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Neurocomputing 38–40 (2001) 1557–1566

NEUROCOMPUTING

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Reading auditory discrimination behaviour of freely moving rats from hippocampal EEG

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Abstract

It has been suggested that hippocampal rhythmical slow activity (theta rhythm) is related to cognitive process and the genesis of P300 response. To test this hypothesis, hippocampal EEG data from CA1 were recorded from rats trained to perform auditory discrimination oddball paradigm. In well-trained rats, significant changes in the hippocampal theta rhythm were observed during an auditory oddball paradigm. Here we used an artificial modular neural network with wavelet coefficients to investigate whether changes in the hippocampal theta rhythm are related to cognition of right tone objectively. However, an objective data interpretation with the modular neural network does not support the hypothesis that changes in theta rhythm are related to cognitive process. In addition, it was confirmed that changes in task-related theta rhythm before/after learning the auditory oddball paradigm resulted from the fact that training changed the character of the motor behaviour. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: P300; Hippocampal theta rhythm; Objective interpretation; Modular neural network

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1. Introduction

Theta rhythm is a local field potential also known as rhythmical slow-wave activity (RSA), a sinusoidal-like EEG signal occurring at frequencies within the bandwidth from 5 to 12 Hz. Theta's long popularity in brain research stems from the hope that it may be linked to higher cognitive functions such as "attention", "motivational states",

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PII: S0925-2312(01)00560-4

or "learning" [7]. Theta rhythm can be recorded from the hippocampal formation of mammals during voluntary motor behaviours such as walking, running, rearing, jumping, swimming, digging, manipulation of objects with the forelimbs, and orienting head and body movements [18]. Theta rhythm from cortical surface in experiments with human subjects during virtual spatial navigation has recently been reported [6], and its possible connection to hippocampal theta rhythm has been discussed [11]. On the other hand, it is widely believed that the late positive component (P300) of event related potentials (ERP) reflects the brain cognitive processing associated with the detection of a target signal and the neuronal activity in the hippocampus is involved in its generation [16]. Several investigators [1–4] suggested that hippocampal theta rhythm is responsible for the genesis of P300 response. However, Vanderwolf [18–20] has suggested that many aspects of the generalized patterns of electrical activity of the hippocampal formation and neocortex (including theta rhythm and neocortical activation) are closely correlated with concurrent motor activity and other aspects are related to sensory inputs independent of overt motor activity. Moreover, predictions from recent advances about neural code [14,13] support Vanderwolf's suggestions. In this paper hippocampal EEG data from rats trained to perform auditory discrimination oddball paradigm were analysed using wavelet transform, and an objective data interpretation with the min–max modular neural network was tried to clarify this long-standing issue.

2. Animal surgery and training

Eight male Long Evans rats between 300 and 400 g were housed in individual cages with food and water provided until the behavioural training. A pair of 80 μm varnish-isolated stainless-steel wires were placed in CA1 region (4.2 mm posterior bregma, 2 mm lateral to midline, 2.5 and 3 mm ventral to the dura) for recording the hippocampal field potentials. Pairs of stainless steel watch screws were fixed into the skull over the cerebellum and nasal bone as ground and reference electrodes. One week after surgery rats were water-deprived and trained in a chamber by means of oddball paradigms [3], in which occasional 'target' stimuli have to be detected in a train of frequent 'non-target' stimuli. We used a low frequency tone of 1 kHz (the so called odd tone) as 'target' stimuli and a high frequency tone of 2 kHz (the so called frequent tone) as 'non-target' stimuli. Tones were given with 50 ms duration and 84 dB intensity. The animals were rewarded by water whenever they discriminate 'target' tone. The recording and training chamber was a box (40 cm × 40 cm × 40 cm) with a round open top of 28 cm diameter and a front glass door. A drinking tube, 3.5 cm above the floor, protruded from the left sidewall. The tones could only be represented after the rat removed its head from the water tube. Drinking was detected by using an infrared light source and phototransistor located above the drinking tube. Up to three drops of water were provided through the tube during each trial. Hippocampal field potentials of 6 s duration including a 1.5 s period before the tone were recorded in freely moving rats, amplified, filtered (1 Hz–1 kHz), digitised (2 kHz sampling rate), and sorted by the stimuli and animal's behaviours. The tip locations of the depth electrodes were verified by light microscopy in the Nissl-stained sections after the experiments.

