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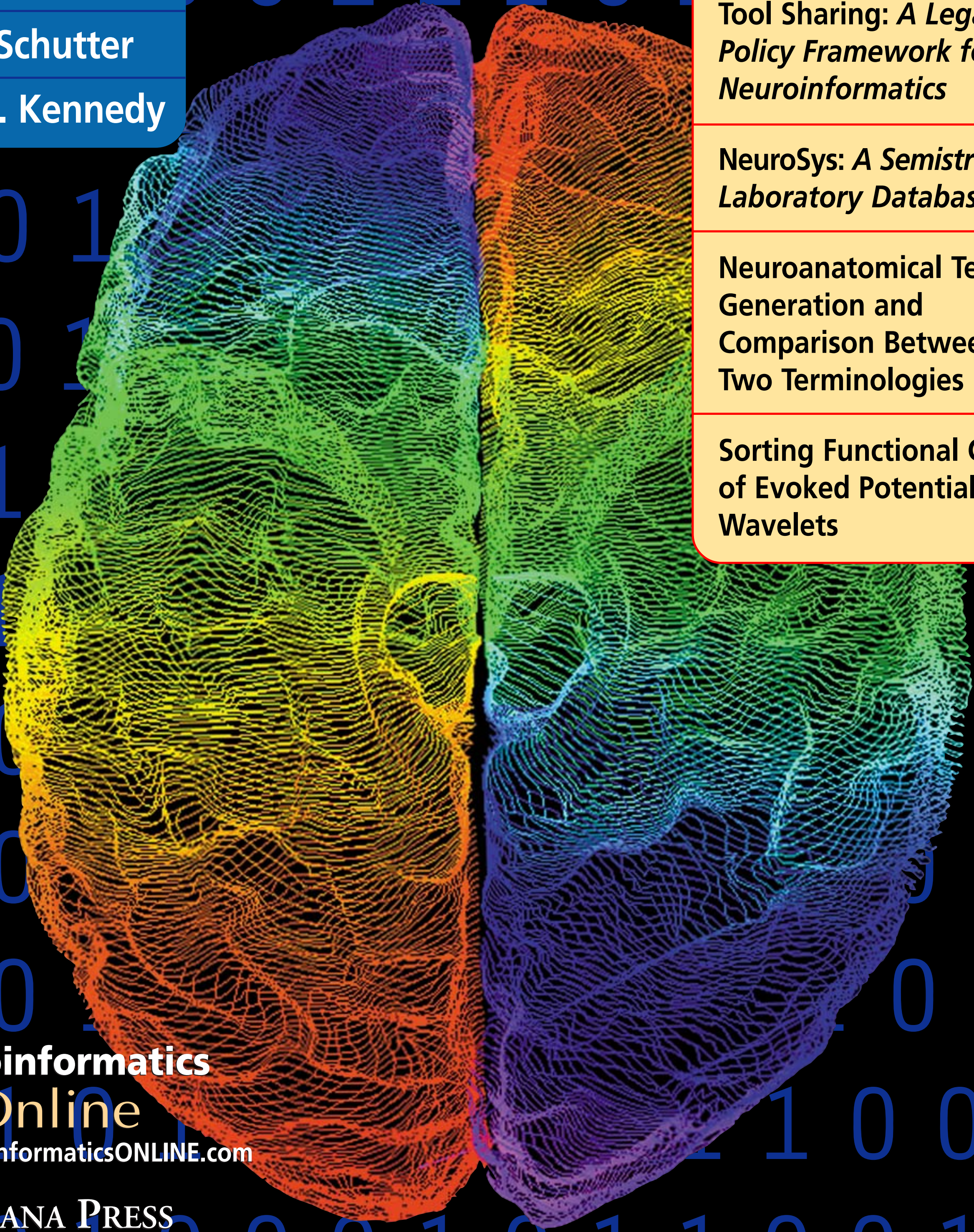

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Original Article

Sorting Functional Classes of Evoked Potentials by Wavelets

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Abstract

Evoked potentials (EPs) recorded within the primary sensory cortex of non-anesthetized rats vary considerably with each peripheral stimulation. We have previously shown that most of this variance reflects the shift of cortical activation between habituated and aroused states. Here we show that a method of matching the potential's course by wavelet functions can reliably differentiate single EPs and may therefore, be used as a probe for indicating the current activation state of the cortex.

