Electroencephalography and clinical Neurophysiology, 1985, 61: 548–558
Elsevier Scientific Publishers Ireland, Ltd.

P300 AND PSYCHOPHYSIOLOGICAL ANALYSIS OF THE STRUCTURE OF BEHAVIOR

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(Accepted for publication: June 17, 1985)

Summary P300 wave was analyzed on the basis of comparison between brain potentials, the structure of behavior and single unit activity within the signal detection task through experiments with humans and animals. The similarity of the late positive components following detected light flashes in humans and rabbits, identified as P300, permitted the use of data concerning single unit activity. The analysis of single unit activity in the visual and motor cortex of rabbits demonstrated that the sequence of behavioral stages in signal detection is based on different sets of units. There is a strong correspondence between the change of set and the P300 development. Since the activity of certain units in behavior reflects the realization of certain functional systems, the modification of the sets of activated units indicates the transformation of the composition of functional systems of different hierarchical levels during the change of behavioral stages. This is the basis for our suggestion that P300 reflects the process of reorganization of the structure of the behavior which is responsible for the transition from one stage of behavior to another.

Keywords: *P300 — behavior*

The use of various EEG potentials in psychophysiological studies must be based on the solution of the problem of their functional significance, i.e., one should know the events in the behavioral organization to which a certain potential is related. The urgent need to understand the meaning of the brain potentials is most obvious in numerous studies dealing with the so-called P300 component. P300 attracts so much attention from psychologists because it is undoubtedly endogenous, has a great ecological validity and an enormous range of psychological correlates (Pritchard 1981). It is due to this long list of correlates that the problem of the 'P300 phenomenon' has emerged. The solution of the problem is believed to lie in the identification of some common factor which will help to explain all properties of P300.

It is supposed that the common factor may be found by defining the behavioral event, common to all experimental paradigms, to which P300 is related, the verification of any relevant hypothesis inevitably including the characterization of brain processes basic for the chosen event (Rebert 1978; Donchin 1981; Pritchard 1981). It must be noted that consideration of the common factor in terms of activity of morphologically identified neuronal assemblies meets certain logical contradictions, i.e., it appears insufficient for an all embracing description of the functional role of P300 (e.g., Donchin 1981). If the common factor is defined by relating P300 to an event in behavior, then unit activity in the context of the problem being considered must also be identified as related to this event. This approach can be based on the fact, observed in many studies of different brain structures, including the cortical ones, that unit activity is related to various behavioral events (e.g., Evarts 1974; Mountcastle 1978; Aleksandrov and Grinchenko 1980; Watanabe 1981; Hyvärinen 1982; Shevchenko et al. 1983); in other words on the phenomenon of the behavioral specialization of neurons (Shvyrkov 1982).

The present study was designed to discover the relation of P300 to the activity of cortical units identified according to the relation of their activity to the succession of the events in the behavior. The problem has been solved in experiments with human subjects and rabbits. We used the signal detection model as it is most widely in P300 studies in humans and is easily adaptable for animal experiments. We sought to:

(1) identify the P300 component in humans

within our experimental model by traditional means: according to the wave form, latency, amplitude and topography (Donchin et al. 1977; Pritchard 1981; Rosier 1983; Sutton and Ruchkin 1984) and to describe the behavioral event related to the appearance of P300;

(2) find out the analog of P300 in rabbits in the signal detection model. Because of the obvious differences between animals and humans in the geometry of the skull and brain considered as three-dimensional conductors and also in the functional specialization of cortical areas, we identified P300 in rabbits according to the following criteria: (a) wave form, and (b) the relation to certain event in the behavior provided the similar structure of experimental models in animals and humans (Neville et al. 1982); it is enough to record EEG at one site in rabbit for that purpose;

(3) correlate the rabbit's analog of P300 with the characteristics of the activity of single cortical units identified with respect to their relation to the succession of behavioral events in the signal detection model. Considering the well-known widespread scalp distribution of P300 it is natural to suppose that the features of single unit activity, basic for this quality of P300, are characteristic for neurons in different cortical areas. That is why the single unit activity was analyzed in visual and motor cortex, their functions being mostly distinct.

Methods

General experimental paradigm and stimuli

In the experiments both with humans and animals an ascending version of the limits methods was used as signal detection task model. The observation or waiting interval was considered as a trial. During a waiting interval soundless light flashes in blocks of 4–7 with constant intervals of 1.2 sec and intensity increasing from 10^{-6} to 10^{-2} nits were presented on a screen. Light flash duration was 50 msec. The experiments were conducted in a dark room after 30 min of dark adaptation. Before the beginning of the experiment the range of intensity increase was adjusted for each subject so that the maximum of hit probability corresponded to the third or fourth flash in the trial. The 2 or 3 flashes preceding the detected one were of near threshold intensity, i.e., the probability of their detection was not zero.

