

Local classifiers for evoked potentials recorded from behaving rats

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Abstract. Dynamic states of the brain determine the way information is processed in local neural networks. We have applied classical conditioning paradigm in order to study whether habituated and aroused states can be differentiated in single barrel column of rat's somatosensory cortex by means of analysis of field potentials evoked by stimulation of a single vibrissa. A new method using local classifiers is presented which allows for reliable and meaningful classification of single evoked potentials which might be consequently attributed to different functional states of the cortical column.

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INTRODUCTION

In this article we present a new approach to the problem of classifying evoked potentials recorded within barrel cortex of awake rat. In our previous research (Kublik 2004, Wróbel et al. 1998, Wypych et al. 2003) we were able to identify two functional classes that represented two states of rat's barrel cortex. The approaches we used so far employed different parts of recorded potentials, ranging in length from 2ms to around 128ms. The part of the potential used depended on the method applied (Kublik 2004, Wróbel et al. 1998, Wypych et al. 2003). The new method for signal classification used here (Jakuczun 2005) creates a set of classifiers which use limited information from the analyzed signals, ranging from a few samples to the whole signal. With this method we were able to localize the parts of the evoked potentials carrying information most important for classification and we found that they were consistent with current understanding of the function of underlying neural circuits.

The article is divided into two main parts. In the first part we describe the theoretical bases of the method with minimum mathematical details. In the second part we apply the method to experimental data. We conclude with physiological interpretation of the obtained results.

THEORETICAL DESCRIPTION OF THE METHOD

The aim of discrimination analysis is to learn more about the differences between the signals belonging to different classes. It should be stressed that we are interested not only in a good classification accuracy but also in understanding the differentiating features of the two signal classes. Widely used classifiers (discriminants) such as decision trees or artificial neural networks are rarely applied to a raw signal classification problem since very often they produce results which are difficult to interpret.

In this section we review a new method for signal discrimination analysis (Jakuczun 2005). It is a combination of the lifting scheme (Sweldens 1998) and Support Vector Machines (Vapnik 1998). The method employs decomposition of analyzed signals with respect to the specially designed bi-orthogonal base. The base has two important features:

- Each base vector is nonzero for only a fraction of indices. This feature called locality is particularly use-

ful when we expect that only a part of analyzed signal is important.

- Expansion coefficients of analyzed signals with respect to each base vector are as discriminable as possible.

Before we proceed to the method description let us introduce some definitions and notations that will be used. Assume we are given a set X of sampled versions of signals that belong to two classes. That is we have

$$X = \{(x_i, y_i) \in \mathbb{R}^N \times \{-1, 1\} : i = 1, \dots, k\} \quad (1)$$

where x_i are sampled signals to be analyzed of length N , y_i is a label indicating the class the i -th example belongs to (for instance "habituated" or "aroused"), and k is the number of signals.

Definition 1. Support of the vector $x \in \mathbb{R}^N$ is the set of indices for which $x_i \neq 0$.

Definition 2. Bi-orthogonal base for space \mathbb{R}^N is the set of pairs of vectors $(\phi_i, \tilde{\phi}_i)$ where $i=1, \dots, N$ such that

$$\langle \phi_i, \tilde{\phi}_j \rangle = \begin{cases} 1 & \text{for } i = j \\ 0 & \text{otherwise} \end{cases}$$

where $\langle x, y \rangle$ is the usual scalar product in \mathbb{R}^N . We can write every vector $x \in \mathbb{R}^N$ as

$$x = \sum_{i=1}^N \langle x, \phi_i \rangle \tilde{\phi}_i$$

ϕ_i are called analysis base vectors, $\tilde{\phi}_i$ are called synthesis base vectors. In this article we present some properties of the analysis part of the bi-orthogonal base. The synthesis part of the base is uniquely determined by the base definition.

Local classifiers

Assume that the dimension N of analyzed signals equals to 2^n for some integer $n > 0$. We choose some integer J such that $J < n$ and construct bi-orthogonal base in two parts. The first part of the base, $(\psi_i, \tilde{\psi}_i)$

where $i \in \left\{1, \dots, \frac{N}{2^J}\right\}$, plays a similar role to the

scaling part of the classical wavelet base and is not used in our analysis. This part of the base spans coarse approximation of the analyzed signals (Sweldens 1998). The second part of the base, $(\phi_{i,j}, \tilde{\phi}_{i,j})$, where

$j \in \{1, \dots, J\}$ and $i \in \left\{1, \dots, \frac{N}{2^j}\right\}$, plays a similar role

to wavelet part of the classical wavelet base. Index j denotes decomposition level of the method. Since we only use vectors $\phi_{i,j}$ in what follows we shall refer to them simply as base vectors. The precise construction of the whole base is given by Jakuczun (2005).

