimulus vs. response locked); consequently, the vertex terminal CNV could be regarded as that part of the RP which precedes S_2 in cued RT-tasks. In contrast, the sensory CNV is assumed to be contingent to S_2, and may only occur when this stimulus is visual.

Several authors have noted the strong relationship between the classical CNV and motor processes (e.g. McAdam, 1974). However, a definite conclusion that the CNV is contingent on a motor response was always held back by the fact that the CNV was also present in sensory tasks. The present results suggest that this negativity can be attributed largely to the SNW, since virtually no negativity precedes S_2 in sensory tasks when long ISIs are used (see Chapter 8.1.). Studies using ISIs of 1 sec have shown that the execution of a motor response to S_2 increases the amplitude of the CNV and that the magnitude of this enhancement is of the same order as the amplitude of the RP preceding voluntary movements (Irwin et al., 1966; Low et al., 1966; Peters et al., 1970; Walter, 1964a).

It was shown that the separation of the classical CNV into two components caused a breakthrough in the investigation of the functional significance of the SPSs in the S_1-S_2 paradigm. It seems that a similar development also takes place for other physiological changes during the ISI, such as heart rate (e.g. Lacey and Lacey, 1974; Coles and Duncan-Johnson, 1977; Duncan-Johnson and Coles 1977), background EEG (Pfurtscheller and Aranibar, 1977), Hoffman reflex and Achilles tendon reflex (Brunia, 1978).

It could be questioned (see Posner in McCallum and Knott, 1976, p. 232) what the value is of longer intervals, since short intervals, of say 0.5 sec, are optimal for a large class of behavioral tasks. Moreover, from a technical point of view recording with short ISIs is less cumbersome (shorter time-constants, easier control of eye movements and blinks, less fatiguing for the subjects), which might be important in, for example, clinical studies. The position taken here is that first the functional significance and other characteristics (topography, time course, etc.) should be determined before studying these SPSs with shorter intervals.

Although with a 1 sec ISI the three SPSs will contaminate each other, the parietal positivity between 200-400 msec, the frontal negativity between 500-700 msec and the vertex amplitude at the end of the ISI will give good estimates of SPW, SNW and terminal CNV, respectively. Of course these SPSs could also be separated by statistical methods (Loveless, 1978). For example, Donchin et al. (1977) using principal components analysis, found with a 1 sec ISI a frontal wave peaking at 475 msec after S_1 and a vertex wave which was most prominent just before the response. Another possibility would be to use the knowledge we now have with regard to the task variables affecting the SPSs. Thus, when the aim of the study is to investigate the terminal CNV, a weak visual S_1 could be used, since we know that this signal does not evoke an SNW, and when S_1 is non-informative the SPW will also be attenuated.

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APPENDIX

- The experiments are not reported in the order in which they were carried out. The chronological order was 1, 4, 2, 5, 3 and then 6.
- Experiments 2, 5, 3 and 6 were carried out together with J. Perdok, and C. Varey assisted in the last experiment.
- In all experiments technical assistance was given by J.Th. Eernst, and A.J. Krul carried out the statistical analysis of the data.
- The following experiments have been published: Experiment 1 in Biological Psychology, 4 (1976): 139 - 154; Experiment 2 in Acta Psychologica, 42, (1978) and Experiment 4 in Psychophysiology, 14 (1977): 563 - 568.

EXPERIMENT 1

EFFECTS OF WARNING-SIGNAL MODALITY ON THE CONTINGENT NEGATIVE VARIATION (CNV)[*]

ABSTRACT

CNVs were recorded during the S_1-S_2 interval of a prolonged simple reaction task. In this task, a warning stimulus S_1 is followed by an imperative stimulus S_2, to which the subject makes a motor response. The differential effects of a visual and an auditory S_1 were investigated under two interstimulus interval (ISI) durations (1 and 3 sec). Under the 3 sec ISI condition, the form of the slow negative wave demonstrated clearly a biphasic character: an orientation wave (O wave) following S_1 with a peak latency at about 650 msec and an expectancy wave (E wave), which reaches its largest amplitude towards the end of the ISI. Under the 1 sec ISI condition the two components of the CNV are confounded. The O wave had a fronto-central distribution, while the E wave was located precentally. The O wave was enhanced after an auditory S_1, as compared to a visual S_1.

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[*] Published in Biological Psychology, 4 (1976): 139-154.

1. Introduction

Several authors (e.g. Tecce, 1972; Näätänen and Gaillard, 1974b) emphasized the importance of investigating the shape of the contingent negative variation (CNV). The morphology of the CNV might contain as much information as the magnitude of the CNV amplitude. The form of the CNV is dependent on the type of subject and on the experimental situation. Two forms of CNV can be distinguished: a quick (A type) and a slow (B type) rise to peak (Cohen, 1969; Donchin, Gerbrandt and Leifer, 1972; Tecce, 1972).

Morphological effects can be investigated conveniently by measuring both the early (at half the interval) and the late (at the end of the interval) CNV amplitude.

Tecce (1972, footnotes 10 and 13) suggested that the early CNV is related to 'arousal processes', supporting this notion with the following evidence: a differential effect on the early CNV is observed after the intake of amphetamine and when subjects have to clench their fist during the interstimulus interval (ISI). Additionally, Gaillard and Näätänen (1976) found that the early CNV is enhanced after an auditory S_1, as compared to a visual S_1. This enhancing effect was explained in terms of the 'arousing' properties of an auditory stimulus (see also Sanders, 1976; Trumbo and Gaillard, 1975).

The early and late CNV also differ as to their topography. While the differences in amplitude between the frontal and vertex derivation are small for the early CNV they are rather large for the late CNV (Low, Borda, Frost and Kellaway, 1966; Näätänen and Gaillard, 1974b). Moreover, in the last study, larger interchannel correlations were found for the early CNV than for the late CNV.

The above results strongly suggest that the CNV is not a unitary phenomenon (see also Borda, 1970; Donchin, Otto, Gerbrandt and Pribram, 1971; Donchin et al., 1972) and that the early and late CNV are produced by different underlying mechanisms; the early CNV seems to be influenced to a greater extent than the late CNV by non-specific activating systems.

Additional evidence for the notion that the CNV is not a unitary potential comes from experiments with long ISIs (Loveless and Sanford, 1974, 1975; Weerts and Lang, 1973). In this situation the CNV has a biphasic character and consists of two distinct components: an orientation wave (O wave) which reaches its peak value within 1 sec after S_1, and an expectancy wave (E wave) which rises in anticipation of S_2. Both Loveless and Sanford (1974), and Weerts and Lang (1973) regard the O wave as a cortical component of the orienting response to S_1, and the E wave as the traditional CNV, and they suggest that the CNV measured with short ISIs (e.g. 1 sec) is a combination of the O and the E wave.

This study investigates the influence of the modality of S_1 on the morphology and on the anterior–posterior distribution of the CNV. Two ISIs (1 and 3 sec) were used to enable the comparison between measures used under short and long ISI conditions. It was thought that the early and late CNV obtained with a 1 sec ISI, would reflect the O and E wave component found when longer ISIs are used. As the modality of S_1 has a differential effect on the early CNV (Gaillard and Näätänen, 1976), it was expected that an auditory S_1 enhances the O wave and that the E wave remains unaffected by the modality of S_1. Similarly, it was expected that the O wave would be located more anteriorly than the E wave, because the early CNV (as compared to the late CNV) is more prominent in the frontal regions (Näätänen and Gaillard, 1974b).

2. Method

2.1. Subjects and apparatus

The subjects were eight male university students aged from 24 to 28 yr. They were tested in a soundproof, air-conditioned and electrically shielded cubicle (Amplifon); a nixie-tube display and a loudspeaker were placed in front of the subject at a distance of about 1.5 m and a response key was mounted on the sloped top of a table, which provided an armrest for the subject. The auditory signals consisted of a 1000 Hz tone at 70 dB (duration 40 msec). For the visual signals a standard red nixie tube was used with all elements activated (duration 40 msec). The luminance of this stimulus was 200 cd/m^2, while the surrounding background had a luminance of 1.75 cd/m^2. Whereas S_1 was either visual or auditory, S_2 was always visual. The intensity of both signals was roughly chosen in the middle of the range of possible intensities. Both signals have been used before in studies on the modality effect (Gaillard and Näätänen, 1976; Trumbo and Gaillard, 1975).

The EEG was recorded with silver–silver chloride electrodes from the frontal (Fz), the vertex (Cz), the parietal (Pz) and occipital (Oz) positions referred to the right mastoid. Vertical eye movements were recorded from above and below the right eye. An electrode on the left ear served as the ground. After a.c. amplification (time constant 6 sec) the EEG and EOG signals were stored on magnetic tape (Philips, Analog-7).

The timing of the signals, including the trigger and measurement of reaction time (RT) (in msec) was done by the PSARP equipment (Van Doorne and Sanders, 1968). This equipment also produced a label, which accompanied the EEG signals and indicated the experimental condition, the trial number and the corresponding RT.

2.2. *Procedure*

All subjects participated in one practice session and in three experimental sessions at the same time at weekly intervals. At the practice session, training continued until the subject reached an asymptote with respect to both mean and variability of RT. The subject was also trained in suppressing eye movements during the ISI. To reduce eye movements the subject was instructed to fixate a mark located in the centre of the nixie tube and to blink after the response was given.

Each test session consisted of six 25 min series, separated by 5 min of rest. During the resting periods the door of the cubicle was opened, but communication with the subject was reduced to a minimum. Within each series four experimental conditions were given in the following order: a 1 sec ISI with an auditory S_1, a 1 sec ISI with visual S_1, a 3 sec ISI with an auditory S_1 and a 3 sec ISI with a visual S_1. The order of presentation was balanced by cyclical permutation.

Each of these four conditions consisted of a block of 33 stimulus pairs (S_1–S_2) in which three or four catch trials were randomly interspersed; in catch trials S_2 was omitted and the subject had to withhold his reaction. The intertrial interval was varied irregularly between 8 and 12 sec to avoid anticipation of the warning signal.

2.3. *Data analysis*

The four EEG and the EOG channels were analysed on line by a LAB8 computer, using a program developed at the Institute. An epoch of 4 sec before S_2 was sampled at a rate of 40/sec. For each of the five channels the means of every five consecutive samples were obtained providing 32 data points at intervals of 125 msec. Due to memory limitations only 11 data points (DPs 1–11) per channel were

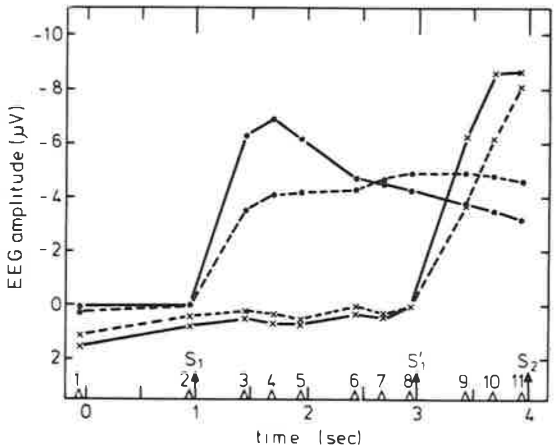

Fig. 1. The vertex EEG amplitude during the 4 sec epoch before S_2, separately for each experimental condition: auditory S_1: 1 sec ISI (X———X); visual S_1: 1 sec ISI (X------X), auditory S_1: 3 sec ISI (●———●); visual S_1: 3 sec ISI (●------●). Each curve is based on the grand means of the 11 DPs indicated in the figure (1–11). The warning singal is denoted by S_1 under the 3 sec ISI condition and by S_1' under the 1 sec ISI condition.

retained for further analysis. Every other mean was used except the 10th, 18th and 26th, while in the first second of the epoch only the 1st and 8th were included (see also fig. 1).

Catch trials, missed signals (RT >1000 msec) and anticipatory reactions (before S_2), as well as the first three trials of a block were omitted from the analysis. The computer also skipped a trial when the EOG amplitude exceeded ±200 μV and when the amplitude of the vertex EEG exceeded ±100 μV (relative to the zero of the a.c. amplifier).

After this selection the 11 DPs of each single trial were averaged over 20 trials. Occasionally, averages were based on less than 20 trials. The 11 DPs of the vertex channel were also averaged over series for each ordinal position to enable the examination of the short-term habituation of the CNV amplitude within a block of trials.

On the basis of the 11 DPs three measures were obtained: the 'early CNV', the average potential within the period 375–500 msec after S_1 (DP 9 for the 1 sec ISI and DP 3 for the 3 sec ISI condition); the 'late CNV', the average potential within the period 125–0 msec before S_2 (DP 11) and the 'O wave', the average potential within the period 625–750 msec after S_1 (the last measure was taken for the 3 sec ISI condition only). All measures were referred to the baseline, the average potential within the period 125–0 msec before S_1 (DPs 8 and 2 for the 1 and 3 sec ISI condition, respectively). Although most EOG artifacts were removed after the rejection on a single-trial basis, EOG activity remained in some averages. Therefore, CNV amplitudes were eliminated when the corresponding EOG amplitude exceeded ±50 μV.

Analyses of variance were completed on the RT, and on the early CNV, the late CNV and the O wave for each of the four EEG derivations and for the EOG channel. The data were analysed according to a factorial design containing the following factors: subjects, S_1 modality, ISI duration, series and sessions. Missing data due to artifacts were estimated by using the least-squares method (Winer, 1962).

3. Results

3.1. S_1 modality effects

The amplitudes of the vertex potential during the 4 sec epoch are presented in fig. 1, separately for the four experimental conditions. Each curve is based on 11 DPs averaged over subjects, weeks and series. Under both ISI conditions the CNV grows faster and reaches a larger amplitude with an auditory S_1 than with a visual S_1.

The waveform of the vertex potential under the 3 sec ISI conditon is rather complicated; with a visual S_1 an initial rise is followed by a more gradual increasing terminal amplitude; with an auditory S_1 the slow wave shows a clear early peak (ca. 650 msec after S_1), followed by a rather steady amplitude decrease. The modality effect on the vertex slow wave lasts until ca. 1450 msec after S_1 (DP 6; see also fig. 1).

An analysis of variance demonstrated that the modality of S_1 had only an effect on the early CNV ($F = 9.81$, df 1,7, $p < 0.02$) and the O wave ($F = 8.99$, df 1,7, $p < 0.02$), while the late CNV was affected by the duration of the ISI ($F = 17.8$, df 1,7, $p < 0.004$). For the late CNV the interaction between S_1 modality and ISI duration was also significant ($F = 5.63$, df 1,7, $p < 0.05$). The late CNV was smaller with an auditory S_1 than with a visual S_1 under the 3 sec ISI condition, but larger under the 1 sec ISI condition (see fig. 1).

3.2. Topographical aspects

Figures 2a and 2b present the curve of the EEG amplitudes separately for the four derivations (Fz, Cz, Pz, Oz). For both S_1 modalities a clear O wave can be observed at the frontal and vertex derivation. With an auditory S_1 the O wave is largely reduced at the parietal derivation and not present in the occipital derivation. With a visual S_1, an early positive wave can be observed at the parietal and occipital derivations. The modality effect on the early CNV was significant for the frontal ($F = 7.7$, df 1,7, $p < 0.03$) and for the parietal derivation ($F = 10.4$, df 1,7, $p < 0.01$), while this effect on the O wave was significant for the parietal derivation ($F = 18.1$, df 1,7, $p < 0.004$), but only weakly so for the frontal derivation ($F = 3.97$, df 1,7, $p < 0.08$).

The anterior–posterior distributions of the O wave and of the late CNV under

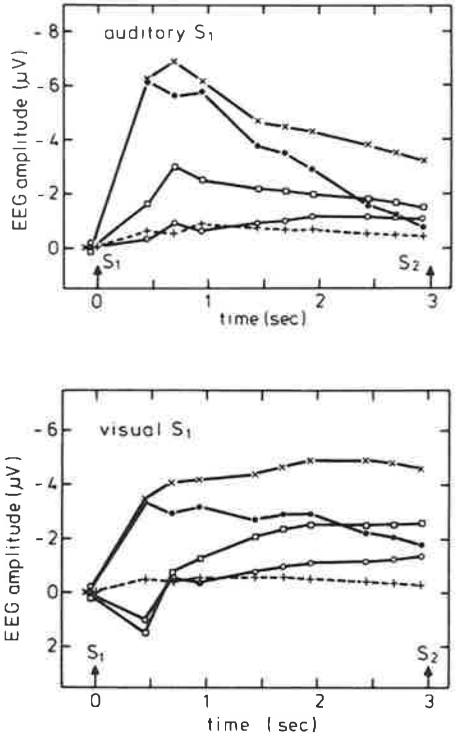

Fig. 2. (a) The amplitudes of the EEG derivations; frontal (●), central (×), parietal (□) and occipital (○); and of the EOG (+) with an auditory S_1, under the 3 sec ISI condition. (b) The same as fig. 2a, but with a visual S_1.

3 sec ISI condition, and of the late CNV under the 1 sec ISI condition are presented in fig. 3 as a function of S_1 modality. It is clearly seen that the O wave is fronto-central dominant, while the E wave is located more posteriorly over precentral regions. The posterior gradient of the distribution of the O wave was steeper and that of the E wave less steep than their anterior gradients. Fig. 3 also shows that the modality of S_1 had no effect on the midline distribution of either wave.

3.3. Effects of series and sessions

The main effects of series and sessions were not significant for the three CNV measures at any derivation (see also fig. 4). For both the early CNV and the O wave, series and sessions tended to interact at all four derivations. During the first session the CNV amplitude was increasing, while it was decreasing during the second and even more during the third session (see also fig. 5). However, this interaction was only significant for the early CNV at the parietal derivation ($F = 2.51$,

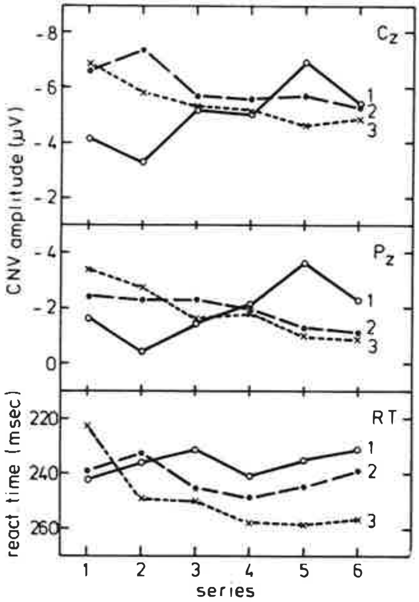

Fig. 5. The vertex and parietal amplitudes of the O wave and the RT as a function of series, separately for the three sessions.

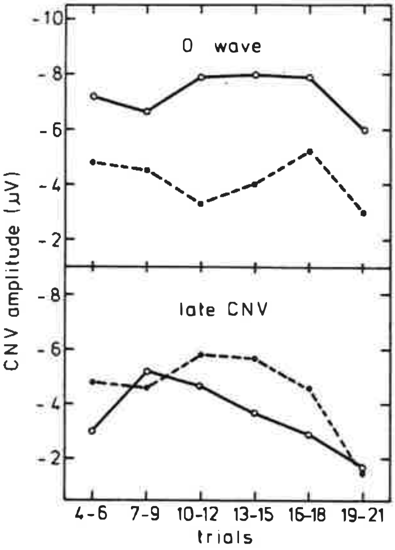

Fig. 6. The vertex amplitudes of the O wave and the late CNV (E wave) under the 3 sec ISI condition, as function of trials within a block, separately for the condition with an auditory S_1 (solid line) and with a visual S_1 (broken line).

