POSTNATAL DEVELOPMENT OF CONGENITAL RHYTHMIC LIMB MOVEMENTS IN RABBITS CAUSED BY STIMULATION OF THE SKIN

L. N. Deryabin

UDC 612.65 : 612.7

To understand the intimate mechanisms of the various functional systems of the adult organism, a thorough study must be made of the congenital reflexes [4, 6, 7, 13, 14]. In highly organized animals and man, the property of variation of the congenital reflexes is well marked, and is transmitted by heredity [5, 6, 9, 10, 11, 13]. Immaturity at birth facilitates the improvement of new coordination relationships in the nervous system essential in the adaptive activity of the organism, formed with the participation and interaction of developing afferent systems [2, 3, 5, 6, 9-13]. From this point of view a convenient object for observations is the rabbit, whose motor coordinations continue to develop for a long period after birth. In a previous communication [1] the author described results characterizing the development of congenital rhythmic activity arising for no visible cause, "spontaneously," in the rabbit in early postnatal ontogenesis.

In the present investigation the dynamics of a congenital rhythmic activity produced by stimulation of the skin of intact rabbits was studied (observations of series I), and the relationship between this dynamics and the maturation of the brain was studied in chordotomized rabbits (series II).

EXPERIMENTAL METHOD

The experiments with the intact animals took place between the 4th-5th and 50th days of life, and those on the spinal animals before the 2nd-3rd months after chordotomy. The operation was performed in the lower thoracic region at various times of postnatal development, within the period of time of examination of the intact animals. The rhythmic movements of the hind limbs of the young rabbits (of "walking" or "running" type), lying on their back, were produced by alternate stimulation of points of the skin of the abdomen and limbs constant for all the animals. Tactile stimulation with the stroke of a hair (five strokes in 5-8 sec) were applied to each point in turn not less than 1 min after the end of the motor reaction to stimulation of the previous point or the reaction arising spontaneously. The rhythmic movements (flexion and extension) of the limbs were recorded in ink on a kymograph.

EXPERIMENTAL RESULTS

The motor response reactions arose in the form of either continuous or periodic rhythmic activity. These forms are shown in Fig. 1. In the first week of life prolonged continuous movements, less than 1 min in duration (Fig. 1A, 1, 2, 5) arose more frequently than during the subsequent weeks. Later the number and duration of the continuous forms decreased while the number of prolonged, interrupted forms, consisting of a series of repeated, shorter bursts of a rhythmic movements (Fig. 1A, 3, 4, 6, 7) increased. By the end of the 2nd or beginning of the 3rd week, the duration of the continuous movements was limited to the time of action of the stimulus. However, at this time after-reactions still appeared in the form of several short bursts arising after stimulation, but these also soon disappeared. After disappearance of these after-reactions, the number of responses during stimulation gradually diminished: to a series of five stimuli, less than 5 separate responses appeared (Fig. 1A, 8-11). Later the reactions disappeared altogether (Fig. 1A, 12). Hence, the shortening of the reaction to stimulation in early postnatal ontogenesis took place in the form of a succession of forms of rhythmic movements in the order in which they are shown in Fig. 1A. At the same time, changes took place in the receptive field, consisting of a decrease in the number of positive responses to stimulation of a standard number of points in the skin (Fig. 2A). It is also clear from Fig. 2 that the maximal number of positive responses fell during the period of maturation of the young rabbits (9th-14th day). By the 6th week of life, stimulation of the skin no longer produced reactions.

I. M. Sechenov Institute of Evolutionary Physiology, Academy of Sciences of the USSR, Leningrad (presented by Active Member of the Academy of Medical Sciences of the USSR D. A. Biryukov). Translated from Byulleten' Éksperimental'noi Biologii Meditsiny, Vol. 62, No. 7, pp. 18-22, July, 1966. Original article submitted December 23; 1964.