Supports of the base vectors from the same decomposition level $\{\phi_{i,j}\}$ are of the same length equal to $2^j L$ for some integer L which is the parameter of the method. Moreover, support of the base vector $\phi_{i,j}$ is shifted to the right by 2^j indices compared to the support of the base vector $\phi_{i-1,j}$. This is a property of vectors constructed for analysis of signals of infinite length. In case of finite length signals the supports of first $L/2$ base vectors are located at the left edge and the supports of last L vectors are located at the right edge.

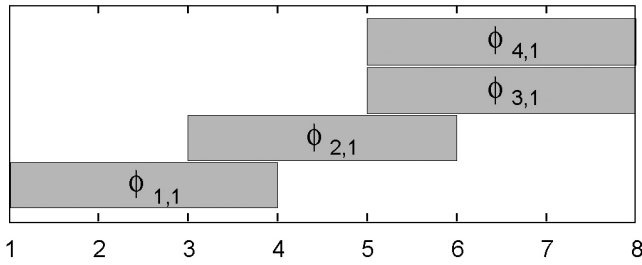


Fig. 1. Supports of all four analysis base vectors for the first decomposition level for $N=8$ data points and $L=2$.

Figure 1 presents supports of four base vectors from the first decomposition level (i.e., for $j=1$) with $N=8$ and $L=2$. Choosing appropriate L and the decomposition level the researcher controls time resolution of the method.

Let X be the training set as defined in Eq. (1). We find each base vector $\phi_{i,j}$ by solving the following optimization problem

$$\min_{\phi_{i,j}, b_{i,j}} \frac{\left| \left\{ x_k : \theta(\langle x_k, \phi_{i,j} \rangle + b_{i,j}) \neq y_k \right\} \right|}{|X|} \quad (2)$$

where $|\cdot|$ means the number of elements of the set, $\theta(\cdot)$ is defined by

$$\theta(t) = \begin{cases} +1 & \text{for } t > 0 \\ -1 & \text{for } t \leq 0 \end{cases}$$

and $b_{i,j} \in \mathbb{R}$. This means that we want to find such base vectors that lead to expansion coefficients that are different for signals from different classes. Each base vector acts as a local classifier because its support is strictly positioned and its length is shorter than length of the analyzed signal.

Filtering local classifiers

In the previous subsection we have introduced the method that finds the bi-orthogonal base $(\psi_k, \tilde{\psi}_k)$, $(\phi_{i,j}, \tilde{\phi}_{i,j})$ given the training set (Eq. (1)). As we have mentioned each base vector $\phi_{i,j}$ can be used as a classifier. In this section we present our approach for selecting the most informative base vectors.

The naive criterion would be selecting those base vectors that have the smallest training error defined as follows

$$\varepsilon_{i,j} := \frac{\left| \left\{ x_k : \theta(\langle x_k, \phi_{i,j} \rangle + b_{i,j}) \neq y_k \right\} \right|}{|X|}$$

where $b_{i,j}$ is defined in Eq. (2). This approach would work best if the number of training examples were large. In case of a small number of training examples there is a risk that small training error is obtained only by chance. To exclude this possibility we propose to use the following procedure:

- For each base vector $\phi_{i,j}$ calculate its training error $\varepsilon_{i,j}^0$.
- For $k=1, \dots, K$ where K is the large number (e.g., 1000) repeat the following:
 - Create a new training set X^k from set (1) by randomly permuting labels y_i .
 - Find the bi-orthogonal base for such modified training set X^k .
 - For each base vector $\phi_{i,j}^k$ calculate its training error $\varepsilon_{i,j}^k$.

For each base vector calculate the following statistics

$$T_{i,j} = \frac{\left| \left\{ k : \varepsilon_{i,j}^0 \geq \varepsilon_{i,j}^k \right\} \right|}{K}$$

This is the estimation of the probability that training error $\varepsilon_{i,j}^0$ was not obtained by chance. Its confidence interval is given by

$$\left[T_{i,j} - u_{1-\alpha/2} \sqrt{\frac{T_{i,j}(1-T_{i,j})}{K}}, T_{i,j} + u_{1-\alpha/2} \sqrt{\frac{T_{i,j}(1-T_{i,j})}{K}} \right]$$

where α is the confidence level and $u_{1-\alpha/2}$ is the quantile of order $1-\alpha/2$ of normally distributed variable u (Feller 1968).

- Choose those base vectors whose confidence intervals contain the desired probability that the training error was not obtained by chance. This desired probability is a parameter of the method.

