RECOVERY CYCLE OF RECRUITING POTENTIALS IN THE CORTEX OF Emys Orbicularis

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The recovery cycle of the surface-negative recruiting potential in the cerebral cortex of the pond tortoise, when investigated by paired stimulation of the nucleus rotundus of the dorsal thalamus, consists of a phase of depression, both absolute and relative (up to 5-8 msec), and a phase of facilitation (10-1000 msec). The facilitation reaches a maximum at intervals of 30-100 msec, and thereafter progressively diminishes, becoming less stable and disappearing after 500-1000 msec. In the character of the recovery cycle and with respect to other previously studied characteristics, the cortical recruiting potentials of tortoises have much in common with the dendritic cortical potentials of mammals arising during stimulation of the nonspecific nuclei of the thalamus.

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The recruiting response expresses the predominant type of functional connection between the dorsal thalamus and cerebral cortex of reptiles. It is very similar to the analogous response in mammals [1, 3].

In the present investigation the recovery cycle of the cortical recruiting potential was studied in response to stimulation of the principal nucleus of the reptilian dorsal thalamus – the nucleus rotundus.

EXPERIMENTAL METHOD

Fifteen acute experiments were carried out under superficial and moderately deep Nembutal anesthesia (10-20 mg/kg, intravenously). The thalamus was stimulated by paired square pulses (2-25 V, 0.1-1 msec, intervals between stimuli 2-1000 msec). Paired stimuli were applied 15-20 sec later, at a frequency of 1-3/sec. The dynamics of the recovery cycle was determined from the amplitude characteristics of the responses to paired stimulation [2, 9]. Steel bipolar electrodes with tips 20-60 μ in diameter, 100-500 μ apart, were used for stimulation. The position of the tips of the electrodes was verified after every experiment histologically. Monopolar recordings were made of the surface potentials of the ipsilateral hemisphere by means of a silver ball electrode 0.5 mm in diameter. The reference electrode was inserted into the neck muscles.

EXPERIMENTAL RESULTS AND DISCUSSION

The recovery cycle of the long-latency, surface-negative cortical recruiting potential of the tortoise (Emys orbicularis) was found to consist of phases of depression and facilitation, followed by recovery 500-1000 msec after stimulation. Immediately after application of the conditioning stimulus, for a short time interval (from 2 to 5-8 msec) the test stimulus produced no response or a potential of lower amplitude than in response to control, unconditioned stimulation (Figs. 1, 2A). In the first case (period of absolute depression) the amplitude of the response to paired stimulation did not exceed the amplitude of the response to a single stimulus (3 msec; Fig. 1). In the second case (period of relative depression) it was greater than the amplitude of the response to each stimulus separately, but less than their sum, because of summation of the response to the first stimulus with the still diminished response appearing to the test stimulus. The period of depression was followed by a phase of facilitation during which the test stimulus evoked a response of greater amplitude than the response to the unconditioned stimulus. The facilitation gradually weakened and disappeared after 500-1000 msec. With short intervals (10-30 msec), in response to paired stimulation one potential appeared, its amplitude greater than the sum of the amplitudes of the responses to each stimulus separately. The fact that the amplitude was higher was interpreted as the result of facilitation of the

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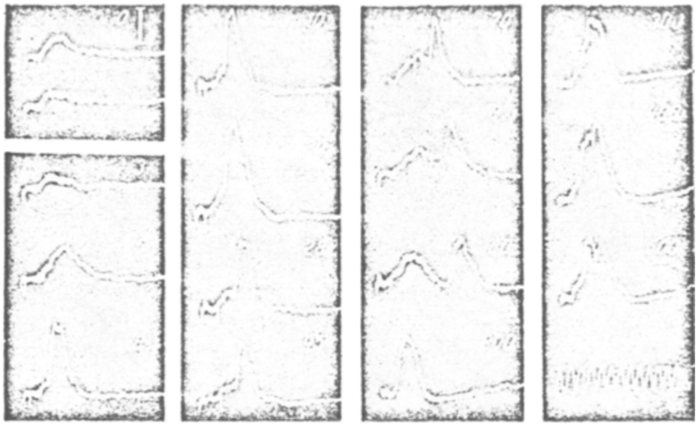