The present modification of the limit method could result in the following alternatives of detection: hits, false alarms and misses of a signal. Phenomenologically the signal detection behavior may be regarded as a succession of two stages: waiting for a signal and report. In such terms hit is the change between two stages in accordance with presentation of the signal, false alarm is the change of the stages without a signal, miss of a signal may be defined as a failure to detect a presented flash and pass to the report stage. As the correct fulfillment of the detection task is the change of successive stages related to the signal presentation, it is obvious that the form of the change does not depend significantly on the mode of onset of the waiting interval and, perhaps, on the concrete form of the behavior at the report stage. This makes possible the consideration of the behavioral structures in humans and animals as comparable ones with respect to the problem involved in spite of some methodical differences arising from the adjustment of the procedure for rabbits vs. human subjects.

Experiment 1

Subjects and procedure

Ten normal adults (7 males and 3 females) aged between 20 and 34 years participated in the experiment and were paid at uniform hourly rate. All subjects had normal or corrected vision. Most of them were quite familiar with the techniques and requirements of the EEG recording.

The subject sat in a comfortable chair 60 cm from a screen and was instructed to fixate the gaze on a fixation point and, having detected a flash, to press a button as quickly as possible. Each trial began by a warning signal followed by the presentation of light flashes over 1–4 sec.

The trials with button pressings with latency of 200–600 msec after a flash (according to data of Pièron (1922) on reaction time to threshold stimuli) were classified as hits. False alarms were the trials with button pressings during the interval between

a warning stimulus and the first flash in a block. The following criteria were used for identification of misses of a signal in humans. First, the trials with no button presses during the whole observation interval, second, fixation of subject's gaze was quite similar to that in hits.

Recording system

The EEG was recorded from 7 electrodes each referred to the linked ear-lobes. The electrodes were fixed at F3, F4, Cz, P3, P4, O1, O2. EEG electrode impedance was below 3 kΩ. Subjects were grounded at the right wrist. Vertical and horizontal eye movements were monitored by recording the EOG from electrodes placed supraorbitally and over the outer canthus of the left eye (see Connolly and Kleinman 1978). In order to exclude trials with incorrect fixation of the gaze the EOG was calibrated by the eye movements approximately to 6° of visual angle, which corresponded to the angular size of the screen. This control was necessary for identification of misses. Any EOG deflection on a given trial exceeding 6° visual angle (as well as blinks) resulted in that trial being discarded.

The EEG was amplified (time constant 2 sec, high-frequency cut-off 1000 Hz) as well as the EOG (time constant 2 sec, high-frequency cut-off 30 Hz). During the previously described behavior we also recorded the marks of warning signal and of the block of light flashes as well as the mechanogram of the button pressing. The button was a force transducer and enabled the recording of 'micropressings' (from 30 g) as well as of pressing after the detected flash (about 3 kg). The whole excursion of the button was 4 mm.

Data collection and processing

The presentation of a warning signal (click of 60 dB, 20 msec duration) and light flashes was controlled by a computer. EEG, EOG, output of the force transducer and the codes associated with clicks and light flashes were sampled on-line and. stored on magnetic tape. The data collection initiated either 2 sec before the click (sampling rate 100/sec, analysis period 10 sec) or from the onset of the first flash in the block (sampling rate 200/sec, analysis period 5 sec). Each sampled epoch was checked before final storage using the display and all epochs showing EOG artifacts were discarded. The data were stored in magnetic memory, including 70 trials of 10 sec epochs and 140 trials of 5 sec epochs for each subject, and finally processed off-line on a computer. The EEG was averaged from the onsets of detected and undetected flashes and also from the beginning of button pressing after the detected flash. Differences in amplitude and temporal characteristics of potentials were evaluated by *t* test.

Experiment 2

Subjects and procedure

Ten freely moving rabbits were used in the experiment. They were trained to wait for a light flash while sitting on a special platform (Fig. 1_6) (the distance from the screen (Fig. 1_3) was 10 cm), where they had to maintain a certain posture. Having seen the flash, the rabbit had to run to the lever (Fig. 1_4) and press it to receive a portion of food. In each trial blocks of light flashes were presented 0.5–10 sec after the onset of the posture. The lever activating the feeder device (Fig. 1_5) was operative only during the presentation of flashes.