We used the base vectors selected this way as the most valuable for discrimination analysis of the signals. Note that since we use bi-orthogonal bases the shape of base vectors cannot be given physiological interpretation easily which is why we do not discuss it.

CLASSIFICATION OF EVOKED POTENTIALS

In this section we apply the method presented above to obtain classification of evoked potentials recorded within the primary sensory cortex of non-anaesthetized rats.

The vibrissa-barrel system of rat is a perfect model for the anatomical and functional study of the mammalian sensory systems. Whiskers on the rat's snout constitute very sensitive and precise sensory organ. They grow in five horizontal rows containing 4–6 big whiskers forming vertical arches. Bending of each vibrissa generates receptor potential and this activation is then represented in clearly defined cell groups within consecutive stages of the sensory pathway. Thus, the somatotopic map in the primary sensory (barrel) cortex mirrors the rows/arches organization of facial vibrissae (Fig. 2A). Such a map allows precise insertion of microelectrodes into the required site in order to record cortical potentials evoked (EP) by the stimulation of a chosen whisker in different behavioral situations. We hypothesized that EPs recorded during well habituated, "idle" state of the cortex and during "active" mode aroused by application of aversive stimulus will differ due to functional reorganization of neuronal network in the cortical column (Wróbel et al. 1998).

Experimental paradigm and recording procedure

Experiment was carried out on 5 male rats weighing 300–400 gram. At the beginning the animals were handled and accustomed to restraining hammock (Fig. 2B). The surgery was then performed during which 3 to 4 electrodes (0.025 mm insulated tungsten wire of ~ 150 k Ω impedance at 1 kHz) were implanted into the barrel cortex at the level of 4th cortical layer. The ref-

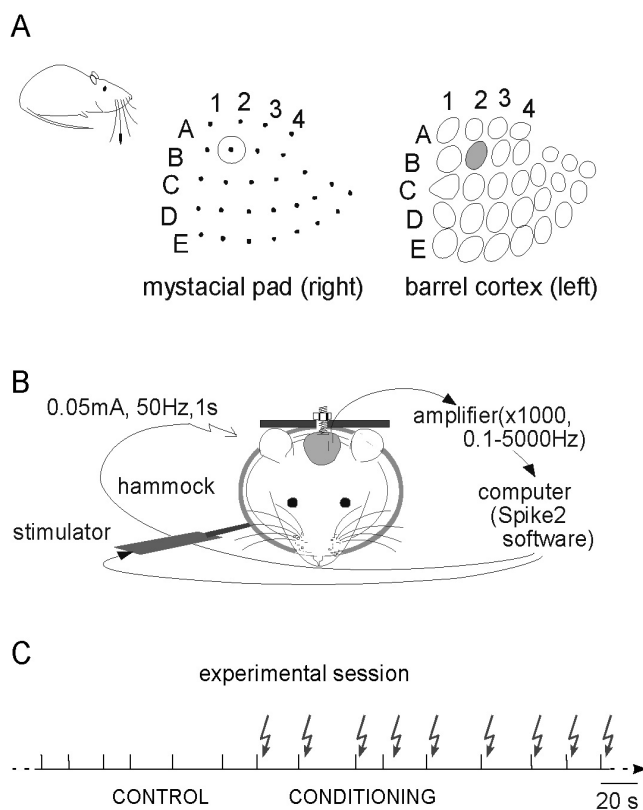


Fig. 2. (A) Schematic maps of vibrissal pad and its representation in the barrel cortex. Left: whiskers grow on the mystacial pad in five rows named by capitals A–E. Consecutive arches of whiskers are numbered from back to front of the snout. Signal from a single vibrissa is transmitted with relatively precise somatotopy through the thalamus to individual functional "barrel" columns of the contralateral primary somatosensory cortex ("barrel cortex"). Right: tangential section of the barrel cortex at the level of layer 4 shows spatial organization of barrel-columns repeating a whisker pattern. Cortical column from which signals are recorded (e.g., B2) and corresponding whisker are addressed to as central (or principal) column and central (principal) whisker. (B) During the experiment rat was restrained in a specially designed hammock, with the head immobilized and principal whisker glued to a piezoelectric stimulator. Signal from electrodes implanted into the barrel cortex was filtered, amplified and stored on an analog tape for off-line analysis. (C) Each daily recording session contained approximately 100 whisker stimulations delivered at different inter-stimuli intervals (15–45 seconds). Experimental session consisted of two parts. The CONTROL part contained 20, 30 or 50 stimulations (vertical lines) without reinforcement. During the subsequent, CONDITIONING part all whisker stimulations were followed by aversive stimulus (a mild electric shock applied onto the skin of the ear).

erence electrodes made of stainless steel screw was inserted into the frontal bone. Recordings started after several days of recovery. Recorded signals were filtered (0.1–5000 Hz), amplified ($\times 1000$) and digitized with sampling frequency of 10 kHz. Down-and-up whisker movements of about ~ 0.1 mm amplitude were produced by piezoelectric slab glued to the whisker about 20 mm from the face and triggered by computer generated square impulse (2 ms duration, 18 V). CED 1401 analog-digital interface (Cambridge Electronic Design) and Spike 2 software were used to control the experiment and to digitize recorded signals.

