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Analysis of Sensory Information by Neurons in the Sensorimotor and Visual Cortex in Rabbits with a Rhythmic Protective Dominant

A. G. Galashina, A. V. Bogdanov, and D. S. Sakharov

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A series of experiments was performed to analyze the linked activity of neurons recorded simultaneously in the sensorimotor and visual areas of the cortex in rabbits with a defensive dominant in the CNS. The dominant focus was formed in the CNS using threshold electrical stimulation of the left paw at a frequency of 0.5 Hz. The analysis showed that trained animals responded to the tone by twitching the paw only when functional connections formed closed circuits, with a variety of different configurations, providing for circulation of rhythmic information, in the intervals between tests. In addition, these studies showed that this information was retained for weeks.

Keywords: rabbits, dominant, multineuron activity, neural codes.

Introduction. A series of our previous studies addressing the mechanisms of transmitting sensory information to the projection zones of the cortex in rabbits showed that in trained animals whose CNS contained a rhythmic defensive dominant, presumptively "postsynaptic" neurons started to generate their action potentials with the same rhythm as the presumptively "presynaptic" neurons, thus creating the conditions for transmission across the circuit from one cell to the other [Bogdanov and Galashina, 1999, 2000, 2008; Galashina andπ Bogdanov, 2012]. As the rhythm had parameters coinciding with those of the stimulation rhythm used to form the dominant, it was concluded that this rhythm was not endogenous, but was some label artificially specified by us; following the movement of this label through circuits of cells provides an approach to studying the directions of movement of sensory information within and between the projection zones of interest to our studies. At the same time, the question of how the pathways along which sensory information moves in neuron microsystems in untrained animals, animals at the initial stage of training, and animals with a formed defensive dominant differ from each other remains open. The aim of the present work was to clarify this question.

Methods. ***Procedure for creating a rhythmic defensive dominant.*** Experiments were performed on nine conscious Chinchilla rabbits weighing 3–3.5 kg. The study protocol complied with the requirements of the Ethics Committee of the Institute of Higher Nervous Activity and Neurophysiology, Russian Academy of Sciences and international rules governing the treatment of experimental animals.

At the beginning of the experiments, each rabbit was placed on a wooden bench with gentle fixation of the head at the neck. The rabbit was in a natural posture on the bench. At 2–3 days after the animal stopped showing signs of restlessness, electrodes were implanted into the rabbits' brains for recording of neuronal activity. Surgery was performed under novocaine anesthesia. After 2–3 days, we progressed to formation of a latent focus of excitation (a defensive dominant) in the CNS of the rabbits. In two rabbits, the dominant was formed prior to surgery. The dominant focus was formed by electrocutaneous stimulation of the left forepaw with series of rhythmic impulses consisting of 15–20 stimuli with interstimulus intervals 2 sec and impulse duration of 0.2 msec. Current strength was threshold for elicit-

Institute of Higher Nervous Activity and Neurophysiology, Russian Academy of Sciences, Moscow;
e-mail: alexandra.38@mail.ru.

