EFFECTS OF PYRAMIDAL LESIONS ON MANIPULATORY MOVEMENTS IN THE DOG. AN ONTOGENETIC APPROACH

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Key words: pyramidotomy, distal forelimb movements, recovery of function, age-determinants

Abstract. The role of age in the recovery of motor functions following unilateral pyramidotomy was studied in groups of puppies operated on at the age of 1, 2, 3 and 5 mo. The animals were trained postoperatively to retrieve with their forepaw morsels of food from test devices varying in shape, diameter and depth. Groups of normal animals of similar ages were trained in parallel. In all age groups the motor impairment following pyramidotomy was proportional to the digital involvement in a given task. Furthermore, the performance of operated dogs was essentially similar in all age groups and no better recovery of function was observed in animals operated on at the age of 1 than at 5 mo. The results are discussed in view of conflicting data concerning the age related differences in the recovery of motor functions after destruction of the pyramidal system in various species.

INTRODUCTION

Considerable evidence in the literature indicates that lesions of the central nervous system sustained in infancy result in less severe functional deficits and are followed by more substantial recovery than similar lesions administered to juvenile and mature organisms (2, 11, 17–19, 29, 33, 41, 50, 61, 63, 68, 69). This phenomenon of “sparing” of function does not appear, however, to be universal, and can be influenced by
such factors as the extent of the lesion and the neural structures involved (11, 18, 19, 22, 29, 41), as well as the kind of task or abilities investigated (18, 29, 33, 50, 69). Thus, although some functions show a progressive pattern of recovery after early postnatal lesions, in others deficits produced by the lesion and the ultimate recovery appear not to be age dependent (11, 19, 22, 33, 50, 69) or even show a “regressive” pattern of recovery, in which the impairment after early postnatal lesions appears only with a delay, as development progresses (18, 50, 69).

Lack of uniformity also characterizes the results of studies concerning the recovery of motor functions after lesions of the pyramidal system at different ages. In pioneer experiments on this problem Kennard (36–39) found that ablations of the motor and premotor cortex in monkeys under four weeks old produced no or little deficit in the animals' ability to use the affected extremities in such motor activities as walking, climbing and feeding. Lesions at later ages produced gradually increasing paresis, but eventual recovery occurred if surgery was done prior to 7 mo. Lesions sustained after 7 mo resulted in severe motor deficits similar to those obtained in adult animals. In rats, unilateral hemispherectomy or unilateral and bilateral lesions of the sensorimotor cortex performed at birth have also been found to produce less deficits in locomotor activities, than similar lesions performed in adult specimens (31, 32). Some sparing of function has been observed even in animals operated at 3 wk (32). In contrast, sectioning the medullary pyramids in monkeys produced a similar impairment in their ability to perform relatively independent finger movements, irrespective of whether the lesion was performed in adult (45) or infant monkeys (44).

One of the possible reasons for the disparity of the results described above may have been connected with differences in the kind of motor functions studied. For example, movements performed in more proximal joints, like those involved in walking and climbing, depend mainly on various nonpyramidal descending pathways (43, 45, 46) and thereby, after cortical lesions, the intact tracts could have subsumed the function of the damaged structures. On the other hand, the ability to perform isolated finger movements in monkeys depends almost exclusively on the integrity of the pyramidal tract (1, 45, 71) and especially on direct corticomotoneuronal connections (3, 42, 44, 45) and, therefore, other descending pathways may not be able to subsume this function, regardless of the animals' age at the time of surgery.

In the present experiments the developmental determinants of the recovery of various forelimb movements after lesions of the pyramidal
tract were studied in dogs. In subprimates direct corticomotoneuronal connections are, in general, lacking (4, 5, 43, 57). Such an organization of the pyramidal tract offers a good opportunity for studying the age-related differences in the recovery of functions after pyramidal lesions, due, for example, to the axonal sprouting of other tracts into sites vacated by the corticospinal fibres or to a remodelling of synapses on common interneurones. Similar mechanisms were observed after some lesions of the central nervous system not only in young (54, 55, 62; for a review of the literature see 19 and 53) but even in adult animals (16, 52, 59, 60, 68) and have been postulated to play a major role in the recovery of various functions. In addition, our previous experiments (27) have shown that pyramidalotomy in dogs differently affects various manipulatory movements, permitting us to assess the recovery of functions controlled to different extents by the pyramidal and non-pyramidal systems. Since evidence indicated that in the dog the pyramidal tract is relatively immature at the age of one month and does not attain maturity before the end of the third month (5, 23, 24, 40), in the present experiment we have compared the effects of pyramidalotomy on animals operated on at the age of 1, 2, 3 and 5 mo. It was assumed, analogous to Kennard's work on monkeys (39), that if recovery of motor functions is age-related, puppies that sustained the pyramidalotomy at the age of 1 mo, and possibly 2 mo, should show better ultimate recovery than the two older groups of animals. We found instead that the effects of pyramidal lesions in the dog turned out not to be age dependent, at least within the age limits studies in the present experiment. Some results had been already published (27, 28).