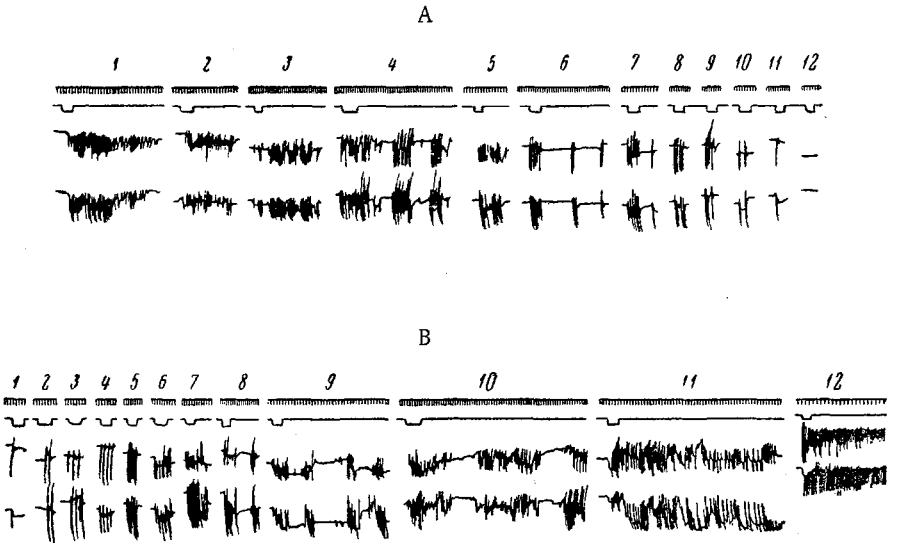

Fig. 1. Forms of rhythmic movements of the hind limbs of young rabbits caused by stimulation of the skin. From top to bottom: time marker (in seconds), marker of stimulation, movements of the left hind limb, movements of the right hind limb. The numbers denote the individual forms of reactions of the hind limbs in response to stimulation of intact (A) and spinal (B) animals. Remainder of explanation in text.

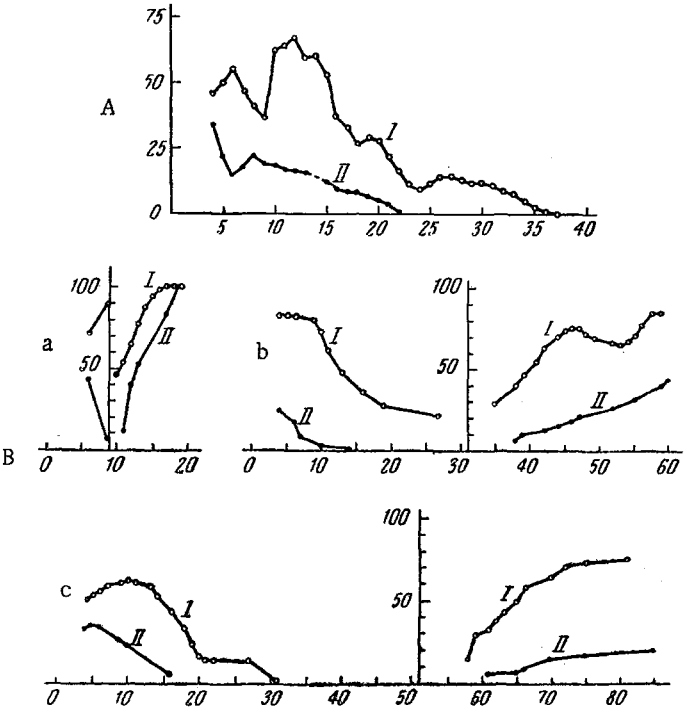

Fig. 2. Number of positive reactions and their duration in the postnatal development of rabbits. Along the axis of ordinates: I) percentage of positive responses; II) duration of successive reactions (in seconds), Along the axis of abscissas: age of animals (in days); A) intact animals; B) with divided spinal cord at the age of five days (a), 31 days (b), and 51 days (c); on the left of the axis of ordinates – before, on the right – after chordotomy.

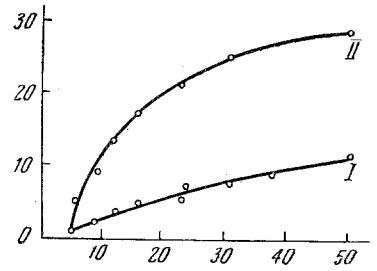

Fig. 3. Times of appearance of the first reaction (I) and reactions of maximal duration (II) to stimulation in rabbits chordotomized at different ages. Along the axis of ordinates – days after chordotomy; along the axis of abscissas – age of animals at the moment of chordotomy. The second-order parabolic curves were plotted from the mean weighted periods (in days).

The results obtained in the observations of series II may be used to study the problem of the portion of the central nervous system with whose development the change in the congenital motor activity described above is connected. As the experiments showed, division of the spinal cord arrested the further development of congenital motor activity as present in the intact animals. In these circumstances, immediately after chordotomy the responses to stimulation of the skin at those points from which rhythmic movements were evoked before operation disappeared temporarily. Later, after a stage of single flexions or extensions, rhythmic bilateral movements of the limbs gradually appeared, identical in their outward form with the "locomotor" movements of the intact young rabbits. The times of appearance of these first reactions to stimulation increased with an increase in the age of the animal at which the spinal cord was divided (Fig. 3, I).