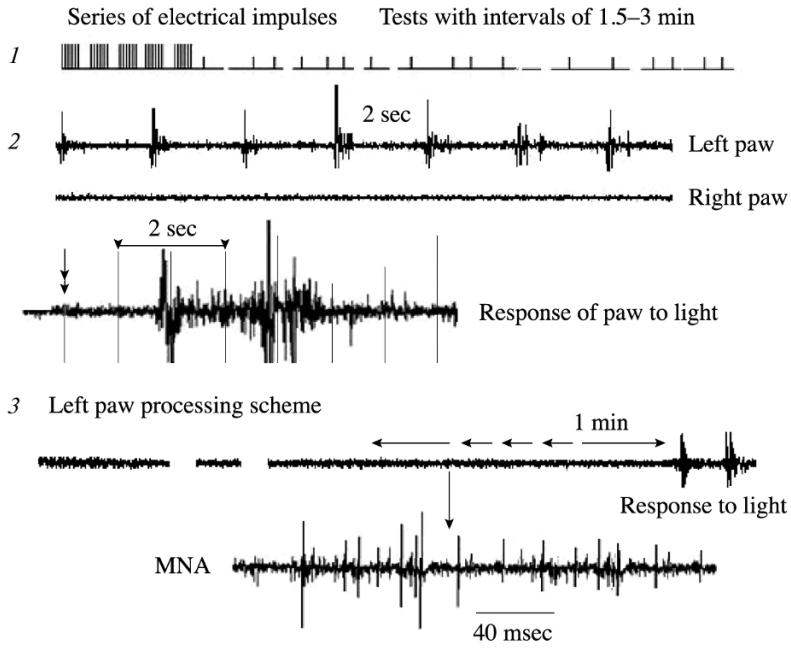

Fig. 1. Scheme of experiment with a rhythmic electrodefensive dominant. *1*) Schedule of electrical stimulation of the paw with subsequent testing with light stimuli. *2*) Responses of the left paw to electrical stimulation. *3*) Diagram showing processing of myogram and multineuron activity in the motor cortex.

ing motor reactions and was selected individually for each rabbit. If response amplitude decreased (the habituation effect), current strength was increased slightly. As a rule, five series were presented with interseries intervals of 2–5 min. Twitching of the paw was recorded using applied piezo elements. After cessation of electrocutaneous stimulation, the animal was presented with a test stimulus in the first and all subsequent experiments – a light; electric shocks were no longer presented. (Fig. 1, *1*). The light was delivered smoothly with changes in the intensity of the incandescent lamps (12 V, 15 W), fed with direct current in conditions of weak illumination of the experimental chamber. Stimulus duration was 8–12 sec. The indicator of whether the animal's CNS had formed a dominant focus was the presence of rhythmic twitching of the left paw (once every 2 sec) in response to the light stimulus to which the animal did not respond before creation of the dominant (Fig. 1, *2*).

Recording of neuron activity. Multineuron activity was recorded using a monopolar method with plates of seven 50-μm nichrome electrodes, glued into a single plane and sharpened to an angle of 35–45°, in factory insulation (PEvKhN-2, GOST 85-98-69). Electrode resistance in the gray matter of the brain was 0.8 MΩ. The indifferent electrodes were made of steel wire 100 μm in diameter. The plate of electrodes was implanted into the sensorimotor cortex at stereotaxic coordinates AP 1–2, L 1–2 (representation of the left forepaw in rabbits). For the visual cortex, coordinates were determined immediately before surgery in zone 17 in terms of the site with the maximal event-related potential in response to flashes of light. Recording of neuron activity started 2–3 days after surgery (Fig. 1, *3*). A four-channel amplifier was used with a bandpass of 400–5000 Hz. Data from morphological monitoring obtained when the experiments were complete showed that the tips of the recording electrodes were located in the lower layers (4–5) of the cortex. Activity was recorded with two electrode plates throughout the experiment – one in the sensorimotor cortex and one in the visual cortex. Spike sequences from four neurons were recorded from each multineuron trace.

Analysis of neuron activity. One-minute segments of multineuron activity recorded between periods of test light delivery were analyzed, to identify how the functional connections between neurons in micronetworks before twitching of the animal's paw in the test were organized. Multineuron traces were processed using a program written by Sakharov in MatLab. Spikes from MNA ere discriminated using a "window" and four impulse sequences were selected (Fig. 2, *1–4*). After removing noise, MNA amplitude was 100 arbitrary units. The width of the window for neurons of the first, highest-amplitude, sequence, was 20–30 Units. Selection was based not only on spike amplitude and shape, but also on spike frequency. Window width for the second spike sequence was 8–10 Units, while widths for the third and fourth sequences were 1–3 Units. The interval between windows varied over the range 7–10 Units; the fourth neuron was no less than 14–20 Units. Spike frequency for the first neuron was in the range 10–14 spikes/sec, compared with 17–22 spikes/sec for the others.