MATERIAL AND METHODS

The experiments were performed on 38 puppies divided into 4 age groups: 1, 2, 3 and 5 mo old. Each age group consisted of two subgroups: puppies that sustained a unilateral (left) pyramidalotomy at a given age, i.e., at 1, 2, 3 or 5 mo and normal subjects that served as a control. The number of normal and operated subjects in each age group is shown in Table 1.

The experimental procedure was similar to that described previously (27). Briefly, subjects were trained to retrieve with the right forepaw pieces of boiled meat (1 × 1 × 1 cm or 7.5 × 7.5 × 7.5 mm, depending on the size of the animal's paw) from several test-devices varying in shape, diameter and depth. All of the 38 motor tasks used in the training were divided into 3 classes: easy, of moderate difficulty
and difficult tasks, according to the degree of digital involvement required to solve them. A brief description of the tasks included in each class is given in the appropriate sections of the Results.

The training of each task was continued to a criterion of 8 out of 10 trials on which the animals were able to retrieve meat by themselves, or to an arbitrarily set total number of movements in tasks in which the animals failed to reach this criterion despite a relatively long training. These numbers varied from 50 to 250 depending on the difficulty of the task. In each trial the number of movements performed in order to get hold of the meat was scored, and each movement was characterized according to its effectiveness and accuracy.

Each dog received four training series. In each series the animals were trained 4 times a week with 40–80 trials daily. The training of all 38 tasks lasted 2–6 wk, depending on the animals' dexterity. In all operated dogs the first training series began 1 month after surgery, while the next training series started 3, 5 and 7 mo postoperatively. Normal animals were trained in parallel to their surgical counterparts, at exactly the same ages. The animals' ages at the beginning of each training series in the various age groups are shown in Table I.

For each dog, class of tasks and training series the following indices of motor performance were calculated: (i) the percentage of tasks solved, i.e., those in which the animal reached the criterion; (ii) the average length of training per task, expressed in the number of movements performed in the training of each task; (iii) the average number of movements per trial performed in the last 10 trials of training of each task and (iv) the average percentage of dysmetric movements, i.e., those in which the animals did not immediately touch the piece of meat, but placed the paw too near, too far, to the side, or did not insert it into the test-device. This latter index concerned the accuracy of movements and not their effectiveness, since dogs most often, after missing the spot where food was placed, corrected their error and

<table>
<thead>
<tr>
<th>Age group</th>
<th>Number of operated animals</th>
<th>Number of control animals</th>
<th>Age at the beginning of successive training series</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>I</td>
<td>I</td>
<td>I</td>
</tr>
<tr>
<td>1 mo</td>
<td>4</td>
<td>5</td>
<td>2 mo</td>
</tr>
<tr>
<td>2 mo</td>
<td>5</td>
<td>5</td>
<td>3 mo</td>
</tr>
<tr>
<td>3 mo</td>
<td>5</td>
<td>5</td>
<td>4 mo</td>
</tr>
<tr>
<td>5 mo</td>
<td>4</td>
<td>5</td>
<td>6 mo</td>
</tr>
</tbody>
</table>
managed to hit the piece of meat when, for example, they retracted the limb. The average percentage of dysmetric movements was calculated from the last 10 trials of training of each task.

The performance of normal and operated animals belonging to different age groups was compared using a three-factor analysis of variance with Surgery, Training and Age as factors. In addition, normal and operated animals belonging to the same age group were compared using a two-factor mixed design analysis of variance (51) and the Duncan tests (12). The methods of surgery, histological verification of lesions and other details of the experimental procedure were as described earlier (27).

RESULTS

Lesions

In the majority of puppies the left pyramid was completely or almost completely transected. Out of the 18 operated animals, the pyramid was transected entirely in 5 puppies; in another 12 puppies the lesion comprised 80–99% of the left pyramid and in 1 animal about 67% (Fig. 1 and Table I). The extent of pyramidal lesions in various age groups was essentially similar. The mean percentages of the cross sectional area of the left pyramid destroyed in different age groups ranged between 88 and 97 (Table II).

In 3 out of 18 puppies pyramidal lesions were followed by some damage to other structures, such as small (about 10%) damage to the opposite (right) pyramid (Nos P-I and P-III) or partial (about 1/4) degeneration of the left medial lemniscus (No P-VIII) due to invasion into the trapezoid body (Fig. 1). In addition, in dog P-III the lesion extended too far laterally, destroying probably part of the left spinothalamic tract (65), while on the right side there was some degeneration of the reticular formation, at the level of the lesion and slightly rostral to it, probably due to the concomitant damage of blood vessels during surgery.

Comparison of motor performance in different age groups

Easy tasks. This class of tasks (10 tasks altogether) consisted of retrieving food placed 5 or 10 cm behind differently spaced vertical bars and from between differently spaced vertical walls (cf. 27). The animals' performance appeared to be only minimally affected by pyramidotomy. Both normal and operated dogs, regardless of their age group, solved all or almost all (88–100% on the average) of these tasks
Fig. 1. Extent of pyramidal lesions in individual puppies operated on at 1-, 2-, 3- and 5 mo of age. L, left; R, right side of the medulla. Dots in the diagram for dog P-III (3 mo) indicate degeneration of reticular formation. TB, trapezoid body; SO, superior olive; nV, nVII, nucleus of the V and VII nerve, respectively.