3. Task-related changes in hippocampal theta rhythm

Shinba et al. [16] have suggested that P450 of rats may correspond to the human P300, and that the neuronal activity in the hippocampus is involved in its generation. Independently, Brankack et al. [3] have found P300-like task-related potentials in the hippocampus of rats performing an auditory oddball paradigm and suggested that hippocampal theta rhythm is responsible for the P300-like response. In well-trained rats it was found that a significant frequency increase of the hippocampal theta rhythm about 300 ms after the odd tone but only if the animal's response was correct [4]. After the non-target tone, no comparable changes have been observed irrespective of the rat's response. In untrained rats any comparable frequency changes after any of the tones no matter how the rats respond were not found. However, conventional averaging-based event-related potential, synchronized to repeated occurrences of a specific event, suffers from two major problems in studying hippocampal EEG; first, ensemble averaging removes information about changes in frequency and amplitude of the hippocampal theta rhythm during an oddball paradigm. Second, it suffers from detecting individual differences of single trial evoked-response potentials (ERPs). For example, it has been found that target-like P300 appears even with nontarget stimuli, which obviously suggest further investigation as to the reliability of selective event-related data averaging when applied to cognitive brain function analysis [8].

To overcome above problems from ensemble averaging, we adopted wavelet time–frequency analysis to investigate both amplitude and frequency changes in hippocampal theta rhythm during an oddball paradigm, which has been found useful in analysing nonstationary signals like task related single trial ERPs and oscillations [17,5]. The hippocampal EEG from rats performing an Oddball-GO/NO-GO reference memory task was convolved by the Morlet wavelets $w(t, w_0)$ with a Gaussian shape both in the time domain and in the frequency domain around its central frequency w_0:

$$W(t, w_0) = e^{(jw_0 t)} e^{(-t^2/2)}. \tag{1}$$

These wavelets can be compressed by a scale factor a and shifted in time by a parameter b. Convolving the signal and the shifted and dilated wavelet leads to a new signal

$$S_a(b) = \frac{1}{\sqrt{a}} \int W\left(\frac{t-b}{a}\right) x(t)\, dt, \tag{2}$$

where W is the conjugate of the complex wavelet and $x(t)$ is the hippocampal EEG signal. These new signals $S_a(b)$ are computed for different scaling factors a. In order to generate maps of theta activity, we extracted signal components between 5 and 12 Hz out of the time–frequency maps. Our data consisted of four classes

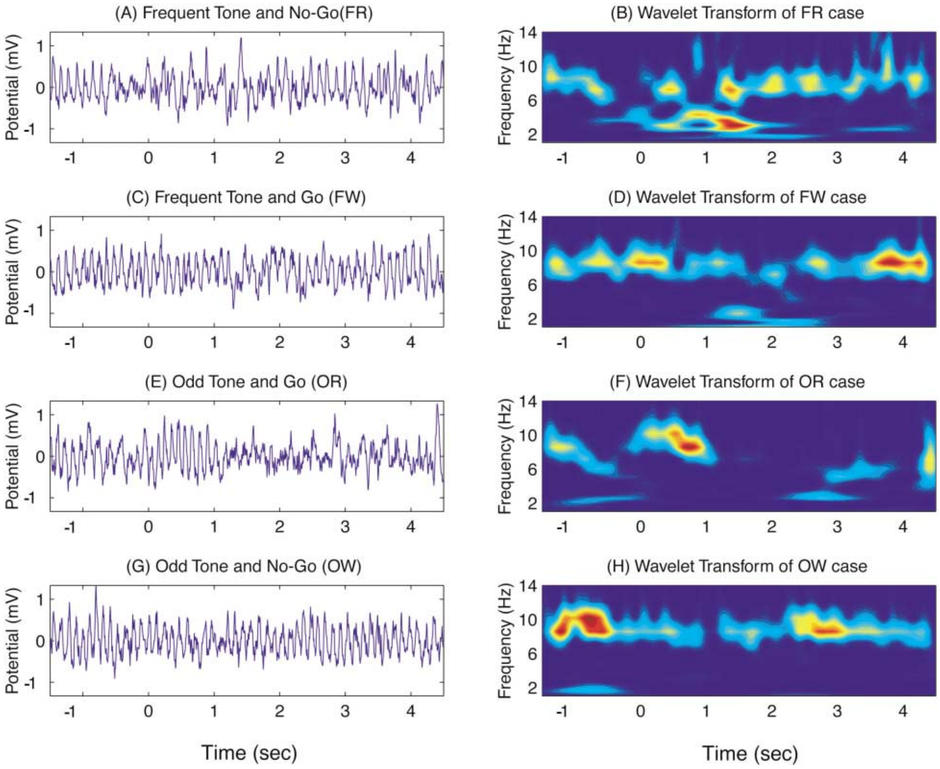

Fig. 1. A typical example (one from each class) of single trial and its wavelet transform of the hippocampal theta rhythm during an auditory discrimination in well trained rats. Tones were given at zero second. Colour coding is blue for close-to-zero values and red for close-to-maximum values.