Primary analysis consisted of constructing cross-correlation histograms (CCH) (Fig. 2, *5*). CCH are based on the

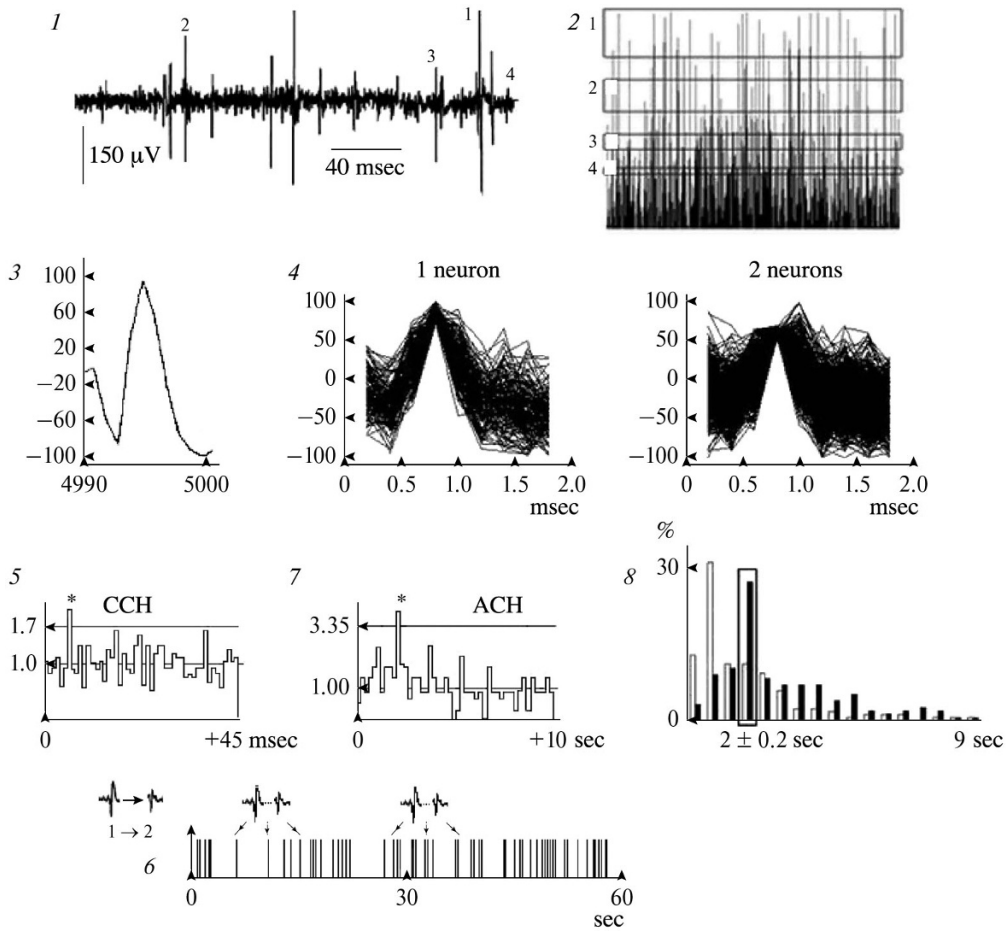

Fig. 2. Schemes showing the processing of multineuron activity. *1*) Multineuron activity; 1–4 – activity of neurons selected for further analysis; *2*) neuron activity discrimination window; *3*) standard shape of largest spike; *4*) spike shapes of neurons 1 and 2 with "superimposition"; *5*) CCH for neurons 1 and 2; *6*) time distribution of spikes collecting to form the peak on the CCH (asterisk); *7*) secondary ACH for these spikes, *predominance of 2-sec peaks; *8*) dark columns show the distribution of peaks showing predominance of 2-sec peaks on secondary ACH in trained animals, light columns show the peak distribution before training.

principle of constructing post-stimulus histograms in which the spikes of one of the neurons (the support sequence) are regarded as the "stimulus" for the spikes of the other (the dependent sequence), such that peaks on CCH could be interpreted as the result of an interaction between "pre-" and "postsynaptic" neurons, thus determining the direction of the influence. CCH were constructed using analysis steps of 0.5–3.5 msec, with 50 points over this range. The analysis included only those CCH in which the mean number of spikes per bin was greater than 20 and the peak evidencing correlated operation of the neurons in the pair included at least 35–70 spikes. Peaks exceeding the mean number of spikes in the histogram with a significance of $p < 0.01$ were assessed. The main criterion for the existence of peaks was their repeated appearance on CCH when the step and analysis epoch were altered. Analysis of correlational relationships (or "functional connections") between neurons, in contrast to all our previous studies, addressed peaks with latencies of less than 80 msec.