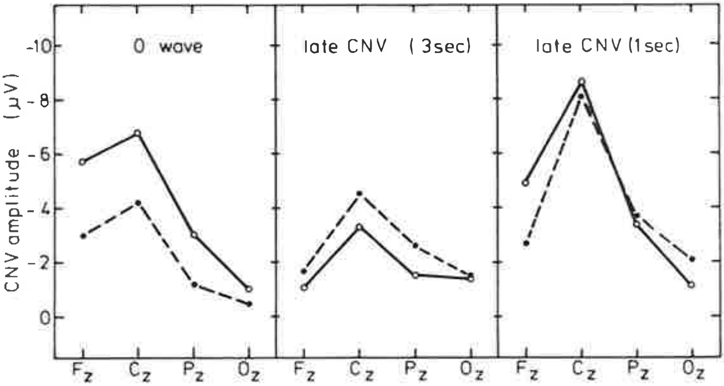

Fig. 3. The amplitudes of the O wave and late CNV under the 3 sec ISI condition and of the late CNV under the 1 sec ISI condition, as a function of derivations, separately for the condition with an auditory S_1 (solid line) and with a visual S_1 (broken line).

df 1,7, $p < 0.01$) and for the O wave at the occipital derivation ($F = 1.99$, df 1,7, $p < 0.05$).

3.4. Effects of ordinal position within a block

To investigate changes in the CNV amplitude within a block of trials, EEG signals corresponding to the same ordinal position were averaged over series. The CNV

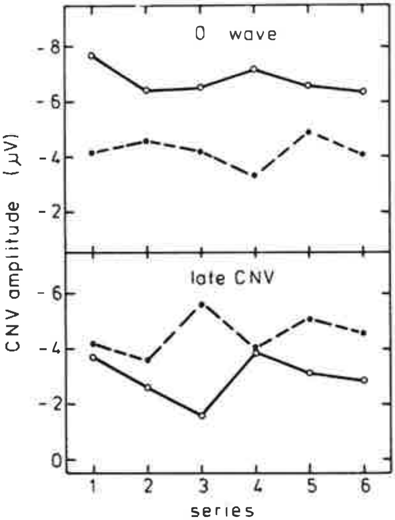

Fig. 4. The vertex O wave and the late CNV (E wave) under the 3 sec ISI condition as a function of series, separately for the condition with an auditory S_1 (solid line) and with a visual S_1 (broken line).

measures were based on three consecutive trials to obtain averages with approximately the same number of trials ($n = 18$) as for the other measures ($n = 20$). Fig. 6 shows that under both conditions the amplitude of the O wave remained constant, while the late CNV decreased within a block of trials.

3.5. RT data

ISI duration had a strong effect on RT ($F = 26.6$, df 1,7, $p < 0.001$), while the modality of S_1 did not have an effect ($F = 2.94$, df 1,7, $p < 0.10$). While the main effect of series was weakly significant, the interaction between series and weeks was very significant ($F = 28.7$, df 10,70, $p < 0.005$). As shown in fig. 5, RT decreased only slightly during session 1 and remained on the same level during session 2. In session 3 RT increased during the 3 h session, the difference between the first and the sixth series being 33 msec. As this interaction was also present in the early CNV and the O wave, RT was negatively correlated with these measures (see also fig. 5).

Catch-trial errors and anticipations were made more frequently during the shorter ISI conditions (1 sec) (t test, $p < 0.01$).

3.6. Eye movements and rejected data

From the single-trial data of eight subjects, 1.8% of the trials were rejected because of eye movements, 1.9% because of excessive EEG activity (clipping of the EEG signal) and 2.3% because of RT failure (1.4% missed signals and 0.9% anticipations). This means that on the average two of the 33 trials were rejected. The data rejected were equally distributed over the series. Thus, no evidence was found for time-on-task effects.

Under both ISI conditions many more eye-movement artifacts occurred with an auditory than with a visual S_1. Table 1 presents the three CNV measures, separately for the four EEG derivations and the EOG amplitudes under the 3 sec ISI condition before and after the rejection of eye-movement artifacts. Generally, the reduction in CNV amplitude was larger with an auditory S_1, as compared to a visual S_1, this reduction being more prominent for the more anterior derivations. After the rejection of eye movements differences in EOG amplitude between the two modality conditions were not significant. No differences between the two modality conditions could be observed in the time course of the EOG signal (compare figs. 2a and 2b).

4. Discussion

This study confirms the results of Loveless and Sanford (1974; 1975; but see also Weerts and Lang, 1974), in that the CNV is not a unitary phenomenon. In

Table 1
CNV amplitudes (in μV) for the four EEG derivations and the EOG under the 3 sec ISI condition with an auditory (A) or visual S_1(V), before and after the rejection of eye-movement artifacts (upper and lower values, respectively).

		Fz		Cz		Pz		Oz		EOG	
		A	V	A	V	A	V	A	V	A	V
Late CNV	before	–2.0	–1.8	–3.7	–4.6	–1.8	–2.6	–1.5	–1.4	– 8.8	–3.5
	after	–1.0	–1.7	–3.3	–4.5	–1.5	–2.6	–1.4	–1.4	– 5.3	–2.8
Early CNV	before	–7.8	–3.3	–7.0	–3.4	–1.8	+1.5	–0.3	+1.0	–13.04	–4.8
	after	–6.4	–3.4	–6.3	–3.5	–1.5	+1.4	–0.2	+0.9	– 6.9	–5.3
O wave	before	–6.8	–3.0	–7.2	–4.2	–3.0	–0.8	–0.7	–0.5	–12.0	–4.2
	after	–5.7	–3.0	–6.8	–4.2	–3.0	–0.8	–1.0	–0.5	– 7.4	–4.4

the slow potential changes prevailing during the foreperiod of a reaction task two distinct components are discernible: an O wave following S_1 with a peak latency at about 650 msec, and a terminal amplitude (E wave) reaching its largest amplitude towards the end of the ISI.

The present modality effect is consistent with an earlier finding (Gaillard and Näätänen, 1976) that an auditory S_1 enhances the amplitude of the early CNV under a 1 sec ISI condition. It is not excluded that the present finding merely reflects the arousing properties of the signal. Indeed, Loveless and Sanford (1975) demonstrated that the O wave is dependent on the intensity of the signal. Detailed comparisons between this study and that of Loveless and Sanford (1975) are not possible because, in the latter study, S_1 remained on during the ISI. This might be one reason why no clear peak of the O wave can be observed in their data.

Further studies are needed to investigate whether the present results are modality specific or are due to intensity differences; for example, by varying the intensity of S_1 within both modalities. A crucial experiment differentiating between these alternatives is difficult to design due to the fundamental problem inherent to cross-modality comparisons. Anyway, the present results are contradictory to the established view that, within wide limits, the CNV is independent of the physical characteristics of S_1 (e.g. Cohen, 1969; Tecce, 1972).

The present results show clearly that the O wave and the late CNV differ in their topography. The fronto-central distribution of the O wave corroborates earlier studies (Low et al., 1966; Näätänen and Gaillard, 1974b) in that the early component of the CNV is located more frontally than the terminal amplitude of the CNV. Accordingly, Walter (1968) reported that the CNV 'spreads' from the anterior frontal cortex posteriorly to the premotor area. In view of the present data it is more likely that the CNV consists of two waves, which are physiologically and functionally independent.

In animal experiments with surface electrodes Borda (1970) and Low (1969) found an anterior-dominant negative shift, and a later potential change in the sensorimotor and the parietal regions (Low, fig. 4–17). These two potentials show a remarkable similarity in both shape and midline distribution to the O and the E waves. Both investigators raise the question as to whether the CNV is a unitary phenomenon. Borda suggests that the frontal and central potentials are unrelated and originate from different subcortical systems. The frontal-dominant potential may arise from activation of a medial thalamus–frontal cortex system. The data of Low are of particular importance because he used rhesus monkeys with enucleated eyes. Low reported that the negative shift in the anterior lead was greater before than after the removal of the eyes.

Also, in the present study, the O wave and the early CNV were reduced in amplitude after the rejection of eye-movement artifacts. It was also shown that an auditory S_1 induces more eye movement than a visual S_1. The latter finding underlines that it is dangerous to compare experimental conditions with different types of warning stimuli. In general, the EOG amplitude, measured in the same way as the

CNV, should be reported separately for each experimental session and if possible before and after rejection.

The present amplitudes recorded were relatively small for both the O wave and the E wave. This might be caused by the relatively long duration of the whole experiment, i.e. three sessions of 3 h. It was expected that the CNV would habituate strongly over such a long testing period. That the E wave did not change over series or only weakly so, might be accounted for in terms of the Hullian concept of 'conditioned inhibition' (Kimble, 1949). This concept implies that subjects knowing that they have to work for a long period, spread their 'energy' over the whole period.

To summarize, so far it has been shown that the CNV is not a unitary phenomenon but consists of two distinct waves, which differ in midline topography and morphology. The O wave seems to be an alerting response dependent on the characteristics of S_1 (e.g. modality and intensity). The O wave could be regarded as an orienting response, which is involuntary but does not habituate over trials. The larger correlations between the vertex and frontal derivation for the early CNV (as compared to the late CNV) found earlier (Näätänen and Gaillard, 1974b) can be regarded as an illustration of this involuntary character. Further research should show whether other components of the orienting response to S_1, i.e. heart rate deceleration and EEG desynchronization, have similar characteristics under the same experimental conditions, namely no habituation over trials and dependence on the modality and intensity of S_1. The frontal dominance of the O wave is consistent with the view that the early phase of the CNV is enhanced to a greater extent than the terminal amplitude of the CNV by conditions known to activate non-specific activating systems (see also section 1).

With regard to both morphology and topography the E wave shows a remarkable similarity to the 'motor potential', which precedes voluntary movements (Vaughan, Costa and Ritter, 1968). Therefore the E wave seems to be mainly related to motor preparation. This view is supported by experimental evidence (reviewed by Loveless and Sanford, 1974; 1975) that the E wave is affected by variables, such as foreperiod duration, time uncertainty, incentives and 'speed/accuracy' instructions, which are known to influence motor preparation, as indicated by RT. For example, Loveless and Sanford (1974) found that both the E wave and the RT were strongly affected by instructions governing the speed/accuracy of response to S_2, whereas the O wave remained unaffected.

In the recordings of many studies, which used a loud auditory S_1, a clear O wave can be observed, especially in the frontal region (e.g. Borda, 1970, fig. 1; Järvilehto and Fruhstorfer, 1970, fig. 2; Low, 1969, fig. 4–15; Syndulko and Lindsley, 1974, figs. 8 and 9). Although the literature will not be reviewed here it is clear that in many instances the relative contribution of the O wave to the late CNV is *not* taken into account. For example, this is the case when experimental conditions are compared where different types of warning signals are used. In view of the present data the differences in CNV amplitude found, for example by Järvilehto and Fruhstorfer

(1970) and by Syndulko and Lindsley (1974), are explained more conveniently as an S_1 modality effect than as reflecting the functional differences claimed by them.

The same argument applies when experimental results based on different ISI durations are compared. Even small changes in ISI duration may produce relatively large differences in the degree to which the CNV amplitude, measured just before S_2 is influenced by the O waves. As the O wave is maximal at about 650 msec after S_1, the contamination of the E wave by the O wave will be relatively large with a 1 sec ISI and will become progressively smaller when longer ISI durations are used, especially with an arousing S_1.

Furthermore, the individual differences in morphology may be explained by the relative contribution of the O wave to the CNV. Thus, subjects with an A-type CNV have a more prominent O wave relative to their E wave, while in a B-type CNV no clear O wave can be observed. This notion can be illustrated by comparing our fig. 1 with fig. 6 in Donchin et al. (1972). Note the remarkable similarity between the types I and II CNV on the one hand, and the slow potential changes with an auditory and visual S_1 on the other.

Owing to the different topography of the O wave and the E wave (see fig. 3) the anterior–posterior distribution of the late CNV will shift towards more frontal regions the larger the contribution of the O wave; thus the posterior gradient will become steeper and the anterior one less steep, when shorter ISIs or more arousing S_1s are used. Although in many instances detailed information regarding the experimental situation is lacking, the contradicting results on the midline distribution might be explained by differences in the relative contribution of the O wave to the CNV amplitude. Topographical studies which found the CNV to be located more frontally or found a steeper posterior than anterior gradient, have used a 1 sec ISI and/or an auditory S_1 (Cohen, 1969; Low et al., 1966; Syndulko and Lindsley, 1974; Walter, Cooper, Aldridge, McCallum and Winter, 1964).

Similarly Donald (1973) reported a shift in midline distribution, when comparing tasks with and without motor response. CNVs were largest in amplitude over the central-parietal scalp, when subjects indicated the detections of S_2 with a manual response, but when they responded 'mentally' with no overt response, the peak of the CNV distribution shifted from central to frontal derivations. Due to the attentuation of the E wave in sensory tasks the relative contribution of the O wave to late CNV will become larger.

Acknowledgement

This study was supported by Organon N.V. (Oss). The author wishes to thank J.Th. Eernst and A.J. Krul for assistance with the analysis of the data. The computer program for the on-line analysis of the CNV was written by H. Van Doorne.

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EXPERIMENT 2

SLOW CORTICAL AND HEART RATE CORRELATES OF DISCRIMINATION PERFORMANCE[*]

ABSTRACT

Slow EEG potentials (F_z, C_z, P_z) and heart rate were recorded during the foreperiod of a reaction task which involved different levels of discrimination difficulty. A simple reaction task was compared with a selective reaction task where either an easy or a difficult discrimination was required. In general, the terminal amplitude of the CNV was not affected by task difficulty. However, a prolonged negative wave was found when the difficulty of the task was not known to the subject in advance but was indicated by S_1. Moreover, the heart-rate deceleration around S_2 was more pronounced the more difficult the discrimination required at S_2.

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[*] To be published in Acta Psychologica.

1. INTRODUCTION

Slow potential shifts (SPSs) develop in the human brain between a warning-signal (S_1) and an imperative signal (S_2), which requires a response (overt or covert). The most familiar SPS is the contingent negative variation (CNV), which was first recorded by Walter, Cooper, Aldridge, McCallum and Winter (1964). Although the CNV has been related to various mental functions, its psychological meaning is still far from clear. From the reviews (Cohen, 1974; Hillyard, 1973, 1974; McAdam, 1974; Tecce, 1972) which attempt to relate the CNV to human behavior it is evident that considerable disagreement prevails as to whether the CNV is related to perceptual processes or not. For example, Cohen (1974) maintains that the amplitude of the CNV is positively correlated with perceptual efficiency, while Hillyard (1973) regards the evidence as too meagre for this conclusion. Indeed, several studies reviewed by Gaillard (1978) show negative results in either reaction time (RT)-tasks or signal-detection tasks, although some investigators reported larger amplitudes on correct than incorrect trials in the latter kinds of tasks.

One possible reason for this is that the CNV is not a unitary phenomenon, but consists of several SPSs. In fact, recent studies which used interstimulus intervals (ISIs) of longer duration ($\geq$ 3 sec) found at least two SPSs which differ not only in their functional significance, but also in their topographical distribution (Loveless, 1975; Loveless and Sanford, 1974; Rohrbaugh, Syndulko and Lindsley, 1976; Gaillard, 1976, 1977). The first potential has the form of an inverted U-curve, which reaches its peak within 1 sec after S_1; the second potential gradually develops during the interstimulus interval (ISI), and reaches its maximum towards the end of this interval. Because of its occurrence towards the end of the ISI and its contingency to S_2 (or to the response to S_2) the second potential seems to resemble more closely the "classical CNV" obtained with short ISI; therefore, it will be called terminal CNV. The term CNV will be used in its original meaning, to denote the negative shift preceding S_2 in studies with short ISIs, which generally did not discriminate between the two negative potentials described here. The first potential will be called slow negative wave (SNW) because of its similarity to the "slow wave" observed in selective listening tasks (e.g., Squires et al., 1977). The SNW appears to be dependent on the characteristics of S_1 in much the same way as the P_{300}. Therefore, both seem to belong to a family of slow potential shifts following S_1. Similar to the SNW the P_{300} will be called slow positive wave (SPW). This notation is preferred because often a clear peak cannot be detected in these slow waves following S_1. Thus, in the present studies three slow potential shifts are distinguished: SPW, SNW and terminal CNV.

The SNW is regarded as a cortical component of the orientation reaction (Sokolov, 1963), because it is affected by the characteristics of S_1, such as modality (Gaillard, 1976), probability (Kok, 1978), duration (Klorman and Bentsen, 1975) and intensity (Loveless and Sanford, 1975). The terminal CNV appears to be determined mainly by the level of motor preparation, since it is affected by task variables such as time uncertainty, (i.e. the duration or irregularity of the ISI), muscle effort and instructions governing the trade-off between speed and accuracy, which are known to influence motor preparation (see also Gaillard, 1978; Ollman, 1977; Pachella, 1974; Sanders, 1977). This notion is supported by the remarkable similarity with regard to both morphology and topography between this terminal CNV and the readiness potential which precedes any voluntary movement (Rohrbaugh et al., 1976).

With short ISIs (e.g. 1 sec), the SNW and the terminal CNV will summate and contaminate each other (Gaillard, 1976). These potentials appear to differ in their functional role and topography, and therefore possible effects of perceptual processes may be obscured because these SPSs may be affected differently. Since almost all studies investigating the relationship between perceptual processes and the CNV have used short ISIs, the present study examined the SPSs preceding discrimination performance in an RT-task, using an ISI of 4 sec. The difficulty of the perceptual judgement at S_2 was varied by using an easy and a difficult visual discrimination task. These two conditions were compared with a simple reaction task, in which no discrimination had to be made, and with a "mixed" condition, where the subject did not know in advance whether an easy or a difficult discrimination was required.

In addition, the phasic changes in heart rate were examined because these also have been related to perceptual processes (Duncan-Johnson and Coles, 1974; Coles, 1974; Lacey and Lacey, 1974).

2. METHOD

2.1. Subjects and apparatus

The subjects were 10 male students of the University of Utrecht, who were paid for their participation. The data of two subjects were discarded because of excessive eye movements. The experiment was run in a soundproof and electrically shielded cubicle (Amplifon).

The subject was seated in a comfortable chair with a head rest; a response button was mounted on the right arm of the chair. The warning signal (S_1) consisted of a 70 dB tone (duration 80 msec), which was delivered by earphones. The frequency of the tone was either 500, 1000, or 2000 c/sec. The imperative stimulus (S_2) always consisted of two vertical bars (width 5.5 cm), which differed in length. This difference was either large (37.5 vs. 5.5 cm) or small (22.5 vs. 20 cm). The longer bar could be either on the left or on the right side of the shorter bar. The stimuli were presented on slides for 1 sec; the slides were projected through the window of the cubicle on a screen at a distance of ca. 1 m from subject's eyes. The stimuli were reasonably intense (luminance 35 cd/m^2), and the cubicle was dimly illuminated (background luminance 3.5 cd/m^2).

Ag-AgCl disk electrodes were attached to three scalp sites (F_z, C_z, P_z) and to the earlobes, which were linked for reference. To prevent the intrusion of artifacts the electrodes were chlorided prior to use and the recording sites were prepared, so that the interelectrode impedance was always less than 5 kΩ. Beckman miniature electrodes were taped to the infra- and supra-orbital ridge for the measurement of vertical eye movements. An electrode above the nose bridge served as a ground. To record the heart-rate, two ECG-electrodes were attached to the rib cage. After amplification (time-constant 6 sec) the EEG and EOG signals were recorded on magnetic tape, together with the ECG.

