RECIPROCAL INNERVATION AND DECEREBRATE RIGIDITY IN EARLY POSTNATAL ONTOGENY

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The study of the development of central coordination and of the reciprocal relations between nerve centers during ontogeny which are its basis represents one of the important problems in physiology.

Much work has been devoted to the problem of the development of reciprocal innervation during ontogeny. S. I. Enikeeva [7] observed simultaneous muscular contractions during the myographic registration of the contractions of the flexors and extensors of decerebrate preparations of newborn animals. Reciprocal inhibition was observed only after a considerable length of time after birth. These data corresponded to the data of I. A. Arshavsky [2, 3] and his co-workers [9] regarding the absence of functional differentiation of the central motor mechanisms in premature infant animals during the first 10-12 days of postnatal life. Other authors observed reciprocal relations in the innervation of antagonistic muscles in embryos even long before birth. According to the data of E. P. Stakalich [11], A. A. Volokhov, G. A. Obraztsova and E. P. Stakalich [6], reciprocal relations can be observed soon after the development of the first reflex movements of the embryos. It is known that newborn puppies, kittens and rabbits crawl well, with alternate movement of all four extremities as in walking.

The development of decerebrate rigidity, in which an increase in the tone of the extensors with simultaneous inhibition of the tone of the flexor muscles is characteristic, indicates that reciprocal relations exist between the nerve centers of antagonistic muscles. According to contemporary theory, decerebrate rigidity is the result of a change in the functional state of the motor nuclei of the medulla oblongata (Deiters' nuclei and reticulate substance), which occurs as a consequence of the elimination of the influences of the higher areas of the brain, especially of the red nucleus. The data of a number of authors allow the supposition that the function of these structures, which are closely involved in the regulation of the tone of skeletal muscles, arising already in the intrauterine period, becomes apparent from the first days after birth [14, 12, 5]. Other authors could not discover a stable decerebrate rigidity during the first days of postnatal life [13, 1].

Data regarding the course of reciprocal reflex reactions of antagonistic muscles and of decerebrate rigidity in newborn kittens are presented in this communication.

EXPERIMENTAL METHODS

The experiments were set up using 23 kittens ranging in age from several hours to 16 days, intact or decerebrate. The kittens were placed in a stand which was padded with cotton and were fastened with gauze bands. The carotid arteries were tied and tracheotomy performed before decerebration. Electrocautery of the sagittal sinus and pressure on the arteries prevented bleeding. After opening the cranium widely under deep ether anesthesia, the cerebral hemispheres were removed and the midbrain cut. The planes of the cuts usually passed: dorsally, along the center of the superior colliculi or between the colliculi, ventrally, close to the anterior border of the pons (Fig. 1, C). The preparations were warmed after decerebration. In order to observe the changes in the tone of the extensors, we fastened the femurs of the preparations, which were laid on their backs, in a vertical position (using small screws which were screwed into the epiphyses of these bones or long needles which were passed through the distal epiphyses of both femurs and fastened in clamps, Fig. 1, B). In cases when the extensors lacked tone the forefeet passively hung down, if tone was present, they took a position midway between flexion and extension.

Fluctuations in the electrical potentials of the extensors and flexors of the knee joint were registered by means of a two-channel cathode oscillograph. The electrodes were needle-like, the distance between them – approximately 5 mm. Defensive reflexes of the hind limbs were produced by mechanical stimulation of the skin on the soles of the feet.