In animal experiments hits were identified as trials in which the rabbit ran to the lever with a latency of 150–700 msec after the flash, which coincided with the distribution of latencies when single flashes of the same intensity were presented. It is important to note here that if the intensity of all flashes in a block was increased, the number of the detected flash decreased until the moment when flash N.1 was always detected. Then the flash detection probability was 0.66, it did not differ from the probability to detect the single flash of the same intensity (0.69). This supports the supposition that the rabbit started to run to the lever after the first detected flash, thus making the run to the lever a very exact mark of detection. False alarms were classified as trials in which the rabbit ran to the lever during the interval between the onset of posture and the first flash in the block. Misses were trials with no run to the lever during the observation interval, providing the fixation of gaze was correct.

Recording system

The EEG was recorded from the visual cortex by nichrome wire electrodes implanted into the skull (upper frequency cut-off being 1000 Hz, time constant 2 sec). A reference electrode was fixed in the nasal bone. Single unit activity was recorded from the visual and motor cortex (VC and MC) (coordinates E — 9 and A + 3 respectively, see Monnier and Gangloff (1961)). Glass microelectrodes with a tip diameter of about 1 μm, filled with 3 M KC1 solution, were used. Electrodes were driven by a mechanical manipulator (Grinchenko and Shvyrkov 1974) with steps of about 5 μm. The micromanipulator was screwed into a special nut fixed to the skull by plastic above a trephine hole 4 mm in diameter. Brain pulsation was minimized by sealing the trephine hole with agar gel. EEG and single unit activity were recorded in the same rabbits, sometimes during the same series and sometimes during successive ones.

During the described procedure the following parameters were also recorded: the marks of light flashes, pressings of the platform and the lever, the marks of food taking, the recording of head movements by a photoelectric technique and/or the electrical activity of masticatory muscles with implanted bipolar electrodes (Basmajian and Stecko 1962). An infra-red light-emitting diode (wave lenght 950 nm, i.e., beyond the range of rabbit's vision (Nuboer and Wessels 1975)) was fastened to the animal's head (Fig. 1_5) and highly sensitive photoelectric plates (Fig. 1_2) were placed in the corners of the experimental chamber. Photoelectric plate potentials recorded by means of DC amplifiers permitted recording of the position and displacement of rabbit's head at any moment. Electrical activity of the masticatory muscles was also used for recording head movement because it activated prior to or simultaneously with the onset of head displacement (Aleksandrov and Grinchenko 1980). It was found that saccadic and vergence eye movements of the rabbit were strictly connected with head movements (Zuidam and Collewijn 1979; Van der Steen 1981). These facts gave a way to check the fixation of the rabbit's gaze by recording of head movements.

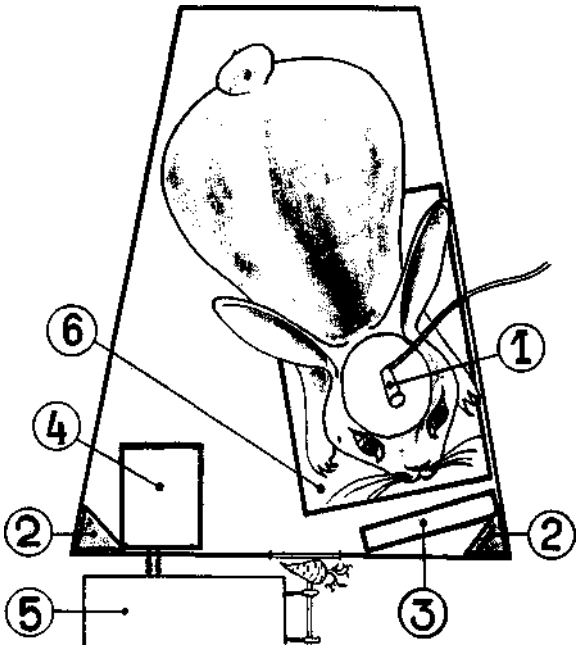

Fig. 1. Design of experimental chamber for studying signal detection in rabbit. 1, infra-red light-emitting diode; 2, highly sensitive photoelectric plates; 3, screen for presenting light flashes; 4, lever for turning on the feeder device (5); 6, platform for waiting for a signal.