(FR, FW, OR, OW), where "FR" means frequent tone and right behaviour (NO GO), "FW" frequent tone and wrong behaviour (GO), "OR" odd tone and right behaviour (GO), and "OW" odd tone and wrong behaviour (NO GO). A typical example (one from each class) of single trial and its wavelet transform of the hippocampal theta rhythm during an auditory discrimination in well trained rats is shown in Fig. 1. Similarly to results using ensemble averaging [4], it was found that a significant frequency increase of the hippocampal theta rhythm about 300 ms after the odd tone but only if the animal's response was correct (Fig. 1F). However, we do not know whether this result is consistent in all single trials. Moreover, the interpretation of the changes in hippocampal theta rhythm during an oddball paradigm with relation to the cognitive brain function has not been confirmed yet.

4. Objective data interpretation by an artificial neural network

It has proved difficult either to verify or to disprove any given hypothesis concerning the operating principles of even the simplest neural system. Major areas are so richly interconnected that there exists no good way of separating one function from another. Moreover, people tend to see what s/he wants to see from this ambiguous situation. Such subjective interpretations have been a crucial bottleneck to understand brain function objectively. The same has been true for hypotheses related to hippocampal rhythmical slow activity. Here we propose an alternative way to get rid of the subjective interpretation problem by using an artificial neural network combined with wavelet transform and try to answer two questions: (a) whether single trial hippocampal EEG data contain sufficient information to distinguish rat's auditory discrimination behaviours, and if so, (b) which is the most plausible one among following three hypotheses related to task related changes in hippocampal theta rhythm,

1. Whether changes in hippocampal theta rhythm are related to recognition of correct tone.
2. Whether changes in hippocampal theta rhythm reflect rat's decision to go.
3. Whether changes in hippocampal theta rhythm are a consequence of the fact that training changed the character of the motor behaviour [18].

In this paper we used the min–max modular network [10] for classification of the hippocampal EEG data. Fig. 2 shows the relationship between the hippocampal EEG single trial data, wavelet transform, and the min–max modular neural network. Two main advantages of the min–max modular network over existing neural networks are that any large and complex problem can be easily divided into a number of independent subproblems small enough as a user expects [9] and all of the subproblems can be efficiently learned by small network modules in parallel. Consequently, a large set of EEG data can be classified effortlessly and efficiently by using the min–max modular network. Each single trial EEG signal was 6 s in duration and was downsampled from 12,000 samples to 400 samples for 6 s, and 5 wavelet coefficients over hippocampal theta bandwidth (5–12 Hz) were extracted. Therefore, 400 × 5 (2000) features extracted from each single trial EEG data are used as inputs. The hippocampal EEG single trial data set consists of 1491 training data and 636 test data. The number of attributes is 2000 and the number of classes is four (FR, FW, OR, OW). Table 1 shows the data distributions in the training and test data sets. According to the task decomposition method [10], the EEG single classification problem was decomposed into 1189 two-class subproblems randomly, where the training data sets belonging to FR, FW, and OR are divided into 49, 6, and 15 subsets, respectively, and the number of subsets belonging to OW is one. The number of training data in each of the subprograms is about 40. Since each of the subproblem can be treated as a completely separate two-class problem in learning stage, all of the subproblems can be learned in parallel. In the simulation, the conventional backpropagation algorithm [12] was used.

The momentums were all set to 0.9, and the learning rates were all selected as 0.03. Training was stopped when the sum of the squared error was smaller than 0.01 or the total number of epochs reached 1000. The 1189 three-layer MLPs were selected as network modules to learn the corresponding 1189 subproblems. Each of the modules