Secondary analysis of cross-correlation histograms. The classical method of constructing CCH gives only a quantitative evaluation of the frequency of spikes arising in multineuron activity one after the other at strictly defined time intervals (linked spikes) and does not provide for assessment of how these pairs of spikes are distributed over the duration of the recording period. Each histogram was therefore subjected to secondary analysis, in which the time sequences of the accumulation of linked spikes in the peak of each histogram could be assessed (Fig. 2, *6*). Secondary analysis used a method of constructing ACH for sequences of linked spikes form neuron pairs (Fig. 2, *7*). This analysis provided for detection of the most common intervals between the moments at which linked spikes appeared in CCH peaks and identification of the rhythm with which they arose in nervous tissue. Analysis of ACH of linked spikes considered only those peaks exceeding the mean level of the set of intervals in the histogram with significance $p < 0.05$ (no less). ACH of linked impulses were constructed with

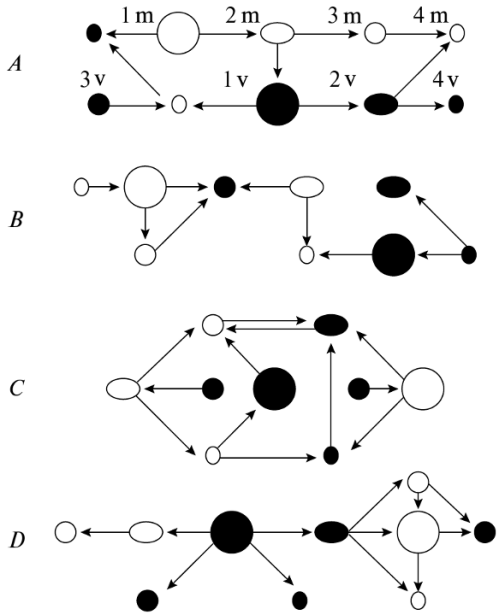

Fig. 3. Schemes of functional connections between neurons in the motor and visual cortex in untrained animals during 1-min traces of multineuron activity. *A*, *B*, *C*, *D*) different rabbits. Light circles how neurons in the motor cortex; dark circles show neurons in the visual cortex. Circle size reflects the amplitude of spikes in multineuron activity. Arrows show the directions of connections. See text for detailed explanation.

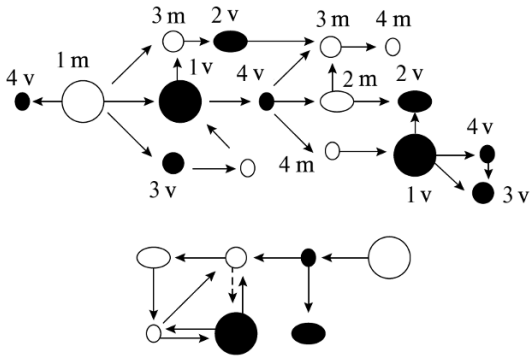

Fig. 4. Schemes of functional connections between neurons in the motor and visual cortex in animals at the initial stage of training. See caption to Fig. 3 for details; see text for explanation.

steps of 0.08–3 msec and histograms with peaks with latent periods of 2 ± 0.2 sec were selected. Our previous studies demonstrated [Bogdanov and Galashina, 1998, 2003] that in contrast to the analysis results obtained in naïve animals, ACH of linked spikes in trained animals were significantly dominated by peaks arising with latent periods close or equal to 2 sec, which coincides with the rhythm with which the left paw was initially stimulated with the electric current (Fig. 2, *8*).

Volume of study. As in previous studies, we compared three phases of learning: naïve rabbits (seven rabbits, 15 segments of multineuron activity traces), trained rabbits (four rabbits, 11 segments of multineuron activity traces), and rabbits with good twitching responses to light (four rabbits, 15 segments of multineuron activity traces). A total of 41 fragments of neuron traces recorded simultaneously from the sensorimotor and visual cortex were analyzed.

