INSTRUMENTAL CONDITIONED RESPONSES IN CATS WITH BULBAR PYRAMID AND RED NUCLEUS LESIONS

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Abstract. Adult cats were trained to insert a forelimb into horizontally mounted transparent cylinders and then either depress a barrier or pull a sliding tray against resistance in order to receive food reward. Unilateral lesions of both bulbar pyramid and red nucleus resulted in severe neurological deficits. However, the instrumental tasks were soon accomplished at preoperative levels of rapidity and strength, although movements of the digits and wrist were reduced and adjustive movements occurred chiefly at more proximal joints. These results support our hypothesis that conditioned and unconditioned behaviors are mediated through different mechanisms.

INTRODUCTION

It has been noted that pyramidal and rubrospinal pathways have similar motor functions and can substitute for each other to some extent (5, 11). Evans and Ingram (2) made lesions in the bulbar pyramid and/or red nucleus of the cat. They claimed that the motor deficits are much more marked after combined lesions of the pyramidal and rubrospinal pathways than when there is a lesion of either pathway alone. Based on the results, they further concluded that in the cat the corticospinal and
rubrospinal pathways are each capable of a degree of compensation for the loss of the other. In summaries of the anatomical and physiological data, Kuypers and Lawrence (5, 6, 7) suggested that there are two distinct main motor systems: medial and lateral. The lateral system consists chiefly of the pyramidal and rubrospinal tracts and acts on the interneurons connected to the distal musculature and to the flexor muscles. A lesion of the lateral system produced deficits in the use of distal flexor muscles; this disturbance was most marked after a combined lesion of the pyramidal and rubrospinal tracts.

On the other hand, it has been demonstrated that animals with pyramidal lesions can be trained for instrumental motor tasks (1, 3, 9, 10, 13-15). However, the role of red nucleus in this situation has not been investigated. In this study, we planned to determine the effects of lesions in bulbar pyramid, red nucleus or both on instrumental responses in cats. A preliminary report was presented (8).

MATERIALS AND METHODS

Adult cats were used. They were subjected to unilateral bulbar pyramidal section, red nucleus lesion or both. Five of them with more accurate lesions are included in this paper.

The animals were trained in a test chamber to insert a forelimb into horizontally mounted leucite cylinders with a diameter of about 8 cm and then either depress a barrier (Cyl. B) or pull a sliding tray (Cyl. T) with a resistance of 7 to 13 ounces in order to receive food reward. Such responses required accuracy in inserting the paw into a narrow opening above the barrier or the tray and also proper foot alignment so that force applied in pressing or pulling was not delivered tangentially to a piston of the barrier or a runner shaft of the tray. The details of the test chamber, the training methods and the performance of normal cats were described in a previous paper (12).

Surgical procedures were performed aseptically under intraperitoneal Nembutal anesthesia (35 mg/kg). The bulbar pyramid was sectioned by a retropharyngeal approach. The red nucleus lesion was made by electrocoagulation through a stereotaxically oriented electrode with a vertical approach. The extent of lesions was determined histologically. All the cats were sacrificed under Nembutal anesthesia by perfusion-fixation technique (4). The alternative celloidin sections of the brain blocks containing the lesion were stained by the cresyl violet and Mahon methods.
RESULTS

*Bulbar pyramid section.* Two cats (No. 10 and 11) with complete right bulbar pyramid section (Fig. 1) were included. Neurologically both cats developed similar deficits in the contralateral limb postoperatively.

![Projection drawings and microphotographs illustrating brainstem lesions](image)

Fig. 1. Projection drawings (A, C) and microphotographs (B, D) illustrating an example of brainstem lesions of the right red nucleus and right bulbar pyramid of cat No. 11 cresyl violet stain. Checkered area, lesion cavity; stippled area, gliosis and cell loss; wavy parallel lines, normal fiber tracts. Abbreviations: BCI, brachium of inferior colliculus; BP, basis peduncle; CA, cerebral aqueduct; CG, central gray; CP, posterior commissure; GL, gliosis; ICP, inferior cerebellar peduncle; IN, interpeduncular nucleus; IO, inferior olive; LGB, lateral geniculate body; LM(ML), medial lemniscus; MGB, medial geniculate body; MLF, medial longitudinal fasciculus; N III, oculomotor nerve; N VII, facial nucleus; NC, cochlear nucleus; NR, raphe nucleus; NRP, parvocellular reticular nucleus; NVL, lateral vestibular nucleus; OT, spinal tract of the trigeminal nerve.
Tactile placing was abolished and proprioceptive and visual placings and hopping were reduced. Extensor tone and supporting reactions were mildly increased. Reaching for food with forelimbs in the free situation, the animals used the uninvolved limbs exclusively and the other only when the preferred limb was restrained. When the cats tried to bat a piece of food held in the air by forceps, the movements were from more proximal joints with greater excursion.