2.2. Procedure

A trial started with the onset of the warning tone (S_1), which was followed 4 sec later by the slide, which remained on for 1 sec. The intertrial interval (S_1-S_1) varied irregularly between 14 and 18 seconds.

The subject was asked to respond as quickly as possible with his right hand. In the simple-RT conditions the subject had to respond to every S_2 and to disregard differences in bar length. In the other conditions he had to respond only when the right bar was longer. This discrimination could be either easy or difficult (i.e., a large or a small difference in bar length).

Moreover, the easy and difficult discrimination was varied either between o within a block of trials. In the latter case the pitch of S_1 indicated whether a difficult or an easy S_2 would be presented. For half of the subjects the high pitch (2000 c/sec) indicated the difficult, and the low pitch (500 c/sec) the easy discrimination and for the other half this relationship was reversed. Finally, there was a "mixed" condition, where the subject had no prior knowledge as t which discrimination he had to make; it could be a difficult or an easy discrimination and the longer bar could be on the right or the left side. In this condition and in the simple RT condition the pitch of S_1 was always 1000 c/sec. Half of the subjects received the experimental conditions in the following order: simple RT, easy (between), difficult (between), easy/difficult (within) (twice) and finally the mixed condition. The other half received the reversed order. There were 40 trials in each of the six experimental conditions. All subjects were trained in a separate session, which included essentially the same program as the experimental session.

2.3. Data analysis

The way in which the data were analyzed, including artifact-rejection and choice of measures was based on previous studies (Gaillard, 1976, 1977).

The three EEG channels, and the EOG channel were digitized at a rate of 25 samples per sec. The analysis period started 1 sec before S_1 and ended at the onset of S_2. For each trial, the number of data points was reduced to 25 by taking the averages of successive groups of 5 points; this yielded one averaged data point per 200 msec. Thirteen of these data points were retained for further analysis (see also Fig. 2).

The computer skipped a trial when a premature RT (before S_2) occured, when a data point in the vertex channel exceeded $\pm$ 100 µV or when the EOG channel exceeded $\pm$ 200 µV (relative to the baseline data point before S_1).

After rejecting artifacts the data points were averaged across 40 trials and the following measures were taken: the amplitude of the terminal CNV (the average during the period 200 msec before S_2), slow negative wave (SNW) (average during the 600-800 msec period after S_1), and the slow positive wave (SPW), (average during the 200-400 msec period after S_1). All measures were referred to a baseline (the average during the 200 msec-period before S_1).

The phasic changes in heart rate (HR) were analyzed separately. The beat-to-beat interval was converted to DC level by a cardiotachometer. This signal was analyzed in the same way as the EEG except that the analyses started 200 msec before S_1 and ended 3200 msec after S_2. After conversion to beats per min (BPM), the data points were referred to the pre-S_1-baseline. The amplitude of the maximum deceleration was taken as a measure, since the latency of the peak deceleration varied across subjects and conditions.

3. RESULTS

3.1. RT data

A two-way analysis of variance (ANOVA) was carried out on the median RT; both main factors were highly significant: easy/difficult discrimination ($F(1/14) = 124$; $p < 0.001$) and the between/within/mixed-conditions ($F(2/14 = 17.2$; $p < 0.001$), while the interaction between these factors was not significant ($F(2/14) < 1$). A post-hoc Newman-Keuls analysis demonstrated that the difference between the mixed- and the within-condition was significant ($p < 0.01$), but that the within- and between-condition did not differ significantly.

As can be seen in Fig.1, RT was increased by 80 msec when the subject had not only to detect S_2 (simple RT), but also had to make an easy discrimination. On the average, a difference of 89 msec was found between the easy and difficult discrimination. When the subject did not know in advance the level of difficulty of S_2 the RT was increased by a further 56 msec. When S_1 indicated the type of discrimination to be made (within-conditions), the RT was increased only slightly, as compared to the between-condition.

The percentage of errors was larger ($t = 2.82$; $p < 0.05$) in the mixed-conditions (4.4%) than in the within- or between-conditions (1.2% in both conditions).

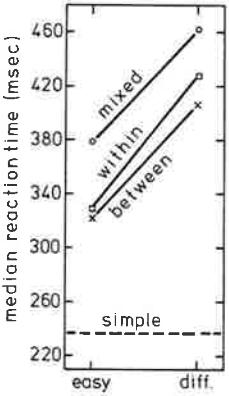

Fig. 1. The median RT for the between, within- and mixed-condition as a function of discrimination difficulty (easy/difficult). For reference the median RT is indicated by a dotted line.

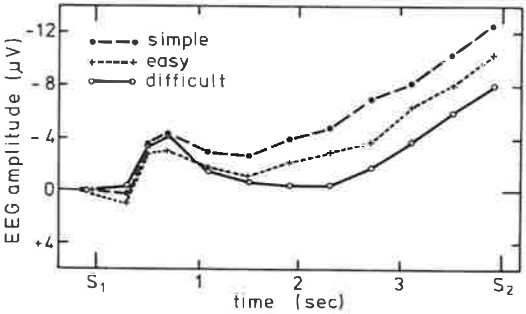

Fig. 2. The vertex amplitude for the simple RT, the easy and the difficult discrimination in the between-condition.

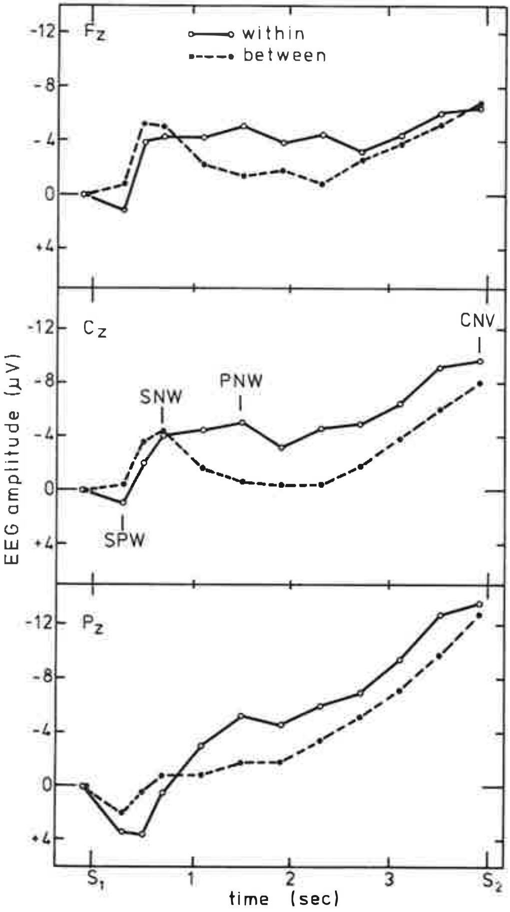

Fig. 3. The EEG-amplitude for the within- and between-blocks conditions of the difficult discrimination, separately for the frontal (F_z), vertex (C_z) and parietal (P_z) derivation.

3.2. Slow potential shifts

Fig. 2 presents the results of the vertex amplitude for the simple RT, and for the easy and difficult discrimination in the between-condition. For clarity the data of the mixed-condition are not shown because they largely coincided with those of the difficult discrimination in the between-condition. In Fig. 3 the EEG curves for the within and between condition of the difficult discrimination are compared separately for the frontal, vertex, and parietal derivation.

The amplitudes of the three measures used are presented in Table 1, separately for each condition and derivation. As in other studies (e.g. Gaillard, 1977; Rohrbaugh et al., 1976) the data show that the slow positive wave (SPW) is located parietally and the slow negative wave (SNW) frontally. However, the amplitude of the terminal CNV was largest parietally, while it was located more anteriorly in other studies. Although this shift in anterior-posterior distribution could be task-dependent, no definite statement can be made because no direct comparison is possible.

Two types of ANOVA were carried out on the three amplitudes of slow potential shifts, for each derivation: the first, a one-way ANOVA, contained the conditions simple RT, easy and difficult discrimination (varied between blocks) and the mixed condition and was aimed at evaluating the effect of task difficulty. The other was a two-way ANOVA, which included the factors of easy/difficult discrimination and between/within blocks. For both ANOVAs no significant effects were found for any of the three amplitude measures or derivations ($p > 0.05$).

As can be seen in Fig. 2, the amplitude of the terminal CNV was largest in the simple-RT and smallest in the difficult condition. This effect approached significance, and 6 of the 8 subjects had larger amplitudes in the simple RT task. Thus, the present data do not support the hypotheses that the CNV is positively related to discrimination or to task difficulty.

Although there were no task effects on the SPW and the SNW, a prolonged negativity was found following SNW when S_1 indicated the type of discrimination. As is shown for the difficult condition in Fig. 3 this prolonged negative wave (PNW) was larger in the within than in the between condition. Although less prominent this effect was also present in the easy condition. To evaluate this effect the second type ANOVA was carried out on the average EEG during the period 1400-1600 after S_1. The between/within effect was significant for all three derivation (F_z : $F(1/7) = 7.2$; $p < 0.03$; C_z : $F(1/7) = 7.5$;

Table 1. The EEG and EOG amplitudes (in μV) for the slow positive wave (SPW), slow negative wave (SNW), prolonged negative wave (PNW), the terminal amplitude of the contingent negative variation (CNV) and the peak deceleration in the heart rate (in BPM), separately for the experimental conditions.

			BETWEEN			WITHIN	
		simple RT	easy	difficult	mixed	easy	difficult
SPW	F_z	+ 1.2	+ 2.4	- 0.8	+ 3.6	+ 2.8	+ 1.2
	C_z	+ 0.2	+ 1.0	- 0.4	+ 2.8	+ 2.2	+ 1.0
	P_z	+ 2.8	+ 3.4	+ 2.0	+ 4.6	+ 4.4	+ 3.4
	EOG	+ 2.0	+ 8.0	+ 2.0	+ 2.0	+ 6.0	+ 6.0
SNW	F_z	- 3.8	- 1.2	- 5.0	- 2.4	- 4.2	- 4.2
	C_z	- 4.4	- 3.0	- 4.4	- 3.2	- 3.2	- 4.0
	P_z	- 0.2	+ 0.8	- 0.8	+ 0.8	+ 1.0	+ 0.4
	EOG	+ 6.0	+14.0	+ 6.0	+ 8.0	+14.0	+16.0
PNW	F_z	- 2.4	+ 0.6	- 1.4	- 0.8	- 4.0	- 5.0
	C_z	- 2.8	- 1.2	- 0.6	- 1.2	- 3.4	- 5.0
	P_z	- 2.2	- 1.2	- 1.8	- 1.0	- 3.8	- 5.2
	EOG	+ 2.0	+10.0	+ 6.0	+ 4.0	+ 8.0	+ 8.0
CNV	F_z	- 7.6	- 5.8	- 6.8	- 5.0	- 6.8	- 6.4
	C_z	-12.6	-10.4	- 8.0	- 8.4	-10.2	- 9.4
	P_z	-12.8	-14.0	-12.8	-11.0	-14.4	-13.6
	EOG	+ 4.0	+ 6.0	+ 4.0	+ 2.0	+ 4.0	+14.0
PEAK DECELERATION		- 2.80	- 2.80	- 3.89	- 3.02	- 3.07	- 3.38

$p < 0.03$ and P_z : $F(1/7) = 6.9$; $p < 0.04$). For the parietal derivation the difference between an easy and difficult discrimination was also significant ($F(1/7) = 6.0$; $p < 0.04$).

3.3. Heart-rate responses

The curves presented in Fig. 4 were shifted backwards to correct for the delay of the cardiotachometer signal. Since the baseline level did not vary systematically across experimental conditions (range: 0.76 BPM) the mean inter-beat interval (i.e. 830 msec) could be taken as an estimate of this delay.

In all experimental conditions a deceleration in heart rate was found which reached it's largest amplitude about the time of the presentation of S_2. However, the expected acceleration during the first part of the S_1-S_2 interval was negligible. This might be due to the slow development of HR-responses, together with the relatively short interval used; that is, before the acceleration could reach its peak the deceleration preceding S_2 had already developed strongly (see Lacey and Lacey, 1974).

It can be seen from Fig. 4 that the deceleration was largest if the subject anticipated a difficult discrimination. In the latter condition the return to baseline was also slower. These effects were most pronounced in the between-condition. The simple RT condition deviated grossly from the other conditions in that the peak deceleration was followed by a much quicker return to baseline level. Averages across subjects of the peak deceleration are

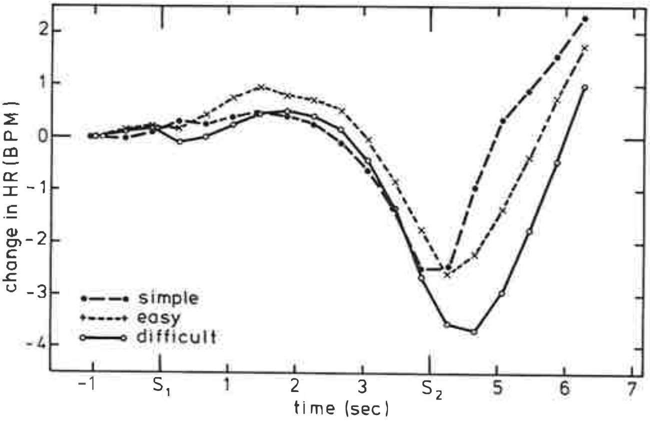

Fig. 4. Change in HR as a function of discrimination difficulty, for the within- and between-blocks conditions.

shown in Table 1.

The same types of ANOVA as used for the EEG data were carried out on the peak deceleration. The second type of ANOVA revealed a significant difference between the easy and difficult discrimination ($F(1/7) = 8.47$; $p < 0.02$).

4. DISCUSSION

Although large and significant differences in RT were found, the amplitude of the terminal CNV was not influenced by the kind of discrimination required at S_2; it did not matter whether the subject anticipated a difficult or an easy discrimination. Since largest amplitudes were observed in the simple-RT condition, where no discrimination was required at all (see also Fig. 2) the present data do not support the hypothesis that the CNV is positively related to perceptual efficiency.

Although not significant, the terminal CNV tended to be even smaller in the more demanding conditions, i.e., difficult discrimination and mixed conditions as compared to simple-RT. Poon et al. (1976) also obtained attenuated amplitudes in a complex RT task ("same-different" responses) as compared to a simple RT-task and similar reductions in CNV were obtained by Roth et al. (1975, 1976) in a memory retrieval task where the size of the memory-set was varied.

These results were explained by the authors as a "ceiling"-effect (Poon et al.) or as a distraction-effect (Roth et al.). An alternative explanation can be given in terms of changes in the level of motor preparation. It may be that under more "difficult" conditions subjects prepare less intensively for the motor response, and therefore the CNV is decreased and the RT increased. When subjects prepare maximally in a choice RT task, almost any stimulus will trigger a response, and consequently they run the risk of making too many errors.

In any event, in line with the findings described in the introduction (see also Gaillard, 1978),the present results do not support the hypothesis that the CNV is associated with the ease of perceptual sensitivity.

Accordingly, these results suggest that the effects of instruction governing the trade-off between speed and accuracy (Gaillard, 1977; Loveless and Sanford, 1974) are mediated by changes in motor preparation. This view is consistent with the fact that practically no CNV is observed in detection tasks where the subject only processes S_2 without making a motor response (Gaillard, 1977; Loveless, 1975; Näätänen et al., 1977; Syndulko and Lindsley, 1977).

In the present study the SNW was only marginally influenced by the discrimination condition. It had been expected that the amplitude of the SNW would be larger when S_1 contained information, but this effect was found not in SNW, but later, ca. 1.5 sec after S_1. The prolonged negativity in the within conditions was especially pronounced when S_1 indicated a difficult discrimination. This effect is very similar to that found by Simons and Lang (1976), not only with regard to the form and latency of this negativity, but also the condition under which it was found. However, in their study the negativity was obtained after the delivery of the stimulus to be discriminated. They interpreted the enhanced slow negativity as "continued attention to the difficult stimulus" (op.cit. p. 63).

In the present study the prolonged negativity is also thought of as reflecting central processing associated with the discrimination to be made at S_2. It is assumed that varying the type of discrimination (easy/difficult) from trial to trial forces the subject to build up a template or neuronal model. This would facilitate stimulus-processing at S_2 and consequently accelerate the reaction process. That some sort of pre-processing takes place is illustrated by the significant increase in RT (ca. 40 msec), when the subject does not know in advance which discrimination will be presented.

In most neurophysiological theories (Pribram and McGuiness, 1975; Sokolov, 1960) there is a close relationship between the orientation reaction and a neuronal model or template. Therefore the present idea of the significance of the prolonged negative wave is congruent with the view that the SNW is a component of the orientation reaction. According to Germana (1968), the orientation reaction is not only a "what is it"-response, but also a "what is to be done"-response. It could be hypothesized that the first aspect is reflected in the SNW and the second aspect in the prolonged negative wave (PNW).

The way in which the orientation reaction is reflected in the HR depends largely on the stimulus characteristics (Graham and Clifton, 1966). In general it can be stated that an acceleration will be observed if the subject rejects environmental information, while HR deceleration accompanies and facilitates the intake of stimulus information (Lacey and Lacey, 1974).

The effects in the present study of discrimination difficulty on the decelerative HR-response are similar to those of Duncan-Johnson and Coles (1974), who used a similar task. These findings may be regarded as support for Lacey's intake-rejection hypothesis, in the sense that a larger deceleration accompanied the more difficult discrimination, where it can be assumed that the intake of environmental input is more critical. However, these results might be contaminated by the motor response, since the peak deceleration occured mostly after S_2. Thus the effect on HR-deceleration might reflect a difference in response latency instead of discrimination difficulty per se. However, a similar effect of easy and difficult discrimination was found in a signal-detection task (Coles, 1974), where the contamination by motor activity is assumed to be minimal.

To examine the psychological significance of the physiological changes during the S_1-S_2 interval, the experimental paradigms used should be classified into general categories (c.f. Hillyard, 1973). The introduction of a warning signal (S_1) enables the subject to prepare for 1) the perception of S_2 (stimulus anticipation), 2) the decision which links S_2 to some kind of overt or covert reaction (decision anticipation), or 3) the execution of a motor response (motor preparation). A physiological measure reflects one of these preparatory mechanisms if it is specifically affected by task variables belonging to that category. For example, a measure reflects decision load if it is influenced by the complexity of the relationship between stimulus and response, e.g., stimulus-response compatibility or the number of stimulus alternatives.

In the present study the phasic changes in HR seem to be connected with stimulus anticipation, in that they are affected by discrimination difficulty. The terminal CNV reflects the level of motor preparation, because it is influenced by such task variables as time uncertainty (ISI duration or variability) and the speed-accuracy trade-off. With regard to the SPW, SNW and PNW the evidence available at this moment suggests that these SPSs following S_1 are unrelated to the three preparatory processes mentioned above, but are affected by the physical characteristics and the information content of S_1.

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EXPERIMENT 3

THE TERMINAL CNV AND STIMULUS DISCRIMINABILITY IN MOTOR AND IN SENSORY TASKS

ABSTRACT

When motor and sensory tasks are compared, it is shown that the terminal CNV is attenuated when the response to S_2 is delayed. Moreover, larger amplitudes preceded a difficult rather than an easy discrimination. In addition, no differences were found in the signal-detection task between correct and incorrect reactions. On these grounds it is concluded that the terminal CNV is not positively related to perceptual sensitivity.