Within each fragment, analysis was applied to activity from six neuron pairs in the sensorimotor cortex and visual cortex (12 CCH for the sensorimotor and visual cortex) and eight mixed neuron pairs including neurons whose activity was recorded simultaneously in the sensorimotor and visual cortex (16 CCH for detection of possible "interactions" between the neurons of these projection zones). Construction of each histogram used different analysis steps. The total volume of the analysis was 2296 CCH. In naïve and trained rabbits with twitching in response to light, 180 CCH were analyzed for the motor and visual cortex and 240 CCH for correlations between the motor and visual cortex; 132 and 176 CCH, respectively, were analyzed in rabbits not showing twitching in response to light. Processing addressed only the first peak on each CCH and ACH.

Results. This study presents schemes for neuronal micronetworks constructed using histograms identifying relationships between the activity of neurons in the sensorimotor and visual cortex of animals with a rhythmic-type defensive dominant formed in the CNS. Construction of schemes used only those histograms which on secondary analysis of peaks on ACH of linked spikes (secondary ACH) showed significant 2-sec bursts. These bursts or peaks on secondary ACH are evidence that the "pre- and postsynaptic" neurons whose activity relationship was identified by CCH demonstrated conjoint activity mostly once every 2 sec. If further correlation analysis of the activity of the "postsynaptic" neuron in this pair was run using some other cell, for which it operated as the "presynapse," identified conjoint activation in the same regime (once every 2 sec), then we had grounds for the suggestion that we were dealing with transmission of information relating to stimulus properties along a circuit from one neuron to another. We will consider the functional schemes in individual experiments from this point of view. On comparison of schemes at different stages of learning, the most obvious point was that the schemes are very simple in untrained animals and become ever more complex at sequential stages of training. This is due not only to increases in the number of connections between neurons in microsystems, but also to increases in the complexity of the configurations and the appearance of closed neuronal circuits.

Untrained animals (Fig. 3, *A*, *B*, *C*, *D*). In rabbit A, a total of 11 functional connections were found: three between neurons in the motor cortex, two between neurons in the visual cortex, and six in mixed pairs. In rabbit B, there were nine functional connections: three in the motor cortex, two in the visual cortex, and four in mixed pairs. In rabbit C, there were 12 functional connections – two between neurons in the motor cortex, one between neurons in the visual cortex, and nine in mixed pairs. In rabbit D there were 12

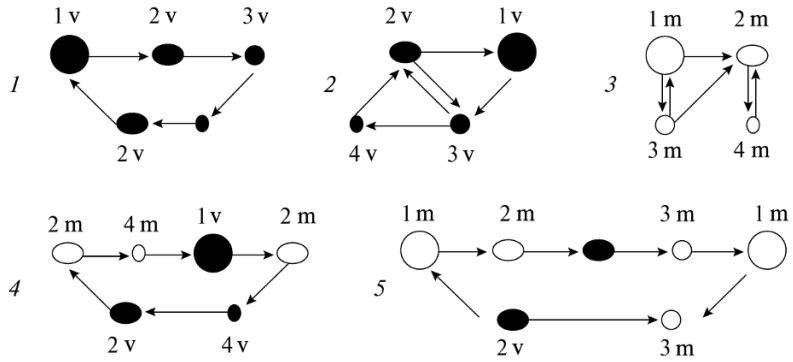

Fig. 5. Schemes of functional connections between neurons in the motor and visual cortex in well trained animals. *1*, *2*) Closed circuits between visual neurons; *3*) no closed circuits between motor neurons; *4*, *5*) closed circuits between motor neurons and visual neurons. See caption to Fig. 3 for details.

functional connections: three between neurons in the motor cortex, three in the visual cortex, and six in mixed pairs.

