LIMB COORDINATIONS DURING LOCOMOTION IN AMYGDALAR, RUBRAL AND FUNICULAR CATS

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Abstract. The registration of the step phases and the relations between them for all of the four limbs were described in the amygdalar, rubral and funicular cats. The evident changes in motor behavior observed after damage of the amygdala and red nucleus did not result from coordination disorders. Conversely, the damage of the medial part of the lateral funiculus in the dorsally hemisected spinal cord disturbed the coordination between fore and hind limbs.

INTRODUCTION

The present studies of lesioned animals were undertaken as a part of an investigation on the control of limbs coordination during locomotion. Performing experiments on various preparations, we noted changes in the motor behavior (including locomotion) caused by lesions of amygdala, red nucleus and spinal cord. Using the method of on-off registration described in a previous paper (2) we tried to examine the role of coordinations in the disturbances observed.

MATERIAL AND METHODS

Five cats after amygdala damage, 4 cats after damage of red nucleus and 6 cats with an incomplete transection of the spinal cord were examined. The operations were carried out under Nembutal anesthesia (35–45 mg/kg). The bilateral brain lesions were made in a stereotaxic apparatus according to the coordinates of the Jasper atlas. The electrodes (wolfram, 0.5 mm diameter at the tip; a direct current of 2.5 ma
for 2 min) were directed toward the ventromedial part of the amygdala (Fig. 1A). In one cat (the same electrode a direct current of 4 ma for 1 min) the lesion was made toward the anterior area of the amygdala.

Fig. 1. Reconstructions and scheme of performed lesions: A, typical small lesion in ventromedial part of the amygdala; B, typical small lesion in red nucleus (symmetrical); C, asymmetrical lesion in red nucleus; D, scheme of spinal cord lesions, V-VL and V-VL-mL preparations respectively.

Lesions in the red nucleus were produced with a steel electrode. A direct current of 3 ma was applied for 20–30 sec. In all cases, lesions were confined to the caudal (magnocellular) part of the nucleus (Fig. 1B). In one case the lesion was asymmetrical and different regions of the magnocellular part of the nuclei were destroyed.
The spinal cord was sectioned at the level of Th₁₀⁻₁₂. The transection was incomplete and in all of the preparations the ventral funiculi were left intact and the ventrolateral and medial parts of the lateral area of the white matter were spared in different degree in various preparations (Fig. 1D).

The amygdalar and rubral cats were given an overdose of Nembutal and perfused with 0.9% saline solution and fixed in 10% formaline. The lesions were reconstructed from frontal serial sections: for the amygdalar cats frozen preparations, 50 μm thick and stained with the Klüver method, for the rubral cats paraffine, 20 μm thick, stained with the Nissl and Weil methods, the funicular animals are still alive.

The locomotion of amygdalar and rubral cats was examined 5–40 days after an operation. The funicular cats were examined one or two years after an operation, i.e., after compensation of their motor functions. All the conditions of pretraining and registration were exactly the same as described in the previous paper (2).

RESULTS

General behavior. Five cats with amygdalar lesions (including the anterior lesioned animal) showed a decrease of food intake, diminished general activity, sometimes apathy and a lack of mobility, so the animals showed general emotional depression. In these cats we observed a decrease of motor efficiency, and some disorders of locomotion: they walked slowly and clumsily without characteristic “cat's smartness”. Three subjects simply dragged their hindlimbs which were spread and inactive. These changes were purely transitory in nature: nearly 10 days later the disturbances gradually disappeared.

The rubral cats during the first 1–2 days after surgery could right themselves. When they started waking they displayed ataxic symptoms: forward and backward oscillatory body movements and rotatory movements of the pelvis. They also frequently stepped on the dorsal surface of the operated paws. These changes in locomotion disappeared 1–2 weeks after surgery. In contrast to locomotion on the ground, the operated animals that were tested on horizontal ladder exhibited much stronger and longlasting impairments. In tests requiring manipulatory movements, two kinds of disturbances were noticed: ataxic symptoms and deficit in the use of distal parts of the forepaw.

The funicular cats tended to drag the hindlimbs behind and were unable to stand upright with the hind part of the body. The recovery of the standing reflex was observed 4–14 days after surgery. However for the first time the hind part of the body staggered and the postural tonus was insufficient to keep it upright, causing the animal to fall
or set. The gradual correction of means and ways of movements of particular hindlimbs was observed in the walking animals. Spreading of the extremities, and persistent overflexion of the hindlimbs enabled standing and walking. The recovery of the functions of the distal part of these limbs was observed 3–10 weeks after an operation: the hindlimb was rarely put on the dorsal surface of the paw. The proprioceptive placing was permanently lost and no corrections of passively done strange positions (e.g., maximal protraction of one of the hindlimb) were observed. On the contrary, during active movements, the position of the hindlimbs was usually correct. Generally, 6 weeks after an operation standing, walking and, in some preparations even galloping were observed in normal daily conditions.