Index Entries: Evoked potentials; wavelet analysis.

Introduction

A common hypothesis posits that many parallel circuits involving functionally repetitious neurons process information in the nervous system. When started by the same sensory event, the activity of these neurons would be synchronized at a given level and their average represented in neighboring neuropil as a local evoked potential (EP; Creutzfeldt et al., 1966; Eckhorn and Obermueller, 1993). If this hypothesis is true, the analysis of EPs might be a more efficient approach for understanding the brain in function than observing spike activities of single neurons. First, the EPs consist of online responses of many cells averaged at a given moment of the dynamic brain state in contrary to poststimulus histograms obtained by summing spikes from unitary responses in many trials over a longer time period, possibly during different functional states of the nervous network. Second, stable EPs can be monitored by means of gross chronic electrodes during long behavioral experiments, which is very difficult to achieve with the precise requirements needed for single neuron recordings (Munk et al., 1996; Wróbel et al., 1998).

We have previously shown that EPs recorded after stimulation of a single vibrissae by chronic electrode implanted at one site in a rat's barrel column, consist of two main components which can be differentiated in time domain by

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a special variation of principal component analysis (PCA; Musiał et al., 1998b). These components (which accounted for about 90% of the signals variance in sleeping and about 70% in behaving animals; Musiał et al., 1998b) were then identified as representing postsynaptic activation of supra- and infragranular pyramidal cells (Kublik et al., 2001). This is owing to the ordered, parallel placement of the apical dendrites of pyramidal cells which sum to form large, easily detected dipoles. Since the peak amplitude of the infragranular component is delayed for about three milliseconds from the supragranular one and both vary in amplitude depending on the behavioral state of the animal; the summed EPs differ accordingly (Kublik et al., 2001). Monitoring the dynamic ratio of activation of the two cell classes which provide the main outputs from cortical column (cortico-cortical and cortico-subcortical) may give insight into online local processing (Wróbel et al., 1998). In order to differentiate between the two EP classes, we have previously compared amplitudes of both subcomponents (Wróbel et al., 1998). This method, however, was not always satisfactory. Thus, in this paper we have tried to check whether the variant of the wavelet method that proved to be useful in other applications to biomedical signals (Wojdyłło, 1998; Szczuka and Wojdyłło, 2001; Wojdyłło, 2002) can be used for reliable classification of temporary EPs recorded in the rat barrel cortex during different stages of conditioning. Wavelet methods are based on the decomposition of the signal by calculating the appropriate coefficients in the wavelet basis and limiting the number of coefficients to the number necessary to preserve the intrinsic information. The method of calculating inner products (i.e. the discrete wavelet transform) combines low computational complexity with the capturing most of the essential information present in field potential data (Wojdyłło, 1998; Szczuka and Wojdyłło, 2001; Wojdyłło, 2002). In the second stage, selected coefficients are used to construct a classification system based on rough set theory (Komorowski et al., 1999). Certainly, the method of wavelet representation of the signal varies and the particular application is usually problem-driven. For instance, the wavelet transform has been used to find essential elements of auditory-evoked potential (Bartnik et al., 1992). The matching pursuit method (Mallat and Zhang, 1993) is designed to locate the elements of a time-frequency dilation dictionary in the signal and was applied to the search for sleep spindles (Durka, 1996). The classification systems for epileptic EEG and detection of rat emotional states were constructed recently by Wojdyłło (1998; *see also* Szczuka and Wojdyłło, 2001 and Wojdyłło, 2002). The wavelet denoising was also used as an analytic tool for evaluating rat auditory EP (Quian Quiroga and Luijtelaar, 2002).

