

ROLE OF RELATIVELY HIGH-THRESHOLD AFFERENTS  
IN FORMATION OF THE DORSAL SURFACE  
POTENTIAL OF THE SPINAL CORD

E. M. Tolkacheva

UDC 612.83.014.423

In experiments on spinal cats and cats lightly anesthetized with hexobarbital, the conduction of impulses in thick afferent fibers was blocked by a direct current. The  $N_2$ -component of the dorsal surface potential of the spinal cord was shown to reflect the integral postsynaptic potential of segmental interneurons of the dorsal horn activated by relatively high-threshold group  $A\gamma\delta$  fibers.

The dorsal surface potential (DSP) of the spinal cord has been investigated in some detail and described [1-8]. Various groups of afferent fibers and central neurons excited by them are known to participate in DSP generation. According to some workers, the origin of the first and largest negative postsynaptic component of the DSP (the  $N_1$ -component) is associated with activity of interneurons, mainly nonsegmental, of the dorsal horn [1, 4]. The question of the genesis of later negative components, especially the second ( $N_2$ ), has not yet been explained.

The role of afferent fibers of various types in the formation of the  $N_2$ -component of the DSP is examined below.

EXPERIMENTAL METHOD

The experiments were carried out on spinal cats and cats lightly anesthetized with hexobarbital (50 mg/kg body weight). Laminectomy was performed in the region of the lumbosacral enlargement. The popliteal, common peroneal, superficial peroneal, and sural nerves were dissected. After the operation the animal was fixed securely to a massive metal frame. Potentials from the dorsal surface and ventral roots were amplified and recorded from the screen of a cathode-ray oscilloscope. Square pulses from an electronic generator with radio frequency output were used for stimulation. The animal's body temperature was maintained at the normal level. The brain and nerves were flooded with mineral oil. To obtain an isolated afferent volley in relatively high-threshold fibers, conduction of impulses in thick afferents was blocked by a direct current. This method has advantages over alternative methods because anodic blocking of a nerve is selective, reversible, and easily controlled [9].

EXPERIMENTAL RESULTS AND DISCUSSION

The relationship between the DSP and strength of stimulation was investigated in the first group of experiments. During weak stimulation of mixed nerves (popliteal and common peroneal) an action potential in the afferent fibers appeared first. As the strength of stimulation was increased, an  $N_1$ -component and P-wave appeared. At a certain intensity of stimulation (1.3-1.5 thresholds), a later negative  $N_2$ -component was formed. A further increase in the strength of stimulation increased the amplitude of the  $N_1$ -component and, at the same time, reduced the later negative waves. The results of one experiment are given in Fig. 1. The strength of stimulation was expressed in multiples of the threshold value (T) for the fibers with lowest

---

Department of Bionics, Dnepropetrovsk University. (Presented by Academician V. V. Parin [deceased].) Translated from *Byulleten' Eksperimental'noi Biologii i Meditsiny*, Vol. 73, No. 2, pp. 3-5, February, 1972. Original article submitted May 14, 1971.

© 1972 Consultants Bureau, a division of Plenum Publishing Corporation, 227 West 17th Street, New York, N. Y. 10011. All rights reserved. This article cannot be reproduced for any purpose whatsoever without permission of the publisher. A copy of this article is available from the publisher for \$15.00.

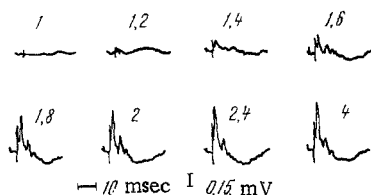


Fig. 1. Changes in DSP in relation to strength of stimulation of popliteal nerve. Numbers show strengths of stimulation in thresholds.

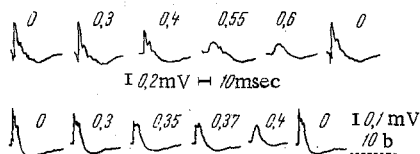


Fig. 2. Changes in DSP in relation to strength of polarizing current blocking conduction in stimulated afferent nerve. Numbers give strengths of polarizing current (in mA); top row - stimulation of popliteal nerve, bottom row - stimulation of superficial peroneal nerve.

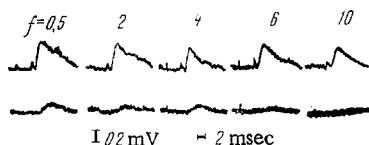


Fig. 3. Dependence of DSP on frequency of stimulation. Top row, DSPs evoked by stimulation of superficial peroneal nerve; bottom row, the same but with polarization of the nerve; numbers show frequency of stimulation.

In the last group of experiments the effect of repetitive stimulation at different frequencies on the character of changes in the  $N_2$ -component of the DSP was studied. Stimuli were applied to the superficial peroneal nerve. Potentials were recorded by superposition of ten sweeps of the beam. As a result of this stimulation the amplitude of the  $N_2$ -component was reduced to a certain steady value, and remained stabilized at a lower level than initially. The records shown in Fig. 3 illustrate the substantial difference between the character of changes in the  $N_1$ - and  $N_2$ -components of the DSPs evoked by repetitive stimulation of the superficial peroneal nerve. At frequencies of 10/sec the amplitude of the stabilized  $N_1$ -component was 75% of the initial value, whereas the  $N_2$ -component was completely suppressed.