**Table II**
Completeness of the left pyramid transection in individual puppies

<table>
<thead>
<tr>
<th>Age Groups</th>
<th>1 mo</th>
<th>2 mo</th>
<th>3 mo</th>
<th>5 mo</th>
</tr>
</thead>
<tbody>
<tr>
<td>Puppy No.</td>
<td>Percent of the pyramid destroyed</td>
<td>Puppy No.</td>
<td>Percent of the pyramid destroyed</td>
<td>Puppy No.</td>
</tr>
<tr>
<td>P-XIX</td>
<td>97</td>
<td>P-V</td>
<td>98</td>
<td>P-I</td>
</tr>
<tr>
<td>P-XX</td>
<td>88</td>
<td>P-X</td>
<td>80</td>
<td>P-II</td>
</tr>
<tr>
<td>P-XXI</td>
<td>99</td>
<td>P-XI</td>
<td>68</td>
<td>P-III</td>
</tr>
<tr>
<td>P-XXII</td>
<td>100</td>
<td>P-XV</td>
<td>100</td>
<td>P-VIII</td>
</tr>
<tr>
<td>P-XVI</td>
<td>96</td>
<td>P-XVI</td>
<td>96</td>
<td>P-IX</td>
</tr>
<tr>
<td>Mean</td>
<td>96</td>
<td>Mean</td>
<td>88</td>
<td>Mean</td>
</tr>
</tbody>
</table>
beginning from the first training series (Fig. 2a). They reached the criterion in these tasks almost immediately (Fig. 2b) and required a similar, relatively small, number of movements per trial to retrieve food (Fig. 2c). The only index of performance which showed a statistically significant effect of Surgery was the percentage of dysmetric movements (Fig. 2d, Table III). The differences between normal and operated animals were, however, mainly limited to the first two training series, while in the third or fourth series the operated animals attained a level similar to normal dogs (Fig. 2d).

![Fig. 2](image.png)

Fig. 2. Motor performance in easy tasks of normal (N) and pyramidotomized (OP) dogs in different age groups. a, mean percentage of solved tasks; b, mean number of movements performed in the training of a single task; c, mean number of movements per trial; d, mean percentage of dysmetric movements. I–IV, successive training series.

The performance of normal and pyramidotomized dogs was, in general, not age dependent. An overall significant Age effect was again obtained only in the percentage of dysmetric movements and this index showed also a significant Surgery × Age interaction (Table III). The dysmetric movements performed in this group of tasks consisted mainly of overstretching the limb or putting it partly over one of the walls (cf. 27). Both normal and operated dogs retrieved meat by raking it back over the floor of the test-devices. However, the operated animals held the paw somewhat more stiffly, without any noticeable flexion of the wrist or toes. These deficits were most prominent in the first period after surgery.

The performance of both normal and operated animals improved in successive training series (Fig. 2). This effect was significant for all the indices of motor performance (Table III), except for the percentage of solved tasks, which reached a maximal level already by the
Values of $F$ statistics for different sources of variations in the animals' performance of easy tasks

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Length of training per task (b)</th>
<th>Number of movements per trial (c)</th>
<th>Percent of dysmetric movements (d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surgery (B)</td>
<td>1.30</td>
<td>1.01</td>
<td>2.55</td>
<td>49.50</td>
</tr>
<tr>
<td>Training (A)</td>
<td>3.90</td>
<td>14.19</td>
<td>65.37</td>
<td>96.83</td>
</tr>
<tr>
<td>Age (C)</td>
<td>3.30</td>
<td>0.25</td>
<td>2.54</td>
<td></td>
</tr>
<tr>
<td>Surgery x Age (BC)</td>
<td>3.30</td>
<td>0.94</td>
<td>0.44</td>
<td>4.57</td>
</tr>
<tr>
<td>Surgery x Training (AB)</td>
<td>3.90</td>
<td>0.79</td>
<td>1.51</td>
<td>1.30</td>
</tr>
<tr>
<td>Training x Age (AC)</td>
<td>9.90</td>
<td>0.22</td>
<td>1.88</td>
<td>0.68</td>
</tr>
<tr>
<td>Surgery x Training</td>
<td>9.90</td>
<td>1.11</td>
<td>0.85</td>
<td>0.66</td>
</tr>
</tbody>
</table>

Underlines denote significant differences: ---, $P < 0.05$; ---, $P < 0.025$; ----, $P < 0.01$; ---, $P < 0.005$; ------, $P < 0.001$.

first training series (Fig. 2a). More detailed statistical analysis showed, however, that in normal animals the effects of training were, in general, limited to the 2nd training series, and the next training series did not improve their performance further (cf. Fig. 2). On the other hand, in operated animals the effect of training was somewhat delayed, especially with respect to the accuracy of movements. A significant decrease in the percentage of dysmetric movements was observed in the majority of groups of operated animals only in the third training series, while the scores obtained in the first two training series were essentially similar.