Methods

Physiological Procedures

The behavioral experiments (*see* detailed description in Musiał et al., 1998a) were conducted on eight rats with electrodes (impedance of about 1 MΩ) implanted at the level of layer 4 (six animals had monopolar recordings against the reference in the frontal bone and two—R33 and R38—bipolar, with electrode tips at the top and bottom of the layer). Histological verification ascribed the recording points from 350 to 700 μm below the cortical surface. Daily experimental sessions on each rat lasted around 1 h. The animal was restrained in a special hammock which kept the head stabilized and allowed for easy vibrissa stimulation. During the session the chosen (principal) vibrissa was bent by means of piezoelectric device (100 μm for 3 ms) a hundred times in random time sequence (15 to 40 s

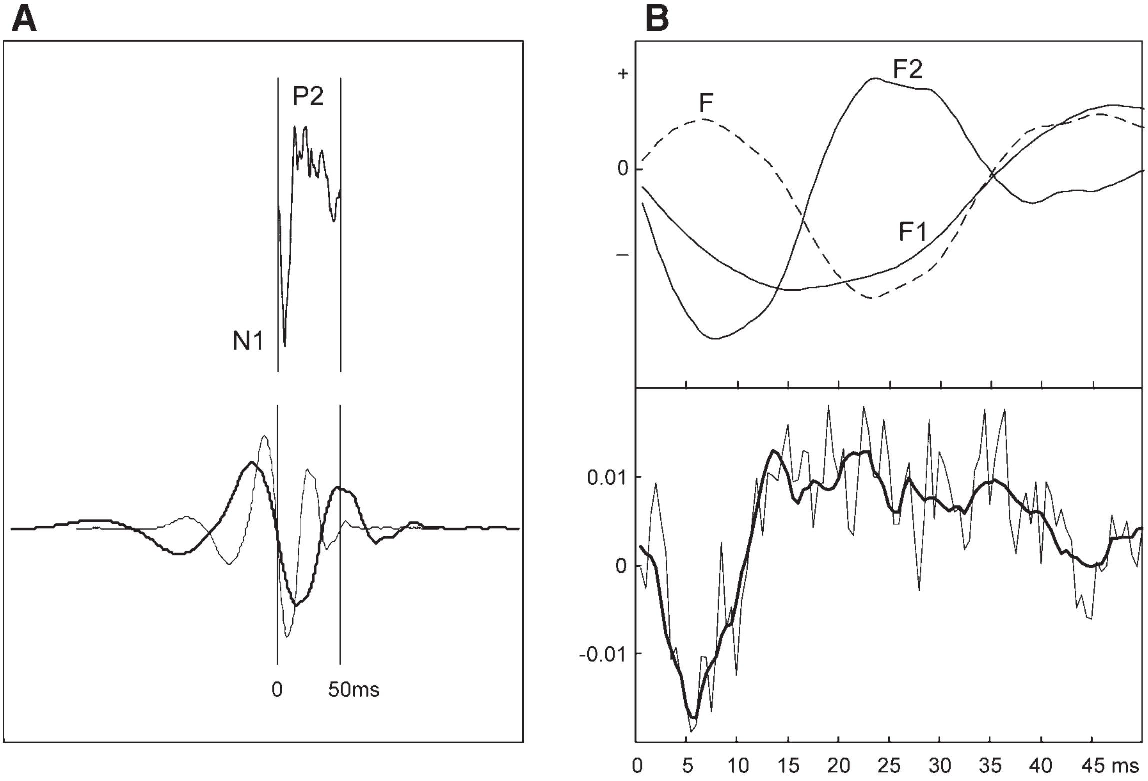

Fig. 1. **(A)** The wavelet method was based on calculation of the inner products (projections) between the EPs (e.g., above for R46, N1 and P2—characteristic waves) and shifted/dilated D5 wavelets (two examples are shown below). Each EP was described by 158 nonzero wavelet coefficients. **(B)** Upper graph: fragments of D5 wavelet (encompassed by window in Fig. 1A) that were chosen as "major" F1 and F2 functions. The final function F (dashed line) for rat R46 is also shown. Lower graph: single, EP (R46) (thick line) and the same EP with gaussian noise added (thin line) drawn at the same time scale as the functions above.

intervals) and thus activated the sensory stream up to the barrel column from which the single EPs were recorded (e.g., Figs. 1B, 2A–C). After the habituation period (3–10 d, to allow the stabilization of mean EP amplitude) the classical conditioning procedure was introduced in one analyzed session called "experimental." This session constituted from three blocks of responses: CONTROL (30 control EPs continuing habituation period), CONDITIONED (30 EPs evoked by vibrissae stimulation which was always followed by a mild electric current applied to the rat's ear; 50 Hz/0.1–0.5 mA/3 ms for 1 s) and REMAINING (including all remaining EPs in the session, each vibrissae stimulation was continuously reinforced by aversive electric stimulus). In one animal (R53PS), electric shocks were applied in a pseudoconditioning scheme, i.e., the reinforcing stimuli were applied with random delay time after bending the vibrissa.