Data collection and processing

During the experiment the single unit activity and EEG, along with marks, were amplified and recorded on a 4-channel tape recorder and finally in computer magnetic memory by means of continuous acquisition at a 5 msec sampling rate. The EEG averaging, comparison of potentials by *t* test, plotting of histograms for unit activity from the onset of posture, the onset of detected and undetected flashes and the beginning of the rabbit's movement to the lever were done by computer.

The mean discharge frequency was calculated and unit activity histograms were analyzed on the basis of time relations to the whole stages of behavior: waiting for a signal (from the onset of posture till the onset of the run towards the lever) and run to the lever (from movement onset to taking food or to some events, related to the realization of these stages, that may be considered as fragments (or substages) of the whole, such as onset of posture, discrete movements during posture maintenance, start of the run to the lever,

food taking. 'Activation' was defined in unit activity histograms as significant ($P \leq 0.05$, t test) activity increase as compared with the interval between the end of mastication and the onset of posture. Only those units were analyzed, the activity of which was recorded in the course of not less than 4 hits.

Results

(I) Comparison of human EEG potentials with those of rabbits during signal detection

(I.1) Human EEG potentials. In the averaging of EEG sections time-locked to the detected flash in hits it was found that a slow negative potential corresponds to the stage of waiting for a signal. This negative wave is completed with a negative-positive potential after the detected flash (Fig. 2A,B). The large amplitude positive component of the potential looked very much alike in all subjects and had the following properties, pooled for all subjects: onset latency 290–340 msec, peak latency 470–640 msec (range of averaged latencies for different locations), peak-to-peak amplitude 14–25 μV, with the maximal amplitude in central (Cz) and parietal (P3, P4) locations (Fig. 2C). Comparison of the amplitudes of this component in different locations revealed that in P3, P4 and Cz it was significantly greater than in F3 and F4 ($P < 0.05$). The amplitude of the component in O1 and O2 was smaller than in P3, P4 and Cz, but greater than in F3 and F4; however, the significance of these differences was $0.05 < P < 0.1$.

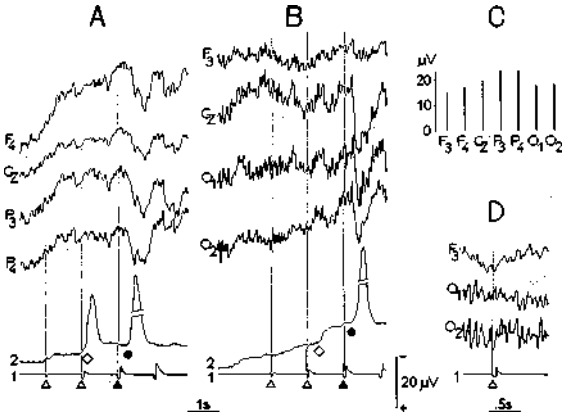

Fig. 2. Human EEG potentials in signal detection task. A and B: hits: original curves for two subjects, averaging from the detected flash (A: n = 31; B: n = 26). C: scalp distribution of the positive component (grand mean for all subjects) in hits. D: misses of signal: averaging from undetected flashes. 1, marks of light flashes: open triangles — undetected, filled triangles — detected; 2, mechanogram of button pressing: open rhombs — micromovements, filled circles — onset of the button pressing after the detected flashes. Mechanogram of the button pressing after the detected flash is shown schematically.

Potential shift in the positive direction in hits coincided with the button pressing during the stage of report. The averaging of the EEG from the onset of button pressing in hits revealed that for a group of subjects the onset of the positive component was distributed over the interval that began 200 msec prior to and finished 50 msec after the movement onset. This demonstrated that there was no strict relation between the onset of the positive component and the onset of button pressing, which was also confirmed by the insignificance of correlation between the mean latency of movement onset and the mean latency of the positive component calculated for each subject (0.2–0.38 for different locations).

One characteristic of the behavior during the stage of waiting for a flash is worth noting: during this stage pressings were recorded in all subjects, phasic up to about 300 g (Fig. 2A, B_2), that were never mentioned in the reports even after special questioning. No large amplitude positive component time-locked to such 'micropressings' occurred. This positive component was also not observed in relation to the flashes that preceded the detected one.

As false alarms occurred in approximately *2%* of trials (mean for the whole group), i.e., in our experimental model they were observed very rarely, we could not record a sufficient number for EEG analysis.

The investigation of misses by means of EEG averaging from the undetected flashes revealed no components similar to those characteristic for hits (Fig. 2D), though the brightness of the flashes and the fixation of gaze were the same on both occasions.