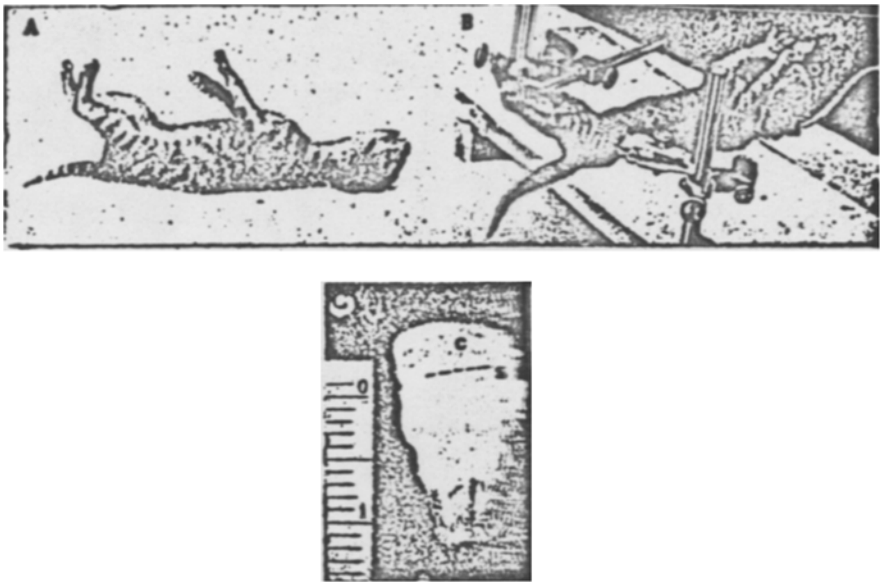

Fig. 1. Decerebrate rigidity in the newborn kitten. Preparation of the kitten on the 3rd day after birth. Weight 134 g.
A) 50 minutes after decerebration: the animal is kept on its back by the right hind limb, the head thrown back, the limbs extended; B) 6 hours after decerebration: the femurs of the animals fastened in a vertical position, the front and hind limbs extended; C) ventral surface of the brain of this animal; c) location of the cut (anterior boundary of the pons varolii); s) surface of the cut.

EXPERIMENTAL RESULTS

Reciprocal innervation in newborn kittens. On registering the electrical activity of antagonistic muscles in kittens with an intact central nervous system during the first days after birth, weak muscle tone, usually dominated by the flexors, is found. We led off differences in potentials with an amplitude of 20–80 μv from these muscles. The form of some of them was monophasic. Typical local reflex reactions, expressed as flexion of the paw, were produced by weak tactile stimulation of the skin on the sole of the foot. An electromyogram from an experiment on a kitten a few hours after birth is shown in Fig. 2, A. An increase in the electrical activity of the flexors (flexion reflex) occurred in response to the slightest tactile stimulation. If the same stimulus was applied to the opposite paw, the differences in the potentials of the flexors were decreased. There would be no changes in the electromyogram of the extensors or a slight increase in the variations of the potentials (crossed extension reflex). On increasing the stimulus we observed more complex reflex reactions. Typical records are shown in Fig. 2, B. In the first moment after the initiation of the stimulus, irregular variations were observed in the potentials of both muscle groups. Visually, the front paws were observed to quiver at this moment. This period of the reflex should be regarded as the result of the diffuse irradiation of the stimulus, characteristic of the early stages of ontogenesis. Then the action potentials of the flexors took on a more regular nature and increased in amplitude, while a decrease in the fluctuations of the potentials of the extensors began simultaneously. Later the electrical activity of the extensors increased, while the fluctuation of the potentials of the flexors gradually dwindled away to nothing. Extension of the limbs corresponded to the last portion of the curves. During the same degree of stimulation of the opposite paw, fluctuation of the potentials of both groups of muscles was observed, although with an obvious predominance of the extensors.

In cases when there was background electrical activity in the extensors as well, it was easy to obtain a typical reciprocal relationship between the reactions of both groups of antagonistic muscles when the force of the stimulation was added (Fig. 2, C).