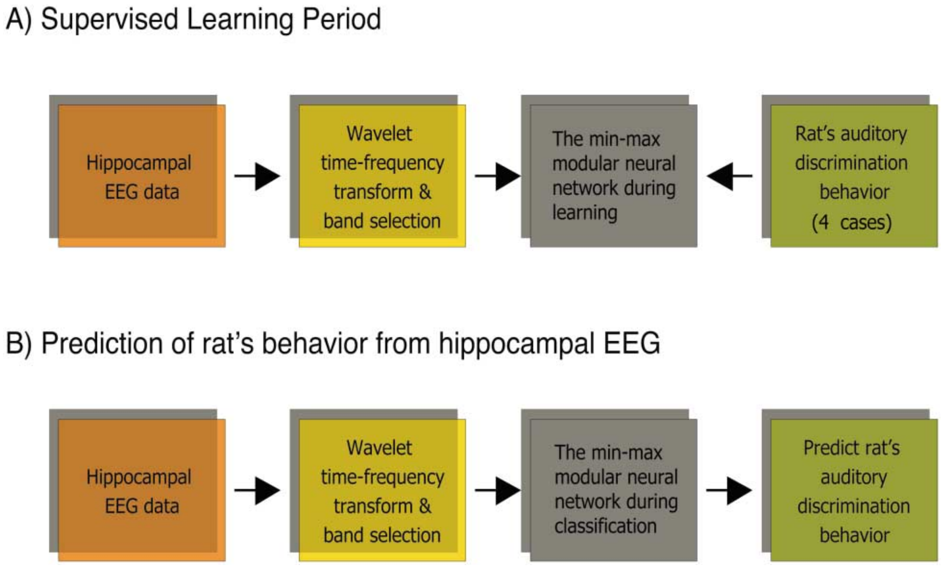

Fig. 2. Block diagrams to show the relationship between the EEG data, wavelet transform, and the min–max neural network. (A) Supervised learning process using training data set; (B) Classification of rat's behaviour using the hippocampal EEG single trial data set.

Table 1
Number of data belonging to each of four classes in the EEG data set and the distributions of incorrect outputs produced by the trained min–max modular network

Classification by combination of stimulus and response	No. of instances		No. of incorrect outputs	
	Training	Testing	Training	Test
Frequent tone/NO-GO (FR)	1027	430	0	26
Frequent tone/GO (FW)	136	68	0	43
Odd tone/GO (OR)	307	128	0	15
Odd Tone/NO-GO (OW)	21	10	0	10
Total	1491	636	0	94

has 2000 input, six hidden, and one output units. The simulation results show that all of the network modules successfully learned the corresponding subproblems within 1000 epochs. The number of average epochs and CPU time used for training each of the network modules are 266 and 95 s at a HP workstation, respectively. Following the module combination principles [10], the 1189 individual trained modules were integrated into an M^3 network shown in Fig. 3. Its success rates on training and test data, i.e., the learning accuracy and generalization performance, are 100% and 85.2%,