(I.2) Rabbit EEG potentials. During hits averaged from the detected flash a large amplitude

positive component was observed. In all rabbits the positive component completed the slow negative deflection corresponding to the stage of waiting for a signal (Fig. 3A); a warning stimulus was not necessary for recording this negative potential (Rohrbaugh and Gaillard 1983). The positive components looked very much alike in all animals and had the following properties pooled for all rabbits: onset latency 113 ± 65 msec, peak latency 414 ± 154 msec, amplitude 86.2 ± 14.3 juV. On averaging the EEG from the start of the rabbit's run to the lever in hits it was found that the onset of the positive component was distributed in the interval that began 150 msec prior to and finished 100 msec after the movement onset. This pointed to the absence of any strict relation between the onset of positivity and the movement onset.

During the false alarms the positive component was found in all animals (Fig. 3B) with an amplitude of 82 ± 19.4 μV; the onset of positivity began 120 msec prior to and finished 140 msec after the movement onset. Comparison of the potentials, averaged from the movement onset, in hits and false alarms, for each animal in the interval which began 500 msec prior to and 500 msec after the movement onset, revealed no significant differences in their wave forms even for $P = 0.2$. After averaging of EEG sections time-locked to undetected flashes (in misses) no such large amplitude potential was found in any animal.

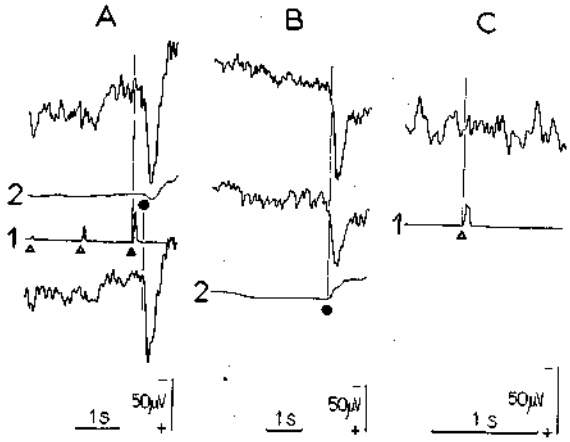

Fig. 3. Rabbit visual cortex EEG potentials in signal detection task. A: hits: above — potential averaged from the onset of the detected flash (filled triangle), n = 20, below — potential averaged from the onset of movement after the detected flash (filled circle), n = 20. B: comparison of the potentials averaged from the onset of the run towards the lever (filled circle) during false alarms (above, n = 31) and hits (below, n = 19). C: misses of signal: averaging from the undetected flashes (open triangle). A, original curves from one animal; B and C, from another one; 1, marks of light flashes; 2, record of rabbit's head movement.

(II) Analysis of unit activity of visual and motor cortex in rabbit

The activity of 61 VC units and 60 MC units was analyzed during signal detection behavior. Eleven VC units and 13 MC units did not change their activity in relation to behavior. The activity of 45 VC and 44 MC units, for which we could

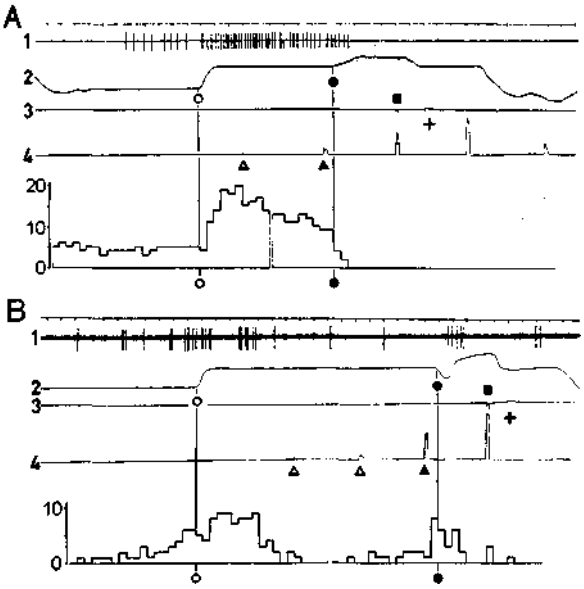

Fig. 4. Relation between rabbit motor cortex unit activity and the stages of behavior. A: example of a unit with activation related to the whole stage of waiting for a flash: from the posture onset until the onset of the run towards the lever, n = 8. B: example of a unit with activation related to fragments of the stages of waiting for a flash and the run towards the lever, n = 8. Above: time scale: A, 200 msec, B, 100 msec; 1, unit activity, 2, record of rabbit's head movement: open circle, posture onset, filled circle, onset of the run; 3, marks of lever presses (filled square) and of food taking (cross); 4, marks of light flashes: open triangles, undetected, filled triangles, detected. A and B below: histograms of unit activity, averaged from the onset of posture (left) and from the onset of the run towards the lever (right); height of the bars — number of spikes in an interval.