**Locomotion.** Five days after an operation, the duration of the step extended to more than 600 msec for some amygdalar cats. They moved slower than the normal cats and never run. Forcing the cats to move faster never succeeded. It was often even necessary to push the cats to start them walking. Three amygdalar cats with slow recovery had obvious difficulties in locomotion: staggering was observed in various experimental conditions and the animals fell off the suspended pathway. Thus, on–off registration was ill fitted for analysis. For two amygdalar cats the registration could be investigated (Table I).

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**Table I**

The observed ranges of the step, swing and stance durations in normal and operated cats (msec)

<table>
<thead>
<tr>
<th>Group</th>
<th>Limb</th>
<th>Time after operation</th>
<th>Step</th>
<th>Swing</th>
<th>Stance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amygdalar</td>
<td>fore</td>
<td>5 days</td>
<td>620–930</td>
<td>220–300</td>
<td>400–630</td>
</tr>
<tr>
<td></td>
<td>hind</td>
<td></td>
<td>620–930</td>
<td>250–380</td>
<td>360–580</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1 month</td>
<td>360–1000</td>
<td>200–300</td>
<td>160–700</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>360–1000</td>
<td>180–330</td>
<td>180–680</td>
</tr>
<tr>
<td>Rubral symmetrical</td>
<td>fore</td>
<td>1 week</td>
<td>680–1080</td>
<td>220–340</td>
<td>450–840</td>
</tr>
<tr>
<td></td>
<td>hind</td>
<td></td>
<td>680–1180</td>
<td>250–400</td>
<td>420–780</td>
</tr>
<tr>
<td>Rubral asymmetrical</td>
<td>fore</td>
<td>1 week</td>
<td>590–880</td>
<td>230–280</td>
<td>360–600</td>
</tr>
<tr>
<td></td>
<td>hind</td>
<td></td>
<td>600–1260</td>
<td>280–480</td>
<td>360–830</td>
</tr>
<tr>
<td>Funicular V-VL-mL</td>
<td>fore</td>
<td>1 or 2 years</td>
<td>680–1030</td>
<td>190–330</td>
<td>470–780</td>
</tr>
<tr>
<td></td>
<td>hind</td>
<td></td>
<td>650–1380</td>
<td>240–490</td>
<td>380–910</td>
</tr>
<tr>
<td>Funicular V-VL</td>
<td>fore</td>
<td>1 or 2 years</td>
<td>540–920</td>
<td>160–220</td>
<td>360–700</td>
</tr>
<tr>
<td></td>
<td>hind</td>
<td></td>
<td>760–1800</td>
<td>270–470</td>
<td>450–1370</td>
</tr>
<tr>
<td>Normal</td>
<td>fore</td>
<td></td>
<td>330–1020</td>
<td>200–320</td>
<td>130–740</td>
</tr>
<tr>
<td></td>
<td>hind</td>
<td></td>
<td>320–1040</td>
<td>180–370</td>
<td>130–700</td>
</tr>
</tbody>
</table>
these animals all of the relations between swing, stance and step durations coincided basically with relations characteristic for normal animals. However, for operated animals they were shifted somewhat toward higher values of the absolute durations of step phases (Fig. 2). Registration performed 1 month later did not show any differences between normal and all of the amygdalar cats (Table I). Two kinds of gait appearing in

![Fig. 2. Relations between swing and step durations for the hind limbs in two amygdalar cats. Each point is the average of 7-15 steps (one trial).](image)

![Fig. 3. Relations between the stance durations for the fore and hind limbs in rubral cats. No 203, asymmetrical cat. Each point is the average of 7-12 steps (one trial).](image)
Fig. 4. Relation between: A, step durations for fore and hind limbs; B, stance durations for fore and hind limbs; C, swing durations for fore and hind limbs. The funicular preparations: No 157, 314 and 10, V-VL-mL; No 337, 320 and 20, V-VL. Each point is the average of 8–15 steps (one trial).
normal cats were obtained as follows: usually the walk was observed (numerical formula 4-3-2-3-4-3-2-3 and in a few cases the trot (numerical formula 2-2).