At the beginning we compared EP amplitudes recorded at a given cortical site by stimulation of each vibrissa and for further experiments we chose the whisker inducing the largest response (called 'principal whisker'). During the following 4 to 8 daily sessions the animals' responses were habituated by repetitive stimulation (100 times during about an hour session) with pseudo-random inter-trial interval (15–45 s). The consecutive "experimental" session included two parts: 1. CONTROL part, during which habituation procedure was continued (this part consisted of the first 30–50 stimulations) and 2. CONDITIONING part, during which each whisker stimulation was followed by a mild

electric shock applied onto the skin of rat's ear in order to evoke arousal state of the animal (Fig. 2C).

The 150 ms fragments of field potentials, starting from the stimulus onset were chosen for the analysis as they encompassed the most characteristic waves of EP (Fig. 4, Wróbel et al 1998). Sweeps contaminated by artifacts (either electronic or of muscular origin) were removed from the data set by means of visual preselection. Table I shows the number of all EPs recorded at an experimental session for each rat together with the number of potentials used for analysis after artifact removal.

Classification experiment

Local classifiers introduced in the first part of this paper were used for classification of preselected potentials from dataset described in Table I. EP sweeps of 150 ms length sampled with the frequency of 10 kHz gave 1500 data points for the analysis.

We used four decomposition levels ($J=4$) and the base length parameter was $L=10$ which corresponds to 20 data points. With these settings the length of base vector support for level 1 vectors was 2 ms, for level 2 it was 4 ms, for level 3–8 ms, and so on. For the discrimination analysis we set the desired probability that the training error was not obtained by chance to 0.9. Since we found no classifiers at the confidence level $\alpha=1$ we reduced it until at least one time-window with satisfactory classifiers for every rat was found. This was obtained for $\alpha=0.95$. Reducing the confidence level even further would result in more classifiers but with increased probability of random responses. We did not investigate thoroughly these additional classifiers.

We used the same data for both steps of the method: training and evaluation/classification due to the relative scarcity of data. Although in principle this approach can lead to over-training we think that the risk here is not high for two reasons: 1) The classifiers used are based on the concept of separating hyperplane with a soft margin which is quite robust to outliers (Vapnik 1998); 2) The classifiers "stability" was checked by the statistical test introduced before.

The evoked potentials from the experimental session were naturally divided into two groups: CONTROL (the first 30–50 potentials) and COND (the remaining 50–70 potentials to the end of the session). Our previous results (Wróbel et al. 1998) showed that in the first (control) part of the experimental session animals remained mostly in the habituated, relaxed

Table I

1	2	3	4	5
Rat	barrel / whisker	No of CONTROL EP all / good	No of COND EP all / good	Number of used classifiers
R33	B2	25 / 22	65 / 62	2
R49	C2	31 / 27	69 / 57	1
R50	C2	31 / 25	69 / 53	2
R52	B2	51 / 42	49 / 40	1
R60	E3	51 / 37	49 / 31	1

Summary of the data set. Consecutive columns show: (1) rat number, (2) recording place and stimulated whisker, (3,4) number of recorded EPs (all) and analysed EP without artifacts (good) in CONTROL and CONDITIONED part of the session, (5) number of classifiers from 11.7–12.8 ms time window accepted for the analysis.

