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

J. YU, C. N. LIU and W. W. CHAMBERS

Audie L. Murphy VA Hospital, and Department of Physical Medicine and Rehabilitation
The University of Texas Health Science Center at San Antonio, San Antonio, Texas
and Department of Anatomy and Institute of Neurological Sciences, University of Pennsylvania, Philadelphia, Pennsylvania, USA

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. This conditioned response survived subsequent unilateral red nucleus and cerebellar interposed nucleus lesions. Dorsal quadrant spinal cord lesion at the cervical level produced initial loss of the conditioned tactile placing but is recovered without retraining. Since those lesions interrupted subcortical afferent and efferent pathways essential to reflex tactile placing, these results indicate that reflex and conditioned responses involve different pathways and mechanisms. Training recruits or activates additional pathways for conditioned responses rather than strengthening those subserving the reflex responses.

INTRODUCTION

Tactile placing (TP) can be tested in a 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. As early as 1933, Bard observed that removal of the
cerebral sensorimotor cortex in cats produced permanent loss of TP in contralateral limbs (2). This result led investigators to believe that TP depended upon the integrity of the sensorimotor cortex and so, this reflex was used to determine the function of this cortical area as well as those of its afferent and efferent systems. Later studies showed that TP can be permanently abolished by combined sensory lesion of both dorsal column — medial lemniscal and spinocervicothalamic systems (10) or by any single motor lesion in the following structures: bulbar pyramid, red nucleus, cerebellar interposed nucleus and cerebral motor cortex (1, 3, 4, 8, 12, 16, 17).

However, despite the persistent loss of TP in the free (unconditioned) situation, the cats after bulbar pyramid section can be trained to place the limb following light touch in a conditioning situation with food as a reward (18). Since the cat with bulbar pyramid section shows normal tactile perception and localization (10), the loss of TP is a motor rather than sensory deficit. On the other hand, the loss of placing following tactile stimuli is not due to the impairment of the musculature essential to placing because the animal can still place following other stimuli, such as bending the joint (proprioceptive placing). Consequently, this conditioned TP represents a phenomenon of central motor compensation through training. The pathways and mechanisms mediating this conditioned response have not been explored.

We planned to determine the pathways mediating the conditioned TP by investigating the effects of subsequent brain or spinal cord lesions on this conditioned response. This paper reports the performance of the conditioned TP in cats after lesions in subcortical sensory and motor structures involved in reflex TP. The effects of cortical and combined cortical and subcortical lesions will be presented in the future. This study was designed to see whether the conditioned TP can survive or can be retrained after a certain lesion or combination of lesions. Although movements were also observed and recorded, the methodology employed afforded only gross characterization. More quantitative and analytical approach will be used in the selected preparations in another investigation to study the nature of this trained behavior.

**MATERIALS AND METHODS**

Adult cats were used. Preparations included lesions in bulbar pyramid, red nucleus, cerebellar interposed nucleus and dorsal quadrant of spinal cord at the cervical level. Five of them with more accurate lesions are included in this paper (Table I).

All the operations were performed aseptically under intraperitoneal
Nembutal anesthesia (35 mg/kg). The bulbar pyramid was sectioned by a retropharyngeal approach. The red nucleus and interposed nucleus lesions were made by electrocoagulation through a stereotaxically oriented electrode with a vertical approach to the red nucleus and a horizontal approach to the interposed nucleus. The spinal cord lesions were done with a sharp knife after laminectomy and incision of the dura mater.

### Table I

Lesions and durations of observation. Abbreviations: R, right; L, left; BP, bulbar pyramid; RN, red nucleus; IP, interposed nucleus; DQ, dorsal quadrant of spinal cord at cervical level. In brackets, days in operative stages.