Fig. 1. Cortical evoked potentials in response to paired stimuli. Numbers denote intervals between stimuli (msec). At zero interval: top potential in response to conditioning stimulus, bottom in response to testing. Starting from interval of 70 msec amplitude of responses to conditioning stimuli increased, and starting from interval of 200 msec responses to second stimulus only. Here and in Fig. 2, negativity is shown by upward deviation of beam; calibration 20 msec, 100 μV.

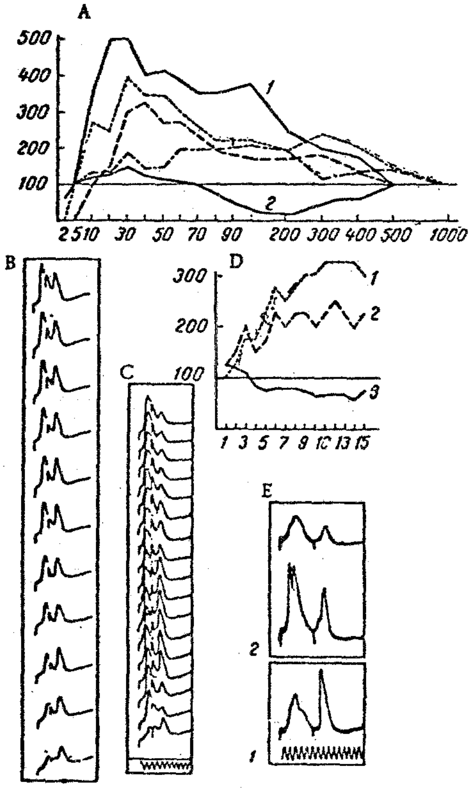

Fig. 2. Effect of intensity of conditioning stimulus and repetitive application of paired stimuli on recovery cycle of recruiting potential. A) Graph showing recovery cycles. Abscissa: intervals between stimuli (in msec); ordinate: ratio between amplitude of response to test stimulus and amplitude of response to conditioning stimulus (in percent). Each curve plotted from data of one experiment: 1) threshold stimulation (4 V, 0.5 msec); 2) supramaximal stimulation (25 V, 0.5 msec) in the same experiment; B) change from facilitation into relative depression following application of paired stimuli (interval 50 msec) at frequencies of 1/sec and (C) 3/sec; D) change in absolute (2) and relative (3) facilitation with increase in amplitudes of responses (1) to conditioning stimuli at 1/sec (oscillogram B). Abscissa: serial number of stimulus; ordinate: ratio between amplitude of response to test stimulus and amplitude of response to conditioning stimulus (in percent); E) responses to paired stimulus at interval of 120 msec; 1) before tetanic stimulation (100/sec, 5 sec); 2) 5 and 15 sec after tetanization. All oscillograms should be read from bottom to top; time marker 20 msec.

response to the second stimulus. With intervals greater than 30 msec, during paired stimulation responses to each stimulus could be distinguished. Facilitation reached its maximum, sometimes amounting to five times the original amplitude, at intervals of 20-100 msec. The facilitation was more marked in magnitude and duration when threshold and above-threshold stimuli were applied, being determined largely by the magnitude of the response to the conditioning stimulus. This was seen particularly clearly in the recovery period, starting at 200-300 msec. When the conditioning stimulus was of considerable intensity (5-10 times above threshold) the degree of facilitation fell sharply, and occasionally facilitation was replaced by depression in the recovery period (Fig. 2A). The degree and duration of facilitation also diminished with deepening of the anesthesia.