Analytical Methods

Rationale

In our previous experiments we have shown that introduction of the aversive classical conditioning stimulus aroused the barrel cortex (Musiał et al., 1998a) and increased the relative

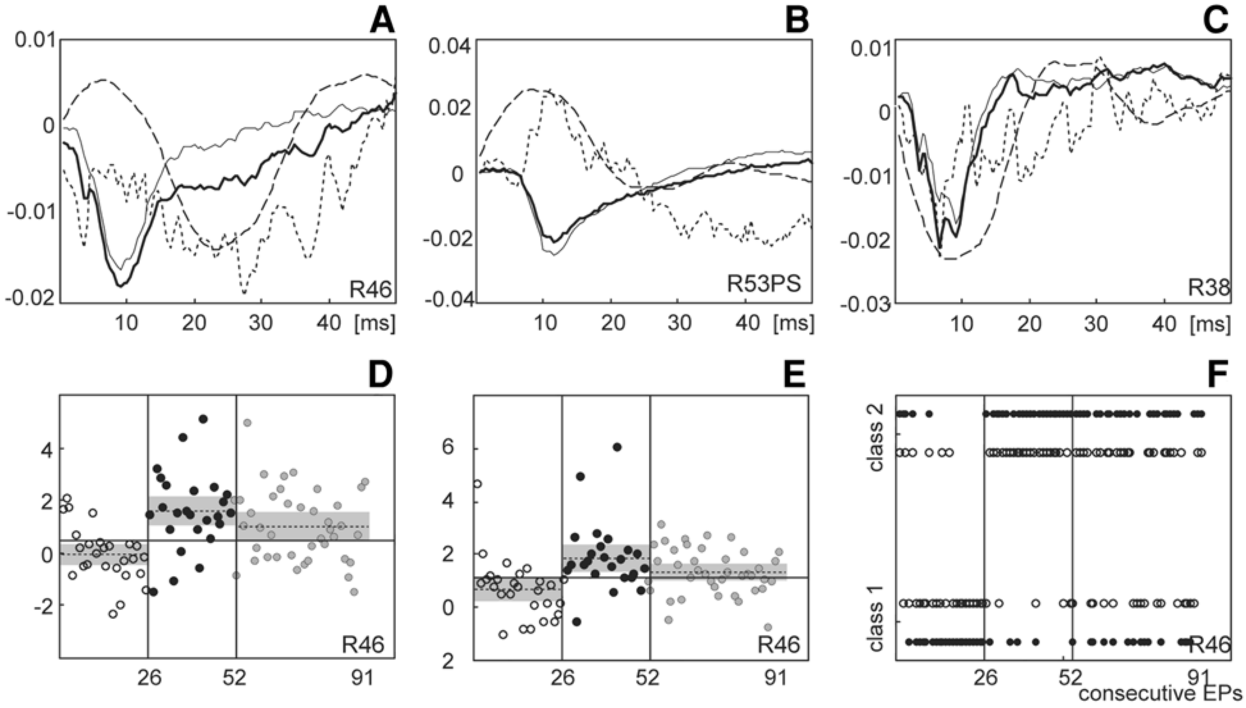

Fig. 2. **(A–C)** Averaged EPs from CONTROL (habituation, thin line) and CONDITIONED (thick line) periods of the experiments for rats R46, R53PS, and R38, respectively. The calculated F functions drawn by dashed lines and differences of mean potentials drawn by dotted lines are presented on the same figures in larger scale for better resolution. **(D,E)** Final parameterization of consecutive EPs as obtained by wavelets and difference of mean potentials methods. (Empty circles = EPs from CONTROL period; Black circles = EPs from CONDITIONED; Gray circles = EPs from REMAINING periods.) Continuous horizontal lines indicate separation thresholds. The mean values for each group are shown as dotted lines with 4SEM corridors (gray). **(F)** Sorting of EPs with help of both classification methods: wavelets (filled circles) and difference of mean potentials (empty circles). D, E, and F are taken from rat R46, vertical lines demarcate the three periods of experiments (CONTROL, CONDITIONED, and REMAINING).