1. INTRODUCTION

From reviews of the literature (Tecce, 1972; Hillyard, 1973) it is evident that considerable disagreement exists with regard to the underlying process or mechanism of the CNV. One of the earliest questions asked was whether the occurrence of the CNV is determined by a motor act at S_2. Walter (1964) showed that much smaller CNV amplitudes were obtained if no motor response was required at S_2. Moreover, CNVs were found in signal detection tasks (Cohen, 1973; Hillyard, 1969; Hillyard et al., 1971) where no stress was laid on the speed of the response. Although the CNVs obtained in these studies were of a fairly low amplitude they were still present.

The results of recent investigations (Loveless and Sanford, 1974; Gaillard, 1976) suggest that more than one slow potential shift can be distinguished during the S_1 - S_2 interval, provided that the interstimulus interval (ISI) lasts at least 3 sec. The first potential, the slow negative wave (SNW), is frontally dominant and reaches its maximum amplitude at about 750 msec after S_1 and it is affected by the stimulus characteristics (Gaillard, 1976; Klorman and Bentsen, 1975; Loveless and Sanford, 1975). The second potential reaches its largest amplitude towards the end of the interval and is called terminal CNV. This label is chosen because this wave resembles closely to the classical CNV and reaches its largest amplitude towards the termination of the ISI. The terminal CNV is most prominent at central regions, over the motor cortex.

Loveless (1975) showed that with ISIs of 4 and 6 sec the terminal CNV was practically absent in a signal detection task, although the SNW ("O-wave" in his terminology) was present in all experimental conditions. In addition, he did not find a relationship between the response categories, i.e. hits, false alarms, correct rejections and misses, on the one hand, and the amplitude of the terminal CNV on the other. This suggests that the terminal CNV is not related to perceptual sensitivity or to sensory mechanisms active in the early stages of information processing.

This finding is contrary to the results of studies by Hillyard and coworkers (1969, 1971), who found larger CNV amplitudes on correct trials in an auditory signal detection task (ISIs respectively 2 and 1 sec). It is very possible that the observed relationship in these studies is in fact due to the presence of the SNW at the end of the ISI. Another explanation for the contrary results may be the fact that the signal detection task used by Loveless was relatively easy (see Loveless, 1975).

In the present study, therefore, the difficulty of target detection was varied. To investigate the dependence of the CNV on a fast motor response sensory and motor tasks were compared. In the sensory tasks the subject was required to delay his response by at least one second, while the stress was on the accuracy of perceiving the stimulus. In the motor tasks the subject was instructed to give a motor response as quickly as possible. Another factor which might be responsible for the small, or almost absent, terminal CNVs in signal detection tasks is the absence of time stress. On the other hand time stress is always present in RT-tasks. Therefore the exposure duration of the stimulus was also varied. It is expected that with short exposures the subject will have to prepare more intensively in order to be able to detect the signal.

2. METHODS

2.1. Subjects and apparatus

Eight male subjects participated in the experimental sessions on payment of a fixed hourly amount. The subjects were tested dimly illuminated (1.7 cd/m^2), soundproof and electrically shielded cubicle (amplifon). The subject was seated in a chair with adjustable head rest. A response key was mounted on the right arm of the chair.

The auditory warning signal was a 1000 Hz tone of 100 msec duration (intensity 70 dB), embedded in white noise (35 dB). S_2 was always a circle of light, which was projected on a screen at a distance of 1 m from the subject's eyes. The circle (thickness 3 mm and 17 cm in diameter) was either concentric or eccentric relative to a fixation point in the center of the screen. This fixation light, which was 6 mm in diameter, was continuously displayed. S_2 was either presented for 80 msec or 500 msec (rise and fall times of the shutter were 10 msec). After stimulus presentation the image of the circle was immediately masked by a black and white random noise pattern. The total presentation time of S_2 plus mask was always 1 second, so that the mask was on for either 920 or 500 msec.

The EEG was recorded with Ag-AgCl disk electrodes from the midline positions F_z, C_z, P_z and O_z. Electrodes attached to the earlobes were linked and served as the reference. The interelectrode resistance was always kept below 5 kohm. Beckman miniature electrodes were taped to the infra- and supraorbital ridge of the right eye for the measurement of vertical eye movements. A ground electrode was attached to the forehead, just above the nosebridge. The ECG was recorded from the rib cage with two electrodes, though those results will not be reported in this paper.

After amplification (time constant 20 sec; high frequency cut off 32 Hz) the EEG and EOG signals were recorded on magnetic tape.

2.2. Tasks

In all experimental conditions the circle was projected in 50% of the trials with the fixation light as its midpoint (concentric circle). In the other half of the trials the circle was shifted upward relative to that midpoint (eccentric circle). The eccentric circle was always defined as the target stimulus (signal). Stimulus discriminability was varied by changing the magnitude of the upward shift.

Both the reaction time (RT-) task and the signal detection (SD-) task consisted of 4 experimental conditions in which the level of stimulus discriminability and the exposure duration were varied in a factorial way: difficult discrimination - short exposure duration (difficult - short), difficult discrimination - long exposure duration (difficult - long), easy discrimination - short exposure duration (easy - short) and easy discrimination - long exposure duration (easy - long).

The magnitudes of the upward shift for the easy and difficult discriminations in the SD-task were determined in the training session and were chosen such that the subject performed just better than by chance in the difficult - short condition (shift about 3 mm) and made only a few errors in the easy - long condition (shift about 9 mm). Of course the other two conditions, difficult - long and easy - short produced intermediate error rates.

Since requiring fast RTs to the difficult discrimination level as used in the SD-task seemed unrealistic, the easy discrimination level of the SD-task was used as the difficult discrimination level in the RT-task. In the easy discrimination conditions of the RT-task, the circle was shifted so that it touched the fixation light. Apart from the delayed response instruction this was the only difference for the SD-task. The same exposure durations were used (80 and 500 msec).

2.3. Procedure

A trial started with the onset of the auditory warning signal which was followed four sec later by the presentation of S_2. The intertrial interval varied irregularly between 11 and 15 sec. The subject was instructed to fixate on the fixation light and to blink or move his eyes for a few seconds after the response was given. To get a stable task performance the subject was trained on one day and then tested on two other days. The order of experimental conditions was balanced with the restriction that the RT-tasks were carried out one one of the two days and the SD-tasks on the other. Each experimental condition consisted of 150 trials, which were divided into 3 blocks of 50.

In the SD-task the subject was instructed to press a button if he thought the target stimulus had been presented, but he had to wait until the noise pattern stopped (i.e. 1 sec after S_1). He was told that the target stimulus would be presented in 50 % of the trials. The subject received a bonus according to a symmetrical pay-off matrix. He received one cent for each hit and correct rejection and lost one cent for each false alarm and miss. After a block of 50 trials he received feedback about his performance.

The RT-task resembled the SD-task closely, except that the subject was instructed to react as quickly as possible to the target stimulus (i.e., a selective RT-task). The same pay-off matrix was used, except that if the subject gave a correct reaction which was shorter than 300 msec, he received 2 cents for it. During this task the subject also received feedback after 50 trials. trials.

2.4. Data Analysis

The way in which the data were analyzed, including artifact rejection and choice of measures, was based on previous studies (Gaillard, 1976, 1977). The four EEG channels, the EOG and the ECG (after converting the R-R intervals to DC level by a cardiotachometer) were digitized at a rate of 25 samples per sec. The analysis period started 1 sec before S_1 and ended at the onset of S_2. For each trial the number of data-points was reduced to 25 by taking the averages of successive groups of 5 points; this yielded one averaged data-point per 200 msec. Thirteen of these data-points were retained for further analysis.

The computer skipped a trial when any data-point in the vertex channel exceeded $\pm$ 100 μV or when the EOG channel exceeded $\pm$ 200 μV (relative to the baseline data-point before S_1). After artifact rejection the data-points were averaged across trials for each condition. Moreover, from the SD-task data-points were averaged separately for the response categories: hits, false alarms, correct rejections and misses.

The following measures were taken: the terminal CNV (the average EEG during the 200 msec before S_2), the slow negative wave (SNW) (average EEG during the 600 - 800 msec period after S_1) and the slow positive wave (SPW) (average EEG during the 200 - 400 msec period after S_1). All measures were referred to a baseline (the average during the 200 msec period before S_1).

3. RESULTS

3.1. Performance

It is evident from Table 1 that the subjects behaved very well according to their instructions in the different tasks. The response latencies are longer than 1 sec in the SD-task, whereas in the RT conditions they were between 310 and 450 msec.

The results concerning response latencies for correct responses and errors (hits and false alarms) corroborate the findings in the literature. The RT for errors in the RT-task is on the average shorter (60 msec) compared to the RT for correct reactions ($t(7) = 3.17$; $p < 0.01$) (see Pew, 1969). The response latencies for false alarms in the SD-task were on the average 200 msec longer compared to the response latencies for hits ($t(7) = 3.25$; $p < 0.01$). Parasuraman and Davies (1975, 1976) found differences of the same magnitude. However, in their studies the overall response latency was shorter, because their subjects were not instructed to delay their responses. It seems to be the case that the subjects not only delayed their response but also their decision.

A two-way ANOVA (discrimination difficulty, exposure duration) revealed that both factors had a significant effect on d' (discrimination difficulty: $F(1/7) = 46.7$, $p < 0.01$ and exposure duration: $F(1/7) = 23.7$; $p < 0.01$). Log β was only influenced by exposure duration ($F(1/7) = 5.5$; $p < 0.05$). The same type of ANOVA was carried out on the RTs and error percentages in the RT-task. RT (weighted mean RT for hits and false alarms) was significantly influenced only by the level of discrimination difficulty ($F(1/7) = 5.35$; $p < 0.05$), whereas percentage of error was affected by both factors (discrimination difficulty: $F(1/7) = 46.7$; $p < 0.01$ and exposure duration: $F(1/7) = 23.7$; $p < 0.01$).

3.2. Slow potential shifts

A factorial ANOVA (SD/RT x discrimination difficulty x exposure duration) was carried out on the SPW, SNW and the terminal CNV.

The amplitude of the SPW was influenced by the type of task, i.e. there is more positivity following S_1 in the RT-task than in the SD-task. This difference in positivity is only significant at P_z ($F(1/7) = 7.6$; $p < 0.03$) and O_z ($F(1/7) = 7.5$; $p < 0.03$). This effect is still present 600 - 800 msec after

S_1 at P_z ($F(1/7) = 6.9$; $p < 0.04$) as well as O_z ($F(1/7) = 8.6$; $p < 0.03$). The SNW, which was hardly present in this experiment, was not affected by any factor. The absence of the SNW is probably due to the fact that the intensity of S_1 was attenuated by the background noise (see also Loveless and Sanford, 1975).

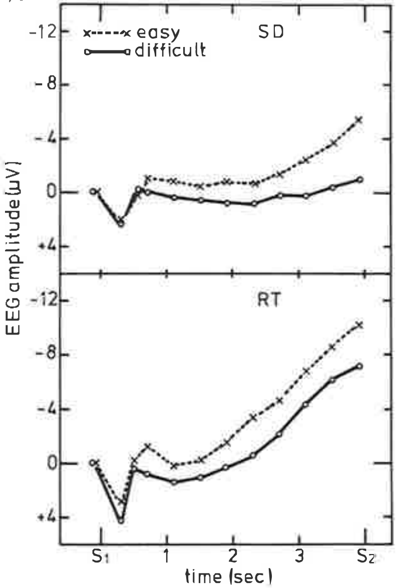

Fig. 1. The vertex slow potential shifts averaged across subjects and short and long exposure duration, separately for the easy and difficult discrimination conditions in the SD- and RT-task.

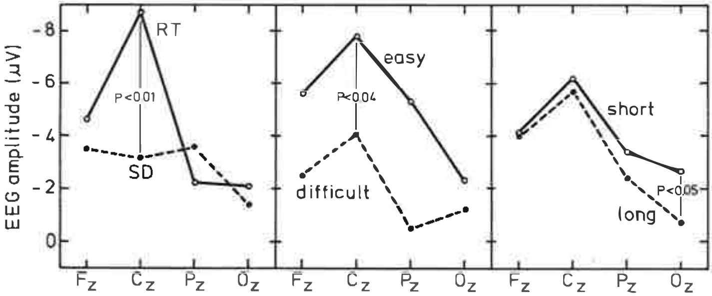

Fig. 2. The midline distribution of the terminal CNV for the RT- and SD-task, for easy and difficult discrimination, and for short and long exposure durations. The amplitude is averaged across the non-involved experimental conditions. Significant effects are indicated by P-values.

Table 1. The means of d' and log β in the SD-task, the percentage of errors in the RT-task and the average response latencies for hits and false alarms (FA) in all experimental conditions.

		DIFFICULT		EASY	
		SHORT	LONG	SHORT	LONG
SD-TASK	RT (HIT)	1388	1296	1357	1375
	RT (FA)	1517	1591	1508	1597
	d'	1.43	2.81	2.09	3.97
	log β	.22	.59	.32	.40
RT-TASK	RT (HIT)	437	486	390	377
	RT (FA)	446	369	311	322
	% errors	32	14	15	6

Table 2. The means (x) and standard deviations (SD) of the terminal CNV amplitudes (μVs) in the four SD tasks, separately for the three derivations and the three response categories. The T-values for the differences between hits and errors, and between correct rejections and errors are also given. The data are based on 5 subjects in the easy - long condition, and on 7 subjects in the other conditions.

		hits			correct rejections			errors	
		x	SD	t	x	SD	t	x	SD
difficult/ short	F_z	- 2.1	12.8	0.47	- 1.0	3.7	0.06	-0.7	11.4
	C_z	- 2.0	8.8	1.72	- 1.5	4.6	1.38	-5.1	6.9
	P_z	- 7.2	14.0	0.58	- 2.7	8.9	0.77	-4.9	8.0
difficult/ long	F_z	- 1.8	12.3	0.88	+ 4.6	12.8	0.15	-3.9	12.0
	C_z	0.0	8.0	0.31	+ 1.0	5.9	0.53	-1.5	13.2
	P_z	- 4.7	5.2	1.49	- 4.9	3.9	1.88	-4.1	12.4
easy/ short	F_z	- 7.4	8.0	1.57	- 4.8	12.1	0.35	-3.0	8.3
	C_z	- 7.7	4.5	2.60*	- 3.9	7.7	0.34	-2.4	5.1
	P_z	-10.5	5.6	0.33	- 3.4	8.4	1.23	-8.9	12.9
easy/ long	F_z	- 1.9	5.7	1.03	- 7.2	11.4	2.19*	-3.3	13.9
	C_z	- 2.2	3.1	1.29	- 6.4	6.6	2.18*	+5.1	14.9
	P_z	- 2.7	6.7	0.06	- 1.8	10.0	0.07	-2.2	15.9

* $p < 0.05$

Fig, 1 gives the averages from C_z separately for the difficult and easy discrimination condition in the RT- and SD-task. Because the exposure durations had no effect on any measure at C_z the curves were collapsed across the long and short exposure conditions. The amplitude of the terminal CNV was significantly influenced by SD/RT ($F(1/7) = 12.4$; $p < 0.01$) and the level of discrimination difficulty ($F(1/7) = 6.5$; $p < 0.04$). The terminal CNV is smallest in the condition in which the most difficult discrimination has to be made and largest in the condition where the discrimination was easy and fast responses had to be given. The observed effects were only statistically significant at C_z (see Fig. 2).

In addition, there was a slight, significant effect of exposure duration at O_z ($F(1/7) = 4.8$; $p < 0.06$) (see Fig. 2). The EOG was not influenced by any factor, which had significant effects on the EEG measures.

In Fig. 2 the topographical distribution of the terminal CNV is shown. The statistically significant differences are indicated in the figure. In the SD/RT comparison the largest difference is observed at C_z. The curves of the easy and difficult discrimination run almost parallel, except for O_z. The same is true for the short/long comparison. In all conditions (except for the SD-task) the decline in amplitude is steeper from C_z to P_z than from C_z to F_z.

To investigate the relationship between the CNV and perceptual sensitivity the EEG data obtained in the SD-task were sorted on a single trial basis into the following response categories: hits, false alarms, correct rejections and misses. If there exists a positive relationship between the accuracy of perceptual processes and the terminal CNV, this should show up when errors are compared to correct responses. Table 2 summarizes the results. The differences between the response categories are marginal and unreliable (there were large differences between subjects in this respect). No statistically significant differences were found between either correct rejections and errors or between hits and errors (see Table 2).

4. DISCUSSION

The results of the present experiment suggest that the terminal CNV is mainly dependent upon the requirement of a speeded response. Small terminal CNV amplitudes were found when the subject was instructed to delay his response (SD-task). This is in line with the results of Näätänen et al. (1977), and of Syndulko and Lindsley (1977). However, in their studies short ISIs (1 sec) were used, so that it could not be observed which wave (the terminal

CNV or the SNW) was influenced by delaying the response.

Besides the type-of-task effect the terminal CNV was affected by discrimination difficulty. The terminal CNV was found to be larger for easier discriminations. Again, this can be attributed to a shortening of the RT in the easy RT-tasks. Surprisingly, the same effect on the amplitude of the terminal CNV was found in the SD-task. This effect can be explained by assuming that it is more difficult to suppress preparatory motor activity when a relatively quick response can be given. In Experiment 6 it will be shown that EMG-activity in the forearm muscles is present before S_2, even when a delayed response is required. Probably the amount of preparatory motor activity and hence the amplitude of the terminal CNV also differed in the conditions considered here.

The analysis according to signal detection categories did not reveal any systematic relationship between the terminal CNV and perceptual sensitivity. This is in contrast to Cohen (1974), who maintains that the amplitude of the CNV is positively correlated with perceptual sensitivity. In addition, the negative results suggest that the relationship found by Hillyard and co-workers (1969, 1971) can be attributed to the SNW, which will contribute to the CNV at the end of the S_1 - S_2 interval when short ISIs are used. This is in agreement with results of Loveless (1975), who found that the index of perceptual sensitivity (d') was correlated with the time-course of the SNW ("O-wave"). In this line of reasoning a positive relationship is not to be expected if the SNW is almost absent, as in the case in the present experiment.

However, an exception has to be made here for the occipital data (O_z): larger terminal amplitudes were found when S_2 was presented for a short time, compared with a long one. It is quite possible that this sensory CNV is limited to the visual modality only. The recent results by Simson et al (1977) are in agreement with this view: in a detection task (ISI 1 sec) a late negative shift was found, with a parieto-occipital dominance, when S_2 was visual but not when it was auditory. Also Syndulko and Lindsley (1977) and Gaillard and Näätänen (1976) provide evidence for an occipital CNV preceding the detection of visual stimuli.

The results regarding the terminal CNV can best be summarized by stating that it is a cortical correlate of motor preparation, while its amplitude gives an index of the subject's planned response speed.

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EXPERIMENT 4

THE LATE CNV WAVE: PREPARATION VERSUS EXPECTANCY*

ABSTRACT

Slow EEG potentials were recorded from different sites along the midline (F_z, C_z, P_z) in the S_1-S_2 interval of a reaction time task. The effects of expectancy on the contingent negative variation (CNV) were investigated by varying the probability that S_2 would be presented. This probability which was indicated by S_1, was either 0.9, 0.5, or 0.0. This was done under instructions governing the trade-off between speed and accuracy. The combined effects of S_2 probability and instructions support the view that the early component of the CNV is a cortical component of the orientation reaction, whereas the late component is mainly determined by the level of motor preparation. The topographical distribution of the early CNV was more anterior than that of the late CNV, which corroborates earlier results.