define the moments of onset and offset of activation in the activity histogram, was analyzed in relation to the stages of behavior or their substages (see Methods). The activations of 25 MC units lasted through the whole stage (12 units were activated during the stage of waiting for a signal, 13 during the run to the lever) (Fig. 4A); activations of the remaining 19 units were related to the substages (Fig. 4B). It is interesting to note that one unit could have activations related to the few substages of behavior. VC units could be grouped as follows: 23 units had their activations related to whole stages (12 to waiting for a signal, 11 to the run to the lever) (Fig. 5A); relation of activity to the substages was demonstrated in 22 units (Fig. 5B). Here we may stress the fact that both types of unit were recorded in all animals in VC as well as in MC. This is in line with the data concerning the similarity of relation of unit activity in various structures of the rabbit's brain to the stages of behavior realization (e.g., Shvyrkov 1977, 1982; Aleksandrov and Aleksandrov 1982). Thus the successive stages of a signal detection behavior are based on different, partly overlapping (due to the units active at substages) sets of the units in agreement with data obtained by Shevchenko (1980).

In order to evaluate the dynamics of the unit activity changes at successive behavioral stages we

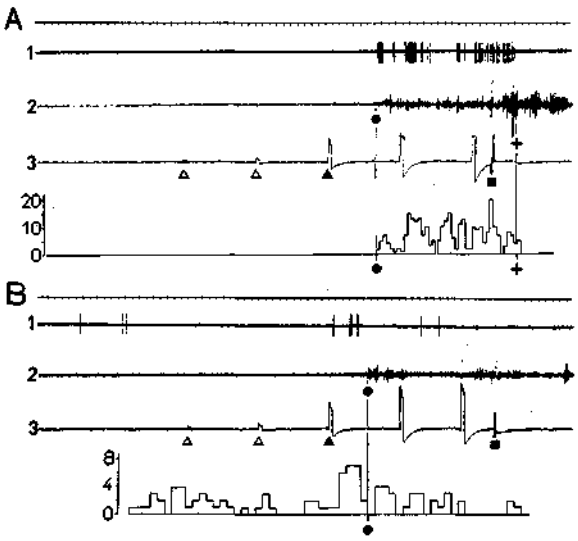

Fig. 5. Relation of the visual cortex unit activity to the stages of behavior. A: example of a unit with activation related to the whole stage of the run towards the lever: from movement onset to food taking, n = 4. B: example of a unit with activation confined to the onset of movement towards the lever, n = 15. Above: time scale 100 msec. 1, unit activity; 2, EMG of masticatory muscles; 3, marks of light flashes. Histograms averaged: A, from the onset of the run towards the lever (left) and from the moment of food taking (right); B, from the onset of the run towards the lever. For other marks see Fig. 4.