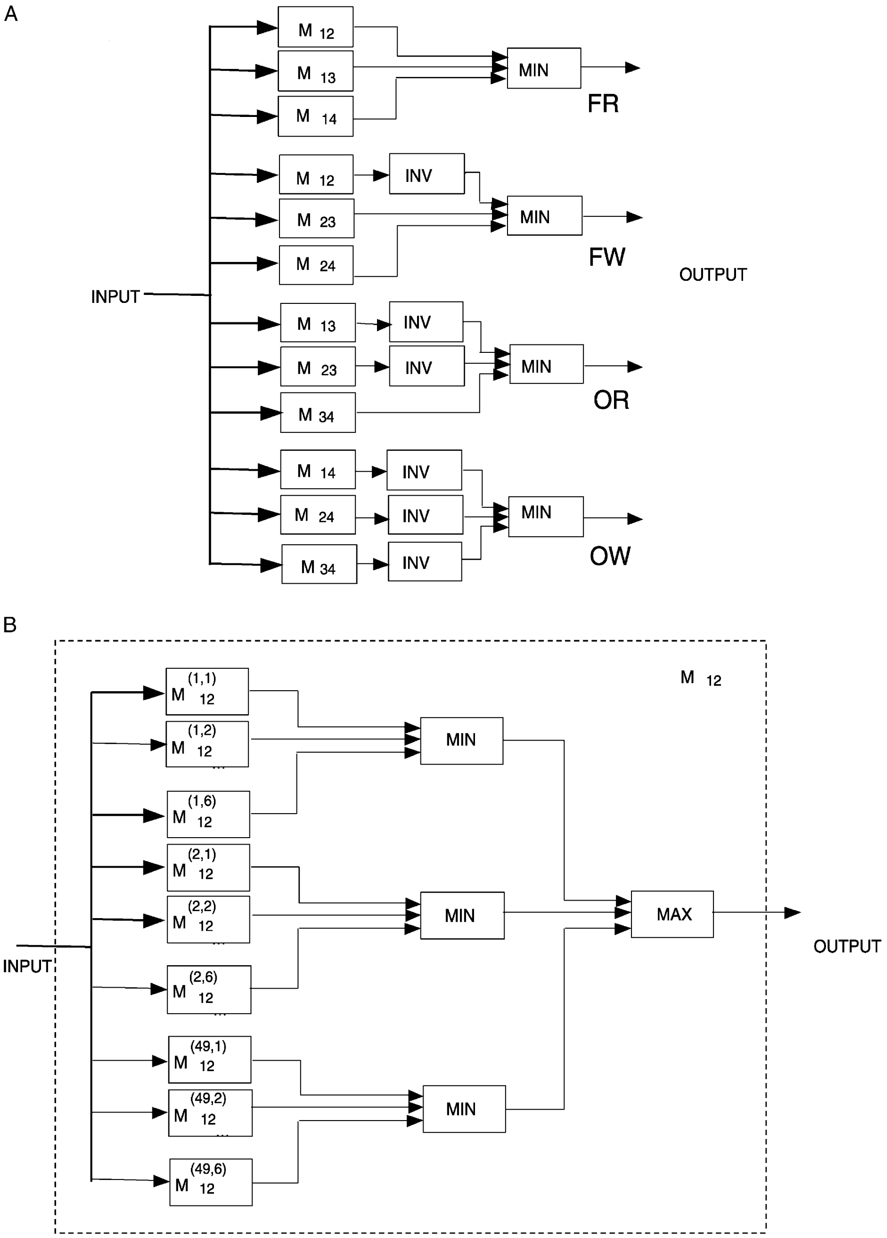

Fig. 3. (A) The min–max modular network for classification of hippocampal EEG signals, where MIN, MAX, and INV denote three integrating units, the functions of MIN and MAX units are to find a minimum value and a maximum value from their multiple inputs, respectively, and the function of the INV unit is to invert its single input; (B) The detail plotting of M_{12} network module in the min–max modular network, where $M_{ij}^{(u,v)}$ denotes the network module trained for discriminating the data belonging to the uth subset of class C_i from the data belonging to the vth subset of class C_j.

Table 2
Detail classification results by the min–max modular network

Class (# of test set)	As “OR”	As “FW”	As “OW”	As “FR”	Don’t know
OR (128)	113	0	0	13	2
FW (68)	3	25	0	38	2
OW (10)	0	2	0	8	0
FR (430)	8	17	0	404	1

respectively. The distributions of the incorrect outputs produced by the trained M^3 network are also shown in Table 1. The neural network distinguished three auditory discrimination behaviours (OR, FR and FW) successfully. Thus, it is quite unlikely that changes in hippocampal theta rhythm are only related to correct perception of right (odd) tone. Considering misclassified cases in Table 2, most OW (NO-GO) cases were classified as FR (NO-GO) cases. But in OR (GO) and FW (GO) cases were not misclassified each other by the neural network. So it is also unlikely that change in theta rhythm reflects rat’s decision to go.

5. Relationship between changes in theta rhythm and motor behaviour

From our video recording of rats’ behaviour during oddball paradigm, it was found that the rats moved around sniffing and exploring the chamber ignoring frequent tones but quickly walking to the water tube after odd tones. Moreover, the duration of theta frequency increase after odd tone is correlated with walking time between odd tones and drinking time in the water tube because no theta rhythm is found during drinking water. As a result, these results support that theta rhythm is related to motor activity and then change in hippocampal theta rhythm is a consequence of the fact that training changed the character of the motor behaviour. Namely, training in this experiment changed rats’ motor behaviour to have quick movements toward the water tube after correct (odd) tone, which result in theta frequency shifts in ensemble average. Furthermore, Shin et al. [15] report that theta frequency change is correlated with spontaneous wheel running speed within single trials even when the relationship between mean theta frequency and mean wheel running speed has no significant correlation. Moreover, theta frequency shifts were observed even during spontaneous deceleration periods without involving any cognitive task and learning.

6. Conclusion

Significant changes in the hippocampal theta rhythm were found during an auditory discrimination oddball paradigm. But, the interpretation of this phenomenon was a real problem: whether these changes represent cognitive process or motor activity? An objective interpretation by an artificial neural network does not support the hypothesis that task-related changes in hippocampal theta rhythm is related to cognition of right tone. Furthermore, shifts of dominant theta frequency were correlated with quick movements toward water after right tone when rat's movements were measured together with task-related theta frequency changes. In other words, changes in hippocampal theta rhythm before/after learning the auditory discrimination oddball paradigm result from a consequence of the fact that training changed the character of the motor behaviour.

Acknowledgements

We thank Dr. M. Ichikawa for continuous support and Shionoya for histology.

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