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*Published in Psychophysiology, 14 (1977): 563-568.

Originally the CNV was regarded as a correlate of expectancy and therefore called "Expectancy Wave" (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). However, relatively little research has been done on the relationship between CNV and expectancy. Most studies used a reaction time (RT) task in which the expectancy of the subject was manipulated by varying the probability that S_2 would occur (e.g. Järvilehto & Mäntysalo, 1976; Karrer, Kohn, & Ivins, 1973). The results of these studies are difficult to evaluate, since the effects of expectancy and motor preparation are confounded: both increase with the probability of S_2.

In an earlier study (Näätänen, Gaillard, & Mäntysalo, 1975), an attempt was made to separate expectancy and preparation, by investigating the effect of S_2 probability on the CNV under two physically identical conditions. In one condition the subject had to react to S_2 as quickly as possible and in the other the subject had to delay his response by approximately 1 sec. In both conditions S_2 was an auditory signal, which was embedded in noise and was difficult to detect. The probability of S_2 had a significant effect on the vertex late CNV, but only when the subjects had to react quickly, suggesting that the CNV is related to motor preparation rather than to expectancy. However, the evaluation of the effect of S_2 probability was hampered by the small CNV amplitudes obtained, especially when the reaction to S_2 was delayed. It was suggested that this was due to the lack of motor preparation in the delayed response-condition and that the difficulty of detecting S_2 suppressed motor preparation when a fast response was required.

In the present study the interaction between expectancy and motor preparation will be investigated with easily detectable stimuli. To avoid possible changes in general activation between the expectancy conditions, the S_2-probability indicated by S_1 was varied from trial-to-trial. Motor preparation was varied by instructions governing speed-accuracy trade-off (see Loveless & Sanford, 1974) and by comparing these conditions with a condition in which the subject had to delay his reaction. Although there is still some uncertainty as to whether stimulus processing is also involved, recent theories (Ollman, in press; Pachella, 1974) assume that speed-accuracy mainly influences the level of motor preparation or, at least, the willingness of the subject to react.

Methods

Subjects and Apparatus

The subjects were 14 male university students, who were paid for their participation in the experiment. The data of 2 subjects were discarded for having too many eye movement artifacts.

The subject was seated in a comfortable chair, which also provided neck- and arm-rest. Both S_1 and S_2 were auditory signals with a duration of 80 msec. S_1 consisted of a 1400, 1000, or 714 Hz tone (intensity 70 dB), while S_2 always was a 1000 Hz tone (intensity 40 dB). A dim

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The author wishes to thank J. Th. Eernst and A. J. Krul for assistance with the analysis of the data.

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fixation light was mounted in front of the subject at a distance of about 1.5 m. Silver-silver disk electrodes were attached with collodion to three scalp sites (F_z, C_z, P_z) and to both ears, which were linked for reference. To prevent the intrusion of artifacts the electrodes were carefully chlorided prior to use and the recording sides were prepared well, so that the interelectrode impedance was always less than 5 KΩ. Beckman miniature electrodes were taped to the forehead, 2 cm above the nose bridge (ground) and to the right supra-and infra-orbital ridge to record the vertical EOG.

The timing of the signals and measurement of RT (in msec) was done by the PSARP equipment (Van Doorne & Sanders, 1968). This equipment also produced a label containing the trial number, the experimental condition, and the corresponding RT. After AC amplification (time constant 6 sec), the EEG and EOG signals were stored on magnetic tape together with their corresponding labels.

Task

Expectancy was manipulated by changing the relative frequency of the occurrence of S_2. The data of a pilot experiment using five probability levels (1.0, 0.8, 0.5, 0.2, 0.0) and also the results of earlier studies (Järvilehto & Mäntysalo, 1976; Karrer et al., 1973; Näätänen et al., 1975) suggested that expectancy operationalized by S_2-probability affects the CNV only to a small extent. Therefore in the present study three extreme probabilities were chosen: "High," "Medium," and "Zero" probability ($p=0.9$, 0.5, or 0.0). A probability of 0.9 instead of 1.0 was chosen because without catch-trials subjects tend to synchronize their reactions with S_2; in this situation fast reactions can be produced even without a high degree of motor preparation (for a demonstration see Näätänen & Gaillard, 1974).

To avoid changes in general motivation between conditions the three probability conditions were varied within blocks; the tone-pitch of S_1 indicated the probability of occurrence of S_2. To avoid stimulus-specific effects, the three tone frequencies were balanced between subjects; for half of the subjects the high probability condition was connected to the 1400 Hz tone, and for the other half to the 714 Hz tone, etc.

The experimental conditions were run under three instructions: "speed," "accuracy," and "detection." Under *speed* instruction the subject was required to react as quickly as possible, even at the cost of some errors. Under *accuracy* instruction the subject was also asked to react as quickly as possible, but to avoid any premature reactions or catch-trial errors. Under *detection* instruction the subject was asked to postpone his reaction by approximately 1 sec. The three instructions were given in balanced order; half of the subjects received accuracy, detection, speed instructions in this order and the other half in the reversed order. In the experimental session two blocks of 45 trials (15 trials per condition) were run under each instruction. Before the two blocks the instruction was repeated and 10–20 warming-up trials were given, during which the subject received feedback from his performance.

A trial started with the onset of a dim fixation light, which remained on until the offset of S_2. The interval between the onset of the fixation stimulus (FS) and S_1, and between S_1 and S_2 were both 3 sec. To avoid eye movements, the subject was instructed to fixate FS as long as it was on, and to blink thereafter. The intertrial interval was varied irregularly between 14 and 18 sec.

In a separate session subjects practiced controlling their eye movements and RT performance. During this session the subject received practically the same program as in the experimental session.

Data Analysis

The three EEG and the EOG signals were analyzed by a LAB8 computer, in the same way as in an earlier study (Gaillard, 1976). The analysis period was 7 sec, starting 1 sec before the onset of FS (sampling rate 25 points/sec). For each trial, the number of data points were reduced to 35 by taking the average of successive groups of five points; this yielded one average data point per 200 msec. Because of memory limitations only the most relevant data points were retained for further analysis (see also Fig. 2).

The computer skipped a trial when a premature RT (before S_2) occurred, when any of the data points of the vertex channel exceeded ±100 μV, or when the EOG channel exceeded a preset level. To evaluate this procedure two levels were used, 100 and 500 μV. Due to the more abrupt development of eye blinks, the averaging of 5 successive samples will attenuate blinks more than eye movements. Consequently, the detection of eye movement artifacts is favored as compared to eye blinks; this is in line with the observation (e.g. Weerts & Lang, 1973) that the ratio between EOG amplitude and EEG artifact is larger for eye movements than for eye blinks.

Since blocks did not have an effect, trials were averaged in sets of 25, reserving 5 trials for artifact-rejection. From the averaged data points the following measures were obtained for each derivation (including the EOG): the early CNV amplitude (average activity in the period 600–800 msec after S_1), late CNV amplitude (average activity in the 200 msec preceding S_2). Both measures were related to a baseline (average activity in the 200 msec before S_1). In the same way these measures were taken in the FS–S_1 interval, referred to a baseline before FS. Additionally, the average EEG activity in the period 400–600 msec after S_1 was taken to investigate the positive wave following S_1 in the parietal derivation. Analyses of variance (ANOVAs) were carried out on the above measures and on the mean RT, using a two-factor design (S_2-probability × instructions). The effect of the two criterion-levels was tested separately. All effects mentioned below were significant at the .05 level or beyond.

Results

Fig. 1 gives the vertex potential averaged across subjects under speed, accuracy, and detection instruction in the high-probability condition. The average EPs to FS are followed by a modest early CNV of less than 2 μV, while no slow potential changes are observed at the end of the FS–S_1 interval. Although both the EPs and the early CNV to FS were somewhat larger under speed and accuracy as

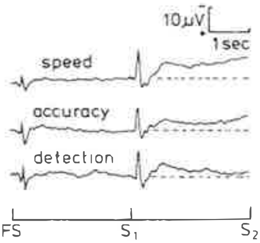

Fig. 1. Vertex potentials averaged over all subjects under speed, accuracy, and detection instruction in the high-probability condition. FS indicates the onset of the fixation light. The duration of the interval between FS and S_1 and S_2 are both 3 sec.

compared to the detection instruction, no systematic effects of either instructions or S_2-probability were found. Thus the task variables did not systematically affect the EEG potentials recorded before S_1. Also the EPs to S_1 were significantly influenced by neither instructions nor conditions. The slow potential changes in the S_1–S_2 interval were clearly affected by instructions; under speed and less so under accuracy instruction an early and late CNV component can be observed, while under detection instruction only the early component is present.

In the analysis (see **Methods**) of the slow potential changes, 1% of the trials were skipped for either excessive EEG activity or premature RTs. Additionally, 3.5% of the trials were rejected for eye movements under the lax criterion and 10% under the strict criterion. Table 1 gives the EEG and EOG amplitudes for the early and late CNV measures for the lax and strict criteria. The criterion level had practically no influence on the early CNV and a modest effect on the late CNV. It is remarkable that this effect is the same for the three derivations. Because of its proximity to the eyes a larger effect was expected in the frontal derivation. To investigate the influence of the rejection procedure on the early and late CNV, the two criterion levels were entered into an ANOVA, together with S_2-probability and instructions. Although a main effect of criterion level was found on the late CNV for the frontal and vertex derivation ($F(1/11)=7.52$ and 7.42), no other main effects or interactions were found for any derivation (including the EOG). The effect of the two criteria was smaller than was expected; this may be caused by the fact that the most severe artifacts were already removed under the lax criterion. Moreover, due to the introduction of a fixation light interval before S_1, only few artifacts may have been present to begin with.

TABLE 1

EEG and EOG amplitudes (in µV) for the early and late CNV measure for the lax (500 µV) and strict (100 µV) rejection criteria for the detection of eye movements
Values are averaged across subjects and experimental conditions

Rejection Criterion	EEG			EOG
	F_z	C_z	P_z	
Early CNV				
500	−5.0	−3.0	—	1.6
100	−5.4	−3.1	—	− 1.0
Late CNV				
500	−0.2	−2.7	−1.7	14.0
100	−1.0	−3.5	−2.2	9.4

Since the differences between the criteria were small, only the data on the lax criterion will be presented; this criterion is preferred because under the strict criterion three times as many trials were rejected.

Fig. 2 shows the composite means (across subjects) of the slow potential changes in the S_1–S_2 interval, separately for derivations, instructions, and the three probabilities. Large differences in waveform are found between the three EEG derivations. An early CNV component with a peak latency of ca. 700 msec is present under all experimental conditions in the frontal and less clearly in the vertex derivation. A late CNV component, which is gradually increasing during the interval, is observed mainly at the vertex and less clearly in the parietal derivation, but only under conditions requiring a fast reaction (high and medium probability under speed or accuracy instruction). Finally, a positive wave is found in the parietal derivation under all experimental conditions; this wave could be regarded as a P300 component evoked by S_1. Thus, the slow potential changes occurring in the S_1–S_2 interval consist of three components, which differ in waveform and midline distribution.

These observations were confirmed by ANOVAs carried out on the amplitudes of the early and late CNV and of the positive wave. The late CNV in the vertex and parietal derivation was affected by instructions ($F(2/22)=10.4$ and 6.8, respectively) and by S_2-probability ($F(2/22)=8.2$ and 4.6, respectively). The interaction between instructions and S_2-probability was significant for the vertex late CNV only ($F(2/22)=3.5$). Post-hoc Newman-Keuls tests demonstrated that these effects on the late CNV were mainly caused by differences between the experimental conditions requiring a fast reaction (high and medium probability under speed or ac-

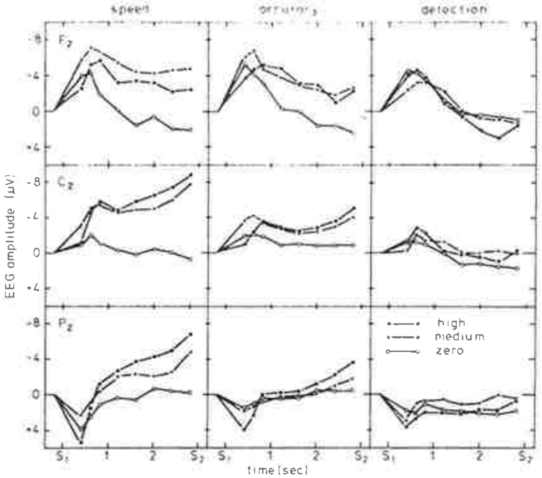

Fig. 2. Composite means across subjects as a function of conditions (high, medium, and zero probability), separately for derivations (frontal, vertex, and parietal) and for the three instructions.

curacy instruction) and the other conditions (detection or zero probability).

Instructions had an effect on the vertex early CNV ($F(2/22)=3.4$); lower amplitudes were found under detection instruction. Although smaller early CNV amplitudes were obtained under the zero-probability condition, the effect of S_2-probability overall did not reach significance. The parietal positive wave was influenced by neither instructions nor probability.

One explanation for these inconsistent results could be that the positive wave and the early negative wave are *instrumentally* related. It can be seen in Fig. 2 that, for example, under both speed and accuracy instructions the parietal positive and the frontal negative wave are more negative under the medium as compared to the high-probability condition, which suggests that under the latter condition the early CNV amplitude is attenuated by the larger positive wave. This observation was supported by the product-moment correlations computed within subjects between the parietal positive wave and the frontal negative wave. Nine out of twelve correlations were positive, of which four were significant. Moreover, when the frontal negative wave was referred to the parietal positive wave instead of the baseline (see **Methods**), more reliable task-effects were found for instructions ($F(2/22)=5.0$) and S_2-probability ($F(2/22)=3.62$).

An ANOVA carried out on the mean RT showed that shorter RTs were obtained under speed than under the accurate instruction ($F(1/11)=12.1$), and also under the high probability as compared to the medium probability condition ($F(1/11)=76.6$). However, the interaction between instructions and S_2 probability was not significant ($F(1/11)<1$). The mean RT was 233 msec, 353 msec, and 1111 msec for the speed, accuracy, and detection instructions under the high probability condition and 288 msec, 396 msec, and 1131 msec under medium probability. Catch-trial errors were only made under speed instruction. Under high probability subjects reacted to 39% and under medium probability to 25% of the catch-trials.

Early and late CNV amplitude as well as RT were not influenced by the order in which the three instructions were given, i.e., it did not matter whether the speed instruction was given at the beginning or at the end of the session. Also the tone-frequency of S_1 had no systematic effect on the early or late CNV.

Inspection of the individual mean RTs revealed large variance among subjects in their speed-accuracy trade-off. This was caused by the large variability in mean RT under accuracy as compared to speed instruction (SD = 113 msec and 39 msec, respectively). Although they were never caught some subjects reacted under accuracy nearly as fast as under speed instruction, while other subjects reacted ca. 200 msec slower. To investigate the influence of these differences in the "strategy" adopted by the subjects, two groups were formed on the basis of the differences between speed and accuracy (in the high-probability condition). Under speed instruction the small and large trade-off group hardly differed either in RT (222 msec and 244 msec, respectively) or in late CNV (9.3 and 8.5 μV), while under accuracy instruction a large difference was found in both RT (268 msec and 438 msec) and late CNV (9.8 and 0.2 μV).

Discussion

The present results provide further evidence for the differential midline distribution of the two components of the CNV reported in recent studies (Klorman & Bentsen, 1975; Rohrbaugh, Syndulko, & Lindsley, 1976; Gaillard, 1976). The early component of the CNV was not only larger but also peaked earlier in the frontal than in the vertex derivation. The late CNV is located precentrally and its anterior-posterior distribution is similar to that of the readiness potential (Deecke, Grözinger, & Kornhuber, 1976; Vaughan, Costa, & Ritter, 1968).

The positive wave observed at the parietal site could be regarded as a late positive wave of the evoked potential to S_1 or alternatively as a temporary resolution of tonic negativity prevailing before S_1 (see Näätänen, 1975, p. 275). Several studies have shown that P300 is maximal over the parietal area, when recorded after S_2 or after S_1 (e.g. Hillyard, Courchesne, Krausz, & Picton, 1976; Rohrbaugh et al., 1976).

The early CNV component was present in the frontal and less clearly in the central derivation not only under the detection instruction, but also in the zero probability condition, which required no further (overt or covert) response. This finding supports the orienting character of the early CNV and is consistent with the appearance of a frontal-dominant negative wave following non-signal stimuli, reported by Loveless (1976) and Rohrbaugh et al. (1976). Thus, the early CNV is evoked by a stimulus, even when it is not followed by an imperative signal. As was suggested by Loveless (1975) the early CNV component seems to be related to stimulus processing and enhances the sensitivity of the organism for the discrimination of subsequent stimuli.

After FS only a modest early CNV wave was found because of the low intensity of the fixation light. It has been shown that the amplitude of the early CNV is attenuated with visual stimulation (Gaillard, 1976) and with lower intensities (Loveless & Sanford, 1975).

Although the early CNV and the positive wave differentiate with regard to their spatial centers (frontal vs parietal) and to their peak latency (700 and 300 msec after S_1) they will contaminate and partially cancel each other. This notion is illustrated by the positive correlations which were generally found between the positive wave and the frontal negative wave. Moreover, when the amplitude of the frontal early CNV was added to the parietal positive wave, significant task effects were found. A further investigation of the relationship between the parietal positive and the frontal negative wave is needed, especially because both have been considered as cortical components of the orienting response (e.g. Loveless & Sanford, 1975; Näätänen, 1975).

Largest differences in the late CNV are found when RT conditions (high-medium probability under speed or accuracy instruction) are compared with either the zero-probability condition or the detection instruction.

These results replicate earlier studies in which S_1 signalled responding vs non-responding. For example, the data reported by Peters, Knott, and Hamilton (1976) show that the effect of non-responding mainly reduced the late CNV, as was also found in the present study.

The small differences between high and medium probability suggest that the CNV is not much affected by occurrence uncertainty, which result was also found by Järvilehto and Mäntysalo (1976), Karrer et al. (1973), and Näätänen et al. (1975). In the RT-situation motor preparation will increase the larger the probability that S_2 will follow S_1. Consequently the amplitude of the late CNV will become larger and the RT shorter. However, under conditions of complete certainty ($p=1.0$) subjects tend to synchronize their reactions with S_2, especially when the S_1–S_2 interval is constant and relatively short (see also Näätänen & Gaillard, 1974). In such a situation short RTs can be produced even without a high degree of motor preparation. This might explain why Järvilehto and Mäntysalo (1976; see also Karrer et al., 1973) obtained lower CNV amplitudes, when no catch-trials were used, as compared to conditions of uncertainty ($p=0.1$ to $p=0.85$). In any event it is possible to explain effects of S_2-probability in terms of motor preparation. Together with the lack of effect of S_2-probability under detection instruction (see also Fig. 2), the present results do not support the hypothesis that the CNV is related to expectancy, at least when expectancy is defined as the probability that S_2 will follow S_1.

The contingency of the late CNV on a motor response is supported by the absence of this component, not only in the S_1–S_2 interval under detection instruction but also in the FS–S_1 interval under all experimental conditions. Although the detection of the weak tone at S_2 and the discrimination of the three pitches at S_1 were relatively easy in the present experiment, at least some late negativity should have been observed if the late CNV component is related to any form of stimulus processing. Moreover, Loveless (1975) also found no late CNV in a signal-detection task, which involved the perception of an auditory signal at threshold level.