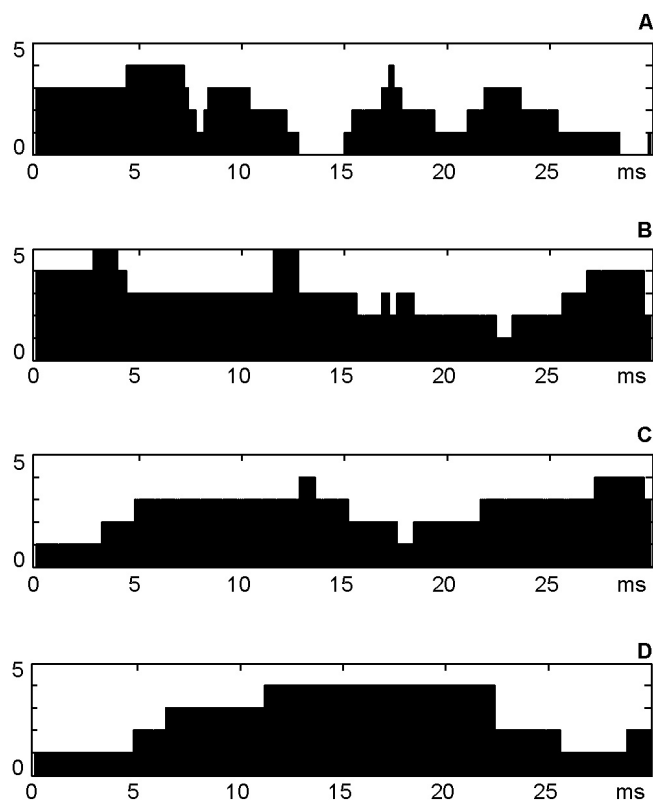


Fig. 3. Histograms showing the sum of time windows in which significant classifiers were found during analysis of datasets from five rats. Results for consecutive base vector levels. (A) level 1 (2 ms resolution); (B) level 2 (4 ms resolution); (C) level 3 (8 ms resolution). (D) level 4 (16 ms resolution). The height of the histogram shows the number of rats for which there was at least one classifier with support at a given time.

state, which we call here INACTIVE state. On the contrary, during conditioned part of the experiment rats were mostly aroused by aversive stimuli and this state we call here the ACTIVE state. Thus each response was evoked at one of the two states and it might easily be assumed that most of EPs recorded during CONTROL period occurred in the INACTIVE cortical state while most of EPs from COND period appeared in the ACTIVE states. Thus, we can think of CONTROL and COND EP groups as good approximations of the INACTIVE and ACTIVE EP classes, respectively. To avoid spurious bias which could be introduced by different sizes of the compared EP groups we have limited the COND group in order to match its size to the CONTROL one.

The main aim of the experiment was to construct a reliable classifier allowing attribution of a given potential to one of the classes and thus recognition of actual

state of the cortex: ACTIVE or INACTIVE. Identification of the EP fragments carrying information most relevant for such classification would then allow for interpretation of the underlying physiological mechanisms.

Figure 3 presents supports of those base vectors which passed the discrimination procedure described above, for the group of five rats. The height of the histogram shows the number of rats for which there was at least one classifier with support at a given time. In a search for the general mechanisms we turned our attention only to those time intervals that were supported by the whole group, and restricted analysis to the first 30 ms after stimulus which contain easily interpretable EP waves. During this time there are only two intervals relevant for the whole group of rats, that is 2.9–4 ms and 11.7–12.8 ms. Both occur at the second decomposition level whose time resolution is 4 ms (Fig. 3B). Activation evoked by the whisker stimulation does not reach the cortex before 5 ms, when the small, positive wave P1, representing the volley of incoming thalamo-cortical fibers is seen in EP. The earlier fragment of EP is most probably a reflection of background cortical activity that is not a subject of our consideration in this project. Thus, for further analysis we accepted only the second interval which falls in with N1 wave of EP, representing stimulus-evoked neuronal activity within the central barrel column. Then, for each rat, we selected base vectors from the second decomposition level whose supports intersected with identified time interval (Table I). Figure 4 shows averaged potentials from groups CONTROL and COND together with the distribution of supports of the analysis vectors accepted for a given rat (each plot presents results for a single rat).

In three animal cases our method gave single significant classifiers with supports intersecting the chosen time interval. In two other cases (rats R33 and R50) two significant classifiers were found (Table I). Each of them could be sensitive to slightly different features in the potential or they could match the same feature but none of them perfectly. Whichever the reason – different classifiers may attribute a given potential to different classes.

There are many ways to avoid ambiguity when more than one classifier is used. For instance one can choose the most efficient one, or attribute the potential to one of the two classes ACTIVE or INACTIVE if majority of the classifiers agreed. We decided to take the most