These initial rhythmic reactions grew longer on the following days as a result of an increase both in the duration of the individual bursts of rhythmic movements and in the number of bursts. At the same time, more elementary rhythmic movements of the limbs appeared, forming complexes of bursts. Parallel with this process, the number of reactions to stimulation gradually increased. It is clear from Fig. 1B that the evoked motor activity of the hind limbs of the young rabbits had a complex periodic character, as in the intact animals. The various forms of this activity are shown in Fig. 1 in the order with which they appeared and were modified after chordotomy: initially two or three alternating movements appeared in response to only one of five stroking stimuli at the same point of the skin (Fig. 1B, 1). Later motor reactions developed in response to 2, 3, 4, and to all 5 members of a series of stroking stimuli of the skin (fig. 1B, 2-5). Later still, brief after-reactions were detected, initially after interrupted responses during the period of action of the stimulus (Fig. 1B, 6), and then after a continuous, confluent response (Fig. 1B, 7). On the following day the reactions were lengthened and formed complexes of periodic bursts, the number and duration of which gradually increased (Fig. 1B, 8-10). Later still, this periodicity of appearance of the bursts of rhythmic movements was disturbed in successive reactions (Fig. 1B, 11), and ultimately disappeared (Fig. 1B, 12). In these circumstances the movements became long and continuous, and approximately at the same frequency.

The pattern of development of rhythmic motor activity described above was generally characteristic of the spinal rabbits undergoing operation at different ages. However, differences were found: with an increase in the age at which the spinal cord was divided, not only the period before the appearance of the first rhythmic limb movements was increased, as discussed above, but also was the time when these movements were longest (Fig. 3, II). At the same time, the duration of the reactions of greatest duration, and also the number of positive responses, fell when the operations were carried out later (Fig. 2B).

For instance, in the young rabbits undergoing operation at the age of 5-10 days, by the first or second day after the operation transient burst of alternating limb movements were found, occurring during stimulation (Fig. 1B, 5), together with complexes of 2 or 3 short bursts and continuous movements with a short after-reaction (Fig. 1B, 6-8). Several days later, the motor activity, having been modified into more complex forms (Fig. 1B, 9-10), attained its maximal duration (Fig. 1B, 11-12) in a high proportion of the experiments.

In the rabbits chordotomized at the age of one month the motor activity of maximal duration developed later than in the rabbits of the preceding group. It also attained the form of continuous movements (Fig. 1B, 11-12), but the duration of these movements did not, as a rule, exceed 1 min. In the animals chordotomized at the age of 40-50 days, the rhythmic movements of maximal duration consisted mainly of single short bursts, lasting not more than 30 sec after the action of the stimulus had ceased. These single bursts of movement did not arise until 3-5 weeks after chordotomy.

Concurrently with the increase in duration of the rhythmic motor responses after chordotomy, the receptive field of the reflexes was restored: at first positive responses were evoked by stimulation of one or two points of the skin, and later reaction appeared from the remaining points.

Consequently, the results show that the time of appearance of the positive responses, and the increase in their number and duration took place more slowly and reached a lower level as the age of the animal at the time of chordotomy increased.

The results of these experiments demonstrate that in early postnatal ontogenesis of intact rabbits the coordination relationships are modified. This is shown by the successive depression of the congenital rhythmic motor activity, as a result of which it completely disappears in the sixth week of life. The disappearance of reflex movements evoked by stimulation of the skin takes place on the average two weeks earlier than the spontaneous congenital movements are inhibited in the same animals [1]. Meanwhile the receptive field is diminished in size, and later abolished. The earlier disappearance of the congenital movements evoked by stimulation of the skin receptors by comparison with the disappearance of the spontaneous activity and the gradual disappearance of the receptive field denote the specific character of reorganization of the coordination relationships in which the tactile afferent system is concerned. It is very probable that some role in this reconstruction, as yet unknown, is played by the development of the optic analyzer and the establishment of its interaction with the tactile analyzer.

The complex rhythm of the congenital movements, changing in the process of development, described in this paper is analogous in its external form to the rhythm of the spontaneous movements of young rabbits in the early postnatal period [1]. This similarity of the rhythms is evidence of common features in the effector apparatuses of these types of congenital movements. For this reason, the conception that the mechanisms of spontaneous and reflex movements are completely separate [15] was not confirmed by the results of these experiments.

The results of these experiments also show that the rhythm of the evoked congenital movements, like that of the spontaneous, underwent not only quantitative but also qualitative changes. Comparison of these quantitative and qualitative changes in the intact and chordotomized animals suggests that removal of the influence of the brain on the spinal cord leads to the revival of the previously inhibited congenital movements, evoked by tactile stimulation, but in the opposite order. The degree and speed of this revival in the chordotomized animals were reduced in the process of postnatal development. This is shown by the fact that the time of appearance of the rhythmic movements after chorodotomy and of their development into movements of maximal duration bore a positive correlation, while the speed and degree of increase in the movements bore a negative correlation to the preoperative age of the animals.

SUMMARY

In the early days of postnatal development of rabbits, irritation of the skin of the abdomen and hind legs of the animals while lying on their backs causes alternating movements of their hind legs, which are variable in rhythm and duration. The growth of animals is accompanied by regular changes and disappearance of forms of the motor activity: at first complex and prolonged forms of rhythmic movements modify and disappear, later the same occurs to simple forms, to the degree of complete cessation of response to stimulation. After chordotomy the reflex movements are revived. This is accompanied by restoration of the forms of movements characteristic of preceding stages of the development. The degree and speed of restoration are inversely proportionate to the time of chordotomy.

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