The influence of speed-accuracy trade-off on the late CNV generally corroborates the study of Loveless and Sanford (1974), except that in the latter study under the accurate instruction less late CNV (3.8 μV) was found than in the present study (5 μV, high expectancy condition). Since it is known (e.g. Henderson, 1970) that under practice RTs become faster under accuracy and remain constant under speed instructions, this discrepancy can be explained by the fact that the subjects in the Loveless and Sanford study did not receive practice under the different instructions. In recent RT-models it is assumed (Ollman, in press; Pachella, 1974; but see also Loveless, 1975) that changes in strategy induced by instructions governing the speed-accuracy trade-off mainly—or even only—influence the level of motor preparation rather than the criterion of a cognitive decision.

The results of the present study suggest strongly that the late CNV is contingent on a motor response and is mainly determined by the level of motor preparation. This notion is supported by the similarity in form and midline distribution of the late CNV to the readiness potential, which precedes voluntary movements. Moreover, Rohrbaugh et al. (1976) found bilateral asymmetries in both the late CNV wave and the readiness potential; greater amplitudes were recorded over the hemisphere contralateral to the responding hand.

It is tempting to assume that the late CNV component and the readiness potential refer to the same neurophysiological generator but are obtained in different task situations and with different averaging techniques. In this view the late CNV could be regarded as that part of the readiness potential which precedes S_2 in cued RT-tasks.

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(Manuscript received November 30, 1976; revision received April 22, 1977; accepted for publication June 29, 1977)

EXPERIMENT 5

SOME EFFECTS OF SPEED-ACCURACY INSTRUCTIONS ON SLOW BRAIN POTENTIALS*

ABSTRACT

The present results corroborate those of Experiment 4, in that a speed instruction enhances the terminal CNV. Moreover, it is shown that reliable measures are obtained when the EEG is averaged backwards from the response rather than for the S_1-S_2 interval. This suggests that the terminal CNV is contingent on a motor response.

It was also found that the amplitude of the SNW increases when S_1 provides information besides its warning function. Thus, the SNW seems to be affected by the psychological significance of S_1.

*Submitted to Biological Psychology.

1. INTRODUCTION

In the discussion of Experiment 4 it was suggested that the terminal CNV and the RP preceding voluntary movements were largely the same neurophysiological phenomenon, which, however, were obtained in different experimental situations and by different averaging methods. In the present study this issue is further investigated by comparing the usual averages time locked to S_2, with movement potentials, i.e. with averages time locked to button presses given in the context of the S_1 - S_2 paradigm. This is done for several task requirements.

The same instructions were given as in Experiment 4, except that a deadline procedure was used (see Ollman, 1977 and Chapter 3, this thesis). The subject was instructed to respond to S_2 before a deadline set by the experimenter. If the subject did not respond before the deadline, a noise burst was given through earphones. In this way the subject received immediate feedback about his reaction performance. This procedure was used to ensure that subjects would follow the instructions throughout a block of trials. Especially under speed instruction subjects tend to slow down their performance during the experimental sessions or even during one block of trials.

Since the RP is usually obtained when the subject produces voluntary movements without external stimulation, an experimental condition was added in which the subject had to synchronize his response with the arrival of S_2. This time-estimation task resembles the S_1 - S_2 paradigm and the voluntary-movement situation. It is generally assumed that the estimation of the arrival of S_2 is an important determinant of the preparatory processes for the response to S_2. The increase of RT with longer ISI is generally explained as resulting from increased difficulty to predict the moment S_2 will arrive (e.g. Näätänen et al., 1974; Näätänen and Merisalo, 1977).

A second aim of the present study was to investigate whether the SNW was affected by the information revealed by S_1. It has been shown that the SNW is influenced by the physical characteristics of S_1, such as intensity, duration and modality of this stimulus (Loveless and Sanford, 1975; Klorman and Bentsen, 1975; Experiment 1, this thesis). It is also conceivable that this wave may be affected by the psychological significance of S_1. Indeed, in Experiment 4 lower amplitudes were found under detection instruction and under the zero-probability condition, which did not require a further overt or covert response.

In the present study the psychological significance of S_1 was varied by making the signal informative. A larger SNW was expected when S_1 was informative as compared to the situation where S_1 only served as a warning that S_2 would soon arrive. S_1 provided information with regard to the instructions to be followed at S_2; this was done in two ways: in one situation the speed and accuracy and in the other situation the speed and detection instruction were varied from trial-to-trial within one block of trials.

2. METHODS

2.1. Subjects and apparatus

The subjects were 10 male University students, who were paid for their participation. The data of one other subject were discarded for having too many eye-movement artifacts. The subjects were seated in a comfortable chair, which also provided a neck- and arm-rest. S_1 was a 70 dB tone (delivered via headphones) with a frequency of either 500 or 2000 Hz. S_2 consisted of slides which were projected (Kodak-carousel) through the window of the cubicle, on a screen at a distance of ca. 1 meter of the subject's eyes. S_2 was always composed of two vertical bars (width 5.5 cm), which differed in length (37.5 versus 5.5 cm).

Ag-AgCl disk electrodes were attached to three scalp sites (F_z, C_z, P_z) and to the earlobes, which were linked for reference. An electrode just above the nosebridge served as a ground. To record the heart rate, two ECG-electrodes were attached to the rib cage. After amplification (time-constant 6 sec) the EEG and EOG signals were recorded on a magnetic tape, together with the ECG.

2.2. Procedure

A trial started with the onset of S_1, which was followed 4 sec later by the slide remaining on for 1 sec. The intertrial (S_1 - S_2) was varied irregularly between 11-14 sec. Under all experimental conditions, except for the synchronization task, the subject was asked to discriminate which of the two bars was longer. He had to respond with his right hand when the right bar was longer and with his left hand when the left one was longer.

To induce changes in the speed-accuracy trade-off two deadlines were used before which the subject had to respond; if he did not respond before the deadline 60 dB noise was given via earphones (duration 500 msec). Under accuracy instruction the deadline interval was twice as long as under speed instruction. The subject was told that only the correct reactions occurring before the deadline would count. Especially under speed instruction, the importance of beating the deadline was stressed, since subjects were found to tend to prefer receiving noise to making errors. With the accuracy instruction the avoidance of making errors was emphasized. The duration of the deadline interval was determined in a separate training session, one week before the experimental session. The deadline under speed instruction was chosen so that the subject made 20 - 30 % errors; in fact the variability between subjects was so low that all subjects could get the same interval of 250 msec under speed, and thus 500 msec under accuracy instruction. In addition the subject received a synchronization task in which he had to respond as closely as possible to S_2; either before or after this signal. The subject was instructed to react with his right hand on half of the trials and with his left hand in the other half. (Since no differences were found between these conditions, the data for right and left hand responding were combined.)

The speed and accuracy instructions were varied either between or within a block of trials. In the latter situation S_1 indicated the instruction the subject had to follow. For half of the subjects the high tone (2000 Hz) indicated a speed instruction and the low tone (500 Hz) the accuracy instruction; this was reversed for the other half.

Finally, the speed instruction was also given within a block of trials, together with a detection instruction; under this instruction the subject was asked to indicate which bar was longer at the off-set of the slide (1 sec after S_2). Again S_1 indicated which instruction had to be followed; the tone which had indicated the accuracy instruction now indicated the detection instruction.

Half of the subjects received the 7 experimental conditions in the following order: synchronization/speed/accuracy (between), speed/accuracy (within), speed (detection)/detection; and the other half of the subjects received them in the reversed order. There were 50 trials in each experimental condition.

2.3. Data analysis

The three EEG channels, and EOG channel were digitized at a rate of 25 samples per sec. The analysis period started 1 sec before S_1 and ended at the onset of S_2. For each trial the number of data points was reduced to 25 by taking the averages of successive groups of 5 points; this yielded one average data point per 200 msec. Thirteen of these data points were retained for further analysis (see also Fig. 1). These data points were averaged across 40 trials, leaving 10 trials for artifact rejection, and the following measures were obtained, separately for each derivation: SPW, SNW and terminal CNV, i.e. the average EEG in the period 200 - 400 msec and 600 - 800 msec after S_1 and 200 msec before S_2, referred to a baseline (average EEG in the period 200 msec before S_1).

On these measures and the mean RT, standard deviation and % of errors two types of ANOVAs were carried out: A two-way ANOVA, which included instructions (speed vs. accuracy) and the between/within conditions. In the second ANOVA the three speed instructions were compared: speed (between), speed (within), speed (detection).

In addition, the EEG was averaged twice (sample interval 14 msec): once time locked to S_2 and once to the response.

3. RESULTS

3.1. RT-performance

Table 1 presents the RT-data separately for the experimental conditions. For both the between and within condition the mean RT was much shorter under speed than under accuracy instructions ($F(1/9) = 110$; $p < 0.001$). Of course, there were much more errors under speed than under accuracy instructions ($F(1/9) = 40.7$; $p < 0.01$), while the standard deviation was much smaller ($F(1/9) = 42.4$; $p < 0.01$). Although the difference in RT and standard deviation between the speed and accuracy instructions were smaller in the within- than in the between-condition, this interaction was not significant ($F(1/9) < 1$). Also the

Table 1. The mean RT, standard deviation (in msec) and the % of errors, separately for the experimental conditions.

	mean RT	standard deviation	% of errors
Synchronization	-5	252	-
Between			
Speed	224	48	29
Accuracy	375	80	2
Within			
Speed	223	46	29
Accuracy	362	83	2
Within			
Speed	231	55	27
Detection	1220	77	2

main effect of between versus within was not significant for either mean RT, % errors or standard deviation. Subjects were quite able to synchronize their responses with S_2; 5 of them reacted within 50 msec before or after S_2, while all reacted within ± 260 msec. Nevertheless, the standard deviation was very large, 5 times more than under speed instruction.

3.2. Slow potential shifts

Fig. 1. shows the composite means of the vertex slow potential, under the synchronization, speed and accuracy instructions (all varied between blocks). Under each instruction a SNW with a latency of ca. 600 msec was followed by a terminal CNV.

In a two-way ANOVA on the terminal CNV the speed-accuracy effect was significant ($F(1/9) = 7.84$; $p < 0.02$), while the variation of instructions between or within a block of trials had no influence ($F(1/9) < 1$). Although the effect of instructions was larger in the between condition (6.4 μV) than in the within condition (2 μV), this interaction did not reach statistical significance ($F(1/9) = 3.54$; $p < 0.09$). No differences were found between the speed and the synchronization instruction, except that in the latter condition the terminal CNV reaches its maximum one data point earlier than under speed instruction, which corresponds with the earlier response.

In contrast to the terminal CNV, the SNW amplitude was not significantly affected by instructions. However, the frontal SNW was influenced by the between/within effect ($F(1/9) = 11.9$; $p < 0.01$). The SNW was enhanced when S_1 indicated the instructions to be followed at S_2. The parietal SPW was affected by both factors. Larger amplitudes were found under speed instruction ($F(1/9) = 4.8$; $p < 0.05$) and under the within condition ($F(1/9) = 5.9$; $p < 0.04$) the interaction between these factors was not significant ($F(1/9) < 1$).

Fig. 2 presents the composite vertex data under the speed instruction, for the three experimental conditions: this instruction was either held constant over a block of trials (between) or varied from trial-to-trial (within) in combination with accuracy or with detection. One-way ANOVAs revealed that the terminal CNV and the SPW were unaffected by these conditions, but the frontal SNW was influenced ($F(2/18) = 5.77$; $p < 0.01$). The amplitude of the SNW was enhanced when S_1 indicated the speed instruction; this effect was most prominent when speed and detection instructions were varied within one block of trials (see Fig. 2 and Table 2).

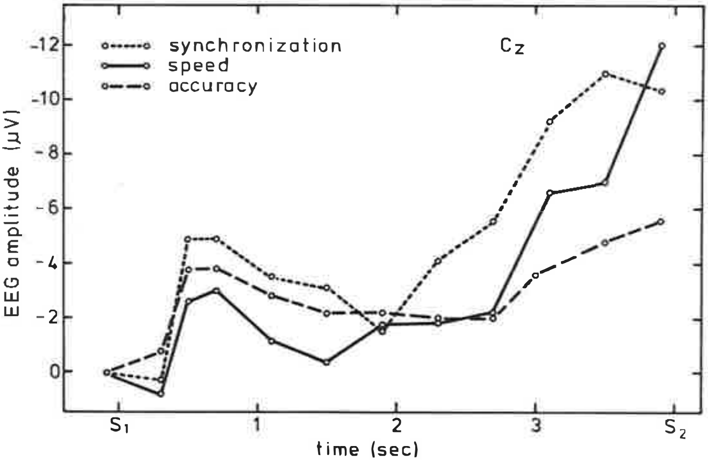

Fig. 1. The composite means of the vertex slow potential under the synchronization, speed and accuracy instructions, all varied between blocks.

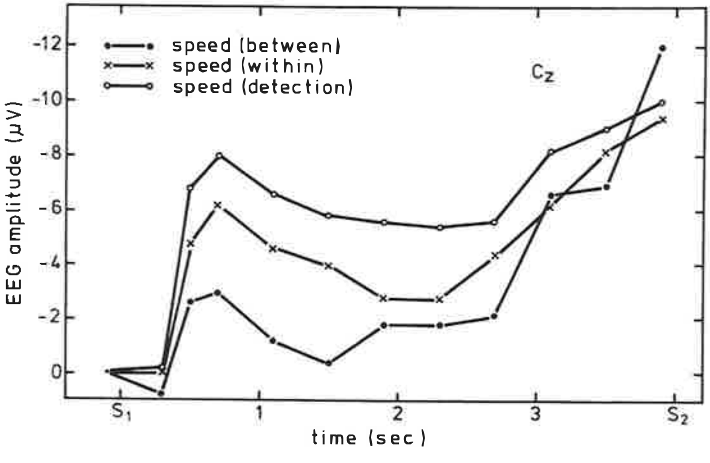

Fig. 2. The composite means of the vertex slow potential under the speed-instruction conditions; this instruction was either held constant over a block of trials (between) or it was varied from trial-to-trial in combination with accuracy (within) or with the detection instruction (detection).

Table 2. The EEG and the corresponding EOG amplitudes (in µV) of the SPW, SNW and the terminal CNV, separately for the experimental conditions.

	Synchronization	Between		Within		Within	
		Speed	Accuracy	Speed	Accuracy	Speed	Detection
SPW							
F_z	- 0.6	+ 0.6	- 0.6	0.0	- 0.6	- 0.4	- 1.2
C_z	+ 0.3	+ 0.8	- 0.8	0.0	- 0.6	0.0	- 1.4
P_z	+ 2.6	+ 3.2	+ 1.0	+ 4.8	+ 3.0	+ 4.0	+ 4.6
EOG	- 2.0	0.0	0.0	0.0	0.0	- 2.0	0.0
SNW							
F_z	- 4.8	- 2.4	- 2.6	- 7.4	- 6.4	- 9.8	- 4.0
C_z	- 4.9	- 3.0	- 3.8	- 6.2	- 4.2	- 8.0	- 2.6
P_z	+ 1.3	0.0	- 2.2	+ 1.2	+ 0.8	- 2.2	+ 2.2
EOG	- 5.0	- 6.0	- 4.0	- 2.0	- 2.0	- 8.0	+ 2.0
CNV							
F_z	- 6.3	- 4.2	- 1.6	- 2.4	- 5.2	- 4.0	+ 1.0
C_z	-10.4	-12.4	- 5.6	- 9.4	- 7.4	-10.0	- 1.4
P_z	- 6.5	- 7.2	- 4.0	- 6.6	- 4.6	- 7.2	- 1.0
EOG	- 6.0	0.0	+ 4.0	+12.0	- 8.0	+ 8.0	+ 8.0

3.3. S-locked vs. R-locked potentials

Figs. 3 and 4 present the vertex potentials time-locked to either S_2 (S-locked) or to the response (R-locked). In all S-locked averages (except under detection) the terminal negativity is followed by the EP complex consisting of an N_1 peak (latency 175 msec) and a large P_3 (latency 325 - 375 msec), sometimes followed by a second large positive component P_4 (latency 525 - 575 msec). The P_2 component is only observed in those conditions (accuracy and detection) where P_3 is reduced and delayed. The latency of the P_3 component was marginally influenced by experimental conditions. The latency was 325 msec under synchronization, 350 msec under both speed conditions and 375 msec under accuracy and detection instructions. These differences in latency are small compared to the differences in RT. For example, the difference in RT between speed and accuracy instructions was 151 msec, while the difference in P_3 latency was only 25 msec.

The EPs to S_2 were largest in the two speed conditions; the N_1 peak was smallest under synchronization, which illustrates the unimportance of S_2 in this condition. The positivity after S_2 (P_3 and P_4) is smallest under detection instruction. It is to be noted that in all conditions P_4 is less positive than P_3, except under accuracy.

As can be seen in Figs. 3 and 4, the R-locked averages show a remarkable similarity in form and time course to potentials synchronized to voluntary movements. As with the potentials time locked to voluntary movements, the response is preceded by a slow negative shift, which could be denoted as readiness potential (RP). This gradual negative shift turns into a sharp negative inflection, which is followed by a slow positive change. Under accuracy instructions this positivity already starts 150 msec before the closure of the button switch. This phenomenon, which was present in 9 out of 10 subjects, looks very similar to the pre-motion-positivity observed by Deecke et al. (1976) in some subjects.

To compare the slow negative shifts in the S- and R-locked averages, the amplitude of the terminal CNV (average EEG 100 msec before S_2) was computed in both averages. These measures were compared to the amplitude of the RP (average EEG in the period 250 - 150 msec before the response) (see Deecke et al., 1976). All three measures were referred to the same baseline (average EEG 2000 - 1800 msec before the response). The topographical distribution of these measures is given in Fig. 5. Largest amplitudes were obtained at C_z for all measures and experimental conditions. There were practically no differences (less than 1 µV) between the three vertex measures under speed instruction. This is not so surprising since both the mean and the variability of the RT in this condition were small, and consequently the discrepancy between the two ways of averaging will also be small. In contrast, under synchronization instruction there was a difference in vertex terminal CNV of 2.4 µV between the two types of averages. Since the variability in response time was large, the enhanced amplitude in the R-locked average suggests that the terminal CNV is contingent on the response and not on the stimulus (S_2). However, under accuracy instruction the amplitudes obtained in the R-locked averages were not larger. This may be caused by the larger time lag between S_2 and the response in this condition (375 msec). As can be seen in Fig. 3, the negativity time-locked to the response still increases after S_2 until 150 msec before S_2. Therefore, the RP measure taken at this moment is much larger than the terminal CNV in both the S-locked and in R-locked averages. Although small in amplitude, the RP preceding the delayed response under the detection instruction shows the same midline distributions as the terminal CNV and the RP under the other instructions (see Fig. 5).