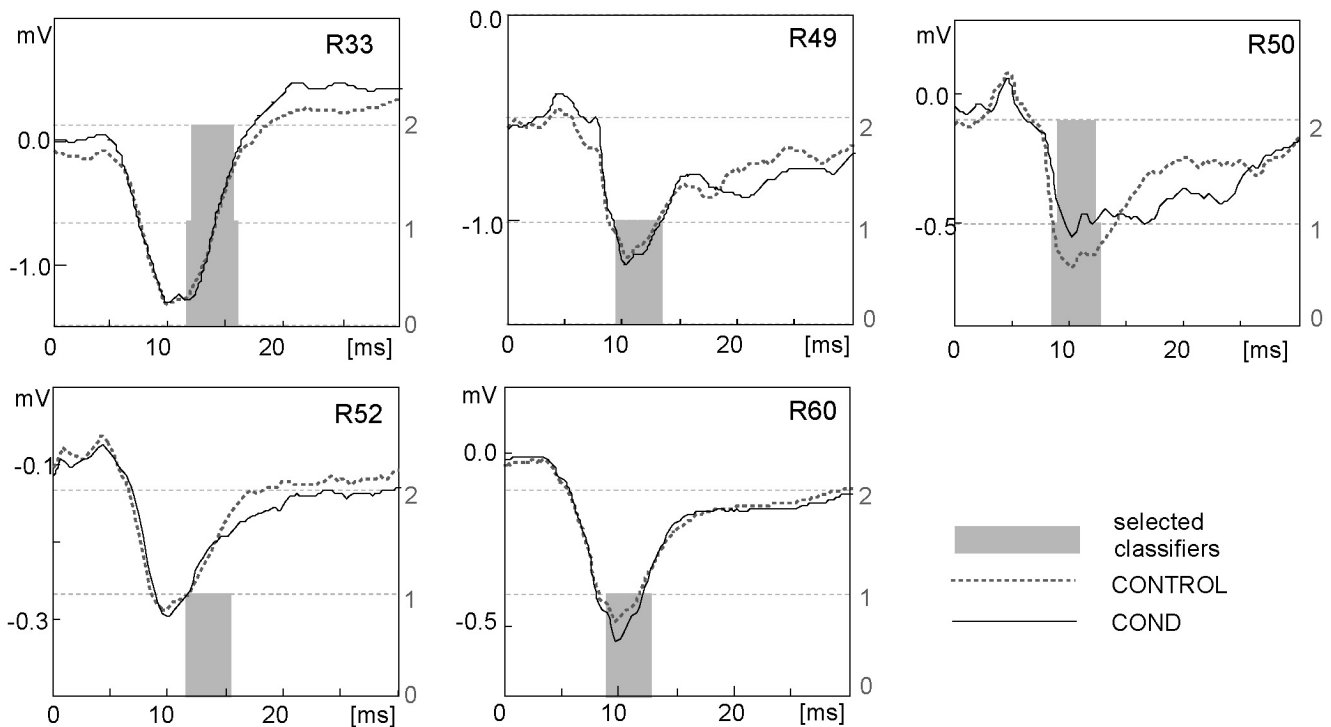


Fig. 4. Averaged potentials from groups COND (solid line) and CONTROL (dashed line). Gray bars indicate time window and number of selected classifiers. Left ordinate – voltage, right ordinate – number of classifiers.

conservative rule, that is to attribute the potential to one of the classes only if all (both in our case) of the classifiers agreed. Otherwise the potential was marked UNKNOWN. Figure 5 shows the results of the classifier voting. We believe that potentials classified by the described procedure as ACTIVE or INACTIVE indeed represent the two different states of rat's barrel cortex. In Fig. 6 we show averaged potentials from the ACTIVE and INACTIVE classes.

Physiological considerations

The idea of dynamic state control of the brain has been proposed a long time ago. Specifically, activation of thalamo-cortical systems has been shown to depend on modulatory influences from different sources (Arieli et al 1996, McCormick and van Krosigk 1992, Moruzzi and Magoun 1949). An active state of the neural network is characterized by widespread, but functionally limited, activation of specific local systems. These states have been characterized in sensory, motor, and association systems of many mammals. Particular interest was directed to the dynamic state changes in the cortico-thalamic loops of sensory systems (Abeles et al. 1995, Arieli et al 1996, Kisley and Gerstein 1999, Livingstone and

Hubel 1981, Waleszczyk et al. 2005). In both behaving and anaesthetized animals random fluctuations between those modes occur (Arieli et al 1996, Livingstone and Hubel 1981, Mukherjee and Kaplan 1995, Wróbel et al. 1998). These dynamic changes are lost or diminished during averaging. It implies that reliable methods for characterizing local brain states are needed in order to study the computational capacities of the conscious brain (Arieli et al 1996, Roland 2002).