contribution of the more lagged (i.e., originating in the infragranular pyramidal cells) from the two main components of EP (Wróbel et al., 1998). Accordingly, we were able to sort the recorded EPs into two classes: "habituated" and "aroused." The classification to the latter class relied on the subtle increase of the local maximum at the peak of the longer latency component and was influenced by concomitant spontaneous changes of the field potential. Nevertheless, it allowed us to show that contextual aversive stimulation abruptly changed the frequency of occurrence of both EP classes: the habituated type EPs were typical for the CONTROL period of the experimental session and aroused EP type dominated during the CONDITIONED period. Due to the habituation to the ongoing aversive stimuli (Knott et al., 2002) the number of aroused type EPs slowly decreased again, in the REMAINING time (Wróbel et al., 1998; *see also* Fig. 2F). In this study we have therefore focused mainly on data obtained from CONTROL and CONDITIONED periods of the experiment.

In a search for a more reliable classification tool, we decided to find a general function

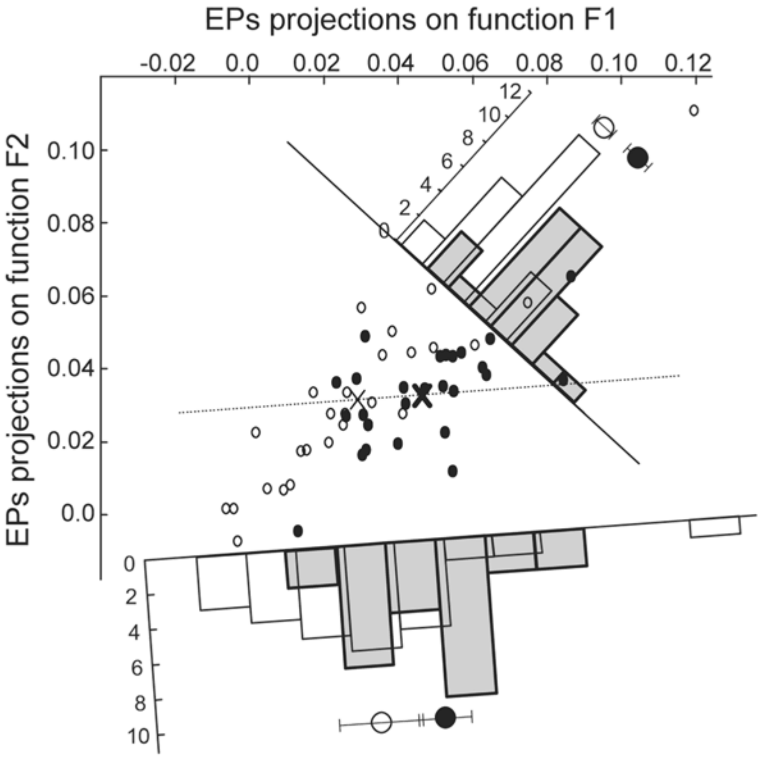

Fig. 3. Two-dimensional subspace where each EP is described by projections on functions F1 and F2. Points corresponding to EPs recorded in CONTROL period are shown as empty circles and those corresponding to CONDITIONED period are filled. Thin and thick crosses mark average EPs from both periods, respectively. The dashed line shows the optimal projection axis F, calculated by the Fisher algorithm. The oblique histogram shows the projection of the two groups (marked by empty and filled bars) on the F axis. Below, the similar histogram is shown which corresponds to projection of the same groups on the axis (dotted) connecting the average EP points. Big circles (with 2 SEM deviations) indicate the projections of mean values (crosses) on both axes.

whose inner product with the recorded EP would give a number characterizing each EP. The resulting numbers for the whole set could then be split into two groups depending on the comparison with the calculated threshold. Two approaches were tested in order to find the required function. In the first approach we utilized wavelet-based function. First we selected the most significant wavelet coefficients of the EPs and then the required function was constructed using only linear rules based on Fisher discrimination analysis. In the second approach we used the difference of the mean EPs from the CONDITIONED and CONTROL parts of each session as it naturally depended on the two potential types to be classified.

