SUMMATION AND ADAPTATION IN STIMULATION OF THE MOTOR CORTEX IN ADULT AND NEWBORN ANIMALS

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The properties of those neurones of the motor cortex which provide the main pathway for the impulses mediating the so-called voluntary motor activity are of great physiological interest. Methods are now available for studying the properties of individual cortical neurones, and the first steps in this direction have been made [14]. However, this in no way lessens the need for a study of the properties of cortical motor neurones "en masse."

In the present article, we report results of an investigation into the properties of motor neurones as affecting summation and adaptation during their "mass" electrical stimulation, and we have recorded the mass response (from the effect on the muscles). Comparatively few works of this kind devoted to a study of the mass properties of cortical neurones have appeared [8, 13], and their results have been contradictory. We have found no articles dealing with the adaptive properties of motor neurones of the cerebral cortex, neither have we found any dealing with the development of such properties of the cortical neurones in young animals. In the most recent work on the properties of individual neurones of the cerebral cortex, these problems have hardly been touched on.

EXPERIMENTAL METHOD

The experiments were carried out on adult and young rabbits of various ages. The motor cortex was exposed under ether anesthesia. The experiments were performed 1-1½ h after the anesthetic had worn off (on unanesthetized animals). The cortex was stimulated with a unipolar electrode (the indifferent electrode was placed on the skull in front of the trepanned aperture, and the active electrode was introduced into the forelimb area of the motor cortex at a depth of about 1 mm). The electrodes were silver, and were chlorided. We recorded the threshold electrical response in the flexors of the elbow of the opposite forelimb.

To study summation, we used rhythmical stimulation by square wave stimuli of 0.2-0.3 msec or of 1 msec duration at various frequencies. In some of the experiments the constant quantity was the duration of a series of impulses (0.7 sec), and in others it was the number of impulses in the series (5 impulses). The threshold values expressed in electrical units* enabled summation curves to be drawn.

To study adaptation, we used long square wave or exponentially increasing potentials. In some of the experiments the stimulation was applied rhythmically at a frequency of 25 impulses per sec (duration of impulses 24 msec). In another set of experiments we used stimuli lasting 0.7 sec. The thresholds of the square wave and exponential voltages (rising at various rates) enabled us to construct adaptation curves. In the experiments we used 17 animals (6 adults and 11 young).

* The threshold values were found from the threshold voltages and resistances of the preparation. We have described the method of determining these quantities in a previous communication (Physiological Journal USSR, Vol. 46, No. 8, p. 933 [in Russian]).

EXPERIMENTAL RESULTS

Studies on adult animals

Summation power. The cortical motor response of adult animals may be studied simply by stimulation of the cortex with short single stimuli (Fig. 1, I). The threshold values are then relatively high. With rhythmical stimulation the threshold is lower, which indicates that summation is taking place (see Fig. 1, I). When the changeover is made from solitary stimuli to stimulation at a frequency of 10 per sec (at an interval of 100 msec) the fall in the threshold is very small (0-30%).

When the frequency is increased from 10 to 100-250 per sec (interval 10-4 msec) the fall of threshold is more marked. With further increase of frequency (shortening the interval), the change of threshold may be of two kinds: sometimes there is a further considerable fall, but much more frequently the threshold rises. Variations of the change of threshold in relation to frequency (interval) of stimulus are observed also when the number of stimuli in a volley is kept constant, or when the duration of the burst of stimuli is constant (then the number of stimuli in a volley increases with increase of frequency).

Plotting the results of the changes in threshold described against the interval between the stimuli gives the summation curves of Fig. 1, II (curves of threshold against interval). Fig. 1, II shows four typical curves. One of them (a) shows the simplest type of threshold change: the threshold falls steadily with decrease of interval. In form, it approaches the classical exponential summation curve of Lapique [12]. Three other curves obtained under other conditions [see footnote to Fig. 1, II], demonstrate another more common type of threshold change. The curve differs from the first by showing a rise of threshold in the short-interval region (2 msec or less), and a more marked reduction of threshold in the region of intervals of 10-20 msec. We will call this second type of summation curve the Y-type curve. The two types of summation curves can be found in a single animal at different periods during the experiment (see Fig. 1, II). We may note that stimulation of the subcortical structures (after extirpation of the "motor cortex") results in similar summation curves (Y-type).