<table>
<thead>
<tr>
<th>Cat</th>
<th>1st lesion</th>
<th>2nd lesion</th>
<th>3rd lesion</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1</td>
<td>L. BP (118)</td>
<td>L. RN (134)</td>
<td>R. DQ (317)</td>
</tr>
<tr>
<td>P5</td>
<td>R. BP (102)</td>
<td>R. RN (67)</td>
<td>L. IP (75)</td>
</tr>
<tr>
<td>Y3</td>
<td>R. BP (193)</td>
<td>R. RN (28)</td>
<td>L. IP (28)</td>
</tr>
<tr>
<td>Y8</td>
<td>R. DQ (146)</td>
<td>R. IP (57)</td>
<td></td>
</tr>
<tr>
<td>Y16</td>
<td>R. BP (68)</td>
<td>R. RN (56)</td>
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</tbody>
</table>

The cats were examined daily for reflex TP in the free situation. They were also positioned in a hammock for testing and training of TP of both forelimbs. The hammock was so constructed that all four limbs hang freely but could not be observed by the animal. The investigator's finger brushed gently against the hair of the paw. Normally, the cat placed the paw on the stimulating finger immediately, exhibited no misplacement, and was capable of adjusting the directionality of movement (medial, lateral, forward, backward) of the paw to correspond to the surface (medial, lateral, anterior, posterior) on which the stimulus was perceived. If the limb was touched at the higher level (wrist or forearm), it was able to lift the paw higher to place there. In the hammock, this adjustment of height was most clearly observed in the forward placing and thus this was tested only on the anterior surface. Conditioned TP was accomplished using food as a reward. The animals were fed only during training or were fed during training with specially preferred food. Since TP could be elicited reflexly in a normal limb and food was always rewarded immediately after each placement, the cat soon recognized this operant situation. In the case of an involved limb, it was easier to activate the limb for placing initially by bending the wrist joint slightly to induce proprioceptive placing and to reward with food following each placement. The training was performed in a room with minimal auditory and visual distractions. Both reflex and conditioned TP were observed for its rapidity, directionality, adjustment of
height and gross movements. Photography, cinematography or videotape recording was used for documentation.

All the animals were killed under Nembutal anesthesia by perfusion (7). The alternative celloidin sections of the brain and spinal cord blocks containing the lesions in cats P1 and P5 were stained by the Cresyl violet and Mahon methods. In the other cats, the blocks were paraffin sectioned and stained with Hematoxylin — eosin and luxol fast blue. The extent of the lesions was identified histologically.

RESULTS

Bulbar pyramid section. Our previous and present observations in 12 cats after complete unilateral bulbar pyramid section (Fig. 1) showed that reflex TP was permanently abolished in the contralateral limbs. However, conditioned TP of the forelimb could be obtained easily with training. Initially, the animal was fed in the hammock without training. It took one to 7 days for cats to get accustomed to the hammock. Another one to 5 days were required to train a cat with pyramid section for TP. Forward placing was usually accomplished first. Stimuli applied to medial or lateral side of the paw often induced forward placing in the early training period but it could soon be shaped into medial or lateral placing. Backward placing was poor in most of the cats; it pushed backward instead of placing backward. However, no special effort was made to train a better backward placing. The conditioned response was as fast as or only slightly slower than reflex TP. The movements were smooth and accurate. There was no deficit in height adjustment. It was noted that this conditioned TP could only be elicited in the training condition despite the length of training. (For control study, two cats with pyramid section and one cat with combined pyramid and red nucleus lesions were tested for TP daily in the hammock without training. The TP was persistently absent.)