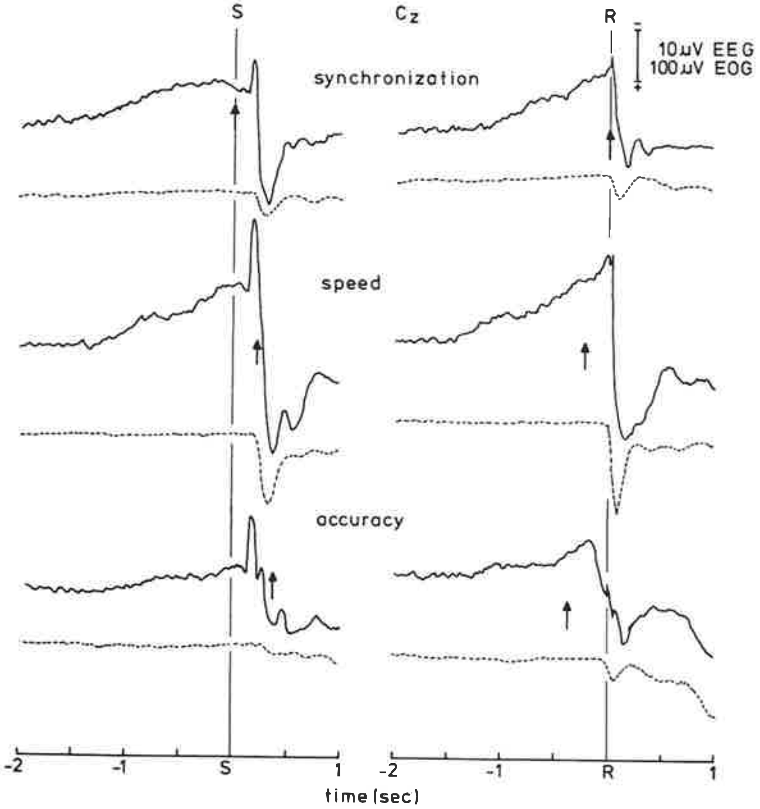

Fig. 3. Averages of the vertex EEG (solid line) and the EOG (broken line) under synchronization, speed and accuracy instructions, either time-locked to S_2 (left side) or to the button press (right side). The arrows indicate average RT (left side) or S_2 (right side).

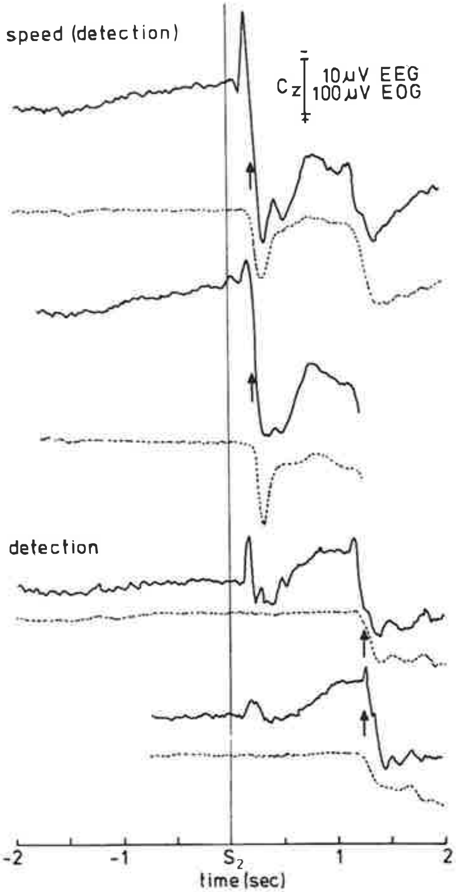

Fig. 4. Averages of the vertex EEG (solid line) and the EOG (broken line) under speed and detection instructions, either time-locked to S_2 (upper curves) or to the button press (lower curves).

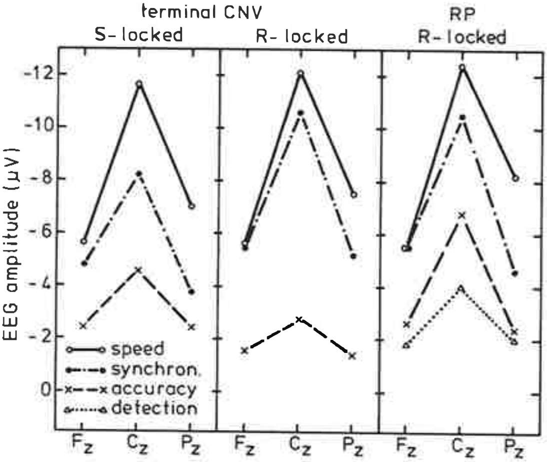

Fig. 5. The midline distribution (F_z, C_z, P_z) of the terminal CNV (the average EEG in the 100 msec period before S_2), obtained from averages either time-locked to S_2 (S-locked) or to the button press (R-locked), and of the RP (the average EEG in the period 250 - 150 msec before the response. All three measures were referred to the same baseline (average EEG 2000 - 1800 msec before the response). These distributions are given for the following experimental conditions: speed-, accuracy- and synchronization-instructions, all varied between blocks of trials. For the detection instruction (crosses) the distribution of the RP only is given because no terminal CNV is present in this condition.

4. DISCUSSION

The present effects of the speed-accuracy instructions were larger for both the terminal CNV and RT than in Experiment 4. This might be due to the deadline procedure, which induced stable and fast RT performance throughout a block of trials. Although not significant, the speed-accuracy effect was somewhat smaller when S_1 indicated the instruction to be followed (within-condition). Some subjects may have found it difficult to change their strategy from trial to trial.

The enhanced terminal CNV under speed instruction may be explained by assuming that under this instruction the level of motor preparation is increased, as compared to the accuracy instruction. Also the absence of a terminal CNV under detection instruction found in this and in the previous study, supports the idea that the terminal CNV is response-related.

The potentials time-locked to the button press to S_2 (Figs. 3 and 4) are similar in form to movement potentials preceding voluntary finger presses (see Deecke et al., 1976; Rohrbaugh et al., 1976). Similar to the RP preceding voluntary movements, the negative shift preceding responses in the $S_1 - S_2$ paradigm is also most prominent at the motor region (C_z). This was also the case when responses were synchronized to S_2 or were delayed by one sec after S_2 (detection instruction). Syndulko and Lindsley (1976) found the same midline distribution under both the RT- and detection instruction; in addition, they showed that this negative shift had a lateral asymmetry contralateral to the responding hand. The present results obtained under the synchronization instruction deviate from Ruchkin et al. (1977), who used a similar task but with an ISI of 900 msec. Their data (Op. cit., Fig. 1) show an inverted U-curve with a peak ca. 700 msec after S_1. Therefore, their data suggest that a gradual rise similar to the RP was not found because the negative shift preceding the response was disrupted by the SNW to S_1 (a click). However, gradual negative shifts were obtained when the EEG was time-locked to the finger presses (Op. cit., Fig. 2). Moreover, these negative shifts in the synchronization task were quite similar to RPs preceding voluntary movements, obtained from the same subjects.

The above findings suggest that the negativity preceding the responses in the $S_1 - S_2$ paradigm is the same as the RP preceding voluntary movements. In this view the terminal CNV obtained from stimulus locked averages largely consists of the increasing limb of the movement related negative shift. Consequently, the terminal CNV could be regarded as that part of the RP which precedes S_2. It is conceivable that with shorter RTs (for example, induced by deadlines or speed instructions) the RP intrudes more into the $S_1 - S_2$ interval and in this way enhances the amplitude of the terminal CNV. This view is supported by the larger negativity in the averages time-locked to the response as compared to the negative shifts in the stimulus-locked averages.

There are, however, also some differences in the negative shifts observed in the present experimental conditions and the RP: the onset of negative shift under speed, accuracy and synchronization instructions was about one sec earlier and this shift reached an amplitude which was about two times larger than the RP reported by Deecke et al. (1976). It could be argued that in the synchronization task, as well as in the RT-tasks, not only motor but also perceptual and decision related processes are involved. However, the terminal CNV seems to be related neither to perceptual nor to decision processes (see Chapter 8).

Therefore, a more likely explanation would be that the present experimental conditions are more <u>interesting</u> than monotonously repeating a large number of voluntary movements. It has been shown that the CNV (Irwin et al., 1966; Waszak and Obrist, 1969) and also the RP (McAdam and Seales, 1969) are influenced by motivation. In the latter study RP-amplitudes preceding voluntary finger presses, increased from 5 μV to 12 μV, when subjects were told that they would receive 10 cents for each response, if given "at the right time". In fact, rewards for these "correct" responses were given in a random fashion. Thus, it could be that the increased RP-values reflect a higher level of motor preparation, caused by an enhanced interest of the subject in the task.

Both above-mentioned explanations assume that terminal CNV and RP are largely produced by the same neurophysiological generator, but according to the first both can be influenced by motor and decision processes, while in the second view they are only determined by the level of motor preparation.

Although the slow potential changes (i.e. terminal CNV and RP) were very similar, especially when the individual averages were compared, the faster phenomena were rather different. Not only the EPs, but also the peaks in the movement potentials had a fixed latency to S_2 or to the button press, respectively, which means that none of the peaks synchronized with each other, if the latency between S_2 and the response is taken into account. Thus, although the slow changes in the S-locked and R-locked averages are correlated, the peaks do not contain the same information.

The shorter latency of the P_3 under speed as compared to accuracy instruction may be shorter because the decision processes are accelerated. In this view the speed-accuracy effect (151 msec) is partly produced by an accelerated decision (25 msec) and for the rest by "fast guesses", i.e. reactions which are given before the decision process is terminated.

On the basis of a trial-to-trial analysis Kutas et al. (1977) compared the RT with the latency of the P_3 on the same trial. They found the correlation between P_3 latency and RT was larger under accuracy than under speed instruction. Moreover, under speed instruction the incorrect RTs mostly preceded the P_3. According to the authors these data suggest that under accuracy instruction the motor processes of selection and execution of the response are tightly coupled with the evaluation of the stimulus (i.e. encoding and decision processes). However, under speed instruction stimulus evaluation, as indexed by the P_3 component, is only loosely related with the execution of the motor response: response may be generated before the stimulus has been fully evaluated. Also in the present study the mean RT (224 msec) preceded the P_3 (350 msec), while these latencies coincided under accuracy (both 375 msec).

In the present study the frontal SNW was strongly affected by the information content of S_1 (see also Fig. 2). The amplitude of this wave was enhanced when S_1 indicated either that a speed or an accuracy instruction had to be followed at S_2. This effect was even larger when speed and detection instruction were varied within one block of trials. The SPW was also influenced by the present conditions, but in a different way, a result also found by Squires et al. (1977). Thus, it was not only enhanced when S_1 contained information, but this wave was also larger under speed than under accuracy instructions. Moreover, in the condition where speed and detection were varied within one block, the amplitude of the parietal SPW did not differ between speed (4 µV) and detection instruction (4.6 µV), while for the frontal SNW a difference of 5.8 µV was found (see also Table 2). Thus, the SPW and SNW seem to be affected by some conditions in the same way and differently in other instances, which suggests that these waves reflect different, but related mechanisms. That different processes are involved is also suggested by the differences in latency (300 - 400 msec vs. 600 - 700 msec after S_1) and midline distribution (parietal-frontal).

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EXPERIMENT 6

THE LATERAL DISTRIBUTION OF SPSs PRECEDING DIFFERENT TASK REQUIREMENTS.

ABSTRACT

In this experiment the lateral distribution ($C_3 - C_4$) was investigated in four experimental conditions: a simple RT-task, a time-estimation task involving a delayed response, a synchronization task and voluntary movements. In all conditions subjects responded to half of the trials with their left hand and to the other half with their right hand. It was found that the terminal CNV obtained from the contralateral hemisphere was larger than from the ipsilateral. This effect was also found in the negative shift obtained from movement potentials time-locked to finger presses in the four experimental conditions.

1. INTRODUCTION

In both Experiments 4 and 5 it was suggested that the terminal CNV, and the readiness potential (RP) preceding voluntary movements, refer to the same neurophysiological processes, although they are obtained in different experimental situations by different averaging methods. In the present study this issue is further pursued by investigating the negative shifts preceding the motor response in movement potentials (in averages time locked to finger presses). This is done for four task conditions: voluntary movements, a simple RT-task, a time-estimation task involving a delayed motor response (detection-instruction) and a synchronization task, similar to the one used in Experiment 5. It is expected that the characteristics of the negative shifts preceding the motor response in the four experimental situations will be about the same.

The specificity of these negative shifts is determined by measuring the lateral scalp distribution, in addition to the midline distribution. Thus, the SPSs preceding left and right hand responses are obtained from the left and right hemisphere (C_3 and C_4) over the motor area. The left and right hand responses were varied from trial-to-trial. This was to prevent the possible adoption of unimanual response-sets which might have caused differential tonic shifts in the resting EEG potential level between the two hemispheres. To obtain differential preparation of only one hand the subjects were instructed to relax the non-involved hand. This was controlled by recording the EMG-activity from the flexor muscles in both arms (see also Syndulko and Lindsley, 1977, p. 125).

2. METHODS

2.1. Subjects

The subjects were 8 male students of the University of Utrecht, who were paid for their participation. The data of 4 other subjects were discarded for having too many eye movements and/or DC-drifts.

Before the experiment the subjects completed a questionnaire about their hand preference. Only the subjects who preferred to use their right hand for several activities (writing, tooth brushing, etc.) were taken. For some activities (e.g. throwing a ball) bimanuality (i.e. no preference for either hand) was allowed.

2.2. Apparatus

In general the apparatus used was the same as in the previous experiment, except that both S_1 and S_2 were auditory stimuli of 70 db with a duration of 100 msec, and were presented either to the left or right ear. A fixation point was mounted on the wall 1.5 m in front of the subject. The EEG derived from 5 scalp sites (F_z, C_z, P_z, C_3 and C_4), and the EOG signals were amplified with a time constant of 10 sec. In addition the EMG was recorded from the flexor muscles (in both the left and right forearm). Before averaging the EMG was integrated using a 10 msec-window.

2.3. Procedure

Left and right hand presses were compared in four experimental conditions. In one condition the subject was asked to give voluntary movements; the subject was trained to do this at intervals not shorter than 6 sec and not longer than 7 sec. The subject gave 48 finger presses for one hand, followed by 48 for the other. The order was balanced between subjects. In the RT-task the subject was required to react as quickly as possible to an imperative signal (S_2) which arrived 4 sec after a warning signal (S_1). In the synchronization task the subject had to respond as near to 4 sec after S_1 as possible. In this task S_2 was only present during the initial phase of the training sessions; thus, S_2 was omitted in the experimental session. In the time-estimation task (TE-task) the presentation of S_2 was delayed on half of the trials. This delay was either 500 or 600 msec, depending on the subjects's performance during training. The delay was chosen such that 5% - 10% errors were made. The subject was instructed to estimate the time interval between S_1 and S_2, and to indicate with a delayed response (1 sec) on one of two buttons whether the interval had been of "normal" duration (4 sec) or had been longer. In the last three tasks S_1 indicated whether the subject had to react with his left or with his right hand. If S_1 was presented to the left ear, a left hand response was required, and a right ear stimulus indicated a right hand response. S_2 was always presented to the same ear as S_1.

The order of rotation of these four tasks was voluntary movements, RT-task, TE-task and synchronization task. The task which was given first was varied between subjects (two subjects each started with the same task).

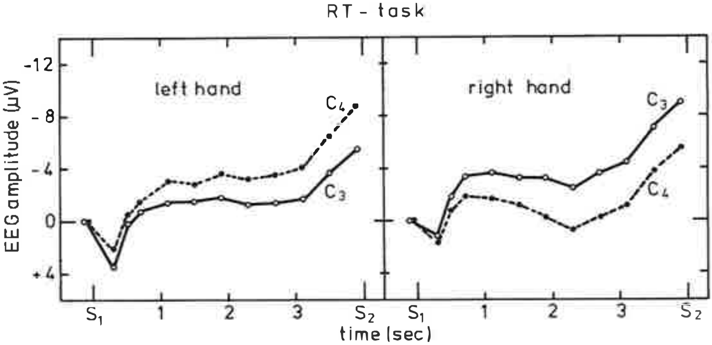

Fig. 1. The slow potential shifts in the RT-task, separately for the left and the right central area (C_3 and C_4) and for left and right hand responses.

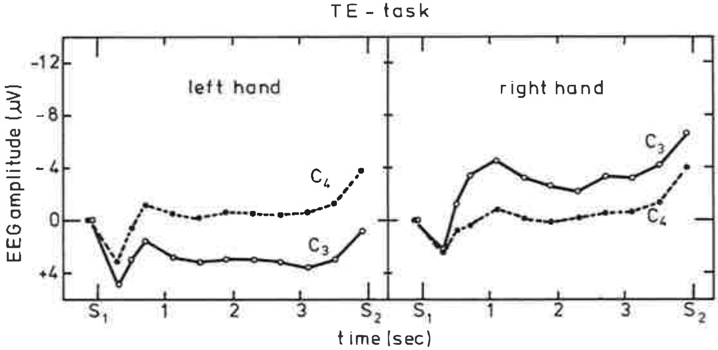

Fig. 2. The slow potential shifts in the TE-task, separately for the left and the right central area (C_3 and C_4) and for left and right hand responses.

3. RESULTS

Two factor ANOVAs (RT/TE-task; left/right hand) were carried out on the SPW, SNW and on the terminal CNV amplitudes for the five EEG-channels and on measures obtained in the same periods for the two EMG-channels and the EOG. Only the significant results will be mentioned.

The terminal CNV was affected by the type of task both at C_z ($F(1/7) = 6.8$; $p < 0.03$) and at P_z; $F(1/77) = 7.4$; $P < 0.03$); larger amplitudes were obtained in the RT-task than in the TE-task. At C_z this amplitude was about two times larger in the RT-task (12.6 µV) than in the TE-task (6.6 µV). The effect of the side of the response did not reach statistical significance for either C_3 or C_4, nor for the midline positions (F_z, C_z, P_z). However, a significant effect was found when the same ANOVA was carried out on the difference between C_3 and C_4 ($F(1/7) = 7.6$; $P < 0.03$). As is shown in Figs. 1 and 2 larger amplitudes were obtained in the hemisphere contralateral to the responding hand. This effect is about the same in both tasks (ca. 3.5 µV, across left and right hand responses).

Figs. 3 and 4 present the integrated EMG for the RT and TE tasks, separately for left and right hand responding and for the activity obtained from the left and right arm flexor muscles (L-EMG, R-EMG). On the one hand, the EMG data run parallel to the EEG data; larger amplitudes are found in the RT-task and in the involved arm, even with a delayed response in the TE-task. On the other hand, the timecourse of the EMG is quite different from the EEG. Instead of a gradually increasing curve, the EMG reaches a peak within one sec after S_1 and remains on a constant level thereafter.

The EMG activity in the 200 msec period before S_2 is larger in the RT-task than in the TE-task, for both the left arm ($F(1/7) = 16.6$; $P < 0.01$) and right arm EMG ($F(1/7) = 8.3$; $P < 0.01$); the effects of response side were also significant for both the left arm ($F(1/7) = 21.1$; $P < 0.01$) and the right arm ($F(1/7) = 18.5$; $P < 0.01$). In addition, for the EMG activity in the period 200-400 msec after S_1 the same results were obtained both for type of task, (Left arm EMG: $F(1/7) = 6.0$; $P < 0.05$. Right arm EMG: $F(1/7) = 7.0$; $P < 0.03$) and response side (Left arm EMG: $F(1/7) = 12.2$: $P < 0.01$. Right arm EMG: $F(1/7) = 6.4$; $P < 0.04$).

In the above mentioned ANOVAs the synchronization task was not included, because in this task rather low amplitudes for the terminal CNV were obtained. This was caused by the large variability in response latencies.