The cat No. 10 was trained before the operation with Cyl. B for 13 days and also with Cyl. T for 7 days. The animal preferred to use the left forelimb for the tasks. The cat was sick after right pyramid section and was not tested in the test chamber until the 11th postoperative day. It used left forelimb in the test chamber and could project the limb into the cylinder without difficulty. Initially, it had difficulty to place the foot on the barrier or tray top properly. Weak and tremorous movements were noted in pushing the barrier or pulling the tray. The tasks were usually accomplished by repetitive partial actions. It also failed to push or pull against 13 ounce resistance. However, the performance improved with time and reached preoperative level of rapidity and accuracy except for fine digital adjustment by three weeks. The other cat (No. 11) was not trained in the test chamber until 5 months after right pyramid section. Cyl. B was tested on the first day of training. The animal learned the task with right forelimb only and was then forced to use the left one. The left forelimb tended to hyperflex in reaching the entrance of the cylinder but had no difficulty to enter it. Up and down oscillations outside and inside the cylinder, poor placement of foot on the barrier and lack of digital movements in pushing the barrier were also noted. Hyperflexing and oscillating movements were reduced by the fourth day. The cat could push the barrier against all levels of resistance by two weeks, but persistently showed poor digital movements. Cyl. T was tested on the 12th day of training. The cat learned to use the left forelimb to pull the tray for a short distance with poor placement of paw and no digital adjustment in two days. Five days later, it could pull the tray against all levels of resistance and demonstrated gross adjustments in placing the paw on the tray top.

Red nucleus lesion. Two cats (No. 13 and 14) were used. Cat No. 13 had a complete right red nucleus lesion and was observed for 3 days postoperatively. Cat No. 14 had a lesion involving rostral three fourth of right red nucleus and surrounding tissue and was observed for 7 days postoperatively. Neurologically, the cats showed deficits in the contralateral limbs. Loss of tactile placing, reduced hopping, vestibular drop and proprioceptive placing were noted. The extensor tone increased and supporting response decreased mildly for 2 to 3 days. Walking was
impaired initially but soon improved to only slight goose steps in the contralateral limbs. In reaching for food with forelimbs in a free situation, the cats preferred to use the uninvolved limbs. When the involved limbs were forced into use, they showed overextension of elbow, wrist and fingers and greater excursion of movements from the shoulder.

Cat No. 13 was trained with Cyl. B and T starting 7 days before the operation. It preferred the left forelimb and could accomplish the tasks in two days. After right red nucleus lesion, the cat was tested on the second day. The instrumental tasks were essentially preserved. The cat still preferred to use the left forelimb and could push the barrier or pull the tray as long as the body was balanced and aligned with the cylinder. However, it is noted that the cat placed the wrist rather than the hand on the barrier or tray top and demonstrated no digital movements. Cat No. 14 was not trained until two days after right red nucleus lesion. The animal soon learned the tasks using exclusively the right forelimb and was then forced to use the left forelimb. Initially, the left forelimb displayed hyperflexion and some vertical oscillations in reaching the cylinder but no difficulty to enter it. The cat placed the wrist rather than the hand on the barrier or tray top and showed no digital movements in placing, pushing or pulling. By the 7th postoperative day, the cat accomplished the tasks at all resistances with some hyperflexion before entering the cylinder, occasional misplacement of the foot and lack of fine digital movements.