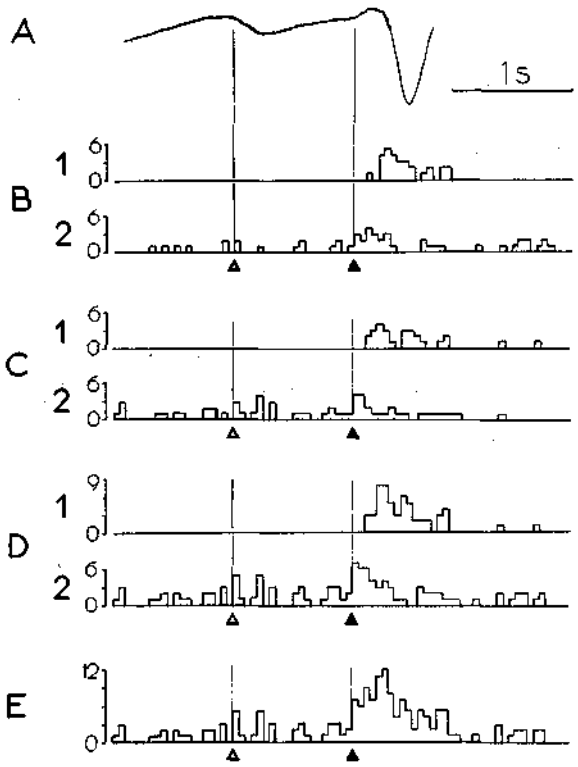

Fig. 6. Comparison of rabbit visual cortex EEG potential and the distributions of the moments of onsets and offsets of unit activation in hits. A: schematic representation of EEG potential; onset and peak latency of the positive component, grand mean for all animals; open triangle, undetected flash, filled triangle, detected one. B–E: histograms of temporal distribution of the onsets and offsets of unit activation; height of the bar, number of such events during the given interval. 1, distribution of units active during either the whole stage of waiting for a flash or the whole stage of the run towards the lever; 2, distribution of units with activation related to fragments of the stages (one unit of this type could have the changes of activity related to the few fragments of the stages). B: distributions for 44 motor cortex units. C: distributions for 45 visual cortex units. D: distributions summing up the data for visual and motor cortex units. E: summarized distribution for both unit types and both cortical areas.

plotted the temporal distributions of the onsets and offsets of the activations in all units analyzed in hits (Fig. 6). We drew attention to the fact that the analyzed distributions were alike for the MC and VC units (Fig. 6B and C).

Although activity changes were seen throughout the whole analyzed interval of behavior, the greatest changes began from the moment of a detected flash and lasted about 800 msec after it (Fig. 6D, E). It is possible to conclude that during this interval the change of the set of active units is most marked — this change is related to the change of the sets of units underlying the successive stages of behavior.

The differences between the distributions of an activity in the units active during whole stages and in the units related to the substages are worth noting. The activity changes in the units related to whole stages were seen mostly during the interval of 200–600 msec after the detected flash (83% of units of this type) (Fig. $6B_1$, C_1, D_1), whereas in the units related to substages the activity changes as a rule were confined to the interval of 0–300 msec (81% of units of this type) (Fig. $6B_2$, C_2, D_2). In other words the large amplitude positive component (Fig. 6A) recorded during hits was related to the changes of activation in the units of both types, but mostly in those having their activity related to whole stages.

As during the interval to which the change of active units' sets is confined both sets of units may be active simultaneously (units related to the stage of waiting for a signal and those related to the stage of a run to the lever) we controlled the relation of the positive component to the change in average level of spike activity. For all units (45 VC and 44 MC units) we correlated the rate of discharge during the 300 msec prior to the detected flash (i.e., always before the onset of the positive change) and during the 300 msec related to the peak of the positive component (i.e., 250–550 msec after the detected flash). Mean rates for VC units during these intervals were 1.03 and 1.12 spikes/100 msec; for MC units — 0.86 and 0.83 spikes/100 msec; these values do not appear different even for $P = 0.2$. These data imply that the development of the large amplitude component during the studied behavior is not related to the change (increase or decrease) of mean rate of discharge.

Discussion

The positive component found in humans in hits with respect to its amplitude and temporal features, specific topography and relative independence of the physical characteristics of the stimulus and the physical movement might be referred to as one of the P300 class and identified as P3b (N.K. Squires et al. 1975; Pritchard 1981). The positive component, due to its characteristics, is quite similar to that recorded during the detection of auditory signals (K.C. Squires et al. 1975) and moving objects (Cooper et al. 1977). In addition to the aforementioned characteristics P300 may be characterized in terms of its relation to the fulfillment of a signal detection task. This component was observed in hits and was observed in the situations of the change of successive behavioral stages (see Methods).

The relation of P300 to a certain stage in behavior is of great importance for the identification of endogenous potentials in animals. The positive component recorded in the animal experiments not only resembles P300 in humans by its temporal characteristics, wave form and its relation to the onset of movement but it is also observed in hits and false alarms and never in misses of a signal. Thus it may be concluded that in our experimental model this positive component recorded in animals may be considered as an analog of the human P300 in spite of the differences in the contents and physical performance of the behavior. The comparability of P300 in humans and animals has been demonstrated previously (Wilder et al. 1981; Arthur and Starr 1984; Neville and Foot 1984); our results may be added to the arguments put forward in these works.

The fact that P300 is observed in the situations of change of the successive behavioral stages makes possible the relation of this component to the characteristics of unit activity analyzed in relation to this event in behavior. Our main finding is that P300 is temporally related to the period of maximal change of the sets of units related to the

realization of the successive stages of signal detection behavior. In order to explain this we think it necessary to analyze in more detail the phenomenon of the behavioral specialization of units.

In terms of functional system theory (Anokhin 1974) the basis of the phenomenon of the behavioral specialization of neurons is supposed to be their involvement in certain functional systems (Shvyrkov 1982). Each functional system is formed during a certain ontogenetic stage as a whole behavioral act, correlated with the needs of the organism, with the organism's motor capabilities and with the characteristics of the environment in which this act is performed (Shvyrkov 1982).