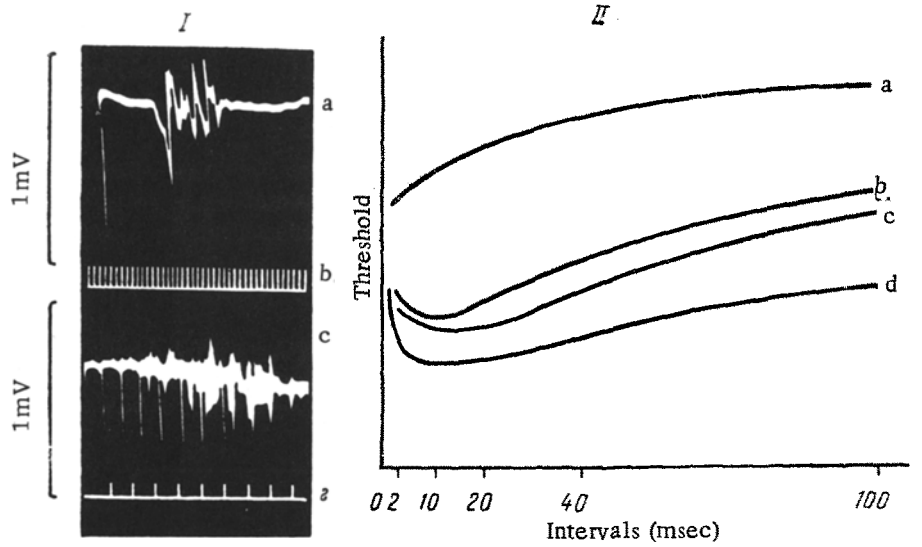

Fig. 1. I: a) Electromyogram of the response of an adult rabbit to a single stimulus; b) time marker 500 per sec; c) electromyogram with rhythmical stimulation (rather above threshold); first stimuli without response, next a response appears through summation; d) time marker, 50 per sec. II) Summation curves obtained in adult animals; a) constant number of stimuli (5), duration of stimuli 0.3 msec; b) same conditions except that duration of stimuli was 1 msec; c) same conditions, but duration of stimuli 0.3 msec; d) duration of group of stimuli kept constant at 0.7 sec, stimulus duration 0.3 msec. Abscissa – time intervals between stimuli; ordinate – threshold and relative amplitude (different ordinate scales apply to the different curves).

Adaptive power. The cortical motor response may be obtained by stimulation of the cortex either by squarewaves or by potentials rising very slowly (as when the voltage is caused to rise by a smooth rotation of the potentiometer knob). This fact by itself demonstrates the low adaptive power of many of the cortical neurones concerned in the motor response. However, these neurones are not altogether without adaptive power, as is clear from the different thresholds for squarewave and exponentially rising stimuli. The thresholds for exponential stimuli rising steeply (time constant of the rise less than 5 msec), which we used with rhythmical stimulation, differed little from the squarewave threshold. Threshold for the slowly rising exponential stimuli (time constant of rise 15 and 45 msec), which we used in measurements of adaptive power with trains of stimuli lasting 0.7 sec, were considerably higher than those for the squarewave pulses of the same duration.

The adaptive power of the motor cortical neurones was such as to give adaptation curves (Fig. 2) which were concave [6]. The accommodation constant λ calculated for the initial portion of these curves was on average about 100 msec (varying from 40 to 190 msec).

Studies on young animals

The adaptive power of young rabbits was illustrated by curves which were of the same type and had the same parameters as those described for the adults. However, in the first 24 h after birth, we found only one of the variants of the summation curves, namely the "exponential shape" (Fig. 3,I). In rabbits aged two days or more, we obtained both types of summation curve, most frequently the Y-type (Fig. 3,II) (as we did with the adult animals).