Fig. 5 gives the vertex movement potentials, i.e. the average potentials

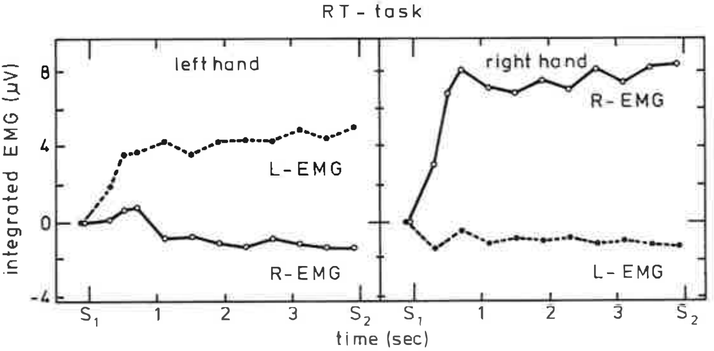

Fig. 3. The changes in integrated EMG in the RT-task, separately for the activity obtained from left and right forearm and for left and right hand responses.

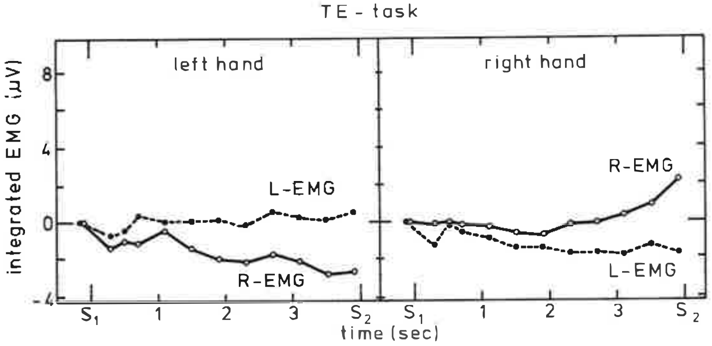

Fig. 4. The changes in integrated EMG in the TE-task, separately for the activity obtained from left and right forearm and for left and right hand responses.

time-locked to finger presses, in the four experimental situations. In general these potentials have the same form, although there are some differences. The negative shift is larger in the RT-task and smaller in the synchronization task, and in the TE-task this negative shift starts somewhat earlier than in the other experimental conditions.

Fig. 6 gives the lateral distribution of the amplitude of this negative shift (average EEG activity in the period 284-144 msec before the response) in the four experimental conditions. In general, the laterality effect ($C_3 - C_4$) is about the same for these conditions and for left and right hand responses.

Fig. 7 presents the EMG activity time locked to the closure of the button switch. The EMG curves obtained from the non-involved arm are not presented, because here virtually no activity was present. As with the movement potentials the EMG shows the same picture in the four experimental conditions. A large peak in the EMG precedes the response by 18 msec for voluntary movements and for the RT-task and by 32 msec for the other two tasks. Although this peak was much larger in the RT-task, the latency of the start of this peak was about the same for all conditions. Although modest in amplitude there is a gradual increase in EMG activity for one to two seconds before the response. This gradual increase runs parallel to the slow negative shift preceding the response, as shown in Fig. 5. This gradual increase in EMG, largest in the RT and TE tasks, is also present in the averages time locked to S_2 for both the RT-task (Fig. 3) and the TE-task (Fig. 4).

Two factor ANOVAs (four experimental conditions; left/right hand) were carried out on the negative shift preceding the motor response for the five EEG-channels, the EOG-channel and the two EMG-channels, and on the difference between C_3 and C_4 and the difference between left and right arm EMG. Experimental conditions did not reach statistical significance in any of the ANOVAs. Response side had an effect at C_3 ($F(1/7) = 5.9$; $p < 0.04$), but not at C_4 ($F(1/7) < 1$) and on the difference between C_3 and C_4 ($F(1/7) = 34.2$; $p < 0.01$). This factor was also significant for the left arm EMG ($F(1/7) = 8.7$; $p < 0.03$), the right arm EMG ($F(1/7) = 9.6$; $p < 0.03$) and the difference between these measures ($F(1/7) = 10.2$; $p < 0.03$).

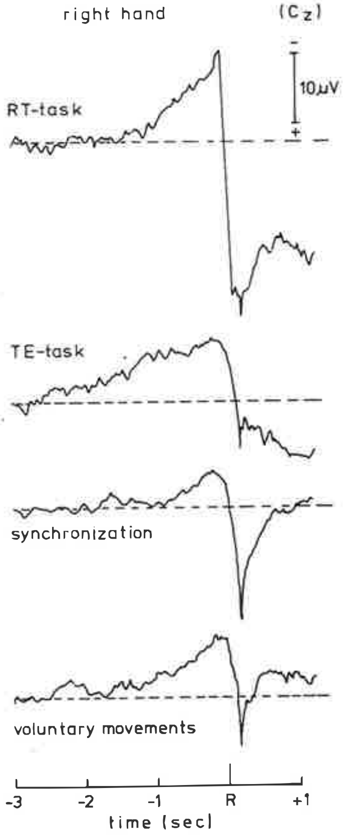

Fig. 5. Vertex movement potentials time locked to right hand finger presses (R) for RT-task, TE-task, synchronization task and voluntary movements.

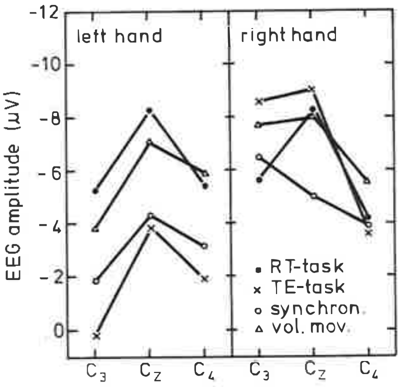

Fig. 6. The lateral distribution of the RP obtained from movement potentials, time locked to finger presses (R) in RT-task, TE-task or synchronization task or to voluntary movements, separately for left and right hand responses The RP-measure is the average EEG activity in the period 284-144 msec before the response, referred to a baseline 3000-2860 msec before the response.

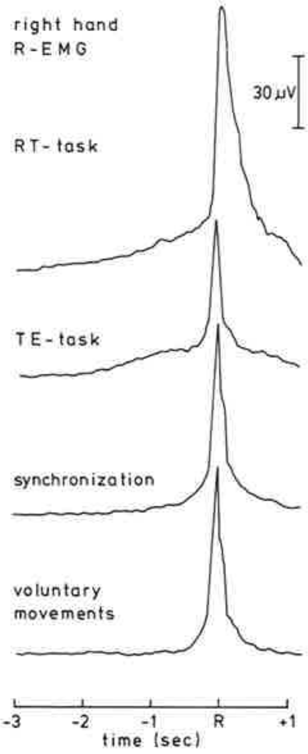

Fig. 7. The integrated EMG activity from the flexor muscles of the right forearm time locked to right hand finger presses in RT-task, TE-task, synchronization task and to voluntary movements.

4. DISCUSSION

The main finding of the present experiment was the laterality effect in the terminal CNV: the amplitude of this SPS was larger contralateral to the responding hand. This finding corroborates the results of Rohrbaugh et al. (1976) who found the same effect, although it was much smaller (1.1 μV). This difference is not easily explained in terms of task difference, since in their study virtually the same RT-task was used, except that S_2 was visual.

One important difference from the Rohrbaugh et al. study is that in the present study the activity in the non-involved response side was controlled by measuring the EMG. Moreover, during the training EMG was monitored and the subjects were informed when there was activity in the non-involved arm. Thus, in the present study care was taken to limit motor preparation to the muscle groups involved in the response (see also Loveless, 1978; Syndulko and Lindsley, 1977). In any event these results show that, with regard to both the lateral and the midline distribution at least, there is no difference between the RP and the terminal CNV. Thus, the negative shifts derived from electrodes over the motor area (C_3, C_z, C_4) in the S_1-S_2 paradigm and those preceding voluntary movements seem to be the same neurophysiological phenomenon, but are obtained with different averaging methods. This notion is supported by the analysis of the movement potentials time locked to finger presses in the four experimental situations. For example, the movement potentials obtained in the RT-task and those accompanying voluntary movements both consist of a gradually increasing negative shift, which starts one sec before the response (see Fig. 5). Also the laterality effect was of the same size. The only difference between the two conditions is that the magnitude of the negative shift in the RT-task is somewhat larger, expecially with left hand responses. As was argued in the Discussion of Experiment 5 this may be explained as a larger involvement of motor systems in preparing the response in the RT-task, than in monotonously executing a series of finger presses. This larger involvement is also suggested by the EMG data time locked to the response. The amplitude of the peak preceding the response and the gradual increase before this peak is larger in the RT-task than preceding voluntary movements.

The EMG data clearly show that the behavioral data, i.e. finger presses closing a button switch, can certainly be used for obtaining movement potentials. The peak of the EMG preceded the response by between only 18 msec to 32 msec. Thus, for slow phenomena no difference in results is expected when the movement potentials are time locked to the EMG.

Although the terminal CNV was largely attenuated in the TE-task, some negativity still preceded S_2. It was assumed that the involvement of motor systems would be minimal in this task, at least before S_2. Therefore, the terminal CNV should be virtually absent if this SPS reflects motor preparation. However, it is not certain that even in the case of a delayed response there is no motor activity at all before S_2.

Sperry (1952) has suggested that, regardless of the manifest behavioral situation, the primary end-product of the brain is motor output. Situations not involving specific, overt motor response may nevertheless produce generalized effector readiness, receptor orientation (fixation of eyes), and non-automatic postural adjustments, in addition to specific motor concomitants of mental processes.

According to Syndulko and Lindsley (1977) the prominence of the vertex terminal CNV in motor tasks is so convincing that the occurrence of this SPS in so-called sensory tasks, which do not involve specific, overt motor responses suggest that the latter tasks also involve at least some "motor" elements. Some support for this notion is provided by the EMG data. The EMG activity in the TE-task, recorded just before S_2, was larger in that forearm which had to give the delayed response.

There is still another point which may obscure the comparison of motor tasks (RT-instruction) and sensory tasks (detection instruction). Although statistically not significant there was a tendency in the present study towards more EMG activity in the baseline before S_1 in the RT-task than in the TE-task. This result may indicate that the level of generalized motor readiness was already larger before S_1 in the former task. If we had controlled this (for example, by giving feedback) the preparation after S_1, and consequently the terminal CNV, should have been larger in the RT-task.

In general, possible differences between preparatory states already present before S_1 have been neglected in CNV-Research. However, it has been found that when S_1 requires a motor response the CNV is attenuated (McCallum and Papakostopoulos, 1972; Otto and Leifer, 1973). This in turn points to the fact that at the moment there is no generally agreed method of determining the DC-level of the brain; Gaillard and Näätänen (unpublished manuscript) attempted to resolve the problem by correlating the CNV-amplitude to the negativity prevailing before S_1; this negativity was referred to the zero of the amplifier and indicated the DC-shifts in the EEG in the period before S_1. Naturally the length of this period is dependent on the time constant of the amplifier, which in that study was 6 sec. It was found that the more positive the DC-level before S_1 the larger the CNV, and vice versa. This result suggests that the CNV is affected by the SPSs occurring before S_1. Further research is needed to investigate whether there are differences in preparatory states between different task situations. These differences could be indicated not only by EEG and EMG, but also by monosynaptic reflexes (see also Brunia, 1978).

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SUMMARY

Slow potential shifts (SPSs) occur in the human brain which are related to the processing of stimuli or to the execution of responses. These SPSs can be systematically investigated by deriving the EEG from the scalp using electrodes, while a subject is performing a task. The present thesis investigates the SPSs which precede the execution of a task. These SPSs are investigated by using the so-called waiting paradigm ($S_1 - S_2$ paradigm). In this paradigm S_1 serves as a warning, whereas S_2 requires some overt or covert response. The best known SPS in this situation is the Contingent Negative Variation (CNV), Originally it was thought that this negative shift was dependent (contingent) upon the association between S_1 and S_2. The aim of the present thesis was to investigate the psychological meaning of the CNV.

Experiment 1 shows that the CNV consists of at least two negative SPSs. When the interval between $S_1 - S_2$ is prolonged (3 sec instead of the usual 1 sec) the slow potential change in the ISI becomes biphasic (see Fig. 4, Chapter 2): The first SPS, the "Slow Negative Wave" (SNW) consists of an inverted U-curve, which peaks ca. 750 msec after S_1. The second SPS, the "terminal CNV", is a gradually increasing potential shift, which reaches its maximum towards the end of the interval.

Firstly, it was shown in the present series of experiments that the CNV is not related to the perception of S_2. This was done by varying the discriminability of S_2: easy vs. difficult discriminations (Experiments 2 and 3) and short vs. long-exposure duration of S_2 (Experiment 3); another method used to study this issue was to compare reaction-tasks with detection-tasks (Experiments 3, 4, 5, 6). In the former the subject is required to react as quickly as possible to S_2, whereas in the latter tasks he has to discriminate S_2 and to delay his response by one sec.

The effects of speed-accuracy instructions were investigated in Experiment 4 and 5. Under speed instructions a subject is required to react as quickly as possible, even at the cost of some errors. Under accuracy instruc-

tions the subject also gives a speedy response, but it is emphasized that he should not make errors. These instructions appear to affect both the RT and the terminal CNV.

In Experiment 1 it was found that SNW is enhanced when S_1 is auditory as compared to a visual S_1. In further experiments it was shown that the SNW is also affected by the psychological properties of S_1. Larger amplitudes are found when S_1 provides information about the task-requirements at S_2; S_1 indicated in Experiment 2 whether S_2 consisted of an easy or a difficult discrimination, in Experiment 4 the probability that S_2 would arrive, in Experiment 5 whether a speed or an accuracy instruction had to be followed.

In order to facilitate the reading of this thesis the descriptions of the experiments are given in a separate section (Appendix: Experiment 1 - 6).

After a short introduction (Chapter 1), a general outline of the methods used is given (Chapter 2) and in Chapter 3 the behavioral evidence on preparatory processes is summarized. Chapter 4 presents the ideas which guided these experiments, and the hypotheses tested in one or more experiments are formulated.

The topographical distribution of the SPSs preceding S_2 was determined in all experiments. The results of this analysis are summarized in Chapter 5.

In Chapter 6 the functional significance of the SNW is discussed on the basis of the present experiments and also of other studies. It is concluded that the SNW is dependent on both the psychological and physical characteristics of S_1. The "SPW", a slow positive wave reaching its peak ca. 300 msec after S_1, appears to be affected by the same factors as the SNW, although there are some differences. The results on the SPW are discussed in Chapter 7.

Finally, in Chapter 8 it is concluded that the terminal CNV reflects the level of motor preparation. Moreover, both its form and topographical distribution suggests that this SPS is produced by the same neurophysiological generator as the readiness potential (RP), which precedes voluntary movements.

SAMENVATTING

In de menselijke hersenen vinden langzame potentiaalverschuivingen plaats, die in verband staan met de verwerking van stimuli of met het geven van bepaalde responsies. Deze langzame potentialen, die afgeleid kunnen worden van electroden geplaatst op de schedel, zijn systematisch te onderzoeken door aan proefpersonen een taak te geven. In het huidige onderzoek ligt de nadruk op de langzame potentiaalverschuivingen, die voorafgaan aan de uitvoering van een bepaalde taak (b.v. zo snel mogelijk reageren op het aanflitsen van een lampje). Deze potentialen worden bestudeerd in het zogenaamde wachtparadigma (S_1 - S_2 paradigma); in dit paradigma wordt een waarschuwingssignaal (S_1), gevolgd door een tweede signaal (S_2), waarop een bepaalde responsie gegeven moet worden.

De meest bekende en onderzochte langzame potentiaalverschuiving is de Contingente Negatieve Variatie (CNV). Dit is een negatieve potentiaalverschuiving, waarvan men oorspronkelijk dacht dat hij afhankelijk was van (contingent was op) de associatie tussen S_1 en S_2. Doel van het huidige onderzoek is de psychologische betekenis van de CNV te achterhalen.

In Experiment 1 wordt aangetoond dat de CNV uit tenminste twee negatieve componenten bestaat: als het interval tussen S_1 en S_2 wordt verlengd (b.v. tot 3 sec) blijkt dat de langzame potentiaalverschuiving bifasisch is (zie Fig. 6, Hoofdstuk 2): de eerste component, de "Slow Negative Wave" (SNW), bestaat uit een omgekeerde U-curve, die zijn piek bereikt ongeveer 750 msec na S_1. De tweede component, "terminal CNV", is een langzaam stijgende negatieve potentiaalverschuiving, die zijn maximum bereikt vlak voor S_2.

Allereerst is aangetoond, dat de terminale CNV niet in verband staat met de waarneming van S_2. Dit werd onderzocht door de waarneembaarheid van S_2 te variëren: makkelijke vs. moeilijke discriminatie (Experiment 2 en 3) of korte vs. lange expositieduur (Experiment 3), alsook door reactietijd-taken met detectie-taken te vergelijken (Experiment 3, 4, 5 en 6). In reactietijd-taken moet de proefpersoon zo snel mogelijk reageren op S_2, terwijl hij bij detectie-taken pas één seconde na S_2, door het indrukken van een knop de bij S_2 gemaakte discriminatie moet aangeven.

In Experiment 4 en 5 werd de invloed van instructies, m.b.t. het snel, dan wel accuraat, reageren onderzocht. Bij een "snel-instructie" moet de proefpersoon zo snel mogelijk reageren en het geeft niet als hij daarbij fouten maakt; bij een "accuraat-instructie" moet hij ook snel reageren, maar er wordt de nadruk opgelegd dat hij vrijwel geen fouten mag maken. Deze instructies blijken, zowel op de reactietijd, als op de terminale CNV, van invloed te zijn.

In Experiment 1 werd gevonden dat de SNW vrijwel alleen optreedt na een auditief signaal. Bovendien blijkt dat de SNW groter is als S_1 niet alleen dient als waarschuwing, maar ook informatie geeft over de taak uit te voeren bij S_2. In Experiment 2 gaf S_1 aan of S_2 bestond uit een moeilijke dan wel uit een makkelijke discriminatie, in Experiment 4 de kans, dat S_2 zou komen en in Experiment 5, welke instructie (snel-accuraat) de proefpersoon bij S_2 moest volgen.

Teneinde de leesbaarheid te vergroten is de beschrijving van de experimenten in een apart deel ondergebracht (Appendix: Experiment 1 - 6).

Na een korte inleiding (Hoofdstuk 1), worden de in het onderzoek meestal gebruikte methoden uiteengezet (Hoofdstuk 2), waarna een samenvatting wordt gegeven over de gedragsresultaten m.b.t. preparatieprocessen (Hoofdstuk 3). In Hoofdstuk 4 worden de uitgangspunten van het onderzoek uiteengezet, en de hypothesen, die in de experimenten getoetst worden, worden geformuleerd.

De topografische verdeling op de schedel van de langzame potentiaalverschuivingen werd in alle experimenten vastgesteld. In Hoofdstuk 5 worden de resultaten van de topografische analyse samengevat.

Op grond van deze experimenten en van ander onderzoek, wordt in Hoofdstuk 6 geconcludeerd dat de SNW bepaald wordt door zowel de fysische als de psychologische betekenis van S_1. In Hoofdstuk 7 wordt de "Slow Positive Wave" (SPW) besproken, die optreedt ca. 300 msec na S_1 en in verschillende opzichten dezelfde kenmerken heeft als de SNW.

Tenslotte wordt in Hoofdstuk 8 geconcludeerd, dat de terminale CNV het niveau van motorische preparatie reflecteert. Bovendien, blijkt deze negatieve verschuiving vrijwel dezelfde vorm te hebben als de "Bereidheidspotentiaal", die voorafgaat aan willekeurige bewegingen. Daarom lijken de terminale CNV en de bereidheidspotentiaal hetzelfde neurofysiologische proces te reflecteren.