INFLUENCE OF CEREBELLAR EXTIRPATION ON THE DEVELOPMENT OF SPECIALIZED MOVEMENTS IN RABBITS

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In a previous article [11] it was shown that in rabbits specialized movements such as cleaning, scratching, licking, and shaking change with age quantitatively and qualitatively; movements of one type are replaced by those of another, and there is a re-organization of their co-ordination.

Guided by the viewpoint of L.A. Orveli [9] who held that re-organization of co-ordination at the highest stages of development is cortical, and related also to the cerebellum, we decided to determine how the development of specialized movements takes place in the absence of a cerebellum.

The functional relationships between the cerebellum and the cerebral cortex has been frequently investigated [1, 2, 6, 7, 10, 17, 18, 20-23], but the part played by the cerebellum in conjunction with the cerebral cortex during such co-ordination has received little attention. Neither has this aspect received any attention in studies on the development of cerebellar function [1, 3, 13, 16, 19].

EXPERIMENTAL METHOD

The cerebellum was removed from rabbits aged 4-7 days. The animals were used for the experiment 1-2 days after the operation.

In the I set of experiments we studied specialized movements developing spontaneously (without stimulation by the experimental), and in the II set we studied specialized movements produced in response to cutaneous stimulation.

The development of spontaneous specialized movements was observed in 29 rabbits from which the cerebellum had been extirpated. As subsequent dissection showed, in 15 of them the cerebellum had been completely or almost completely removed, while in 14 only a portion was missing, i.e., only the vermis or only the hemispheres, or a portion of the vermis and of the hemispheres. A control group consisted of 30 intact rabbits.

EXPERIMENTAL RESULTS

In the first few days after the operation the decerebillate differed but little from the controls in respect of motor activity; both groups were unstable in movement, swayed, crawled, and fell on one side. However the controls became daily more stable, whereas the decerebillate group became more unstable; they swayed more, whether crawling or walking they fell almost the whole time, and later nystagmus occurred.

In the partially decerebillate these disturbances gradually diminished, and cerebellar insufficiency was almost completely compensated. In rabbits from which the cerebellum had been completely extirpated there was no such compensation, and until the end of the period of observation, i.e., until the 30-50th day of life they remained severely affected. Thus in rabbits recovery of movements takes the form of organic compensation, as was shown by Lucian [21]; however, there was very little functional compensation. This shows that in the rabbits which we studied, cortical compensatory processes are inadequately developed [3, 7].

Time of Appearance of Specialized Spontaneous Movements in Rabbits

Group of animals	Mean age of rabbits at time of appearance of movements (in days) M ± m	Significance of the difference between the experimental and control groups (P)
Control	7.3 ±0.35	–
Incomplete cerebellar extirpation	8.4 ±0.57	< 0.01
Complete cerebellar extirpation	9.1 ±0.35	< 0.001

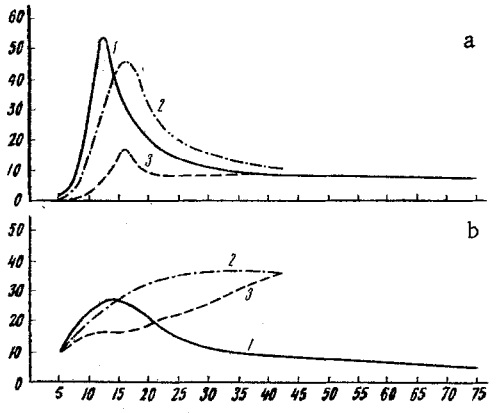

Fig. 1. Change with age in the number of specialized movements. a) Spontaneous; b) Movements evoked by cutaneous stimulation. Ordinate – number of movements (on average in 1 rabbit during the experiments); 1) Control group; 2) Rabbits with partial cerebellar extirpation; 2) Rabbits with complete cerebellar extirpation.

In the operated animals specialized movements appeared later than in the controls, on average on the 8-9th day of life, instead of on the seventh (see table).