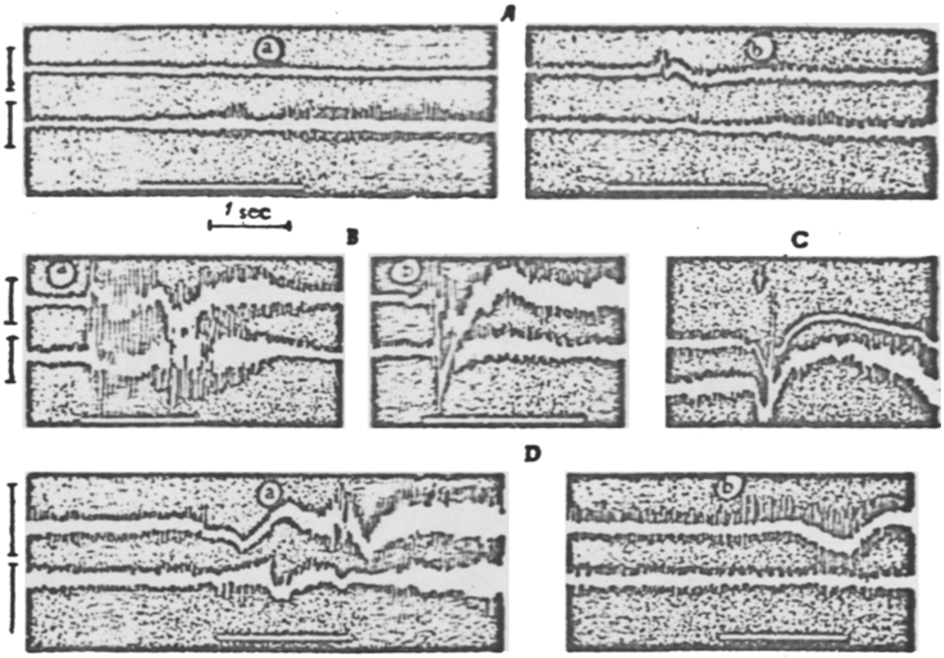

Fig. 2. Reflexes of antagonistic muscles of the hind limbs of newborn kittens during cutaneous stimulation.
A) Reflexes during very mild tactile stimulation of the skin of the left (a) and right (b) soles of a kitten with an intact central nervous system several hours after birth; B) the same during stronger stimulation; C) reflexes during tactile stimulation of the left sole of a kitten with an intact central nervous system the day after birth; D) reflexes during weak pinching of the left (a) and right (b) soles of a kitten decerebrated several hours after birth.
Curves (top to bottom): electromyograms of the left quadriceps femoris, electromyograms of the flexors of the kneejoint of the left limbs.
Calibration is 50 μv of the effective voltage of an alternate sinusoidal current.
Stimuli indicated by the light lines below or by an arrow. Film speed 1 cm/sec.

Similar, but even more distinct, reflex interrelations were obtained with decerebrate preparations of newborn kittens, if they were in good functional condition (see below). We show the curves obtained with a kitten several hours after birth (Fig. 2, D). Rhythmic motions of the limbs of a "walking" type, which could arise without additional stimulations and which sometimes lasted over 10 minutes, were observed repeatedly in the decerebrate preparations.

Often in response to skin stimuli, as well as during strong spontaneous movements, simultaneous contractions of the antagonistic muscles of the newborn kittens would occur. Coordinated contractions of these muscles of a synergistic type, as well as of an antagonistic type, could be observed among decerebrate kittens at various stages of the experiment on a single preparation using the same stimuli. It is known that simultaneous contraction of antagonistic muscles is observed as a regular occurrence in adult decerebrate animals as well [4, 8, 10].

Consequently, the nerve centers of newborn kittens are able to bring about reciprocal reflex reactions of antagonistic muscles of the type of a flexion reflex, of a crossed extension reflex, and of a rhythmic reflex of the walking type. The nerve centers of newborn kittens differ from adult animals in their greater tendency toward irradiation of excitation, lesser speed and clarity of the organization of the reciprocal relations.

On decerebrate rigidity in newborn kittens. Almost all the authors who experimented on decerebrate preparations of adult animals pointed out the diversity of their condition and the irregularity with which decerebrate rigidity appeared. This pertains to newborn ones to a considerably greater extent.

Some time after decerebration (from 2 to 30 minutes), reflex excitability, defensive and knee reflexes would appear. Usually shortly after decerebration, the extensor tone was not dominant; more often the flexor tone was stronger. However, in 10-40 minutes, as a rule, tonic contraction of the extensor muscles appeared and increased in strength. The head would be thrown back, the front and then the hind limbs would be extended (Fig. 1, A). During the passive flexion of the head and limbs, the resistance of the contracted extensor muscles could be felt. A kitten which was placed on its feet and lightly kept from falling on its side by holding its nose and tail could keep its body above the surface of the support for some time (up to 30 seconds). The tone of the extensor muscles was considerably more apparent in the forelimbs than in the hind.

However, the period during which the extensor tone increased usually was replaced after a few minutes by a predominance of the flexor tone or by complete slackness of the skeletal muscles. Often this was accompanied by a decrease in the excitability of the animal's reflexes and by loss of the ability to give coordinated reflex responses. In order to evoke a reflex in these cases, a strong pinch of the limb was required, when brief jerky quiverings of the entire musculature would occur. After some time the condition could improve, as judged by the appearance of muscle tone and coordinated reflex responses. In some cases (10 preparations) respiration was disrupted during one of the periods of muscle atony. Infrequent spasmodic motions with long pauses would appear. After some time, respiration would cease and the kitten would die.

In other experiments, stable decerebrate rigidity would develop after the initial period of unstable functional condition, 30 minutes to 3 hours after decerebration (9 preparations). It would be preserved, although with interruptions, for a long time (sometimes over 9 hours). The state of decerebrate rigidity was characterized by the following signs. The extensor muscles were in a state of tonic contraction. The forefeet of the preparations were kept at an angle of 60-120° to the femurs which were fastened in a vertical position (see Fig. 1, B). The tone of the occipital muscles was stronger. Constant fluctuations in the potential differences of the extensor muscles, typical of decerebrate rigidity, were found with the help of a cathode oscillograph. Corresponding sample electromyograms are shown in Fig. 3, A and B. Frequently in the initial stages of the experiment, fluctuations of the differences in potential of the flexors and extensors both would be registered. Later, after several hours, differences in potential could be found only among the extensor muscles. Weak stimulation of the muzzle, chest, abdomen, taps on the stand, alternate flexion and extension of the hind limbs at the knee produced an increase in the extensor tone and increased the fluctuation of the differences in the potentials of these muscles (Fig. 3, C). This should be regarded as a sign of the dominant state of the extensor nerve centers, typical of decerebrate rigidity. It is necessary to observe that decerebrate rigidity could weaken or disappear temporarily in the last group of preparations. However, it would always return spontaneously or after additional stimulation.

