THE EFFECTS OF BRAIN LESIONS ON THE "HOPPING REACTION" IN NEWBORN AND ADULT RABBITS: A MODEL FOR STUDYING AGE DEPENDENT RECOVERY

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Abstract. In 5 groups of rabbits (0-1, 2-3, 4-5, 6-7 and 12-13 weeks old) the left frontal, parieto-temporal and occipital cortex were removed. Beginning two weeks after the operations the hopping reaction was tested during 15 weeks. It was found in the groups operated 0-1, 2-3 and 4-5 weeks after birth, that the hopping reaction developed normally. This was not the case in the animals operated 6-7 and 12-13 weeks after birth. Brightness discrimination with the left and right eye was tested in the same animals, beginning 12 weeks after the operation. Contrary to the motor system, no age-development recovery was found in the visual system. In all age groups, brightness discrimination with the eye contralateral to the lesion was impaired.

In 1927 Rademaker published an article on "the physiology of reflex standing" (12). He described that if we place a dog with one leg in strong abduction on a table, this leg will feel flaccid and the elbow will be partly flexed. If we now move the trunk into the direction of the leg, the stretched adductor muscles relax at the same time as the abductors become stretched and the elbow and the shoulder will extend. The nearer the leg approaches the median position, the stronger the supporting tonus will become. On the other hand, if a leg stands in the median
position and we move the trunk sideways, the supporting tonus decreases. If we move the trunk far enough, the supporting tonus will disappear and the leg will be lifted and brought back into the medial position. Rademaker argued that this reaction is probably caused by the intense stretching of the abductors and should therefore be named “proprioceptive correcting movement”.

The article “on the physiology of reflex-standing”, is an almost verbatim translation of an article in the Dutch language “Over de physiologie van het staan” (13). In this article the “Proprioceptieve bewegingen” were for the first time named “Hinkreacties” (hinken = to hop). Rademaker found that the hopping reactions were lacking in de cerebrated dogs, but present in dogs in which the cerebral cortex had been removed previously, albeit that the reactions “appear somewhat late”. These reactions explain the puzzling phenomenon in thalamus-animals that, although they lack the placing-reflexes and correcting movements on stimuli emanating from the body-surface, they always place their legs in the proper way in standing, walking and falling.

The hopping and placing reactions were described in greater detail in Rademaker's book “Das Stehen” in 1931. The hopping reaction was there described as “Hinkebein Reaktionen” (14).

Analogous observations were made in the cat. Dusser de Barenne, like Rademaker, working in Magnus' Laboratory in Utrecht (8) studied the behavior of cats in which the neocortex had been removed several months before. The animals could walk, but the legs were often in an abnormal position, like strong adduction. Abnormal positions were less rapidly corrected than in normal animals. While walking on a slippery floor, especially the forelegs often slid away without the normal corrective responses. Anatomically it was found in those animals that the neocortex was largely removed. In addition, there was considerable damage in the nucleus caudatus and the globus pallidus (7).

Hopping and placing reactions of the cat were extensively studied by Bard (1, 2, 3). He found that cortex lesions could result in permanent profound depression of the hopping reaction. Complete removal of one hemisphere did not show any disturbance in the legs ipsilateral to the lesion.

The number of studies on the hopping reaction after cortical lesions in the rabbit is relatively small. Brooks and Woolsey (4-6) found that the hopping reaction was easily elicited in the forelegs. The reaction was less developed in the hind legs.

In our laboratory the hopping reaction before and after cortical ablation was recently studied in rabbits operated at different stages of postnatal development (9, 10, 15).
The hopping reaction of the forelegs was tested by means of a conveyor-belt moving at a speed of 2.5 cm/s. The rabbit was held in such a way that the experimenter's hand supported the animal and one of its forelegs. The other forepaw touched the surface of the conveyor-belt and supported the body. The animal was held at right angles to the direction of movement of the belt.

The hopping contains a passive component in which the leg follows the conveyor-belt and an active one in which the leg is lifted and returned to its standing position. It was found that the hopping reaction in the rabbit is easier to elicit by adduction than by abduction. Therefore the hopping reaction was studied with the conveyor-belt adducting the foreleg in all experiments to be described.

It was found that the effects of hemidecortication on the hopping reaction depend on the age at which the animals are operated. In five groups of rabbits (0-1, 2-3, 4-5, 6-7 and 12-13 weeks old) the left frontal parieto-temporal and the occipital cortex were removed. Beginning two weeks after the operation the hopping reaction was tested during 15 weeks. In the groups operated 0-1, 2-3 and 4-5 weeks after birth, the hopping reaction was found to develop normally. This was not the case in the animals operated 6-7 and 12-13 weeks after birth.

Contrary to the motor system, no age-dependent recovery was found in the visual system. In all age groups brightness discrimination with the eye contralateral to the lesion was impaired.

Age-dependent recovery as found in the motor system of the rabbit does not seem to be present in the rat. Bard and Brooks (3) discovered that completely decorticated rats rarely assumed abnormal leg positions, but the hopping reaction could be elicited when a displacement led to abduction, but the response to adduction was only slightly retarded. In rats in which the rostral third of one cortex had been removed, only the contralateral legs were deficient.

Brooks and Peck (4) found that complete removal of that area of the cortex, which in rats 1 to 5 days old corresponds to the sensorimotor area of the adult rats, results in a permanent deficiency of the placing and hopping responses. This deficiency was indistinguishable from that caused by a similar operation on the other hemisphere of the same rat, after it had reached maturity.

In other words, the age dependent recovery, which is found in the rabbit, does not exist in the rat.

The motor system of the hemidecorticated rabbit is also a suitable preparation for studying the effects of drugs on functional recovery after brain damage. Ever since Macht (11) described the temporal reappearance of placing reactions in brain damaged animals after injection
of amphetamine, a large number of studies have appeared in rats and cats. In a pilot study in our laboratory it was found that the beneficial effect of d-1 amphetamine sulfate is also present in the hemidecorticated rabbit. In Fig. 1 the effect is shown of a subcutaneous injection of 5 mg/ kg of d-1 amphetamine sulfate on the hopping reaction contralateral to the hemidecorticated side of the brain in 11 adult rabbits. One hour after the injection the hopping reaction was still negative in all animals. Two hours after the injection the hopping reaction was positive in all animals. The effect had disappeared 24 hours after the injection.

![Graph showing the effect of a subcutaneous injection of 5 mg/kg d-1 amphetamine sulfate on the hopping reaction contralateral to a hemidecortication in 11 adult rabbits. Hopping was tested 1/2, 1, 1 1/2, 2, 4, 6, and 24 hours after the injection. The squares above and below the dotted line indicate the number of animals in which the hopping reaction was positive and negative respectively.]

It was also found that the effect of amphetamine on the appearance of the hopping reaction could be completely blocked by a simultaneous subcutaneous injection of 0.6 mg/kg Pimozide.
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