Analysis of these results shows that the  $N_1$ - and  $N_2$ -components of the DSP reflect the activity of different structures in the spinal cord. The relatively low amplitude of the  $N_2$ -component indicates that the interneurons generating it are located in deeper layers of the dorsal horn. This agrees with the observations of Selzer and Spencer [10] that cells generating the  $N_2$ -component lie in Rexed's layer V. The

thresholds contained in the peroneal nerve. As Fig. 1 shows, the  $N_2$ -component appeared in response to stimulation with a strength of 1.4 T and reached its maximum in response to stimulation with a strength of 2 T. A further increase in the strength of stimulation led to a reduction in the  $N_2$ -component, while the  $N_1$ -component increased to its maximum.

This phenomenon suggests that the  $N_2$ -component reflects activity of interneurons excitable by relatively high-threshold fibers with a lower velocity of impulse conduction.

To confirm this hypothesis, in the second group of experiments the thick low-threshold fibers were blocked by dc polarization of the nerve. Experiments on the mixed nerves showed that as the strength of the polarizing current was increased the afferent peak disappeared first, followed by the  $N_1$ -component when the strength of the current was 0.4-0.6 mA. The remaining  $N_2$ -component was a low-amplitude (100-150  $\mu$ V) potential and was followed by a positive wave. Its maximum was shifted into the region of longer times (40-50 msec) and its amplitude was reduced on the average by one-third compared with the P-wave of the ordinary DSP. As Fig. 2 (top row) shows, polarization of the popliteal nerve by a current of 0.6 mA led to complete disappearance of the  $N_1$ -component. The mean latency of the  $N_2$ -component, measured in nerve polarization experiments, was 6.3 msec. Calculations showed that the conduction velocity in fibers responsible for generation of the  $N_2$ -component varied between 18 and 38 m/sec, with a mean value of 28.5 m/sec, whereas the conduction velocity in fibers responsible for generation of the  $N_1$ -component averaged 53 m/sec. Fibers exciting interneurons generating the  $N_2$ -component thus belong to the  $A\gamma\delta$  group.

In the next experiments the role of cutaneous fibers in the formation of the  $N_2$ -component of the DSP was studied.

Polarization of cutaneous nerves (superficial peroneal and sural) led to changes in the DSP similar to those observed in the experiments with the mixed nerves. Examination of Fig. 2 (bottom row) shows that polarization of the superficial peroneal nerve by a current of 0.35 mA reduced the amplitude of the  $N_1$ -component by almost 50% compared with the control. An increase in the current to 0.4 mA led to disappearance of this component while the  $N_2$ -component and following positive wave remained intact. Simultaneous recording of the DSP and ventral root potentials showed that at a certain strength of polarizing current stimulation of the afferent nerves caused the appearance only of the  $N_2$ -component and of the corresponding polysynaptic action potential in the ventral roots.

correlation now established between changes in the  $N_2$ -component and the polysynaptic reflex response confirms the view that the  $N_2$ -component reflects the integral excitatory postsynaptic potential of segmental interneurons excited by relatively high-threshold afferents with a lower conduction velocity. The decrease in amplitude of the  $N_2$ -component after a certain strength of stimulation is reached can probably be attributed to primary afferent depolarization developing in the terminals of relatively slow-conducting fibers following activation of presynaptic inhibition mechanisms by the preceding volley of impulses in fast-conducting fibers.

The more marked inhibition of the  $N_2$ - than of the  $N_1$ -component at low frequencies of stimulation is possibly connected with the functional properties of synapses formed by the thinner afferents responsible for generation of this component and also with the deeper homosynaptic depression developing in them.

#### LITERATURE CITED

1. P. G. Kostyuk, *Fiziol. Zh. SSSR*, No. 9, 800 (1956).
2. P. E. Motsnyi, *Fiziol. Zh. SSSR*, No. 3, 346 (1955).
3. A. K. Florov, Author's Abstract of Candidate's Dissertation, Dnepropetrovsk (1966).
4. C. G. Bernhard, *Acta Physiol. Scand.*, 29, 106 (1953).
5. C. G. Bernhard and W. Koll, *Acta Physiol. Scand.*, 29, 30 (1953).
6. C. G. Bernhard and L. Widen, *Acta Physiol. Scand.*, 29, 42 (1953).
7. J. Hughes, G. McCouch, and W. Stewart, *Am. J. Physiol.*, 118, 411 (1937).
8. U. Lindblom and J. Ottosson, *Acta Physiol. Scand.*, 29, 180 (1953).
9. L. Mendell and P. Wall, *J. Physiol. (London)*, 172, 274 (1964).
10. M. Selzer and A. Spencer, *Brain Res.*, 14, 331 (1969).