**Tasks of moderate difficulty.** In this set of tasks (12 in total) the animals had to retrieve food from troughs of different depths (2, 3, 4 and 5 cm) and inclinations of the front wall ($45^\circ$, $67^\circ$ or shaped like a quarter of a cylinder) (cf. 27). Normal puppies, irrespective of their age group, solved almost all ($93-100\%$ on the average) of these tasks by the first training series (Fig. 3a). On the other hand, groups of operated puppies solved on the average only $68-85\%$ of these tasks in the first training series (Fig. 3a), despite their longer training per task (Fig. 3b) and more movements performed in a single trial to retrieve food (Fig. 3c). Their movements were also less accurate, as shown by an increase in the percentage of dysmetric movements (Fig. 3d).

Although the overall effect of Surgery was significant for all the
indices of motor performance (Table IV), more detailed statistical analysis showed, in fact, that in the majority of age groups and indices significant differences between normal and operated animals were essentially limited to the first and/or second training series. The only exception to this was the percentage of dysmetric movements. In this latter index the differences between normal and operated animals persisted up to the third or even fourth training series (cf. Fig. 3d).

Fig. 3. Motor performance in tasks of moderate difficulty of normal (N) and pyramidotomized (OP) dogs in different age groups. Denotations as in Fig. 2.

Like in easy tasks, in tasks of moderate difficulty the animals' performance was not age-related. Both normal and pyramidotomized dogs of various age groups obtained very similar scores (Fig. 3) and neither the Age nor the Surgery × Age interaction were found to be significant sources of variation in their performance (Table IV).

The overall effect of training series was significant in all of the indices of performance (Table IV). In most indices there was also a significant Surgery × Training interaction (Table IV); the performance of operated animals was more influenced by the training than that of normal subjects (Fig. 3). The least influenced by the training in operated dogs was the accuracy of movements. As shown in Fig. 3d, in all age groups, except 5 month-olds, the percentage of dysmetric movements remained on a high, essentially unchanged level during the entire period of postoperative training. This index also showed a significant Surgery × Training × Age interaction.

As in the easy tasks, the main error in accuracy of movements consisted of overstretching the limb and/or putting it on a side-wall of the through (cf. 27). Also both normal and operated dogs retrieved
Values of \( F \) statistics for different sources of variations in the animals' performance of tasks of moderate difficulty

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Percent of solved tasks (a)</th>
<th>Length of training per task (b)</th>
<th>Number of movements per trial (c)</th>
<th>Percent of dysmetric movements (d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surgery (B)</td>
<td>1.30</td>
<td>33.96</td>
<td>35.76</td>
<td>10.74</td>
<td>34.37</td>
</tr>
<tr>
<td>Training (A)</td>
<td>3.90</td>
<td>35.24</td>
<td>41.16</td>
<td>33.51</td>
<td>22.96</td>
</tr>
<tr>
<td>Age (C)</td>
<td>3.30</td>
<td>2.65</td>
<td>2.00</td>
<td>1.87</td>
<td>1.64</td>
</tr>
<tr>
<td>Surgery ( \times ) Age (BC)</td>
<td>3.30</td>
<td>0.39</td>
<td>0.00</td>
<td>2.06</td>
<td>0.72</td>
</tr>
<tr>
<td>Surgery ( \times ) Training (BA)</td>
<td>3.90</td>
<td>16.65</td>
<td>11.28</td>
<td>0.29</td>
<td>4.81</td>
</tr>
<tr>
<td>Training ( \times ) Age (AC)</td>
<td>9.90</td>
<td>1.64</td>
<td>1.08</td>
<td>1.32</td>
<td>1.09</td>
</tr>
<tr>
<td>Surgery ( \times ) Training ( \times ) Age (ABC)</td>
<td>9.90</td>
<td>0.30</td>
<td>0.34</td>
<td>0.83</td>
<td>2.33</td>
</tr>
</tbody>
</table>

For explanations of underlines see Table III.

food from troughs by raking it over the ascending front wall. However, since in pyramidotomized animals movements of distal limb muscles were mainly affected, the most difficult tasks for these animals consisted of retrieving food from deep (4 and 5 cm) troughs with the front wall inclined at 67° or shaped like a quarter of a cylinder. The operated animals failed as a rule to solve these tasks in the first training series. On the other hand, from the very beginning of the training they were able to retrieve food from troughs of similar depth with the front wall inclined at 45° since these latter tasks required less involvement of distal limb muscles.

Difficult tasks. This class of task consisted of 4 sets of tests in which the animals had to retrieve food from: (i) holes shaped like inverted truncated cones of different depths (2, 3, 4 and 5 cm) and diameters (2 and 4 cm at the bottom); (ii) a horizontal tube, 7 cm in diameter and 6 cm deep, situated at the level of the animals' shoulder; (iii) oblique tubes 7 cm in diameter and 3, 4 and 6 cm deep and (iv) similar vertical tubes, 3, 4, 5 and 6 cm deep (16 tasks in total). Since some tasks included in this class required an extensive use of distal limb muscles, the performance of both normal and operated dogs was much worse than in the tasks of moderate difficulty.

