ACTA NEUROBIOLOGIAE EXPERIMENTALIS

Acta Neurobiol Exp 2004, 64: 229-238

Contextual impact on sensory processing at the barrel cortex of awake rat

Ewa Kublik

Department of Neurophysiology, Nencki Institute of Experimental Biology, 3 Pasteur St., 02-093 Warsaw, Poland, Email: e.kublik@nencki.gov.pl

Minireview

Abstract. In order to understand the processing of sensory information in different behavioral situations we recorded evoked potentials (EP) to stimulation of a single vibrissa in the barrel cortex of non-anesthetized rat. We attributed the two principal components of the first negative wave (N1) of the cortical EP to the activation of two pyramidal cell populations (supra- and infragranular) of the central barrel-column. A positive wave of longer latency (P2) reflected the activation of the neighboring columns of the barrel cortex. The EPs recorded continuously throughout the experiment could be sorted into two classes dominated by the activity of either infra- or supragranular pyramidal cells. The introduction of an aversive contextual stimuli increased the amplitude of the second component of the N1 wave, which is built up by activation of infragranular cells, and the amplitude of the P2 wave representing excitation of neighboring columns. We hypothesize that increased activity of infragranular cells activates a cortico-thalamo-cortical loop going through the POm nucleus, which finally excites wider areas of primary somatosensory cortex. This spread of activity enables the comparison of information from neighboring vibrissae at the mystacial pad. The general cortical activation caused by the introduction of the contextual stimuli might be induced by noradrenergic and/or cholinergic systems. Prolonged contextual stimulation causes habituation processes, which return the cortical network to an idle state.

Key words: somatosensory cortex, evoked potentials, principal components, cortical surface cooling, aversive reinforcement, functional cortical states

INTRODUCTION

Introduction of new, possibly dangerous, stimuli in an animal's environment induces changes in sensory information processing necessary for a fast analysis of the new situation. These changes can be seen already at the level of the primary sensory cortex. For monitoring modifications of early sensory processing, we have utilized the method of chronic recordings of the evoked potentials (EP) from the vibrissa-barrel system of the rat. The relatively simple and well known anatomy of this sensory pathway permits precise electrode placement. The EPs comprise information about the electrical events dominating within a monitored population of cells in consecutive moments of time.

VIBRISSA-BARREL SYSTEM

The vibrissa-barrel system in rodents (Armstrong-James and Fox 1987, Jones and Diamond 1995, Simons 1978, 1995, Welker 1971, Woolsey and Van der Loos 1970) offers excellent conditions for studying the mech-