The adaptive power of the neurones mediating the motor response to stimulation of the cerebral hemispheres in young rabbits does not differ essentially from that found in adult animals (Fig. 2b). The constant λ varies between 50 and 150 msec. We must note that in the young rabbits the motor response to the electrical stimulus was not of purely cortical origin. Some of it was related to stimulation of the subcortical structures [7] which in these animals contain a higher percentage of mature neurones than does the motor cortex [2, 3]. The results obtained in these experiments on the young animals must be related to the mass of relatively mature cortical and "striopallidal" neurones.

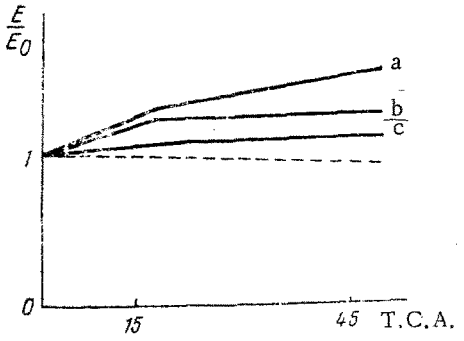

Fig. 2. Adaptation curves. a and c) Obtained from adult rabbits; b) obtained from a 2-day-old rabbit (T.C.A.—time constant of adaptation).

The two kinds of summation curves found in our experiments reflect the two types of summation occurring in the body of the neurones on electrical stimulation: a) direct summation of subthreshold stimuli (local responses), and b) indirect summation of nerve impulses arriving from nerve fibers which had received a threshold stimulation, and which were near the stimulating electrode. The direct summation of stimuli in nervous structures is strictly subject to the laws formulated by Lapique [1, 2], so that the relationship of threshold to interval is expressed by an exponential curve [4]. The indirect summation in the complex structures (but not in a single synapse!) is very similar. However, it is complicated by the phenomena of refractory and supernormal (exaltatory) phases in the conducting structures. The relative refractoriness of the neurites leads to an increase of threshold for stimulation at intervals of 2 msec or less, or to a reduction of the effects of stimulation of standard strength [5, 10]. The phases of exaltation are due to a fall in threshold for stimuli applied at intervals of 4-10 msec.

On this account, indirect summation gives a Y-type curve of threshold against interval. With cortical stimulation these types of summation are associated, and the extent to which either preponderates will depend upon many circumstances.

The discovery of the principally Y-type summation curves in adult non-anesthetized animals on stimulation of the motor cortex indicated that under these conditions summation was indirect. It corresponds to the electrophysiological result which showed that under such conditions the pyramidal neurones of the cortex are excited first of all "through fibers" lying above the cortical layers [1, 9]. This agrees with our results [7] where we showed that under such circumstances short electrical stimuli affect primarily the fibers of the elements of the cerebral cortex.

We must note that the same Y-type summation curves were obtained by Lilly and his co-workers [13] when they stimulated the cortex of unanesthetized apes. However, under deep dial or nembutal anesthesia these same authors obtained summation curves for cats and apes which were nearly exponential. We must suppose that the anesthetic interferes with synaptic transmission in the motor cortex.