As illustrated in Fig. 4, groups of normal animals solved on the average 66–79% of the tasks in the first training series, while in the
fourth they reached the level of 87–93\% of solved tasks (Fig. 4a). They also required much longer training per task (Fig. 4b) and more movements per trial (Fig. 4c) than in tasks of moderate difficulty (cf. Fig. 3a–c). The percentage of dysmetric movements was likewise the highest in this group (cf. Fig. 4d and 3d).

The performance of operated animals was inferior to that of normal animals. In the first training series they solved on the average only 45–59\% of the tasks, while in the fourth training series 66–85\% (Fig. 4a). In other indices, the performance of operated dogs was also inferior to normal puppies, since they required longer training per task (Fig. 4b), more movements per trial to retrieve food (Fig. 4c), and performed more dysmetric movements (Fig. 4d). In all of these indices the overall Surgery effect was significant, with no significant Age effect or Surgery × Age interaction (Table V). Moreover, since in this class of tasks the performance of normal animals was relatively poor, especially at the beginning of the training, in some indices the differences between normal and operated dogs increased rather than decreased, as the training progressed. For example, in the percentage of solved tasks (Fig. 4a) significant differences between normal and operated subjects were obtained from the majority of age groups only in the last or the two last training series, whereas at the beginning of training their performance was similar. This contrasted with the set of tasks of moderate difficulty, in which the differences between normal and
operated animals were mainly observed in the first two training series.

The effects of training series were also significant in all the indices of motor performance (Table V). A significant Surgery X Training interaction was obtained only in the percentage of dysmetric movements. This index showed an improvement as a result of training series only in normal animals, while in pyramidotomized ones the scores remained essentially unchanged throughout the whole postoperative period (Fig. 4d). The number of movements per trial and the percentage of dysmetric movements showed also a significant Training X Age interaction.

### Table V

Values of *F* statistics for different sources of variations in the animals' performance of difficult tasks

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Percent of solved tasks (a)</th>
<th>Length of training per task (b)</th>
<th>Number of movements per trial (c)</th>
<th>Percent of dysmetric movements (d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surgery (B)</td>
<td>1.30</td>
<td>20.70</td>
<td>21.61</td>
<td>20.28</td>
<td>26.07</td>
</tr>
<tr>
<td>Training (A)</td>
<td>3.90</td>
<td>23.30</td>
<td>19.70</td>
<td>15.28</td>
<td>22.45</td>
</tr>
<tr>
<td>Age (C)</td>
<td>3.30</td>
<td>1.03</td>
<td>1.86</td>
<td>0.92</td>
<td>1.56</td>
</tr>
<tr>
<td>Surgery x Age (BC)</td>
<td>3.30</td>
<td>0.73</td>
<td>0.82</td>
<td>0.08</td>
<td>0.08</td>
</tr>
<tr>
<td>Surgery x Training (BA)</td>
<td>3.90</td>
<td>0.30</td>
<td>2.46</td>
<td>0.56</td>
<td>2.73</td>
</tr>
<tr>
<td>Training x Age (AC)</td>
<td>9.90</td>
<td>1.30</td>
<td>1.31</td>
<td>2.50</td>
<td>2.64</td>
</tr>
<tr>
<td>Surgery x Training x Age (ABC)</td>
<td>9.90</td>
<td>0.55</td>
<td>0.66</td>
<td>1.28</td>
<td>1.50</td>
</tr>
</tbody>
</table>

For explanations of underlines see Table III.

As was described previously (27), the inferior performance of pyramidotomized dogs was most conspicuous in tasks that required the most extensive use of distal limb muscles. However, these tasks were very difficult for normal animals too, so that they learned to solve them only gradually. Table VI shows the percentages of normal and pyramidotomized dogs able to solve particular tasks classified as difficult in consecutive training series. Since this index did not show any Age effects (Table V), all of the normal and of the operated dogs were grouped together, regardless of their age at the beginning of training.

The least affected by pyramidal lesions was the ability to retrieve food from the set of large cones and the horizontal and oblique tubes. All or almost all of normal animals solved these tasks as early as the
first training series, independently of the depth of test devices. The percentage of pyramidotomized dogs solving these tasks was somewhat smaller and ranged from 78–100 and 89–100 in the first and fourth training series respectively. In general, the difficulties in solving these tasks by pyramidotomized dogs increased as a function of the depth of the test devices, but this effect was not very strong.

The retrieval of food from narrow cones represented a much more difficult task both for normal and pyramidotomized dogs and the difficulty of these tasks increased markedly as a function of the depth of the cones (Table VI). In the first training series 100 and 90% of normal dogs were able to retrieve food from 2 and 3 cm deep cones, while only 65 and 60% of dogs from cones 4 and 5 cm deep. Among operated dogs, 89 and 55% of the subjects solved the former two tasks, while 22 and 17% the latter two tasks. The differences between normal and operated dogs decreased with training, but in the fourth training series the percentage of pyramidotomized dogs able to retrieve food from cones 4 and 5 cm deep was still smaller than in normal animals (78% vs 95%).