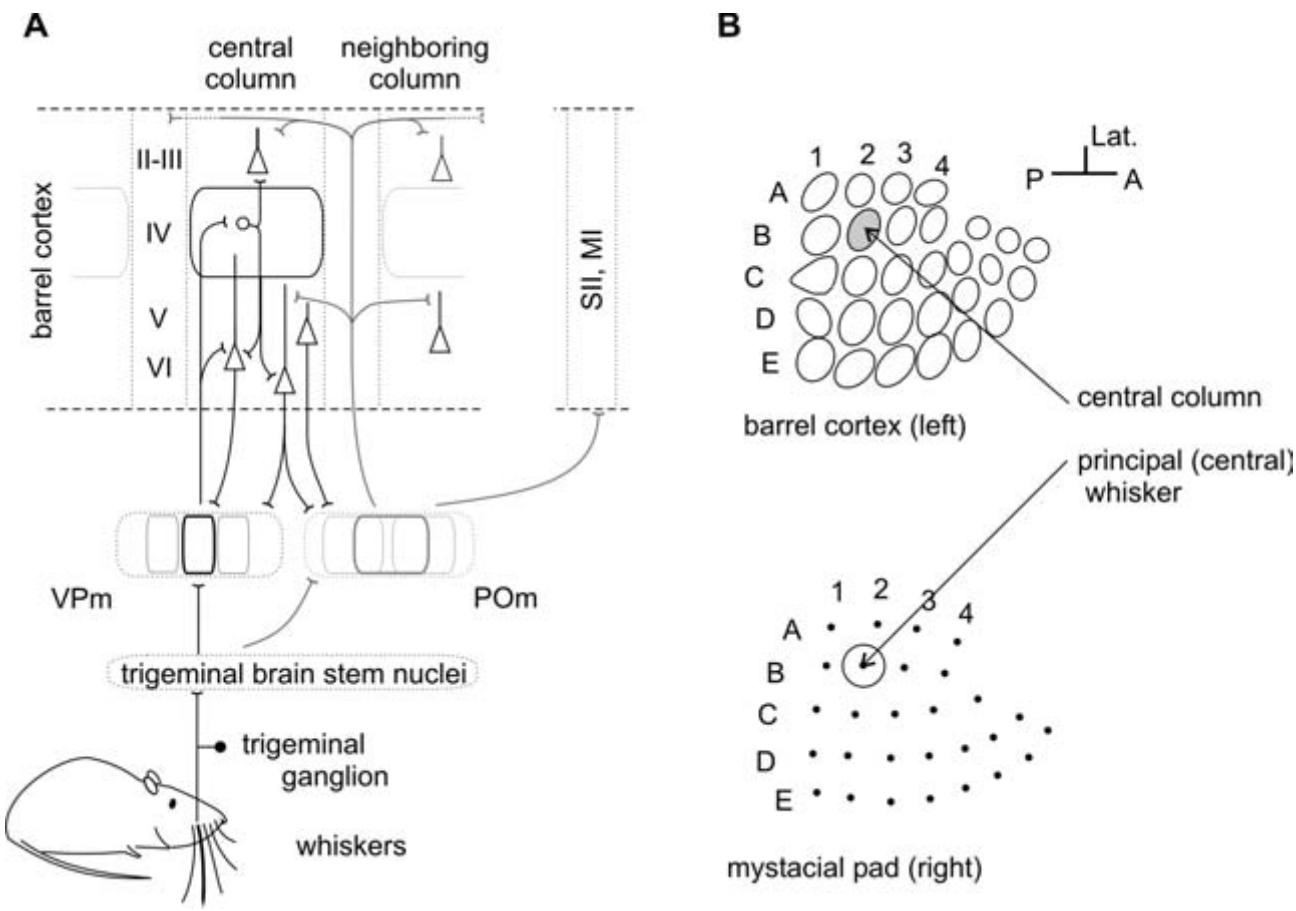

Fig. 1. Simplified schema of the rat's vibrissa – barrel system. (A) Signal from a single vibrissa is transmitted by the lemniscal pathway with a relatively precise somatotopic mapping: going through separate "barreloids" in the ventral posteromedial nucleus (VPm) of the thalamus to individual "barrels" in layer IV of the primary somatosensory cortex ("barrel cortex"). Less precise somatotopic organization can be found within the secondary, paralemniscal pathway: cells in the medial posterior nucleus of the thalamus (POm) receive information from many whiskers and send their axons to layers I and Va of the large portion of the barrel field and additionally to the secondary somatosensory cortex and other cortical regions (SII, MI). Pyramidal cells in layers II-III are called "supragranular", in layers V-VI "infragranular". Axons from infragranular cells send cortico-thalamic fibres from layer VI to VPm, and from layer V and VI to the POm. (B) Lower panel: whiskers grow on the mystacial pad in 5 rows labeled A-E. Consecutive whiskers are numbered from back to front on the snout. Upper panel: a scheme of the tangential section of the barrel cortex at the level of layer IV showing spatial organization of barrel-columns repeating a whisker pattern. Whiskers and corresponding columns located in the same position within the pattern (e.g., B2) are referred to as central (or principal) whisker and central (principal) column.

anisms of sensory information processing. Single whiskers are represented by relatively well defined groups of neurons at each step of this sensory pathway. In the principal trigeminal nucleus of the brain-stem these groupings are called "barreletts" (Ma 1991, Ma and Woolsey 1984); in the ventral posteromedial (VPm) nucleus of the thalamus – "barreloids" (Chmielowska et al. 1989, Diamond 1995, Land et al. 1995) and finally, in layer IV of the primary somatosensory cortex (the "barrel cortex") they are called "barrels". The "barrel-column", which forms the cortical unit processing of the single vibrissa, is composed from the corresponding neurons below and above layer IV (Fig. 1A). Such columns form a similar spatial pattern within the sensory cortex as the whiskers on the mystacial pad (Fig. 1B). Less precise somatotopic organization can be found in the medial posterior nucleus (POm) - another thalamic nucleus that process tactile information from the whiskers. POm neurons also send their axons to the barrel cortex (and to other cortices like SII) but in a more diffuse manner (Deschênes et al. 1998). The VPm and the POm are strongly influenced by the level of cortical activity, both receiving strong cortico-thalamic input: VPm from layer VI and POm from layer V and VI (Diamond et al.1992, Kublik et al. 2003, Temereanca and Simons 2004, Yuan et al. 1985, 1986). The reciprocal connections within cortico-thalamo-cortical systems were proposed to underlie gate/gain mechanisms at the early stage of sensory pathways and during contextual facilitation (Lindström and Wróbel 1990, Wróbel et al. 1998).

RESPONSES EVOKED IN THE BARREL CORTEX BY WHISKER STIMULATION

Local field potentials (LFP) recorded from a cortical tissue summate excitatory and inhibitory postsynaptic potentials of many cells in the neighborhood of the electrode's tip (Martin 1995). When the activity of these cells is synchronized by a sensory stimulus, it produces a visible characteristic sequence of waves (the evoked potential, EP). Figure 2A shows the averaged evoked potential after whisker stimulation, recorded by electrodes implanted in layer IV of the rat's barrel cortex. The EP consists of three main waves: P1 (5 ms latency after stimulation), N1 (10 ms) and P2 (18-40 ms). Single unit recordings have shown that stimulation of a single vibrissa activates cells in more then one barrel-column, and *vice-versa* – neurons from one column respond to more then one whisker with different latency and magnitude (Armstrong-James 1995, Armstrong-James et al. 1992, Keller 1995). This is also true for the EPs: maximal peak-to-peak amplitude can be obtained after stimulation of the corresponding whisker (Fig. 1B). The EPs evoked by stimulation of whiskers surrounding the principal one have smaller amplitudes (Fig. 3). These potentials can be attributed to passive electric field flow from the surrounding columns and/or activation of neurons in the central column by the lateral routes from the neighboring whiskers. Thus, the single EP recorded from the

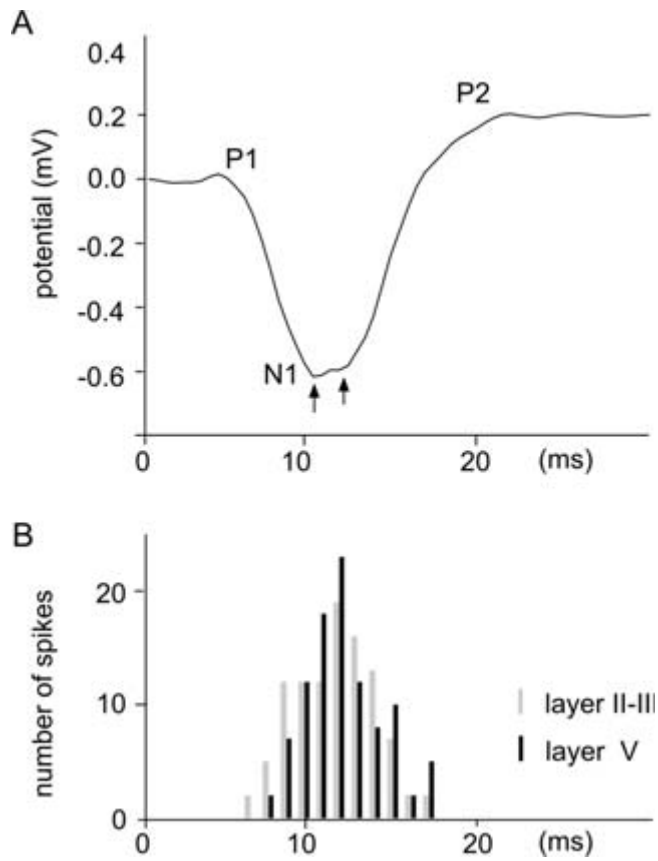

Fig. 2. Responses evoked in the barrel cortex by single whisker stimulation. (A) An evoked potential averaged from 83 vibrissa stimulations during one experimental session. Main negative wave (N1) of the EP corresponds in time to the distribution of response latencies of single pyramidal cells located in the central column (shown in B). (B) Latency histograms of the pyramidal cells' responses to whisker stimulation (gray – supragranular cells, black – infragranular cells) drawn on the basis of the data reported by Shimegi et al. (1999). Note small time shift between single-unit activation of cell populations from upper and lower layers in the PSTH and corresponding small ripples in the N1 wave minimum of the EP (arrows in A).

barrel cortex encompasses postsynaptic fields from heterogeneous groups of neurons, located not only within central but also in neighboring cortical columns.