Initial Adjustment of the Data

The piece of continuously registered local field potential starting from the vibrissae stimulation and lasting 50 ms was considered as EP (Fig. 1A,B). This potential window was digitized with 2 kHz frequency, which resulted in 100 values per one EP. One hundred EPs from the experimental session of each rat were analyzed. Due to overlapping transient artifacts (evoked by animals' movements), some EPs from each session were excluded from the analysis as judged visually from the recorded signal. This left an average of 28 EPs in CONTROL and CONDITIONED periods and 37 EPs in REMAINING time, for further analysis. For a given animal the average level of all field potential values measured during 50 ms just prior to the movements of the vibrissae was taken as reference (zero). The EP amplitudes were then normalized by dividing them by the Frobenius norm (square root of the sum of the squares of the elements of an N column matrix where each EP was represented by 100 values in one column) and multiplying by $\sqrt{N}$.

Since all chronic electrodes were placed in slightly different cortical depths and data were recorded with either mono- or bipolar electrodes, the EPs registered from different animals also differed (*see* Fig. 2A–C). We have therefore decided to fit a specific function for each animal.

Wavelets

The signal is decomposed in the orthonormal basis formed by the translations and dilations of the mother wavelet Ψ. The elements of this basis are specified as:

$$\Psi_{jk}(x) = 2^{j/2}\Psi(2^{j}x - k)$$

Since the basis is orthonormal, coefficients of the signal s are given by inner products:

$$c_{jk}(x) = \int_{-\infty}^{\infty} s(x)\psi_{jk}(x)dx$$

For wavelet Ψ, we chose Daubechies D5 wavelet (Daubechies, 1992) because it is continuously differentiable and has adequate length of support. Our previous research also proved that using this wavelet for biological signal processing preserves essential input signal information (Wojdyłło, 1998).

Although most of the applications of wavelet methods use a tree algorithm of decomposition, we directly calculated the inner products between measured signals and translated/dilated D5 wavelets (or its appropriate fragments). This procedure allowed us to generate coefficients from short-time EP signals associated not only with high but also with low frequencies (below 20 Hz).

At each level of dilation (N=2,...,7) we were using a D5 wavelet $9{\cdot}2^{N}$ points long (lasting $9{\cdot}2^{N}/2$ ms). The beginning of the wavelet was positioned at the beginning of the signal and their inner product was calculated. Next, the wavelet was shifted 2^{N} points to the left or right (until it did not overlap the signal) and consecutive inner products were calculated.

Two elements of this basis are shown in (Fig. 1A, bottom). The analyzed EPs (represented by 100 numbers each) can be understood as vectors in 100-dimensional space, and the chosen wavelets as an overcomplete set of functions (not a basis) since each EP was characterized with 158 non-zero coefficients.

In order to reduce the number of coefficients, we have chosen two elements of the wavelet basis, with the highest absolute values of inner products for most EPs (i.e., for all 743 signals obtained from 8 rats). This was done by finding a threshold that was reached by the coefficients obtained for 70% of EPs with only two wavelet functions. Such functions were expected to be the most sensitive for identifying the systematic differences expected between EPs recorded in both (CONTROL and CONDITIONED) periods. We called these "major" functions F1 and F2 (Fig. 1B, top).

Each EP was then described by two parameters, the inner products which can be intuitively understood as projections on each of the selected major functions. All EPs recorded from each of the animals could then be represented as points in the two-dimensional space (Fig. 3). Separate representation was prepared for data from each animal and allowed finding direction of an axis which optimally differentiated EPs from CONTROL and CONDITIONED EP-groups (Fisher discrimination analysis, Dillon and Goldstein, 1984). This direction was obtained by such a rotation of the axis connecting averages from both groups (which is equivalent to difference of means in the subspace), which gave the best separation of the groups:

Where:

$$V = (M2 - M1) \cdot \left(\frac{[n1-1] \cdot C1 + [n2-1] \cdot C2}{n1 + n2 - 2} \right)^{-1}$$

V = direction vector,

$M1,\ M2$ = means of the groups,

$n1,\ n2$ = numbers of elements in the groups, and

$C1$, C2 = covariance matrices for the groups.

This axis was described in the F1/F2 space by the straight line equation $F=A\ F1+B\ F2$ ($V=[A,B]$ here). The projection of each EP-point on the F axis gave us a new parameter, characterizing each EP with single number *f*. This projection corresponded to calculating inner products of consecutive EPs with function F (function F is a combination of functions F1 and F2 with coefficients A and B). The value f could be then found by calculating $A\ f1+B\ f2$, where $f1$ and $f2$ are the projection values of a given EP on the major functions.