Red nucleus lesion. Four cats (P1, P5, Y3, Y16) were subjected to red nucleus lesion. Cats P5 and Y3 were trained for the conditioned TP in the hammock after complete right pyramid section. Subsequent ipsilateral complete red nucleus lesion in P5 (Fig. 2) produced little initial impairment. The conditioned TP was preserved in forward direction, questionable in medial and lateral and absent in the backward direction. When the anterior surface of the forearm was touched to test for height adjustment, the cat attempted to lift the limb up for placing but never high enough. By one week, the animal showed good conditioned forward, medial and lateral TP. By 10 days, it could also push backward when the posterior surface of the paw was touched. However,
Fig. 1. A photomicrograph showing right bulbar pyramid and left cerebellar interposed nucleus lesions in the cat P5. Mahon Stain (Degeneration of left medial lemniscus is due to a later lesion in the spinal cord which will be reported in a future paper.)
Fig. 2. A photomicrograph showing right red nucleus lesion in the cat P5. Mahon stain.
adjustment of height was continuously poor. The cat Y3 had a large red nucleus lesion involving surrounding tissue and was very impaired neurologically after the surgery. The animal was not tested in the hammock until the seventh postoperative day. The conditioned TP was noted only in backward direction at that time but also in forward and medial directions the following day. With daily testing, conditioned TP recovered in all directions by one week though with difficulty in adjustment of height.

The other two cats (P1 and Y16) were not trained after pyrami
tomy. The cat P1 with complete left pyramid section received a complete left red nucleus lesion 118 days later. The cat was tested and trained in the hammock 18 days after the red nucleus lesion. The conditioned TP was obtained on this first training day. The response was slow; it took 3 to 4 up and down hair strokes to elicit the response. This improved with time and required only one light hair touch by two weeks. Contacting the medial or lateral surface of the paw induced forward placing initially but it could soon be shaped to medial or lateral placing. It always responded with pushing backward instead of placing when the posterior surface was touched. The cat Y16 with complete right pyramid section was tested in the hammock 22 days after the subsequent complete right red nucleus lesion. Training was not started until 6 days later when the animal became accustomed to the hammock. The cat learned the task on the 1st day though it often moved forward in medial placing. By two weeks, movements were smooth and accurate.

Throughout the observation period, all cats with combined pyramid and red nucleus lesions showed loss of tactile placing and impaired proprioceptive placing in the free situation.

Dorsal quadrant spinal cord lesion at cervical level. Dorsal quadrant spinal cord lesion at cervical level was made in two cats (Y8 and P1). Such a lesion interrupted both the dorsal column-medial lemniscal and spinocervicothalamic systems as well as the corticospinal and rubrospinal tracts. The cat Y8 was trained for the conditioned TP for two days preoperatively. After a right spinal cord lesion at C3 level removing dorsal quadrant with extended gliosis to the surrounding areas (Fig. 3), the animal showed ipsilateral limb flaccid paralysis with no tactile or proprioceptive placing initially. The cat was tested almost daily in the hammock starting on the 6th postoperative day when it could stand and eat actively inside the home cage. No conditioned TP was observed in the right forelimb. Four days later the limb started to move in response to touch but without placing. Gradually some movements of placing were noted. By 21st postoperative day, conditioned TP was occasionally
found in forward, medial and backward directions. Conditioned TP in all directions was present 29 days after surgery despite the persistent loss of TP and very impaired proprioceptive placing in the free situation (Figs. 4 and 5). The movements of the conditioned response tended to be fast and flailing with big excursion but usually reached the endpoint accurately.

The cat P1 had a well defined right dorsal quadrant lesion at the C4 level (Fig. 3) subsequent to left pyramid and red nucleus lesions. The animal was not tested regularly in the hammock so that the effects of retraining could be minimized. There was no conditioned TP when tested on the seventh and 29th postoperative day. At the third time which was 43 days after surgery, conditioned forward and backward placings were noted sometimes. On the 64th postoperative days when the animal was tested for the sixth time in the hammock, the conditioned TP was present in forward, backward and sometimes also medial and lateral directions but without height adjustment. By 5 mo postoperatively, it did attempt to adjust the height in the conditioned TP but could not lift the limb high enough.