In order to understand the consecutive activation steps of cortical processing one should first dissociate the components forming up each evoked response. Local field potentials in the cortex are dominated by activity of the pyramidal cells, whose apical dendrites form large dipoles extending through the most of the cortical depth (Barth and Di 1991, Barth et al. 1989, Di et al. 1990, Martin 1995, Wróbel 1997). The course of the N1 wave corresponds in time to the distribution of the shortest latencies of the single unit responses of pyramidal cells located in the central column (Fig. 2B) (Armstrong-James 1995, Armstrong-James et al. 1992, Shimegi et al. 1999). N1 amplitude dropped rapidly when we stimulated vibrissa located far from the principal one, which suggests that this short latency wave is related mainly to the activity evoked in the central column by the principal whisker and is not transmitted within the barrel field. For the P2 wave we found the opposite: despite the fact that peak value of its amplitude was smaller then that of N1, it's extent on the cortical surface was much wider (Fig. 3). We concluded that this wave resulted from activation of the columns in a large portion of the barrel-field transmitted by long distance intra-cortical connections within supragranular layers or by multi-whisker thalamic input. Our unpublished data showed also that the P2 was more pronounced in non-anesthetized rats and it may therefore represent surrounding activity transmitted by the cortico-cortical connections engaged in higher order functions. These results are in line with data reported by other authors who found that P2 is reduced during SII inactivation (Jackson and Cauller 1998).

Current source density (CSD) analysis attributed two main sources of cortical evoked potentials (EPs) to two pyramidal cell groups in "supragranular" (II-III) and "infragranular" (V-VI) cortical layers (Barth et al. 1989, Di et al. 1990, Mitzdorf 1985, Wróbel 1997). Our own results are in line with these observations. Cortical response to stimulation depends on the current state of the local network that is constantly modulated by the ongoing activity (Arieli et al. 1996, Musiał et al. 1998b). This can explain the variability of the potentials evoked by the same stimulus in consecutive applications. When a number of sources contribute to an EP, each of the resulting subcomponents can be influenced by the background activity in a different manner. In order to reveal

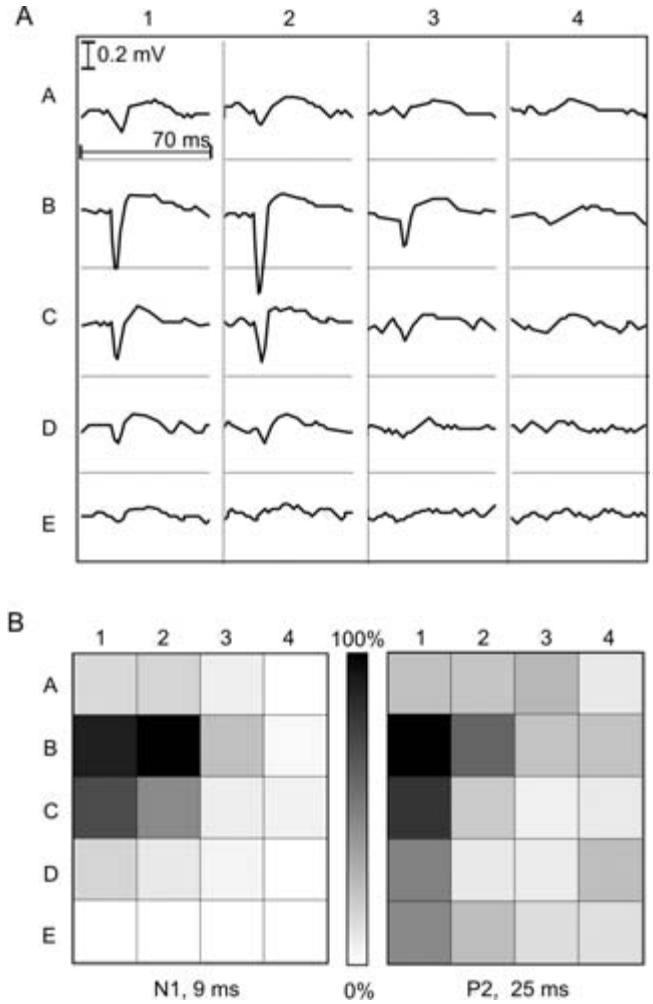

Fig. 3. Averaged evoked potentials (A) recorded from the electrode located in cortical column B2 after consecutive stimulation of every vibrissa on the mystacial pad. Maximal peak-to peak amplitude was obtained after stimulation of corresponding B2 whisker ("principal whisker"). (B) Gray level in each small square represents the relative value of N1 (left panel) and P2 (right panel) amplitudes expressed as percentage of their maximal value. The P2 wave can be traced in a larger area of the barrel field than the N1 wave.

the subcomponents of the EPs recorded in the barrel cortex we applied a special version of Principal Component Analysis (PCA), developed in our laboratory (Fig. 4A) (Musiał et al. 1998b). This analysis used the trial by trial variability of the EPs recorded from one location in the barrel cortex to find a unique course of activity of distinct populations of cells. Using this method we were able to extract two subcomponents within the N1 wave. Both subcomponents had a similar course but the second lagged behind the first by about 1.5-4 ms (Figs. 4 and 7B). The two subcomponents were similar to those