The total number of specialized movements changed with age (Fig. 1a). In the control animals it increased rapidly, reaching a maximum by the 13th day, and then fell. In the partially decerebellate group the number of movements increased more slowly, and reached less high values than in control animals, and the maximum occurred several days later, on average on the 16th day. Reduction in the number of movements also occurred later than it did in the controls. In the totally decerebellate the maximum number of movements was very small. Such a considerable reduction in their number can be explained partly as being due to a disturbance of motor function: it is very difficult to superimpose the specialized rabbit movements on a condition of severe instability with a staggering gait and frequent falls. But this effect must not be attributed to the later appearance of specialized movements or the later period at which they were developed maximally. Evidently here we are concerned with a disturbance of relationships within the nervous system so grave as to lead to a delay in the development of specialized movements.

The operated rabbits differed from the controls not only in the number of specialized movements, but also in their character (Fig. 2). During the first days of the investigation in both the control and operated groups, the chief movements were scratching, and later were replaced by licking movements. However in totally decerebellate the changeover from scratching to licking occurred much later than in the control group, on average by the 22nd day, instead of the 16th. At the same time there was a considerable increase in the proportion of the shaking movements at all ages. In some rabbits the percentage of shaking movements was so high as to exceed all others. In rabbits from which only part of the cerebellum had been removed the development of specialized movements did not differ essentially from what was found in the control groups.

Thus early removal of the cerebellum leads to a slowing down in the development of spontaneous specailized movements, and to a change in their nature.

In the experiments of group II we studied the specialized reactions evoked by cutaneous stimulation. The experiments were carried out on 17 young rabbits, from 6 of whom part of the cerebellum had been removed, and in whom the disturbance of co-ordination of movements had been compensated in the course of time; in 11 of them the extirpation had been more complete, and the disturbance of the movements had not been compensated during the period of observation.

The control group consisted of 34 intact rabbits.

Cutaneous electrical stimulation was applied always to the same part of the skin, the part most effective in eliciting the scratching reflex [4]; it was situated towards the back of the side of the neck.

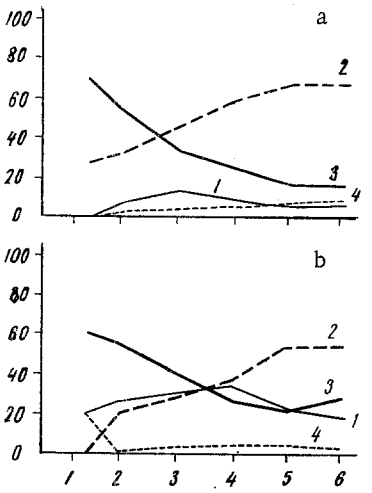

Fig. 2. Change with age in the form of specialized spontaneous movements. a) Control group; b) Completely decerebellate rabbits. Ordinate—number of movements (percentage); Abscissa—age (in weeks). Type of movements; 1) Shaking; 2) Licking; 3) Scratching; 4) Cleaning.

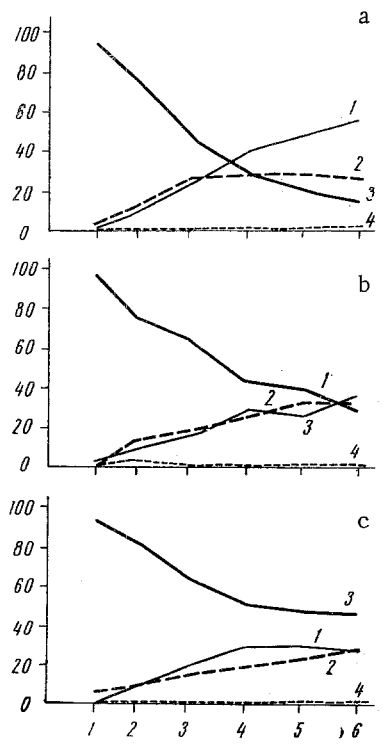

Fig. 3. Change with age in the type of specialized movements evoked by cutaneous stimulation. a) Control group; b) Partially decerebellate rabbit; c) Completely decerebillate rabbits; Remaining indications as in Fig. 2.

