THE EFFECTS OF CEREBRAL SENSORY AND MOTOR CORTICAL LESIONS ON CONDITIONED TACTILE PLACING IN CATS WITH PYRAMID SECTION

J. YU

Department of Physical Medicine and Rehabilitation, University of California Irvine Medical Center
101 City Drive South, Orange, CA 92668, USA

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Abstract. Cats after unilateral bulbar pyramid section showed permanent loss of tactile placing in the contralateral limbs. However, the cats could be trained to place the forelimb following light touch in a conditioning situation with food as a reward. Subsequent unilateral or bilateral cerebral cortical lesions involving sensory and/or motor areas did not abolish this conditioned response. Since these cortical areas are essential to reflex tactile placing, the results indicate that reflex and conditioned responses can be mediated differently at the cerebral cortical level.

INTRODUCTION

Cats after unilateral bulbar pyramid section showed permanent loss of tactile placing (TP) in the contralateral limbs. However, the cats could be trained to place the forelimb following light touch in a conditioning situation with food as a reward. This conditioned TP survived subsequent lesions which interrupted subcortical afferent and efferent pathways essential to reflex TP, such as red nucleus lesions, cerebellar interposed nucleus lesions, and dorsal quadrant spinal cord lesions at the cervical level (7). These results indicate that reflex and
conditioned responses involve different subcortical pathways and mechanisms. In this paper, similar findings at the cerebral cortical level are reported.

MATERIALS AND METHODS

Adult cats were used. Reflex TP was tested in the cat by contacting (light hair touch) part of the unsupported limb with the edge of a table. The normal cat will place the paw on top of the table forward, backward, medially or laterally with adjustment of height according to the part of the limb touched. The cats were also positioned in a hammock for testing and training of the conditioned TP of both forelimbs with food as a reward. Both reflex and conditioned TP were observed for its rapidity, directionality, adjustment of height and gross movements. The detailed methods were described previously (7).

All operations were performed aseptically under intraperitoneal Nembutal anesthesia (35 mg/kg). The bulbar pyramid was sectioned by a retropharyngeal approach. Cerebral cortical ablations were done by gentle aspiration after craniotomy and opening of dura mater. The sensory cortical ablations involved SI and SII (according to the ref. 4) and the motor cortical ablations involved areas 4 and 6 (as outlined in the ref. 5). At the termination of the experiments, the cats were killed under Nembutal anesthesia by perfusion (2). The extent of the cortical lesion was inspected and plotted for the areas involved and its depth was determined histologically using paraffin or frozen sections stained with Hematoxylin-eosin and luxol fast blue or cresyl violet.

RESULTS

Motor cortical ablation. Three cats (Y89, Y41 and P5) were used. Cat Y89 was trained for conditioned TP in the hammock starting the 9th day after right bulbar pyramid section. The involved left forelimb could perform the conditioned response in two days and showed no difference from the intact limb by 10 days. The right motor cortex was ablated (Fig. 1) 35 days after the pyramid section. The conditioned TP in the left forelimb disappeared for one day and returned without retraining on the second postoperative day, although the response was slow and inconsistent. Rapidity recovered in the following seven days, but the limb moved with more extension and larger step than the right. By 42 days, no difference was observed between the two forelimbs. Cat Y41 had a right bulbar pyramid lesion extending to the surrounding tissue, and was trained for the conditioned TP starting on the 23rd
postoperative day. It took 14 days to train the involved left forelimb for placing in all directions. Left motor cortex was ablated 63 days after the right pyramid lesion. The conditioned TP was observed in the left limb, but not in the right on the 7th postoperative day when the animal was tested for the first time after surgery. With further testing and training, the conditioned TP was obtained in the forward direction in two days, in the lateral in 7 days, in the medial in 8 days and in all directions by 13 days. Cat P5 was trained for conditioned TP after right pyramid section. The conditioned response survived the subsequent right red nucleus and left cerebellar interposed nucleus lesions as described in the previous paper (7). The right motor cortex was then ablated 75 days after the cerebellar lesion. The cat was not tested in the hammock until the 3rd postoperative day. The conditioned TP in the involved left forelimb was preserved, but the response was slow initially. The limb tended to be stiff, often oscillating before placing, and could not be raised high enough for height adjustment. The left motor cortex was ablated 52 days after the right motor cortex lesion. Loss of reflex TP was now noted also in the right limbs. Both forelimbs were extended in the hammock, more so in the left. The conditioned TP disappeared initially and returned in the right limb in forward, medial and sometimes backward directions on the 7th postoperative day when the cat was tested in the hammock for the second time. By the 11th day, the right limb could perform the conditioned TP in all directions but showed no height adjustment. No conditioned TP was obtained in the left limb until the 11th day when the limb responded to repeated hair stroking but could not always be elevated to place. The conditioned response improved with time. By 24 days after the last surgery, the left limb could perform the conditioned TP in all directions but still stiff and difficult to elevate. When the right paw was supported by the investigator's hand with the elbow in full extension, the left limb showed less extensor tone and performed the conditioned TP faster and smoother.