Combined bulbar pyramid and red nucleus lesions. Two cats (No. 11 and 12) were subjected to unilateral combined lesions in two stages. Cat No. 11 was operated with red nucleus lesion 175 days after pyramid section. Both lesions were complete (Fig. 1). Cat No. 12 had a complete pyramid section and a subsequent partial red nucleus lesion 163 days later. After the second lesion, cat No. 11 was observed for 54 days and No. 12 for 92 days. The cats with combined pyramid and red nucleus lesions were very impaired neurologically. Initially, the cats walked very awkwardly with the contralateral involved limbs dragged. The forelimb often stepped on the dorsum of the foot and hindlimb often slipped out of position. Though improving with time, the cats still walked with some goose stepping in the involved limbs and occasionally stepped on the dorsum of the forefoot. The animals could never walk on elevated horizontal bars. Throughout the observation period, the contralateral involved limbs showed loss of tactile placing and marked impairment of proprioceptive, visual and abduction placings. The involved limbs might hang down the edge of the table (on which the cat was lying) without trying to lift them up. The impaired forelimb could passively be internally rotated, extended, adducted at the shoulder and
placed on its back. The forelimb was used reluctantly to bat a piece of meat held in forceps and usually only after restraint of the normal limb. The movements were coarse swipes and chiefly aimed and directed from the shoulder.

In marked contrast to the severe neurological impairments was the satisfactory performance in the conditioning situation. Cat No. 11 was trained and tested after right pyramidotomy as described above. After subsequent right red nucleus lesion, marked impairment was noted only initially. The left forelimb tended to overflex and showed tremorous movements in reaching the cylinder. The left hand was used as a loose mass from the wrist distally and the forearm supinated. The hand placed on the barrier or tray top with its ulnar aspect and usually did not place on the center of the top. Pushing the barrier or pulling the tray was weak, unsuccessful and without any digital movements. The left hindlimb frequently slid out of position, especially when the left forelimb lifted up from the floor for the tasks. However, rapid recovery occurred. By the 8th postoperative day, the cat could accomplish the tasks though without digital movements. By the 18th postoperative day, the cat could push or pull steadily against all levels of resistance as long as the body maintained its balance. Cat No. 12 was not tested or trained in the test chamber after right pyramid section and not until 20 days after subsequent right red nucleus lesion. The cat used only its right forelimb and was then forced to use the left one. The pattern of movements in the test chamber was essentially the same as cat No. 11 except for no tendency to overflex the limb. The cat could push and pull against all levels of resistance by one week after starting training. In both cats, the performance in the conditioning situation was not altered with vision occluded.

DISCUSSIONS

As noted by other investigators, (2, 5–7) our animals with combined bulbar pyramid and red nucleus lesions were very impaired neurologically. This indicates that pyramidal and rubrospinal tracts are essential for skillful movements in an unconditioned situation. These two pathways may compensate for each other to some extent when one is damaged.

On the other hand, despite severe neurological impairments, the cat with the combined pyramid and red nucleus lesions could maintain its balance, project the involved forelimb into the cylinder, place on the barrier or tray top and push the barrier or pull the tray against resistance in the test chamber even with vision occluded. A similar result was
found in another experiment (15). As mentioned previously, the cats with the combined pyramid and red nucleus lesion could not step on the elevated horizontal bars; this persisted during an observation period extending up to three months. However, animals with identical lesions which had been trained with food as a reward, could walk on the bars as early as two weeks postoperatively. These findings support our hypothesis that conditioned and unconditioned behaviors are mediated by different mechanisms. Training activates a parallel system essential to conditioned responses rather than strengthening the original pathways subserving the normal responses (14). The observation that the subsequent red nucleus lesion in the cat with pyramid section resulted in the severe initial impairment of instrumental responses suggests that rubrospinal tract also compensates for the pyramidal deficits in the training situation. However, other systems can be activated with training in the absence of rubrospinal control.

In this study, we found that digital movements were impaired after bulbar pyramid and/or red nucleus lesion both in the conditioned or free situations. Since the instrumental tasks were not designed specifically to test or train for the digital movements, we were not sure whether such movements could be obtained through training. In our other study with unilateral pyramid sectioned monkeys (10, 14), digital movements were trained with the following strategies: 1) the sound limb and medial three digits of the impaired limb were restrained to force the animal to use only the thumb and index finger; 2) a food pellet was put in small wells in a wooden board and the animal was required to use an individual finger to dig out the pellet or to oppose the thumb and index finger to retrieve it and 3) a baited drawer was used and the animal was required to grasp a knob with opposition of the thumb and one other finger to open it. Although the movements were weaker and somewhat ataxic, the monkey could finally perform discrete digital movements.

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REFERENCES


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