In the operated rabbits as well as in the control group specialized responses to stimulation were observed even from the first day of observation, i.e., from the 5-6th day of life onwards. The change in the number of reactions occurred differently in the operated and in the control groups (Fig. 1b). In the control group the number of reactions rose rapidly, reaching a maximum by the end of the second week of life, then gradually regressing. In the operated rabbits the number increased more slowly, and did not reach a maximum before the 5-6th week, i.e., at a time when there was very little reaction in the control group. As a result, by the 4, 5, and the 6th week the number of reflexed movements in the decrebellate rabbits was considerably higher than it was in the control group of the same age, and it was even greater than at the period of the maximum in the control group.

With the exception of the washing reflex, which was almost entirely absent, the specialized reflexes were observed in the operated and control groups during the whole period of the investigation; it was only the relationship between them that changed with age (Fig. 3). In the very first experiments stimulation of the posteriod lateral portion of the surface of the neck elicited almost exclusively scratching movements both in the decerebellate and control groups. At the end of the first week licking and shaking reactions occurred. Then in the control group (Fig. 3a) the scratching reflex gradually gave way to a shaking response, and by the end of the 3rd week, stimulation of the same receptor zone caused mainly shaking movements only. In rabbits lacking only part of the cerebellum (Fig. 3b) a reduction in the relative number of scratching movements and an increase in the number of shaking responses occurred more slowly than it did in the control group. The number of shaking reactions did not approach the number of scratching responses until the end of the 6th week. In completely decerebellate rabbits (Fig. 3b) the preservation of the scratching responses until a late age was shown still more strongly; scratching remained the principle form of response during the whole of the period of observation, and replacement of one kind of response by another did not occur.

No appreciable differences between the operated and control groups were observed with respect to the licking reflex.

Thus as a result of cerebellar extirpation the number of specialized reactions increased more slowly, and after three weeks of life, instead of a reduction in the number of reactions there was a further increase. Also, for a long time a high percentage of scratching movements was maintained.

A similar phenomenon—the preservation of a large number of scratching reactions until a late age—may, as has already been pointed out [12], take place occasionally in intact rabbits, an effect which is evidently due to an incomplete expression of the subordinate relationships within the central nervous system.

It is known [4] that in healthy adult rabbits it is very difficult to evoke specialized movements such as washing, scratching, licking, or shaking, but such movements may readily be evoked from decerebellate preparations. The same phenomenon was also observed in hemidecorticate cats [15]. Reduction of oxygen tension [4], enucleation [5], destruction of the labyrinths [14], ionizing radiation [8], or, in fact, any influence which weakens the cerebral cortex will lead to the appearance of specialized reflexes in adult animals.

We may suppose that in our experiments also, the long preservation of a large number of specialized movements in decerebellate rabbits indicates a weakening of the function of the cerebral cortex, which without the assistance of the cerebellum cannot cope with the problem of suppressing specialized movements. Evidence of cortical weakening is shown by the preservation of the scratching reflex as the preponderant form of response in the operated animals. Normally the cortex suppresses the scratching reflex earlier than other specialized reflexes; in decerebellate animals there was interference with the suppression of the scratching reflex.

The results we have reported indicate that cerebellar activity is one of the factors exerting an influence on the reorganization of the co-ordinated relationships in the growing organism. For a more complete understanding of the mechanism of reorganization of co-ordination during development further studies will be needed.

SUMMARY

Extirpation of the cerebellum from rabbits 4 to 7 days old led to marked changes in the development of the behavioural reflexes (cleaning, scratching, licking, and shaking). Evidently, in the absence of the cerebellum the cerebral cortex is incapable of adequate reorganization of relations in the developing nervous system.

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