*Sensory cortical ablation.* Three cats (Y4, Y29 and Y36) received right sensory cortical ablation subsequent to right pyramid section. The left limb showed loss of TP and tactile localization throughout the observation period. Cat Y4 was trained for the conditioned TP starting 4 mo after pyramid section and was subjected to a sensory cortical lesion (Fig. 1) 17 days later. The cat was not tested in the hammock until 14 days after the cortical ablation when the conditioned TP could not be found in the left forelimb. However, the forward and medial conditioned TP were obtained at times after retraining on the following day, and
so were the lateral and backward placings in two more days. Height adjustment was poor and forward movements were common in medial and lateral placings. By the 31st postoperative day, the conditioned TP was well performed in all directions in the left forelimb with height adjustment improved. Cat Y29 was trained for the conditioned TP starting two and a half months after right pyramid section and was subjected to a right sensory cortical ablation 17 days later. When the cat was tested for the conditioned TP on the second postoperative day, the forward and lateral placings were present with exaggerated steps.

By 7 days after the cortical lesion, the left forelimb could perform the conditioned TP in all directions with height adjustment, although the limb tended to move forward in lateral or medial placing. Cat Y36 was trained for the conditioned TP starting two months after right pyramid section and was subjected to a right sensory cortical ablation 12 days later. The conditioned TP survived the sensory cortical lesion only in the forward direction when tested on the second postoperative day. Since the forelimbs were usually restless in the hammock, it was difficult to evaluate the response. However, the conditioned TP did return in all directions with height adjustment by 37 days.

Sensory and motor cortical ablation. A combined sensory and motor cortical lesion was done in 5 cats (Y43, Y44, Y60, Y48 and Y8). Cat Y43 was trained for conditioned TP starting 21 days after left pyramid
section. The left sensory and motor cortical ablation was done two months after pyramid section and produced no change in the conditioned TP in the left forelimb. The right forelimb was more active than the left, and tended to persist in stepping forward until placing on the investigator's finger, probably not a response to touch. The real conditioned TP was recognized in the forward direction on the 29th postoperative day but not in all the directions until 84 days after the cortical lesion. Cat Y44 had a left pyramid section with few fibers spared and showed recovery of reflex TP in the right forelimb 51 days after surgery. Left sensory and motor cortical ablation (Fig. 1) was performed 57 days after pyramid section and produced a permanent loss of reflex TP in the right limbs. The cat was trained for conditioned TP starting 22 days after pyramid section and could not perform the conditioned TP with the right forelimb after the cortical lesion. However, the conditioned TP returned in the forward and backward directions by the 5th postoperative day and in all directions by the 15th day. The right forelimb moved more rigidly than the left and could not be elevated for height adjustment. Cat Y60 had a right sensory and motor cortical ablation 41 days after right pyramid section. This cat was trained for the conditioned TP starting 33 days after pyramid section and was not tested in the hammock until the 14th day after the cortical lesion when the conditioned response was noted to be absent in the left forelimb. The left forelimb responded to touch by withdrawal by 29 days after the cortical lesion and by placing only in the forward direction starting on the 42nd day. By 66 days after the cortical lesion, the cat could place the limb in all directions following touch in the hammock, slower in response in the medial direction. The cat attempted to adjust the height in placing with hypermetric steps when the forearm level was touched but could not raise the limb high enough. Cat Y48 was trained for conditioned TP starting 27 days after right pyramid section and was then subjected to a bilateral sensory and motor cortical ablation in two stages. The right sensory and motor cortical lesion (Fig. 1) done 41 days after the right pyramid section resulted in loss of the conditioned TP in the left forelimb until the 53rd postoperative day. The left forelimb was overextended and hypermetric in placing. The left sensory and motor cortex was ablated 78 days after the right cortical lesion. The conditioned TP was lost in the left forelimb for 10 days and in the right forelimb for 46 days. The right limb was not as stiff as the left but neither limb could adjust for the height in placing. The left limb was still hypermetric in placing by 85 days after the left cortical lesion. Both cats Y60 and Y48 frequently showed stepping movements ("bicycling") in the hammock after sensory and motor cortical
ablation. Cat Y8 with a right dorsal quadrant spinal cord lesion at the cervical level and a subsequent right cerebellar interposed nucleus lesion was described in the previous report (7). The left sensory and motor cortex was ablated 58 days after the cerebellar lesion. When the cat was tested in the hammock for the first time on the 9th postoperative day, the conditioned TP was normal in the left forelimb but was only present in the forward and backward directions in the right. Touching the medial side of right paw induced forward placing of the right limb but often was accompanied with the left. By the 27th day, the right forelimb could perform the conditioned TP in all directions as before the cerebral cortical lesion with stiffness and no height adjustment.

**DISCUSSION**

The right TP has long been known to depend on the cerebral cortex (1), and more particularly on the sensorimotor cortex (3). The reflex is permanently lost in cats after either sensory or motor cortical ablation. However, the conditioned TP in cats with pyramid section could still be obtained after these cortical lesions. The results indicate that the reflex and conditioned responses can be mediated differently at the cerebral cortical level. This is supported by findings from an earlier study of the effects of cerebral sensory cortical ablation on the instrumental conditioned reflex in cats with cerebellar lesions (6). Those cats were able to project forelimbs into cylinders and taking food placed inside even without vision despite abnormal muscle tone, ataxia and sensory impairment noted in the free situation.

We found that the conditioned TP in cats with pyramid section disappeared after combined sensory and motor cortical lesions and required retraining to regain it. This probably indicates that the sensorimotor cortex plays a role in the conditioned TP, although other areas can be recruited by training when the sensorimotor cortex is ablated. Since either sensory or motor cortical ablation did not abolish the conditioned TP, this suggests that sensory and motor cortical areas may be redundant to each other in mediating the conditioned response.

4. ROSE, J. E. and WOOLSEY, C. N. 1949. Organization of the mammalian thala-


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