The result of our analysis showed that the evoked potentials recorded in our experiment from each rat were not homogeneous. Despite (or thanks to) the great variance of the EPs from the experimental session, classification experiment showed that they can be divided into two distinct classes (ACTIVE/INACTIVE) which appear with different frequency during habituated and aroused periods of the experiment. We want to stress that potentials of the ACTIVE class were recorded also in the control part of the experiment and the INACTIVE ones during conditioning part of the session. It was the frequency of the appearance of the ACTIVE EPs that increased rapidly when the cortex was aroused by the aversive stimulation (Fig. 5). Such a result supports the hypothesis that the state of the cortex (identified here by class of record-

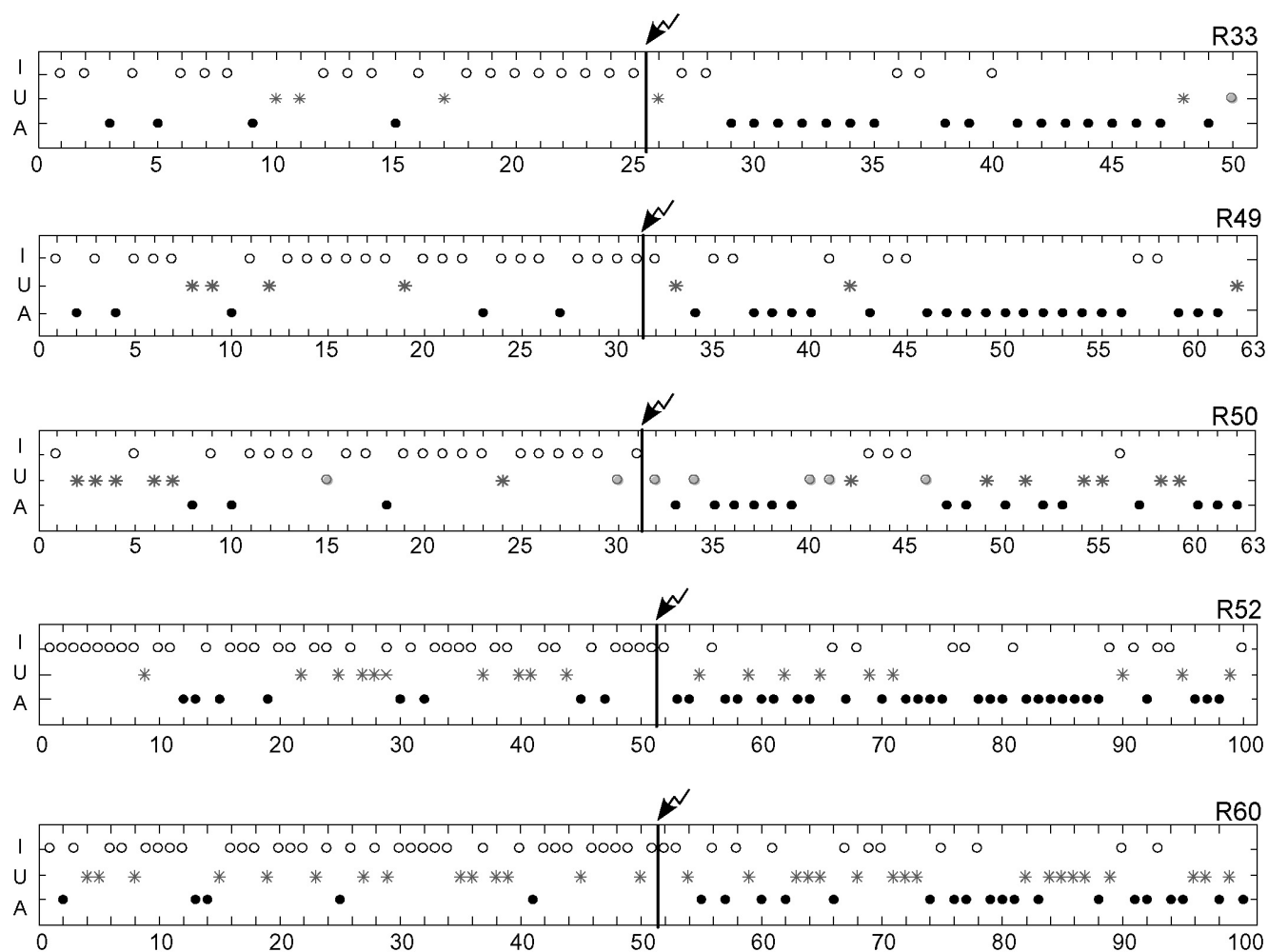


Fig. 5. Results of the classification. Filled circles indicate EPs classified to ACTIVE state (A), empty circles – EPs classified to INACTIVE cortical state (I). Gray circles mark EPs which were not classified by the method (UNKNOWN) and gray asterisks mark those which were removed from the sample during arbitrary preselection. Vertical line at each plot marks the time when the aversive shock was introduced.

ed evoked potentials) is a dynamic feature constantly modulated by external and internal influences. This finding matches our previous results with classifications based on different analytical methods (Kublik 2004, Wróbel et al. 1998, Wypych et al. 2003) and is in accordance with the other reports showing dynamic changes of the brain states (Abeles et al. 1995, Arieli et al. 1996, Kisley and Gerstein 1999).