Thus, after section of the midbrain of kittens ranging in age from several hours to 16 days of postnatal life, the phenomenon of decerebrate rigidity was observed for a long time in approximately half of the cases. The appearance of decerebrate rigidity was also observed among the remaining preparations, but only for a short time. Stable rigidity could be ovserved only among those preparations on which the decerebration operation was performed faultlessly (without hemorrhage, with minimal cerebral trauma, etc.). Additional trauma of the preparation (for instance, cuts in the skin), as well as cooling or overheating, easily led to deterioration of the functional condition and to the disappearance of the rigidity.

Our experiments show that the central nervous system of kittens during the first days of postnatal life develops sufficiently to respond to external stimulation by reciprocal reflex reactions of the skeletal muscles. They confirm the idea that animals of this age are capable of elementary reflex acts: defensive reflexes (flexion and crossed extension), the simplest locomotion and after-discharge, connected with the central mechanisms of the medulla oblongata and midbrain. At the same time it is necessary to note the incomplete coordination of the

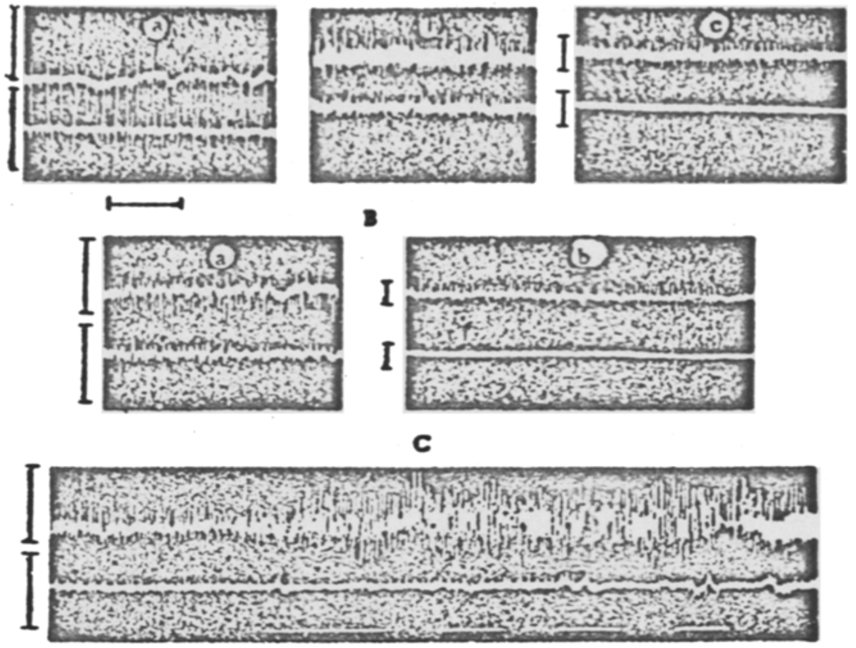

Fig. 3. Tonic potential fluctuations of the extensors and flexors of the kneejoint after decerebration.
A) Preparation of a kitten several hours after birth: a) ½ hour after decerebration, b) after 1½ hours, c) after 2½ hours; B) preparation of a kitten 1 day after birth: a) 1 hour after decerebration, b) after 2½ hours; C) the same preparation: increased fluctuation of the extensor potentials during weak tactile stimulation of the abdominal skin.
The same curves and calibration as in Fig. 2.

contractions of the skeletal muscles, evinced as the ease of onset of diffuse irradiation of excitation in comparison with the adult animals, as well as the relative inconstancy of the developement of decerebrate rigidity in newborn animals. Apparently, the variations in the phenomena observed after decerebration at this age should be considered a sign of the low functional stability of the corresponding nerve centers.

A considerable degree of differentiation of the functional properties of their nerve elements is a condition requisite for reciprocal relations between the centers. The facts which we obtained do not correspond to L. A. Arshavksy's and his collaborators' ideas regarding the functional state of the motor apparatus of newborn animals. Apparently, the methods they used to study the state of the reflex arcs at early stages of ontogenesis were not exact enough to show the dynamics of the functional differentiation of the elements of the central nervous system.

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