Firing of an individual unit is considered as a retrieval from memory of a certain functional system as a whole. The set of neurons active at a certain stage of a behavior may be used to characterize the set of actualized systems and their interrelations which are related to the structure of behavior at that stage.

From this viewpoint the fact that in the successive stages of signal detection behavior the activity of different, partially overlapping, sets of neurons are involved means that at these stages different systems and intersystemic relations are realized, which correspond to two different states of the subject (Shvyrkov 1982). The relation of unit activity to the whole behavioral stages or substages makes possible the association of unit activity with the functional systems of the different hierarchical levels (Aleksandrov and Grinchenko 1980) and makes also possible the division of the unit pool into two groups, related to the systems of higher hierarchical level (with the activity related to the whole stage) and to subsystems (with the activity related to the substages).

The change of systems during the transition from one behavioral stage to another, as shown in our study, starts from the 'lowest' systems to the 'highest' ones, the change of the systems of the higher hierarchical level being probably possible only when the systems of lower hierarchical levels are changed. Moreover, reorganization of some units' activity is observed through the whole analyzed interval of behavior, which reflects the permanent existence of the dynamics of intersystemic relations. The changes of the behavioral stages and P300 probably take place, however, only when the reorganization of intersystemic relations embraces all levels of the behavioral organization and may be associated with the reorganization of the state of the subject.

The change of unit activity during the interval of P300 development takes place in such a way that during the change of sets of active units some activations overlap in time but some are separated by an interval. Therefore we did not observe any significant increase or decrease of firing during this period for the whole group of analyzed units. It is reasonable to suppose that the mode of change of the sets may vary with the experimental situation and the brain structure and may be accompanied either by an increase (Halgren et al. 1980) or decrease (for review see Rebert 1978) of firing or, as we have demonstrated, with unchanging discharge activity.

The fact that the dynamics of the activity changes in VC units closely resembles that in MC units is in line with the thesis of the functional system theory concerning the similar temporal organization of the activity in different brain structures during behavioral realization (Anokhin 1974; Shvyrkov 1977,1982). It is this characteristic of activity changes that may be basic for the widespread topographic representation of P300.

Thus the hypothesis states that the change of state of the subject's behavior is the factor determining the manifestation and the principal characteristics of P300.

In spite of the great spectrum of tasks which subjects have to perform according to various instructions, most of the experimental models designed for the studies of P300 have somewhat common structures. As a rule the instruction demands the subject to respond in a certain way (to press the key by left or right hand, to count) to particular kinds of stimuli (of different modalities, of different levels of intensity or to verbal stimuli). In the continuum of any experimental situation the successive behavioral stages may be phenomenologically distinguished (as in the present work) as follows: waiting for the presentation of the signal and report (or autoreport). In other words the change of the state of subject that determines both the occurrence of P300 and its characteristics is present in any model.

Probably an attempt to consider P300 as a manifestation of the processes of reorganization of behavioral structure shows the way to integrate the behavioral, psychological and neurophysiological evidence in order to understand the psychophysiological functional role of P300.

Résumé

P300 et analyse psychophysiologique de la structure du comportement

L'onde P300 a été analysée en comparant les potentiels cérébraux, la structure du comportement et 1'activité unitaire dans une tâche de détection de signal au cours d'expériences sur 1'homme et 1'animal. La similitude entre les composantes positives tardives qui suivent la détection d'éclairs chez 1'homme et chez le lapin, identifiées comme P300, a permis d'utiliser les données relatives à 1'activité unitaire. L'analyse de cette dernière dans le cortex visuel et moteur du lapin a montré que la succession d'étapes comportementales dans la détection du signal se base sur différents ensembles d'unités. Il y a une correspondance importante entre le changement d'ensemble et le développement de la P300. Puisque 1'activité de certains neurones dans le comportement reflète la réalisation d'un certain système fonctionnel, la modification des ensembles d'unités activées signe la transformation de la composition des systèmes fonctionnels de différents niveaux hiérarchiques pendant le changement d'étape comportementale. Ceci conforte notre suggestion que la P300 reflète le processus de réorganisation de la structure du comportement qui est responsable de la transition d'un stade à 1'autre du comportement.

We thank Dr. L.I. Aleksandrov for his helpful comments and for his invaluable assistance in preparation of this report for publication. The authors are indebted to Dr. T. Järvilehto for his critical reading of the manuscript.

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