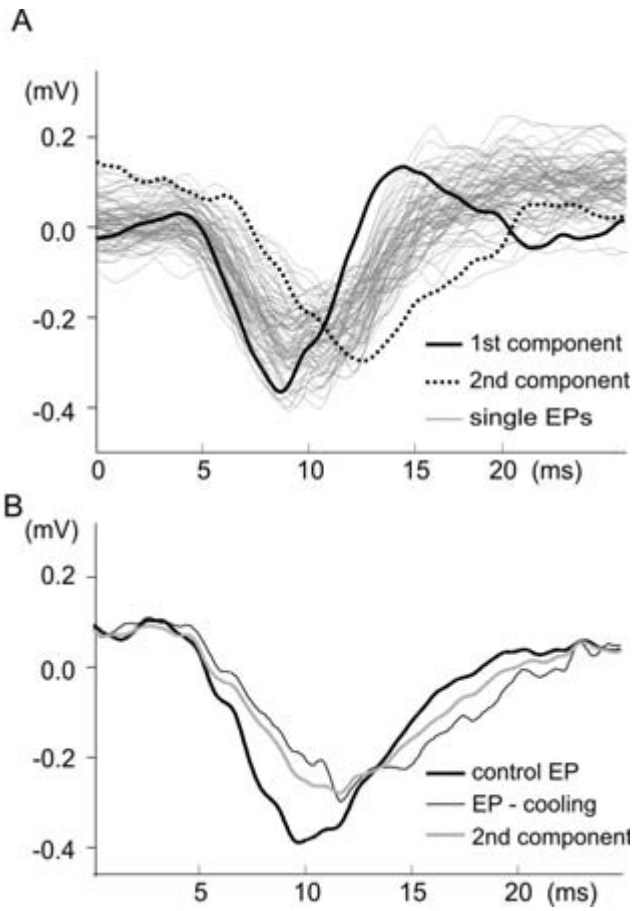

Fig. 4. Principal component of the EPs recorded from the rat's barrel cortex. (A) Individual EPs (thin gray lines) recorded during one session from the barrel cortex of non-anesthetized rat. Application of Principal Component Analysis allowed for decomposition of the two principal components within the N1 wave, representing cell's excitation in the supra- (N1s, black thick line) and infragranular layers (N1i, dotted line) (adapted from Musiał et al. 1998b). (B) Inactivation of the cortical surface by cooling inactivated superficially located supragranular cells and diminished the first principal component. The infragranular cells, not affected by the cooling pulse, produced EPs composed of the second principal component (adapted form Kublik et al. 2001).

found previously by Di et al. (1990) and their timing was also congruent with extracellular unitary recordings from supra- and infragranular cells as found in previous studies (Armstrong-James 1995, Armstrong--James at al. 1992, Shimegi et al. 1999). We have therefore concluded that the first, earlier, subcomponent of N1 wave could be produced by postsynaptic excitation of the supragranular cells (abbreviated as N1s). The second subcomponent could be attributed to postsynaptic activation of the infragranular cells (N1i).

To confirm further the origin of N1 subcomponents, we decreased the activity of neuronal elements in superficial layers by means of cooling the surface of the barrel cortex of urethane anesthetized rats (Kublik et al. 2001). The mild cooling pulse decreased exclusively the amplitude of the earlier component (N1s) showing that it is indeed generated by the pyramidal cells located in more superficial, supragranular layers (Fig. 4B). The longer latency principal component (N1i), disappeared only with strong cooling pulses, and therefore could be attributed to the postsynaptic activity of infragranular pyramidal neurons. The small P1 wave was the only component to remain after the deepest cortical cooling. Therefore, we assume that it reflects the incoming volley from the thalamo-cortical fibers.

MODIFICATION OF THE CORTICAL EPS BY INTRODUCTION OF CONTEXTUAL STIMULUS – CHRONIC EXPERIMENT

In the following experiments rats with chronically implanted electrode were used to monitor the contextual modification of the barrel cortex activity (Fig. 5). Before the experiments rats were accustomed to a restraining hammock. Recordings began after implantation of an electrode into the barrel cortex at the approximate level of layer IV and a few days of convalescence. The principal vibrissa was selected as the one evoking the biggest N1 amplitude in the EP. The chosen whisker was glued to a piezoelectric device and stimulated approximately 100 times at different inter-stimulus intervals (20-40 seconds). The experiment consisted of about 10 daily sessions.

During a few days of a control period, the amplitude of EPs evoked by repetitive stimulation declined slowly (Musiał et al. 1998a). In the experimental session a mild electric shock was introduced and followed each consecutive vibrissa stimulation (n = ~66 aversive stimuli). For analytical convenience this session was divided into three parts: the first, control part, contained approximately 33 stimulations without reinforcement; the second conditioning (C1) during which each whisker stimulation (n = ~33) was followed by the reinforcement; and third part of the session which we called remaining (n = ~33).

In the conditioning part of the session EP's amplitudes increased and then dropped again towards control level during remaining period (Fig. 6A). This effect was most pronounced when measuring the amplitude of P2