The *f* parameters, each corresponding to one EP, were finally divided into two classes in such a way that led to a minimal number of EPs of class 1 in CONDITIONED group and of class 2 in CONTROL group. The separating value was set as the value resulting in the minimal sum of the squares of the parameters that were classified as opposed to the majority of the group (compare Fig. 2D,F).

Difference of Mean Evoked Potentials

A similar classification as described previously was obtained using the difference between averaged EPs from groups CONDITIONED and CONTROL instead of function F, in each animal's data (Fig. 2A–C). The example of resulting projections of the consecutive EPs on that difference is shown in Figure 2E. The separating threshold was found similarly as in the wavelet method (compare Fig. 2E,F).

Results and Discussion

Efficiency of EP Sorting in Classical Conditioning Paradigm

In this paper, we attempted to check whether the wavelet method could be used for reliable classification of single EPs recorded online from a behaving rat. Up to the present, the most popular method for EP classification has simply relied on the measure of their amplitude (e.g., Castro-Alamancos and Connors, 1996). We have previously shown that the parameter based on comparison of the amplitudes of EP's main components might be a good measure of the current activation of the sensory cortex (Wróbel et al., 1998). However, this method needed perfect recordings, which were not always secured in chronic experiments. The wavelet and difference methods that use the information from the EP shape within the whole time window were perfect candidates for such ongoing classification of evoked potentials. To test whether this method will work in typical behavioral experiment, we used the classical paradigm from our previous studies where the recorded EPs were shown to depend on contextual aversive stimulation, absent in CONTROL time, and systematically accompany the sensory stimuli during the CONDITIONED period of experiment (Wróbel et al., 1998; Kublik et al., 2001).

Since both the wavelet and difference methods were able to discern the data into classes even if the difference was incidental; we have therefore compared results of classification (measured in index of sorting efficacy for both methods) of experimental data and of the same

Table 1A. Classification with Wavelet Method

Rats	R33	R38	R46	R49	R50	R52	R53PS	R59
Exp. Data	73.7	73.3	82.7	65.5	60.7	69.1	71.7	73.5
Control Data	63.3–4.5	60.6–4.0	60.6–4.2	61.0–4.2	61.6–4.2	58.6–3.5	61–4.2	60.1–3.7
Significance	p<0.014	p<0.002	$p<10^{-6}$	p<0.15	p<0.57	p<0.003	p<0.007	p<0.001

Table 1B. Classification with Difference of Means

Rats	R33	R38	R46	R49	R50	R52	R53PS	R59
Exp. Data	78.9	70.0	78.8	79.3	64.3	83.0	80.0	76.5
Control Data	70.3–4.1	67.9–3.4	67.1–4.3	70.4–4.2	70.8–4.6	66.3–3.3	66.4–4.1	66.1–3.7
Significance	p<0.02	p<0.27	p<0.005	p<0.002	p<0.92	$p<10^{-6}$	p<0.001	p<0.004

data appointed randomly by half to PSEUDO-CONTROL and PSEUDO-CONDITIONED groups. Such a random distribution was done 100 times and each time different EPs were accounted as belonging to both PSEUDO-groups.

The efficacy indexes for experimental and random data are presented in Table 1A and B. Both classification methods successfully differentiated the experimental and randomized data. In both cases six significant results ($p<$ 0.05, Student t-test) were obtained. We also compared total efficacy indexes obtained for experimental data from the whole group of rats with indexes obtained in all PSEUDO-experiments. These total results were significant: $p<10^{-11}$ in wavelet method and $p<10^{-7}$ in difference of mean EPs method (Student t-test). We conclude that both methods used in the analyses are useful tools for differentiating functional changes of sensory evoked potentials influenced by contextual, aversive stimulation. The efficacy index did not reach one in any experiment, which was to be expected when taking into account dynamic fluctuation of the incoming neuromodulatory activity and other spontaneous inputs continuously reaching the recorded tissue.

Sensitivity for Noise

The intrinsic noise of signals recorded from each animal were estimated by independent observers and, more objectively, by calculating the ratio of FFT mean amplitudes under vs over 100 Hz (not shown). This noise was small for data from rats R33, R46, R53PS, R59, average from R49, R50, R52, and high from the R38. When compared to the efficacy indexes, this estimation indicated that the intrinsic noise was noteworthy, but not a major obstacle for our sorting analyses.