Trained animals (Fig. 4). In the first experiment, when rabbit C was being presented with the light only, the paw did not yet twitch in the test, but the number of connections during the period prior to delivery of the test increased form 12 to 21 (Fig. 4, upper). The scheme of the functional connections was more complex, though no closed loops had yet appeared. In the fourth experiment, this same rabbit (Fig. 4, lower) showed twitching of the paw in response to light. (We need to remember that in all experiments apart from the first, the rabbit was presented only with light tests, i.e., no electrical stimulation of the paw.) And although the number of connections was small – only 10 – closed circuits appeared around which information on the duration of the interstimulus interval (2 sec) could return to the cell from which it started its journey in this micronetwork: a figure-of-eight can be identified from two closed loops intersecting at the third motor neuron – one loop 3m → 2m → 4m → 3m and the second loop 3m → 1v → 4m → 3m (neurons closing circuits of connections are shown in bold).

The next illustration (Fig. 5) shows an example of eight experiments in rabbit E during the interval prior to delivery of one of the test stimuli. In this experiment, the rabbit's paw clearly twitched in seven tests out of nine. The picture before the test was increased in complexity and 29 functional connections appeared. We will address these in detail. While no closed loops were seen in the six functional connections of four neurons among the neurons of the motor cortex (Fig. 5, *3*) (considering forward and reverse connections), the visual cortex showed two closed circuits between four neurons. One was simple (Fig. 5, *1*) – 1 → 2 → 3 → 4 → 2 → 1 (five transfers) and the second (Fig. 5, *2*) was of the figure-of-eight type - consisting of the same four neurons (six transfers), at the center of which was the third visual neuron – 3 → 2 → 1 → 3 → 4 → 2 → 3. An even more complex situation was seen between neurons in the motor cortex and neurons in the visual cortex (10 connections in the direction from motor cortex neurons to visual cortex neurons and six in the reverse direction); eight closed circuits of different complexities could be identified from four motor and four visual neurons. For example, one figure-of-eight through the second motor neuron (Fig. 5, *4*) 2m → 4m → 1v → 2m → 4v → 2v → 2m and the second through the first motor neuron (Fig. 5, *5*) 1m → 2m → 2v → 3m → 1m → 2v → 3m → 1m.

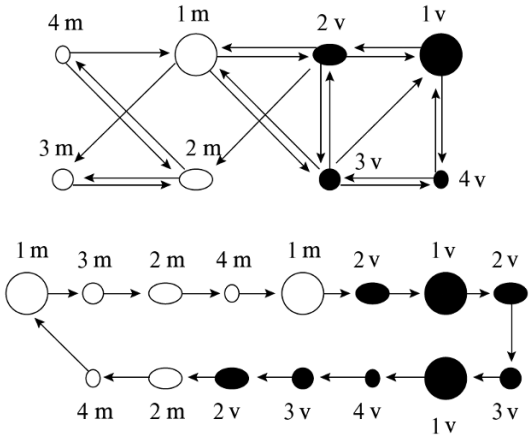

Fig. 6. Scheme of pathways by which information on stimulation parameters can repeatedly pass through the motor and visual cortex in a well trained rabbit (reverberation of sensory information). See text for detailed explanation.

Finally, the last example (Fig. 6) of 12 experiments is rabbit F, in which the paw twitched in response to nine of 13 test stimuli. The fragment before presentation of the light contained 28 functional connections. The illustration (Fig. 6, upper) shows all variants of connections in the motor (6) and visual (9) cortex. For example, closed circuits in the motor cortex were of the type 4 → 1 → 3 → 2 → 4 – while those in the visual cortex were of the figure-of-eight type – 1 → 2 → 3 → 1 → 4 → 3 → 2 → 1. There were 13 connections joining the motor and visual projections, though only five are shown, to avoid complexity. Of these five, there was one closed circuit 3v → 2v → 1m → 3v. The lower part of the figure shows one of the longest circuits, including 15

connections: six within the motor cortex, seven within the visual cortex, and two between them. As in the previous figures, light circles show motor neurons and dark circles show visual neurons. We will pay particular attention to one long circuit connecting the two projection zones. This fragment contained a total of five closed circuits with different levels of complexity. These results provide evidence for our view that even within cortical microregions, neurons can be connected into closed circuits of different lengths and configurations, providing the basis for spike activity reverberation when animals are trained.