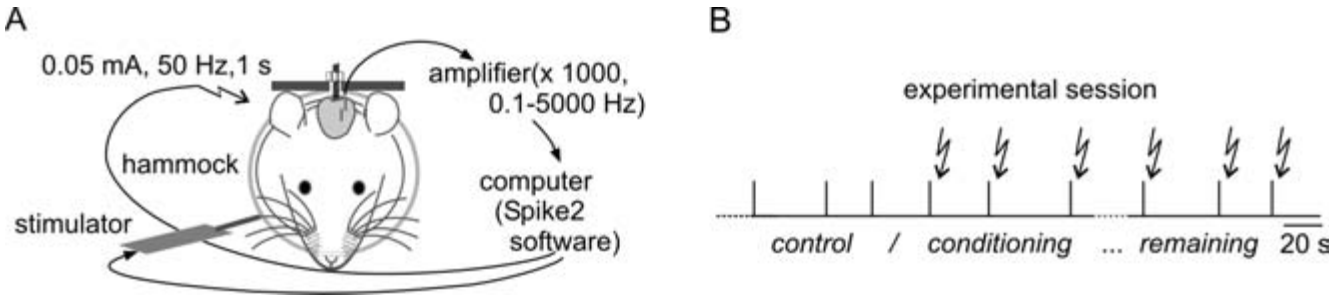

Fig. 5. Experimental design for the chronic recording of evoked potentials in non-anesthetized rat. (A) During the experimental session a rat was restrained in a specially designed hammock with the head immobilized and a chosen whisker glued to a piezoelectric stimulator. Signals from electrodes implanted into the barrel cortex at the approximate level of layer IV were filtered (0.1-5,000 Hz), amplified (x 1,000), digitized on-line and stored on analog tape for off-line analysis. (B) The experimental session contained approximately 100 repetitions of whisker stimulation delivered at different inter-stimulus intervals (20-40 s) and consisted of three parts. The first, control, contained approximately 33 stimulations without reinforcement. All the subsequent whisker stimulations were followed by aversive stimulus (a mild electric shock). This part of session was set apart for analytical reasons in order to create groups equal in stimulations number to the control portion. For all figures and text the first ~33 whisker stimulation with reinforcement was called conditioning, and the rest were called the remaining part of the session.

(Fig. 6B). We also observed a slight increase of the average amplitude of the N1 wave for the whole group of rats (~113% of control value) (Fig. 6A), but it was not statistically significant. We therefore concentrated on the subtle analysis of the two subcomponents of N1 in order to study the changing ratio of neuronal activity within both groups of pyramidal neurons within the central column. As a result of the time difference between the two components attributed to supra and infragranular activity, small ripples were visible on the minimum of the N1 wave (Figs. 2, 7 and 8). Both components were differently influenced by the changing state of the brain. It appeared that the rising trend of N1 amplitude in the conditioning part of the session was exclusively due to enhancement of the second subcomponent (Fig. 7). On average the infragranular cells seemed to be more strongly influenced by the introduction of the reinforcement then the supragranular cells. In order to characterize the dynamics of this activation, each EP recorded in session C1 was classified with the specially designed analytical method which utilized the contribution of both subcomponents to the integral of the analyzed N1 fragment (Fig. 8A). Potentials dominated by the supragranular component (with N1s bigger then N1i) were sorted to class 1, those dominated by the infragranular component – to class 2 (Fig. 8) (cf. Wróbel et al. 1998). Class 1 EPs occurred more frequently during the control period of the experimental session. Contextual aversive stimulation abruptly changed the frequency of occurrence of both EP classes favoring appearance of class 2 EP immediately after onset of the reinforcement (Fig. 8C). This type of EP was clearly related to the increased arousal of the animal that could possibly be mediated by neuromodulatory action (Wróbel and Kublik 2000). As for the amplitude changes, this effect was also

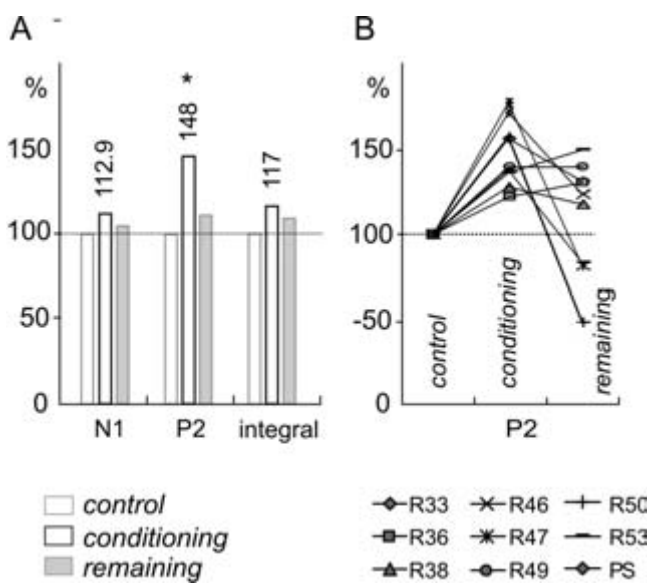

Fig. 6. Modulation of amplitudes of EPs with introduction of reinforcement. (A) Amplitudes of N1 and P2 waves and the integral magnitude of evoked potentials (calculated as a sum of the absolute values of measurements taken in all time points within a 50 ms sweep containing both waves). The amplitude was averaged for the group of rats (n = 9) separately for the control, conditioning and remaining periods of experimental session. On average the contextual stimulus increased all EP parameters tested. (B) In all the experiments the amplitude of P2 increased significantly in the conditioning portion of the session (9/9, P=0.02).