Four rubral cats also had slower locomotor movements after an operation (Table I). In some trials the hindlimbs fell out of the step, and performance of fewer steps than the forelimbs were noted. In one animal this happened only incidently, while in the other subject with an asymmetrical lesion, it became a rule after a few trials (Table I). The correlation between the stance phases for the fore and hind limbs seems to be direct and the ratio was 1:0.7 (Fig. 3). A weak correlation was found between the swing duration for the fore and hind limbs. The relations between the swing and stance durations for the two fore or two hind limbs were normal.

The locomotion of the funicular cats could be classified as a walk since the numerical formula was 4-3-2-3-4-3-2-3. The formulae 3-2 and 2-2 were not observed. The preparations could be divided into two groups. In the first, the step duration for the fore and hind limbs was similar (Table I). However, the hindlimbs of these animals moved at a slightly slower speed (the step duration was longer) than the forelimbs. In the second group of the animals the step durations for the fore and hind limbs considerably differed (Table I, Fig. 4A). Both the swing and stance phases for the hindlimbs were elongated in these preparations but both were related to the speed of an animal.

The correlation between the stance durations for the fore and hind limbs was direct and the ratio seems to be normal for these animals in which the duration of the step for the fore and hind limbs was nearly the same (Fig. 4A). The correlation between the stance phases for the animals in which the hindlimbs performed fewer steps than the forelimbs was also direct, but for each animal of this group the set of points approximated a straight line with the slope ca. 0.7 (Fig. 4B). On the contrary to the normal relations, no correlation between the swing durations for the fore and hind limbs in all of the funicular preparations was observed. For each cat the points were grouped below the center along the abscissa and in some cats in parallel to the abscissa (Fig. 4C). The relations between either swing and stance or swing/stance and step durations were normal for the forelimbs.

**DISCUSSION**

Animals after different lesions were used in this experiment. We choose three groups of animals with visible changes in motor behavior caused by lesions in structures connected with the emotions (amygdala), manipulation (red nucleus) and locomotion itself (spinal cord).
The problem of *amygdala* influence on the motor activity is still unclear. Some motor responses (e.g., head turning, biting, sniffing, chewing) claimed to result from the amygdaloid stimulations appear to be associated with seizures activity of the amygdala (3, 16). However, a few marked disturbances in the motor functions were observed in animals after amygdala operations. Dogs with dorsomedial amygdala lesions were apathetic, atonic, lying down in the first few days, then standing motionless where placed, or sitting taking cataleptic-like position. They walked slowly with significant difficulties (6). Some of these anomalies in motor behavior were observed in our amygdalar cats. The registration of locomotion showed that these changes did not result from coordination disorders. However, the evident tendency to elongate the swing phase in relation to stance (Fig. 2F) seems interesting (in amygdalar cats we observed many steps in which that tendency appeared). It is probably necessary to examine more exactly postural and flexor tonus in amygdalar cats.

The role of the *red nucleus* in motor behavior has been a subject of several investigations. Lesions in the red nucleus in cats produced an increase of extensor tone, impairments of some postural reflexes as well as ataxic symptoms (4, 5, 11, 12). In conditioned reflex experiments, damage of the red nucleus yielded impairments of instrumental movements (13, 15). According to Kuypers (14) the rubrospinal tract together with the corticospinal tract belong to the lateral descending system controlling movements of distal musculature. In our previous experiment (9), lesions of the red nucleus were followed (among others) by transient impairments of locomotion and postural reflexes. In this study “falling out of the step” was observed in two animals. Interestingly these disturbances closely resembled those observed in the V–VL funiculcral preparations. As it is known, the structures neighboring on the red nucleus, as nucleus interstitialis of Cajal or medial longitudinal boundle, are related to locomotion itself (10). It is worthwhile investigating which structure is “responsible” for these fore and hind limbs discoordinations.

In all of the funicular preparations the relations between swing, stance and step durations for the fore and hind limbs separately were in accordance with those of normal animals, whereas the magnitudes of these durations were shifted towards higher values, a fact which may be connected with the observation that these animals moved slowly or very slowly.

In one group of the funicular cats coordinations of the limbs were not disturbed, but the step duration of hindlimbs was more or less longer than for the forelimbs. In these animals we intended to leave
the ventral, ventrolateral and medial part of the lateral funiculi. In the second group in which the ventral and the ventrolateral tracts were left, the coordination between fore and hind limbs was destroyed. "Falling out of the step" what was sporadically observed in the rubral cats, was noticed constantly in these V-VL funicular animals (see 1). Differences of swing/stance relations and of motor control (7, 8) of the fore and hind limbs in normal animals support the hypothesis that control mechanisms for the hind limbs were disturbed both in asymmetrical rubral and funicular preparations.

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