Retrieving food from vertical tubes appeared to be a very difficult task for normal dogs and an almost unsolvable problem for the operated ones. In the first training series only 30 and 20% of normal dogs were able to retrieve food from tubes 3 and 4 cm deep, and 5% from the depth of 5 and 6 cm. These percentages increased as a function of training, so that in the fourth training series 85 and 80% of the normal animals solved the two former tasks, while 50% solved the latter two. On the other hand, the operated animals were, in general, unable to solve these tasks in the first two training series, except one dog (No P–XII, 5 month-group) that reached the criterion in the 3 cm deep tube and in tubes of all depths in the 1st and 2nd training series respectively. In the 3rd training series the performance of operated animals improved slightly, but still remained on a much lower level than in the normal dogs. At the end of the training only 7 out of 18 operated dogs were able to retrieve food from the most shallow tube, while 5, 4 and 2 subjects retrieved from tubes 4, 5 and 6 cm deep, respectively.

The inferior performance of pyramidotomized dogs in this class of tasks was a function of two factors: the decreased accuracy of movements and the deficit of distal limb movements. Since in all tasks belonging to this class the animals had to insert the paw into relatively small openings, the percentage of dysmetric movements was much higher in both normal and operated dogs, than in the remaining two classes of easier tasks (cf. Fig. 2, 3, 4). In the test of cones, the subjects
### TABLE VI

Percents of normal and pyramidotomized dogs solving various sets of difficult tasks in successive training series

<table>
<thead>
<tr>
<th>Kind of test-device</th>
<th>Its depth (in cm)</th>
<th>Normal dogs ($n = 20$)</th>
<th>Pyramidotomized dogs ($n = 18$)</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Successive training series</td>
<td>Successive training series</td>
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<td>I</td>
<td>II</td>
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<td>Large cones (4 cm diameter)</td>
<td>2</td>
<td>100</td>
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<td>3</td>
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<td>4</td>
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<td></td>
<td>5</td>
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<tr>
<td>Narrow cones (2 cm diameter)</td>
<td>2</td>
<td>100</td>
<td>100</td>
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<tr>
<td></td>
<td>3</td>
<td>90</td>
<td>100</td>
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<td></td>
<td>4</td>
<td>65</td>
<td>85</td>
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<td></td>
<td>5</td>
<td>60</td>
<td>85</td>
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<tr>
<td>Horizontal tube</td>
<td>6</td>
<td>95</td>
<td>100</td>
</tr>
<tr>
<td>Oblique tubes</td>
<td>3</td>
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<td>6</td>
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<tr>
<td>Vertical tubes</td>
<td>3</td>
<td>30</td>
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usually overstretched the limb and only when pulling it back could the paw fall into the openings. In task consisting of retrieving food out of the tubes, the dogs often scraped the external walls of the tubes or their edges, before inserting the paw (cf. 27). This manner of behavior, although also present in normal dogs, was much more frequently observed in operated subjects. One of the factors which additionally interfered with the operated animals' ability to insert the paw into the tubes was their tendency to spread, instead of to adduct, the toes at the final stage of the movements.

The functional deficit of distal muscles rendered movements of the operated animals also less effective, particularly in tasks that required the most extensive use of distal muscles. Normal animals raked food over the front wall of the devices, the toes remaining flexed and adducted (cf. 27). On the other hand, the pyramidotomized dogs, even if they succeeded in inserting the paw into the openings, either only displaced the meat toward the front wall or were able to pull it up only for a short distance, and then “lost” it, so that food fell back into the devices. This deficit explains why the animals' performance was particularly impaired in the tasks of deep narrow cones and of vertical tubes.

Comparison of motor performance in individual dogs

The performance of individual normal and operated dogs is shown in Fig. 5, which gives the percentages of all the 38 tasks solved in successive training series by animals belonging to different age groups. The data in the Figure illustrate again the effects of Surgery and of training series and lack of age effect on the animals' performance. In the first training series the vast majority of normal animals solved 80–90% of the tasks, while the operated dogs 60–80%; in the fourth training series, most of normal animals solved 95–100% of the tasks, while the pyramidotomized dogs 80–95%. All animals, except a few, generally improved their performance in successive training series. The performance of animals operated at the age of 1 mo was not any better than of animals that sustained the surgery at older ages.

The lack of age effects in the performance of operated animals was not due to differences in the completeness of pyramidal lesion in various age groups. The mean percent of the left pyramid destroyed was 96% in 1 month-old animals; 88% in 2 month-olds; 93% in 3 month-olds and 97% in 5 month-olds (cf. Table II), while the mean percent of tasks solved in these groups was 76, 73, 68 and 72, and 86, 93, 88 and 89 in the first and fourth training series respectively.
The lack of correlation between the completeness of transection of the left pyramid and the animals' performance was also seen in comparing the performance of individual animals within particular age groups (cf. Table II and Fig. 5), as well as of all operated subjects regardless of their age at the time of surgery. The Spearman correlation coefficients between the percentage of the pyramid transection and the percentage of tasks solved by each subject were not significant either with respect to the first or fourth training series (first series: $T = 0.77, P > 0.05$; fourth series: $T = 0.06, P > 0.05$). On the other hand, the impairment of the reticular formation seemed to influence the animals' performance, especially shortly after the surgery (cf. Fig. 5 and 1, dog No. P-III, group 3 month-old). In other animals with some additional impairment of the right (ipsilateral) pyramid and of the medial lemniscus (dogs P-I and P-VIII, group 3 month-old), the performance was within the range of other operated dogs.