Hence, the recovery cycle of the cortical recruiting potentials of pond tortoises, like the cortical recruiting potentials of mammals, have a dominant phase of facilitation. In tortoises this dominance is even more distinct, for in the recovery cycle the phase of facilitation, unlike that in mammals, is not subdivided by a period of relative refractoriness [5]. On the other hand, the depression after facilitation was found extremely rarely in the tortoises.

According to data in the literature, facilitation at short intervals, when the second stimulus is applied during the response to the first, is attributable to temporal summation of the effects of two successive stimuli on account of the state of local subthreshold excitation in some of the neural units. Facilitation at longer intervals is regarded as a supernormal phase of recovery of excitability after relative refractoriness [5, 6]. However, in the last case, because of spatial summation, many locally excited units become involved in the response [4]. Taking this into consideration, it was natural to assume that facilitation in the recovery cycle of the cortical recruiting potential in the tortoise is also, at least partially, connected with an increase in the number of units responding to the second stimulus. To test this hypothesis, paired stimuli were applied in a frequency of 1-3/sec at intervals at which facilitation of the response to the test stimulus took place. Augmentation of the responses to the conditioning stimuli, characteristic of the recruiting response, developed. As this augmentation proceeded, the facilitation of the responses to the test stimuli diminished progressively relative to the preceding response in the pair (relative facilitation). In the course of repetitive stimulation it disappeared and was followed by depression. Absolute facilitation (relative to the response to the first conditioning stimulus) either increased or diminished, but to a far lesser degree than relative facilitation (Fig. 2B-D). Similar changes in the recovery cycle were observed when paired stimuli were applied after preliminary tetanic stimulation (100/sec). After the end of tetanization the response to the conditioning stimulus increased considerably, while the potential produced in response to the test stimulus not only was not facilitated compared with the first response, but was actually depressed, even though facilitation had been present before tetanization (Fig. 2E). In rare cases when, during repetitive stimulation at 1-3/sec, the amplitude of the responses to conditioning stimuli progressively diminished, a parallel decrease took place in the absolute facilitation. The relative facilitation was less strongly affected and showed a tendency to increase. This phenomenon, known as recruitment against a background of subnormality, has been found in the visual system of mammals [6, 8]. This type of response is not characteristic of recruiting responses in tortoises. It is well marked in them in the behavior of cortical responses to stimulation of the optic nerve.

The progressive decrease in the degree of relative facilitation during repetitive application of paired stimuli is probably associated with progressive involvement of new units in a state of subthreshold excitation and constituting a potential facilitation reserve. If this reserve was completely exhausted, facilitation disappeared and the depressor phase of the recovery cycle appeared. This is a characteristic property of every discharging neuron in the central nervous system [5], but it is masked when summated recruiting responses of new neural units are studied. Probably changes in the recovery cycle of recruiting potentials when paired stimuli are applied after tetanic stimulation and when supramaximal stimuli are used may have the same mechanism.

Although facilitation occupies a considerable part of the recovery cycle of the recruiting potential and is maximal at shorter intervals (20-100 msec), the optimal frequency for development of the recruiting response in the reptilian cortex is 3-7/sec, corresponding to a longer interval between stimuli. The response reaches its maximum usually not at the second, but at later stimuli, developing gradually. At a frequency above optimal, the response to the second stimuli is always maximal, followed by a rapid decline of the response. In mammals the recruiting response also develops on account of the phase of late facilitation in the recovery cycle. Bishop and co-workers [6] consider that both the phase of late facilitation and development of the recruiting response are connected not only with an increase in the number of reacting units, but also with an increase in excitability of units already taking part in the response. To understand the mechanisms of facilitation during paired and repetitive stimulation of the test system, the summated response must be compared with the behavior of single units.

All the changes described above in the recovery cycle of the cortical recruiting potentials of the tortoise are probably associated with units in the surface layer of the cortex, receiving impulses during stimulation of the nucleus rotundus. This hypothesis is supported by the fact that the recovery cycle of responses of the cortical surface in the tortoise to its direct stimulation is completely analogous to the recovery cycle of the recruiting potential we have investigated [8].

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