In order to estimate the sensitivity of both methods to the outer disturbance, all normalized experimental signals were summed with white gaussian noise of high amplitude: with mean zero and 0.004 standard deviation (Fig. 1B, top). Similar analyses as those used for the original data were then applied and their results are presented in Table 2A for wavelets and Table 2B for mean potentials method.

The contamination of the original EP data with noise did not result in change of the chosen major functions F1 and F2. The efficacy indices calculated for the disturbed signals were smaller than for the originally recorded signals, but did not change for the control PSEUDO- groups. However, the number of rats in which significant differences between EPs in CONTROL and CONDITIONED groups were found decreased to four. On the other hand, the difference of averaged EPs for disturbed signals was much noisier (especially in high frequency range, not shown) than obtained for original recordings (Fig. 2A–C). Such a variability of the function which was

Table 2A. Classification with Wavelet Method, Noised Data

Rats	R33	R38	R46	R49	R50	R52	R53PS	R59
Exp. Data	71.1	71.7	84.6	65.5	66.1	69.1	66.7	70.6
Control Data	63.1–5.3	60.0–3.9	60.6–4.3	61.0–4.7	61.4–4.2	58.3–3.9	60.2–4.6	60.3–3.8
Significance	p<0.07	p<0.002	$p<10^{-6}$	p<0.16	p<0.13	p<0.004	p<0.07	p<0.005

Table 2B. Classification with Difference of Means, Noised Data

Rats	R33	R38	R46	R49	R50	R52	R53PS	R59
Exp. Data	81.6	75.0	82.7	79.3	76.8	86.2	83.3	77.9
Control Data	79.4–5.0	72.4–4.0	72.0–4.5	74.7–4.2	75.8–4.3	74.1–3.6	74.2–4.7	76.8–4.3
Significance	p<0.33	p<0.26	p<0.011	p<0.14	p<0.41	p<0.0009	p<0.03	p<0.39

used for the final sorting of disturbed signals did not change much of the efficacy index for experimental groups but increased the index for the control (PSEUDO- groups) data in such a way that only three significant results were obtained. However, the total group-results in both methods were significant ($p<10^{-9}$ and $p<10^{-4}$ in wavelet and mean potentials method, respectively).

The wavelet method appeared to be more resistant to added noise than the one using difference of mean potentials. There might be three reasons for such an observation. First, in contrast to naturally noisy difference function, function F contains only low frequencies and therefore is less sensitive to the added high frequency noise. Second, by using the wavelet method we were able to reduce dimension of the space (from 100 to 2) without significant loss of information. Third, the important step influencing the efficacy of the classification depended on finding the best angle for projection of the two-dimensional non-symmetric distributions shown in Figure 3 on the final axis. The Fisher analysis was specially designed for such an evaluation (dashed line in Fig. 3) whereas projections on the difference of mean potentials (in this two-dimensional subspace) are equivalent to projections on the line connecting the calculated means (crosses in Fig. 3). The projection histograms are presented in Figure 3. It is clear that Fisher analysis resulted in more compact and better separated groups.

Functional Considerations

In this paper we have presented the new method of classification of single EPs, which can reliably account for the recorded responses to one of the two classes. This result confirms our previous observations that contextual stimulation changes the EPs recorded in the barrel cortex by vibrissae stimulation from habituated to aroused-type (Wróbel et al., 1998; Wróbel and Kublik, 2000). Note that in both (wavelet and difference of mean potentials) analytical approaches a significant difference was also found for rat R53PS, which was trained in a pseudoconditioning regime. This indicates that change of EP type was not owing to the conditional pairing of the two stimuli, but rather resulted primarily from the unspecific arousal accompanying novel (aversive) stimulation. Thus a single EP course may serve as an online indicator of the underlying activation state of the cortical tissue within different parts of the behavioral paradigm. The calculated function F was found to be highly correlated with the change of EP-courses (difference of means) at different arousal states (Fig. 2A–C). This function reached local extreme values at the latencies of peak responses for N1 (around 10 ms) and P2 (from 20 to 40 ms) characteristic EP waves and therefore should also be most sensitive to dynamic variations of the underlying physiological mechanisms (Wróbel et al., 1998; Wróbel and Kublik, 2000).

Acknowledgments

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