Fig. 5. Percentages of all the 38 tasks solved by individual normal (N) and pyramidotomized (P) dogs in different age groups. I-IV, successive training series. For comparison of the extent of lesions in individual dogs see Fig. 1 and Table II.
DISCUSSION

The main result of the present study is the lack of age dependent differences in the recovery of motor skill after unilateral pyramidal lesions in the dog. In all four age groups studied, the performance of operated dogs was essentially similar, irrespective of whether the lesion was made at 1, 2, 3 or 5 mo of age. This held true for each of several training series, which involved a period from 1 to 8 mo after surgery, as well as for different classes of manipulatory tasks. Overall significant Age effects or significant Surgery × Age or Training × Age interactions in performance were obtained only in a few instances and when present, they mainly concerned the accuracy of movements, i.e., the ability to direct precisely the limb to a given spot. In other indices of performance, mainly related to the effectiveness of manipulatory movements, such as the percentage of solved tasks, the length of training per task and the number of movements per trial performed in order to retrieve food from the test-devices, the effects of age were not significant. Similar results concerning the lack of age-related differences in the recovery of manual dexterity after transection of medullary pyramids have also been obtained in monkeys (44).

Effects of pyramidotomty. With respect to the effects of pyramidotomty on manipulatory movements in the dog, the present experiments amply confirm our previous results obtained in a much smaller number of subjects (27), showing that in the dog, as in other species (1, 6, 25, 35, 45, 71), the pyramidal tract mainly controls movements of distal muscles. In all age groups the motor impairment following pyramidotomty was proportional to the degree of digital involvement in a given task. In easy tasks, in which the use of distal limb movements was not necessary, the performance of operated dogs was similar to normal animals, except for a transient impairment in the accuracy of movements. In tasks requiring movements of foretoes the effects of pyramidotomty were much more evident. The operated animals solved less of these tasks, despite their longer training per task and more movements performed in a single trial in order to retrieve food. Their movements were also less precise, as evidenced by an increase of dysmetric movements. The tasks most affected after pyramidotomty proved to be those which required the most extensive use of foretoe flexion and adduction, as retrieving food from deep and narrow inverted truncated cones or vertical tubes. In these tasks the differences in performance between normal and operated dogs persisted until the end of postoperative examination, i.e., for 8 mo after sugery. These
results show that even in species with rudimentary manipulative abilities of the paw, like in the dog, the pyramidal tract is particularly important for the control of distal muscles. Similar results were obtained in experiments with stimulation of the motor cortex in pyramido-tomized dogs (26). For a more detailed discussion of this problem, see (27).

Developmental consideration. The lack of age-related differences in the recovery of motor functions obtained in the present study might have been due to several factors. One of them is the age at which the youngest group of puppies sustained surgery. In all studies concerned with the developmental determinants of nervous plasticity, the animals' age at the time of surgery constitutes a critical factor. It is generally assumed that the more immature the structure to be damaged, the more recovery of function should be obtained. In the present experiments the earliest transection of the pyramid was done in one month old puppies. The choice of this age derived mainly from our pilot data, showing that manipulatory movements could not be trained systematically in puppies younger that two months, since the animals would not “work” hard enough to retrieve food from the test-devices. On the other hand, we were hesitant to extend the interval between the surgery and the beginning of training beyond a period of one month, in order not to overlook the timing of some recovery processes, if such were to take place. This experimental paradigm was, however, compatible with available anatomical data showing that in 4 wk old puppies the corticospinal tract is still very immature; its fibers, although well visible in the white matter as fibers of passage, hardly enter the spinal gray (5). Other developmental studies in the dog also strongly suggested that at this age the corticospinal tract is far from being mature. Fibers in the lateral corticospinal tract are not yet myelinated (15) and their conduction velocity in 4 wk old dogs attains approximately one third of the values characteristic for adult animals (30). Likewise, movements elicited by stimulation of the motor cortex hardly resemble at that age those of adult dogs, although they already possess some adult characteristics (23, 24). Various forms of placing reactions only begin to appear in puppies in this period, and if present they are performed irregularly (9). Since evidence also pointed out that the pyramidal tract in the dog does not attain its full maturity before the age of three months (5, 15, 23, 24, 30), it was assumed that if the recovery of motor functions after pyramidal lesions were age dependent, the animals that sustained the surgery at the age of 1, and possibly 2 mo would show better recovery of function than animals operated on at 3 or at 5 mo. In cats, for example, an increased capacity for sparing the ability to solve some tasks after lesions of the hippocampus was
obtained in animals operated at 6 wk of age, and this structure is also considered to attain its maturity at the age of approximately 3 mo (33). Similarly, lesions of the visual cortex were reported to produce considerable sparing of function even in cats which sustained surgery at the age of 2 mo (70). In rats, in which the timetable of development of the pyramidal tract is much shorter than in the dog (32), unilateral lesions of the sensorimotor cortex and adjacent structures performed in 3 wk old animals were also followed by some sparing of function when compared to adult (2 mo old) operates (32). Therefore, the results obtained in the present study seem to suggest that the lack of increased capacity for recovery of function in puppies operated at the age 1 mo might have been due to other factors than the maturational status of the pyramidal tract at this age. For example, it has been postulated (18), that the capacity for compensation depends not so much on the maturational status of the damaged structures, but rather on the functionally related structures that remain undamaged. In the dog the transition period between the 3rd and 4th wk of life is characterized by a very rapid development of motor functions. The animals at that age begin to display an adult pattern of locomotion and of muscle tone (13, 14). Also at the age of 3 wk all pathways in the spinal cord are already myelinated, except for the lateral corticospinal tract and the fasciculus gracilis (15). It might be possible, therefore, that if other extrapyramidal pathways were to subsume the function of the lesioned pyramidal tract, the surgery should be performed before dogs reach the age of 3 wk. This problem is now under investigation, but our preliminary results with puppies operated in the 2nd postnatal week do not show any better sparing of manipulatory movements than in animals described in the present paper, operated at later postnatal periods.