Cerebellar interposed nucleus lesion. Three cats (P5, Y3 and Y8) received unilateral cerebellar interposed nucleus lesions with resultant ipsilateral neurological impairments. All the lesions were complete with some involvement of the surrounding tissue including part of the dentate nucleus (Fig. 1). Cats P5 and Y3 had left interposed nucleus lesion subsequent to right pyramid and red nucleus lesions. Tactile perception and localization were still intact after the cerebellar lesion. The cat P5 was tested daily in the hammock beginning on the seventh postoperative days. The conditioned TP was absent for only the first 2 days. The movements were very hypermetric with elbow hyperextended. The cat Y3 was first tested on the 3rd postoperative day and showed conditioned TP in forward and medial directions. The lateral placing was also present when it was tested again on the 8th postoperative day. The
Fig. 4. Testing reflex tactile placing in the cat Y8 with right dorsal quadrant spinal cord lesion at cervical level. Note that the reflex is present in the left limb but not in the right.

Fig. 5. The cat shown in Fig. 4 was trained to place the involved forelimb following light touch in a conditioning situation despite persistent loss of reflex tactile placing.

cat was thereafter tested daily. By 12 days after surgery, the conditioned TP was noted in all directions with height adjustment. The movements were fast and stiff (jerky) and sometimes oscillated in reaching the endpoint for placing.

The cat Y8 was subjected to right interposed nucleus lesion 146 days after right dorsal quadrant spinal cord lesion at C3 level. There was no conditioned TP noted when the cat was tested for the first time in the hammock 11 days after surgery. However, the conditioned forward, lateral and backward placings were present when the animals was tested again two days later. The conditioned TP was noted in all directions on the 21st postoperative day when it was tested for the third time. The movements were very hypermetric, overshooting the endpoint and jerky.

DISCUSSION

The conditioned TP was obtained with training despite persistent loss of reflex TP in cats after bulbar pyramid section. This conditioned response survived subsequent red nucleus and cerebellar interposed nucleus lesions. Dorsal quadrant spinal cord lesion at the cervical level
produced initial loss of the conditioned TP but it recovered without retraining. These results indicate that reflex and conditioned TP involve different pathways and mechanisms. Bulbar pyramid, red nucleus, cerebellar interposed nucleus, dorsal column-medial lemnisoal and spinocervicothalamic systems are essential to reflex TP but not involved in the conditioned TP. It seems, therefore, that training recruits or activates additional pathways for conditioned responses rather than strengthening those subserving the reflex responses.

Spontaneous recovery of function after central nervous system lesions could theoretically be achieved by reorganization or re-establishment. Actual cases of recovery may involve both processes in varying degrees. Possible mechanisms of reorganization, re-establishment or both in higher animals are sprouting, denervation supersensitivity, disappearance of shock or diascisis, equipotentiality or mass action, redundancy, alternative pathway or vicarious function, behavior substitution, etc. (5, 6, 11, 15). Spontaneous recovery of a motor system may involve one or more of the above-mentioned mechanisms. On the other hand, the mechanisms for neuromuscular recovery with training have not been well investigated. Previous studies (6, 14, 15) demonstrated that further functional improvement beyond spontaneous recovery can be obtained with training in experimental animals following brain damage. Training may increase functional level even with no change of reflex status. Liu and Chambers (9), Goldberg (6) and Yu (14) proposed that the underlying mechanism in recovery with training is the activation of parallel systems essential to conditioned responses. Our findings in this study support this hypothesis.

We have found that the conditioned behavior is difficult to transfer to an unconditioned or another conditioned response in animals with brain lesions (14, 15, 17, 19). In this study, such a phenomenon was demonstrated even more clearly. The reflex TP could never be elicited in the free situation in the cat which was trained to place the limb following light touch in a conditioning situation after pyramid section with or without other subsequent lesions. It is interesting to note that failure in obtaining generalization was observed earlier in conditioning normal animals. Experiments have shown that the phenomenon of generalization does not occur when a similar stimulus is applied against a different situational background (13).

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REFERENCES


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J. YU, Department of Physical Medicine and Rehabilitation, the University of Texas Health Science Center at San Antonio, 7703 Floyd Curl Drive, San Antonio, Texas 78284, USA.

C. N. LIU and W. W. CHAMBERS, Department of Anatomy and Institute of Neurological Sciences, University of Pennsylvania, Philadelphia, Pennsylvania 19174, USA.