Discussion. Recent years have seen ever more active studies of the mechanisms encoding sensory information by neuron populations in the CNS. In seeking answers to the question of how the nervous system encodes sensory information, researchers focus on neuronal structures located in very different areas: the spinal cord [Raastad and Kiehn, 2000], brainstem [Chang et al., 2000], and subcortical nuclei [Nadasdy, 2000; Reich et al., 1997; Roman et al., 2004; Tetko and Villa, 2001], and, finally, the cortical projections [Amassian and Stewart, 2003; Ikegaya et al., 2004; Shu et al., 2003]. Methods such as intracellular and extracellular single- and multiple recording of activity have been used [Donoghue et al., 1998; Lestienne and Tuckwell, 1998; Maldonado et al., 2000]. This variety of approaches comes from the fact that the question of clarifying the mechanisms of encoding and the course of information processes (studies of synaptic modification, gradual oscillations of membrane potentials, or spike sequences) is still a long way from being answered [Kretzberg et al., 2001; Tiesinga and Sejnowski, 2004]. Exponents of one direction take the view that continuous oscillations of membrane potential carry more information than action potentials [Kretzberg et al., 2001]. Supporters of another hold that the mechanism of information encoding may be completely based on interactions between GABA receptor-mediated, hyperpolarizational, synaptic processes and tuning of intrinsic oscillatory mechanisms in pyramidal cells to particular frequency ranges [Cobb et al., 1995]. A third group seeks the key to information encoding mechanisms in patterns of neuronal inputs [Ikegaya et al., 2004] and their mono- and polysynaptic modifications [Roman et al., 2004]. However, a significant number of investigators, including ourselves, are of the opinion that information on the properties of sensory stimuli may be encoded in the dynamics of sequences of action potentials generated by neurons [Chawla et al., 1999; Kreiman et al., 2000; Nirenberg and Latham, 2003; Reich et al., 1997; Romo et al., 2003], and, indeed, the dynamics of spike sequences not only of individual units, but also the spikes of neuron pairs or groups, whose correlated activity has been demonstrated by a variety of statistical analysis methods [Brecht et al., 1999; Donoghue et al., 1998; Gochin et al., 1991; Gochin et al., 1994; Nirenberg and Latham, 2003].

On the basis of the results reported here, as well as those from our previous studies providing evidence that the dynamics of the linked neuron activity reflect the parameters of the stimulation used in the experiments [Bogdanov and Galashina, 1999, 2000; Galashina and Bogdanov, 2012], we believe that data presented in the current report can be interpreted in terms of "neuronal codes" and "neuronal encoding."

Rusinov, analyzing the nature of the trace processes underlying memory, suggested that maintenance of the rhythm in a dominant occurs by means of a reverberation mechanism in which the structure of nerve cells assimilates the stimulus parameters and retains a model of the stimulus in memory [Rusinov, 1987]. The important role of the reverberation mechanism in processes associated with the analysis, recognition, and remembering of external stimuli is not denied by contemporary investigators. Reverberation as a basic mechanism operates at the level of whole structures in the central nervous system [Slama and Delgutte, 2015; Schlecht and Habets, 2015] and at the level of the cell membrane [Maciunas et al., 2016].

Analysis of interaction schemes between different neuron pairs showed that learning produces not only an increase in the number of "functional connections" between neurons, but also an increase in their complexity – with the appearance of neuronal circuits connecting cells for circulation of sensory information within cortical microregions (forward and reverse connections) and for conducting this information from one projection zone to another. We note that trained animals start to respond to light with twitching of the paw only when these circuits become closed and form microsystems of cells of different configurations in the intervals between tests. We believe that thanks to these closed circuits, sensory information can repeatedly pass through the same pathways (reverberate), creating the conditions for remembering the image of the stimulus used for formation of the rhythmic defensive dominant.

Conclusions. Analysis of schemes of interactions between different neuron pairs in the sensorimotor and visual cortex showed that learning was associated with not only an increase in the number of "functional connections" between them, but also that trained animals respond to the test light with twitching of the paws when functional connections form closed circuits of different lengths and configurations during the intervals between tests.

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