System-dependent recovery of function. The lack of age related differences in the recovery of the ability to perform relatively isolated finger movements after pyramidotomy has been also reported in monkeys operated at the age of 4 days to 5 wk (44), although in this species the development of the pyramidal tract and of direct corticomotoneuronal connections lasts at least 8 mo (42). These results, together with ours, seem to speak in favor of the hypothesis that, irrespective of the organization of the pyramidal tract in various mammals, i.e., the presence or absence of direct corticomotoneuronal connections, movements of distal limb muscles are hardly compensated after lesions of this system, regardless of the age at the time of surgery. This hypothesis is substantiated by the fact that out of various descending pathways in the spinal cord, only the rubrospinal tract shows some analogy in the anatomy and function with the pyramidal tract with respect to
movements of distal limb muscles (43, 57, 58). However, lesions of this tract produce much smaller impairment in distal movements than lesions of the pyramidal tract (25, 43, 45, 46, 67) and, therefore, this system may play only a minor role in the compensation of function after pyramidal tract lesions. On the other hand, general motor activities which usually involve more proximal muscles may offer a much better opportunity to study the age-related differences in the recovery of motor functions after various lesions, since they are controlled by multiple systems (43, 46) that may replace each other. This difference in the underlying mechanisms subserving various motor functions may explain the disparity of results concerning the age-related differences in the recovery of motor functions in the work of Kennard (36–39) and Lawrence and Hopkins (44) on monkeys. A similar hypothesis concerning “compensable” i.e., mediated by multiple systems and “noncompensable” functions after early brain lesions was put forward with respect to other brain functions (33).

Species differences. The final point concerns the species differences in the plasticity of the nervous system after early postnatal lesions. So far the majority of studies concerning this problem have been done on rodents, and specifically on rats and hamsters, since these species are born with a much less developed central nervous system than other mammals with a longer gestation period (30, 64). In rats, for example, the major growth of the corticospinal fibres into the brain stem and rostral cord occurs in the 2nd and 3rd wk postnatally, while at the time of birth only a small number of corticospinal axons has reached the pyramidal decussation and the cervical cord (10, 32). Consequently unilateral lesions of the sensorimotor cortex and adjacent structures or unilateral pyridotomy performed in newborn rats are followed by the development of a small, aberrant ipsilateral corticospinal projection from the opposite hemisphere, which terminates in the spinal gray in regions similar to the normal contralateral distribution (7, 8, 31, 32, 47, 49) and form normal-looking synapses (48, 56). A small anomalous projection was present even in animals operated at 20 days postnatally (47). The function of this aberrant corticospinal tract in movements of distal limb muscles in the rat has not been ascertained, but it has been postulated to play a role in locomotion (31) and especially in precise limb positioning when walking on a difficult terrain (32). In hamsters, having a gestation period shorter than rats, transection of the medullary pyramids performed during the first 2 wk after birth was found to be followed by a regrowth of pyramidal fibres, which coursed an abnormal route, but nevertheless reached and formed synapses in their normal, terminal areas in the spinal gray (34). Func-
tionally these animals, in contrast to those lesioned as adults (35), showed a considerable sparing of manipulative abilities of the fore-paw (61). It is possible, therefore, that if in other mammals, as carnivores and primates, pyramidal lesions were performed in a similar developmental period as in neonate rodents, for example, in the period of intense axonal growth and before the corticospinal fibres reached their terminal sites, such lesion would be also followed by a reorganization of corticospinal fibres and by sparing of function, similarly to that found with respect to prenatal prefrontal cortex lesions in primates (20, 21). The resolution of this problem has to wait, however, for much better knowledge of developmental stages of the pyramidal tract in various mammals both pre- and postnatally.

The authors wish to thank Dr P. S. Goldman for her helpful criticism in preparing the manuscript, Drs J. Brennan and P. Jastreboff for suggestions concerning the statistical analysis of the material. This investigation was supported by Foreign Research Agreement No. 05.001.0., annex 284A of the U.S. Department of Health, Education and Welfare under PL 480 and by Project 10.4.01.7 of the Polish Academy of Sciences.

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Accepted 10 March 1982