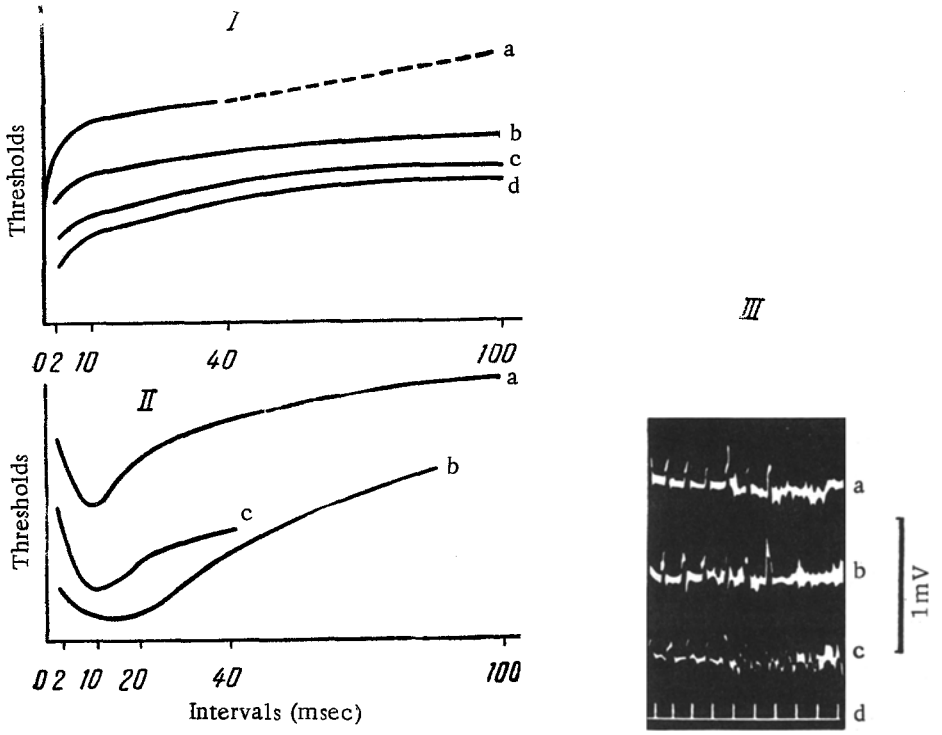

Fig. 3. Summation curves obtained in rabbits of various ages. I. a) in 24-h-old rab - bits while the duration of the group of stimuli remained constant at 0.7 sec, stimulus duration 0.2 sec; b and c) ditto except that the stimulus duration was 1 m sec; d) constant number of stimuli (5), stimulus duration 1 m sec. II. a) in a 24-h-old rabbit with a constant number (5) of stimuli, stimulus duration 1 m sec; b) in a 2-day-old rabbit, stimulation period constant at 0.7 sec, duration of individual stimulus 1 m sec; c) 9-day-old rabbit under the same conditions. Remaining indications as in Fig. 1. III. a,b,c) electromyograms of the response to rhythmical cortical stimulation in rabbits aged 3 days (the response occurs at the end of a group of stimuli as a result of summation); d) time marker, 50 per sec.

Our discovery in the present experiments of the preponderance of "exponential" summation curves in newborn rabbits indicates that summation of neuronal stimulation is chiefly direct, and that it determines the motor response from one hemisphere of these animals. This result is evidence of the low excitability of the fibers in the hemispheres of newborn animals.

Summation curves of the exponential type obtained at a constant number of stimuli may be interpreted as the mirror image of the extinction of the local reaction of neurones to subthreshold stimuli (the decay curve of the local response may be obtained by rotation of the summation curve through 180° about the abscissa). Under the complex conditions of our experiments this standpoint can be accepted only with qualifications. All the parameters of the corresponding curves lead us to conclude that the local responses to electrical stimuli of the cortical (and subcortical) neurones have a considerable duration (tens of milliseconds), which are comparable with the duration of the EPSP [11].

The low adaptive power of neurones responsible for the motor response following stimulation of the hemispheres of adult or newborn animals indicates the possibility of their multiple response to prolonged electrical stimulation. We may note that multiple response of a pyramidal neurone of the cortex of the cat to suprathreshold squarewave stimuli of 10 msec has been demonstrated in experiments with intracellular recording [14]. We may suppose that the multiple response of such weakly adapting neurones could also be obtained with sufficiently strong EPSP's.

A comparison of the results obtained on adult and newborn animals leads to the conclusion that by themselves the neurones responsible for the motor response associated with stimulation of one hemisphere may vary in different animals with respect to summation and adaptation, but that the conducting structures (neurites, synapses) are not well developed in the higher centers of the newborn rabbit.

SUMMARY

In rabbits and their progeny an investigation was made of summation and adaptation of the neurones of the motor cortex; unipolar stimulation was used, and the muscular response recorded. Two types of summation curves were found: "exponential" and "Y-shaped," and were related to the "direct" and "indirect" summation of stimulation. In adults, "Y-shaped" summation curves were more frequent, whereas in rabbits aged 24 h "exponential" curves preponderated. We found very little capacity for adaptation at any age.

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All abbreviations of periodicals in the above bibliography are letter-by-letter transliterations of the abbreviations as given in the original Russian journal. *Some or all of this periodical literature may well be available in English translation.* A complete list of the cover-to-cover English translations appears at the back of this issue.