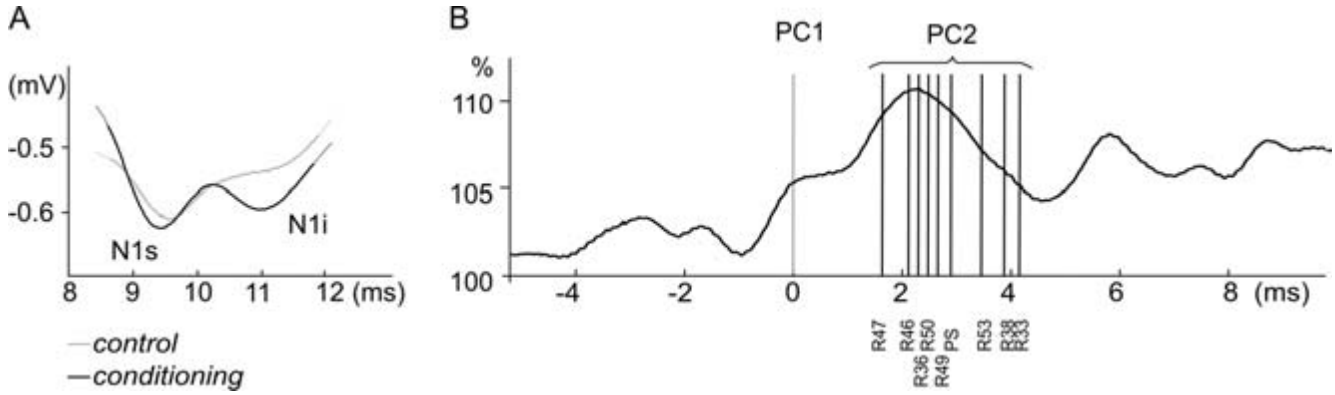

Fig. 7. Introduction of reinforcement induced an increase of the N1 wave in the extent of the infragranular subcomponent. (A) The fragment of averaged evoked potential at the minimum of the N1 wave (conditioning – black line, control – gray line). The two ripples may result from summation of the supragranular (N1s) and infragranular (N1i) subcomponents (an example from rat R49). Note the slight increase of the N1i in the conditioning as compared to control situation. Similar effect was observed in all the experiments. (B) The relative amplitude of the N1 wave for the whole experimental group (n = 9). For each rat, the relative values of every time-point of N1 wave in the conditioning part of the session was calculated as percent of the value of the control level, illustrating change of N1 shape and amplitude resulting from the introduction of reinforcement. The time scale was normalized for all rats, with the maximum amplitude of the first principal component (PC1, gray vertical line) indicating a common zero point and then the group average was calculated. Black vertical lines indicate occurrence of the peak amplitude of the infragranular principal component for each rat (PC2). Note the approximately 10% increase of N1 amplitude at the time of domination of the infragranular component.

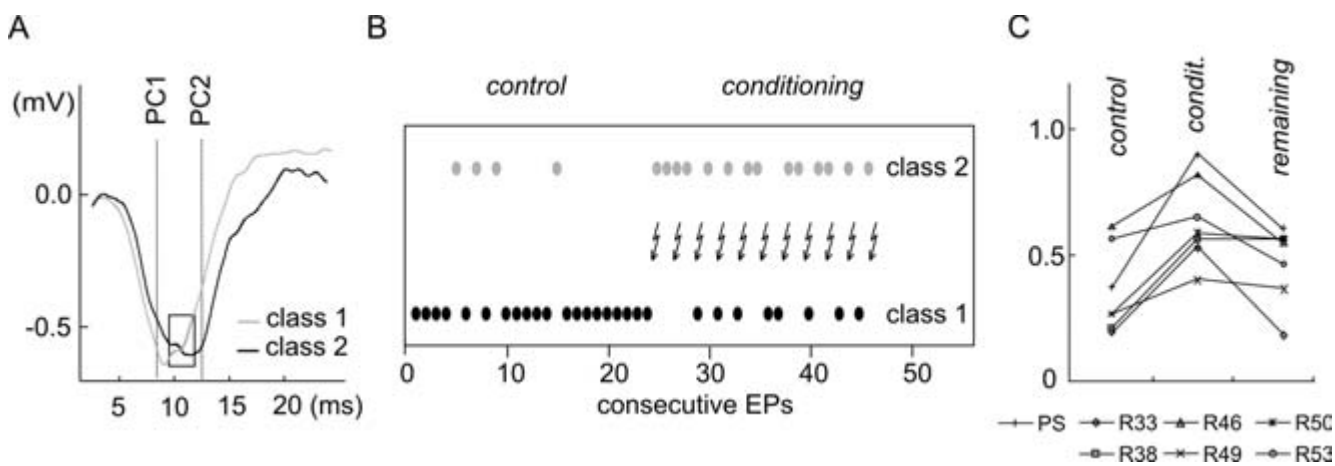

Fig. 8. Dynamic change of cortical state during the introduction of aversive stimulation. (A) Evoked potentials averaged within the groups classified according to predominance of one of the two N1 subcomponents. This average should be compared with Fig. 2A showing an averaged EP from all the potentials recorded in the same session. The two vertical dotted lines indicate the latencies of the maximal amplitude of the two Principal Components of EPs (PC1, PC2). The small rectangle shows the 2 ms window chosen for the analysis. For each individual EP, the sweep within this time window was normalized by subtracting its mean value. It was then multiplied by the differentiated Hanning window. If the earlier, supragranular subcomponent dominated over the second component, the number resulting from the calculation was positive and we placed the EPs in class1. If the infragranular subcomponent was bigger than the supragranular one, the result of the analysis was negative and the EP was placed in class 2 (Wróbel et al. 1998). (B) The classification of consecutive EPs in control and conditioning parts of the experimental session in one rat. (C) The ratio of class 2 EPs to the total number of EPs in the control, conditioning and remaining parts of the conditioning sessions in 7 experiments.

fast, raising immediately with the first reinforcing stimulus, and transient – the ratio of the occurrence of the two EP classes slowly reversed during the remaining part of session, towards the control value (Fig. 8B,C). Classification of each EP recorded in consecutive moments of the experiment allowed us to follow the ongoing dynamics of the cortical states. Note that within the control (habituated) part of the session we recorded a few "aroused" EPs (attributed to class 2), and after introduction of the reinforcement, some of the recorded responses were attributed to non-aroused class 1.

Since the described method of classification was based on a small difference in shape of the N1 peak, it could be also very sensitive to spontaneous changes of the underlying field potential and noise. We therefore searched for other classifying algorithms that would take into account the differences of the entire course of EPs (Wypych et al. 2003). The two functions tested reached local extreme values at the latencies of peak responses for N1 and P2 waves and were shown to be sensitive to dynamic variations of the underlying physiological mechanisms (Wróbel and Kublik 2000, Wróbel et al. 1998, Wypych et al. 2003). All these approaches proved to be effective in classifying the recorded evoked potentials into "aroused" and "habituated" classes and confirmed our preliminary conclusion that contextual stimuli transiently changed the route of sensory processing in the barrel cortex.