The time window in which significant classifiers were found for each rat was between 11.7–12.8 ms (Fig. 3 and 4). This period matches the late phase of N1 wave of recorded EPs (Fig. 4). It has been shown to be composed from two main components which can be attributed to supra- (layers II–III) and infragranular (layers V–VI) pyramidal cell sources (Kublik et al. 2001, Musiał et al. 1998). The infragranular cell com-

ponent is delayed of about 3 ms to the supragranular component and peaks at 12–13 ms after sensory stimulation in the behaving rats (Musiał et al. 1998). This component has been shown to increase considerably during the activated state of the barrel cortex (Wróbel et al. 1998). On the other hand we have also shown that P2 component that represent the activation of columns neighboring the principal one (Kublik 2004) grew in COND part of a session. It is not surprising that dishabituation evoked by arousal stimuli involve transmission of information of the reinforced sensory stimulus to the surrounding network (Kublik 2004, Wróbel et al. 1998). Thus, the results of present analytical method match our previous findings. It promises to become an adequate tool for differentiating local brain states during behavioral experiments.

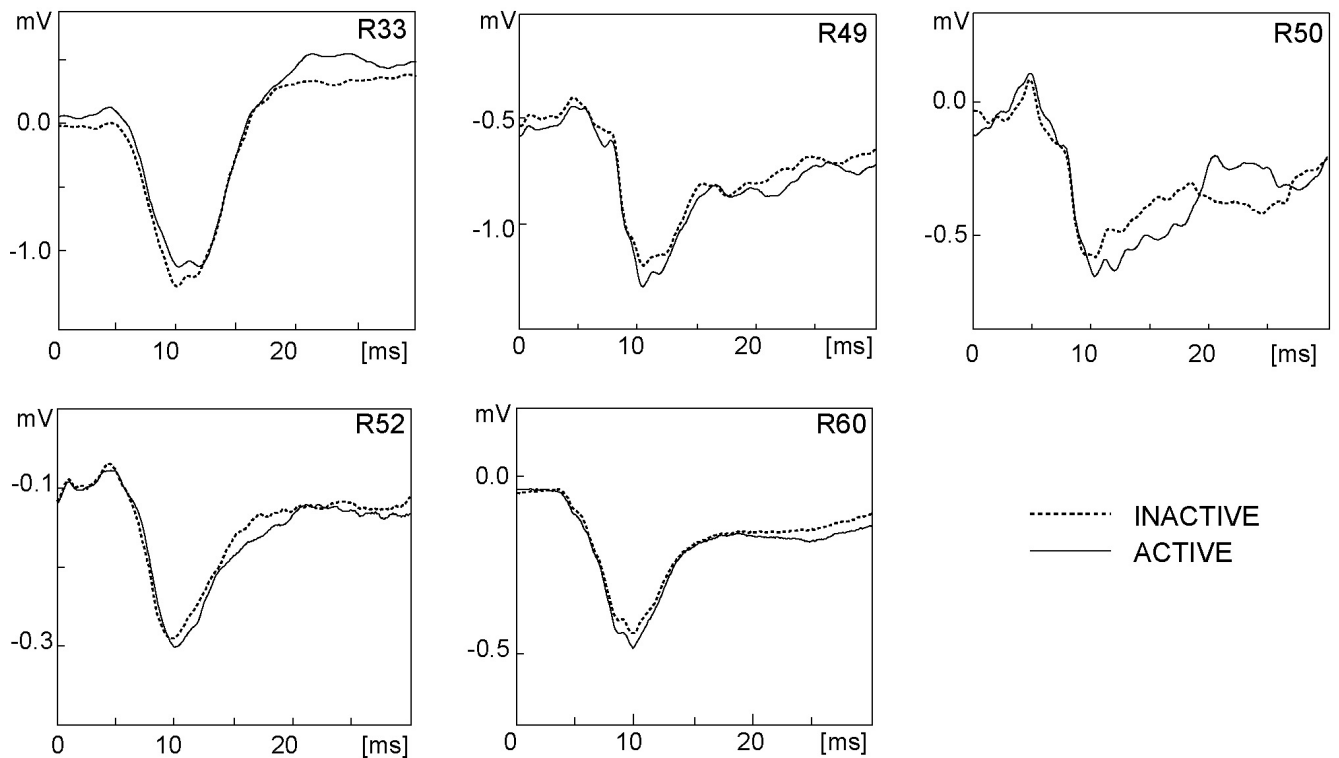


Fig. 6. Averaged evoked potentials classified as ACTIVE and INACTIVE.

CONCLUSION

In this paper we have found that the new method of local classifiers is a viable tool for classification of single evoked potentials in behaving animals.

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