MODEL OF SENSORY PROCESSING IN THE BARREL CORTEX

The experiments described here have shown that introduction of an aversive, contextual stimulus transiently favored the appearance of EPs dominated by a second component of N1 and induced the increase of the P2 wave amplitude (Musiał et al. 1998a, Wróbel et al. 1998). Various researchers have reported that an increase of EP amplitude resulting from a conditioning procedure does not cease until after a few days of extinction (John et al. 1969, Mark and Hall 1966, Popova 1970). In our experiment observed parameters of the EP already drop towards the control level during the first "conditioning" session despite the continuation of the reinforcement. We therefore conclude that the observed phenomena are an electrophysiological illustration of fast nonspecific activation rather then a plastic change resulting from classical conditioning. Since the early description of the "synchronized" and "desynchronized" types of electroencephalographic signal (Moruzzi and Magoun 1949) it is widely believed that the cortex may exhibit distinct functional states (addressed nowadays as "activated" and "non-activated"). Two types of evoked potentials recorded in our experiment after whisker stimulation reflect responses characteristic of such different functional states of activity within the barrel cortex. In the control situation the barrel cortex remains in non-activated mode typical for the conscious, quiescent rat. In that mode the repetitive, meaningless whisker movement evokes habituated responses. In our experimental model it is characterized by small P2 amplitudes indicating that information is not transmitted any further after it reaches pyramidal cells at the central barrel-column. A salient change in the animal's environment (like the aversive reinforcement) may provoke general arousal. All previously habituated stimuli would then gain a new meaning. Facilitatory action of neuromodulatory inputs activated by new stimulation (McCormick 1992, Kublik et al. 1998, Sara et al. 1994, Steriade et al. 1993, Vankov et al. 1995, Webster et al. 1991, Woody and Gruen 1993, Wróbel and Kublik 2000) switches the brain to aroused state which facilitates intense information processing for quick evaluation of the modified situation. Our data point out that this excitatory influence is directed mainly to the infragranular cells (increased N1i subcomponent in "aroused" class 2 EPs). The increased activity of these neurons subsequently influences the cells in the thalamic sensory nuclei. According to other authors (Castro-Alamancos 2002, 2004, Temereanca and Simons 2004) relatively precise functional connection to VPm may be engaged in shaping the receptive fields and enhancing precise pattern discrimination, thus functioning mainly in active whisking during exploratory behavior. On the other hand, axons from layer V pyramidal neurons which project to the cells in the POm (Deschênes et al. 1998) could in turn increase the gain for information flow to surrounding cortical columns of the barrel field and to other cortical areas like SII, MI (Diamond 1995, Wróbel et al. 1998). In our experimental model this surround activation was reflected by the enhanced magnitude of the P2 wave.

We therefore hypothesize that nonspecific contextual reinforcement actuate the cortico-thalamo-cortical loop through the POm and therefore facilitate information flow from the thalamus to extended portion of the primary somatosensory cortex and other cortical fields. Such a facilitating action should also promote gathering and/or comparison of various, possibly important sen-

sory information. After a relatively short time (minutes), the habituation to modified environmental input would close the loop again, and set the cortical network back to an idle state.

Recording and classification of consecutive EPs allowed us to conceive the dynamic fluctuation of the cortical functional states depending on behavioral salience of the contextual stimuli in the animal's environment and internal habituation processes within the cortical network. Detailed analysis of the EP subcomponents pointed to a switching/gating mechanism in the infragranular cells of the primary sensory cortex.

ACKNOWLEDGEMENTS

These experiments were supported by the Polish State Committee for Scientific Research (KBN), grant no. 6 P05A 090 20.

REFERENCES

Arieli A, Sterkin A, Grinvald A, Aertsen A (1996). Dynamics of ongoing activity: explanation of the large variability in evoked cortical responses. Science 273: 1868-1871.

Armstrong-James M (1995) The nature and plasticity of sensory processing within adult rat barrel cortex. In: The barrel cortex of rodents. (Eds. E.G..Jones and I.T. Diamond) Cerebral Cortex, vol. 11, Plenum Press, New York, p. 333-373.

Armstrong-James M, Fox K (1987) Spatiotemporal convergence and divergence in the rat S1 "barrel" cortex. J Comp Neurol. 263: 265-81.

Armstrong-James M, Fox K, Das-Gupta A (1992) Flow of excitation within rat barrel cortex on striking a single vibrissa. J Neurophysiol 68: 1345-1358.

Barth DS, Di S (1991) Laminar excitability cycles in neocortex. J Neurophysiol 65: 891-898.

Barth DS, Di S, Baumartner C (1989) Laminar cortical interactions during epileptic spikes studied with principal component analysis and physiological modeling. Brain Research 484:13-35.

Castro-Alamancos MA (2002) Different temporal processing of sensory inputs in the rat thalamus during quiescent and information processing states in vivo. J Physiol 539: 567-578.

Castro-Alamancos MA (2004) Absence of rapid sensory adaptation in neocortex during information processing states. Neuron 41: 455-464.

Chmielowska J, Carvell E, Simons DJ (1989) Spatial organization of thalamocortical and corticothalamic projection systems in the rat SmI barrel cortex. J Comp Neurol 285: 325-338.

Di S, Baumartner C, Barth DS (1990) Laminar analysis of extracellular field potentials in rat vibrissa/barrel cortex. J Neurophysiol 63: 832-840.

Deschênes M, Veinante P, Zhan ZW (1998) The organization of corticothalamic projections: reciprocity versus parity. Brain Res Rev 28: 286-308.

Diamond ME (1995) Somatosensory thalamus of the rat. In: The barrel cortex of rodents (Eds. E.G. Jones and I.T. Diamond) Cerebral Cortex, vol 11. Plenum Press, New York, p. 189-219.

Diamond ME, Armstrong-James M, Budway MJ, Ebner FF (1992) Somatic sensory responses in the rostral sector of the posterior group (POm) and in the ventral posterior medial nucleus (VPM) of the rat thalamus: dependence on the barrel field cortex. J Comp Neurol 319: 66-84.

Jackson ME, Cauller LJ (1998) Neural activity in SII modifies sensory evoked potentials in SI in awake rats. Neuroreport 9: 3379-3382.

John ER, Shimokochi M, Bartlett F (1969) Neural readout from memory during generalization. Science 164: 1534-1536.

Jones EG, Diamond IT (1995) The barrel cortex of rodents. Cerebral Cortex, vol 11. Plenum Press, New York, 462 p.

Keller A (1995) Synaptic organization of the barrel cortex. In: The barrel cortex of rodents. (Eds. E.G. Jones and I.T. Diamond) Cerebral Cortex, vol. 11, Plenum Press, New York, p. 221-262.

Kublik E, Musiał P, Wróbel A (1998) Contextual stimuli change the DC potential recorded at the primary sensory cortex. Eur J Neurosci 10: 140.

Kublik E, Musiał P, Wróbel A (2001) Identification of principal components in cortical evoked potentials by brief surface cooling. Clin Neurophysiol 112: 1720-1725.

Kublik E, Świejkowski DA, Wróbel A (2003) Cortical contribution to sensory volleys recorded at thalamic nuclei of lemniscal and paralemniscal pathways. Acta Neurobiol Exp (Wars) 63: 377-382.

Land PW, Buffer SA Jr, Yaskosky JD (1995) Barreloids in adult rat thalamus: three-dimensional architecture and relationship to somatosensory cortical barrels. J Comp Neurol 355: 573-588.

Lindström S, Wróbel A (1990) Frequency dependent corticofugal excitation of principal cells in the cat's dorsal lateral geniculate nucleus. Exp Brain Res 79: 313-318.

Ma PM (1991) The barrelettes - architectonic vibrissal representations in the brainstem trigeminal complex of the mouse. I. Normal structural organization. J Comp Neurol 309: 161-199.

Ma PM, Woolsey TA (1984) Cytoarchitectonic correlates of the vibrissae in the medullary trigeminal complex of the mouse. Brain Res 306: 374-379.

Mark R, Hall RD (1966) Acoustically evoked potentials in the rat during conditioning. J Neurophysiol 30: 875-892.

Martin JH (1995) The collective electrical behavior of cortical neurons: the electroencephalogram and the mecha-

nisms of epilepsy. In: Principles of neural science (Eds. R.K. Kandel, J.H. Schwartz nad A. Jobert), Appleton & Lane, Norwalk, Connecticut p. 777-791.

McCormick DA (1992) Neurotransmitter actions in the thalamus and cerebral cortex and their role in neuromodulation of thalamocortical activity. Prog Neurobiol 39: 337-388.

Mitzdorf U (1985) Current source-density method and application in cat cerebral cortex: investigation of evoked potentials and EEG phenomena. Physiol Rev 65: 37-100.

Moruzzi G, Magoun HW (1949) Brain stem reticular formation and activation of the EEG. Electroencephalogr Clin Neurophysiol 1: 455-473.

Musiał P, Kublik E, Panecki SJ, Wróbel A (1998a) Transient changes of electrical activity in the rat barrel cortex during conditioning. Brain Res 786: 1-10.

Musiał P, Kublik E, Wróbel A (1998b) Spontaneous variability reveals principal components in cortical evoked potentials. Neuroreport 9: 2627-2631.

Popova NS (1970) Dynamics of the form of evoked potentials in the course of defensive conditioning to an intermittent photic stimulus (in Russian). Zh Vyssh Nerv Deiat Im I P Pavlova 20: 545-554.

Sara SJ, Vankov A, Herve A (1994) Locus coeruleus-evoked responses in behaving rats: a clue to the role of noradrenaline in memory. Brain Res Bull 35: 457-465.

Shimegi S, Ichikawa T, Akasaki T, Sato H (1999) Temporal characteristics of response integration evoked by multiple whisker stimulations in the barrel cortex of rats. J Neurosci 19: 10164-10175.

Simons D (1978) Response properties in vibrissa units in rat SI somatosensory neocortex. J Neurophysiol 41: 798-820.

Simons D (1995) Neuronal integration in the somatosensory whisker/barrel cortex. In: The barrel cortex of rodents. (Eds. E.G. Jones and I.T. Diamond) Cerebral Cortex, vol 11. Plenum Press, New York, p. 263-297.

Steriade M, Amzica F, Nunez A (1993) Cholinergic and noradrenergic modulation of the slow (0.3 Hz) oscillation in neocortical cells. J Neurophysiol 70: 1385-1400.

Temereanca S, Simons DJ (2004) Functional topography of corticothalamic feedback enhances thalamic spatial response tuning in the somatosensory whisker/barrel system. Neuron 41: 639-651.

Vankov A, Herve-Minvielle A, Sara SJ (1995) Response to novelty and its rapid habituation in locus coeruleus neurons of the freely exploring rat. Eur J Neurosci 7: 1180-1187.

Webster HH, Rasmusson DD, Dykes RW, Schliebs R, Schober W, Bruckner, Bieshold D (1991) Long-term enhancement of evoked potentials in racoon somatosensory cortex following co-activation of the nucleus basalis of Meynert complex and cutaneous receptors. Brain Res 545: 292-296.

Welker C (1971) Microelectrode delineation of the fine grain somatotopic organization of SmI cerebral neocortex in albino rat. Brain Res 26: 259-275.

Woolsey TA, Van der Loos H (1970) The structural organization of layer IV in the somatosensory region (SI) of mouse cerebral cortex. The description of a cortical field composed of discrete cytoarchitectonic units. Brain Res 17: 205-242.

Woody CD, Gruen F (1993) Cholinergic and glutamatergic effects on neocortical neurons may support rate as well as development of conditioning. Ping Brain Res 98: 365-370.

Wróbel A (1997) Collective electrical activitry of the brain (in Polish). Kosmos 46: 317-326.

Wróbel A, Kublik E (2000) Modification of evoked potentials in the rat's barrel cortex induced by conditioning stimuli. In: Plasticity of the barrel cortex. (Ed. M. Kossut) FP Graham Publishing Co. New York. p. 229-239.

Wróbel A, Kublik E, Musiał P (1998) Gating of the sensory activity within barrel cortex of the awake rat. Exp Brain Res 123: 117-123.

Wypych M, Kublik E, Wojdyłło P, Wróbel A (2003) Sorting functional classes of evoked potentials by wavelets. Neuroinformatics 1: 193-202.

Yuan B, Morrow TJ, Casey KL (1985) Responsiveness of ventrobasal thalamic neurons after suppression of S1 cortex in the anesthetized rat. J Neurosci 5: 2971-2978.

Yuan B, Morrow TJ, Casey KL (1986) Corticofugal influences of S1 cortex on ventrobasal thalamic neurons in the awake rat. J Neurosci 6: 3611-3617.

Received 6 February 2004, accepted 28 March 2004