FUNCTION OF CAT’S CAUDATE NUCLEUS IN TASKS INVOLVING SPATIAL DISCONTIGUITY BETWEEN LOCATION OF CUE AND RESPONSE

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Abstract. Cats were trained on go-left, go-right tasks with auditory frequency (F) or auditory location cues. The latter were used either with cue-response spatial discontiguity (LspD) or contiguity (LspC). Bilateral lesions located in the ventral segment of the caudate produced severe impairments on F and LspD tasks performance. Similar lesions, however, had no effect on the performance of the LspC task. Our findings show that spatial discontiguity between the location of cue and response is a crucial factor producing deficit on spatial tasks performance.

INTRODUCTION

The discovery that damage to anterior caudate nucleus in monkeys resulted in behavioral impairments similar to those found after cortical prefrontal ablations (15) led to further research on the functional role of this nucleus. The experimental findings supported the view that these two structures belong to the same functional system (1-4, 14, 16).

The analysis of a delayed response type performance, a task often used in studies concerning functional relationship of the prefrontal cortex and anterior caudate, identified temporal separation between cue and response, and spatial discrimination, as the critical factors involved in the tasks (11, 17, 22). Further studies with monkeys or dogs were
focused on the animal's orienting response in spatial requirements (6, 7, 9, 13). An orienting response directed toward the source of cue has been considered as a possible factor of impairment produced by either prefrontal or anterior caudate lesions (13).

Subsequent investigations were concerned with dissociation between the temporal and spatial factors in prefrontal tasks. The findings with non-delayed spatial tasks in which the location of the cue signaled a differing direction for the instrumental response, i.e., a spatial discontinuity between these elements, identified a different cortical focus for these tasks than for delayed responses (5, 12, 18–20).

The present investigation is concerned with determination of the function of the cat's anterior caudate nucleus in the performance of spatial tasks.

Three tasks were used which had the same response requirements. The cat had to approach one of the two feeders and to place his right paw on the lever located on that feeder. The tasks were differentiated by cues and/or cue-response spatial relationship.

METHODS

Subjects. Thirty three naive adult male cats of 2–4 kg body weight were employed. They were fed once a day, after the experimental session, in their single home cages.

Surgery and histology. One-stage bilateral electrolytic lesions were made under nembutal anesthesia (35 mg/kg) in aseptic condition. Anodal current was applied for 1.5 or 2 min through stereotically directed monopolar-platinum electrode, enamelled except for one millimeter on the tip. The intended location of damage was either dorsolateral (DL), dorsomedial (DM) or ventral (V) segment of the head of the caudate nucleus.

After the post-operative testing had been completed, the cats were anaesthetized with nembutal perfused through the heart with saline and 10% neutral formalin. Brains were cut into 50 μm frozen sections stained according to Klüver-Barrera technique to identify the location and extent of damage.

Apparatus. Behavioral testing was carried out in an open field compartment (Fig. 1) measuring 80 cm long by 60 cm wide and 60 cm high. The left and right side wall, contained a protruding feeder with a lever on its vertical wall. The feeders were 70 cm apart from each other. There were three speakers connected with an acoustic generator; one fixed at the center of the ceiling and two others located on the side walls, 25 cm above each feeder.
Acoustic stimuli could be delivered and the feeders operated by remote control. The animal's behavior could be watched on a TV set.

**Procedure.** During adaptation sessions food (2–3 g of raw meat) was delivered in a pseudo-random order, 17 times in each feeder. Food delivery was signaled by a click emitted when the well with meat was placed in position. Animals learned to approach food and to retrieve it from the well. When they responded without error to a 100 consecutive food presentations, two auditory stimuli were introduced as cues for instrumental responses. One cue of a pair signaled reward in the left, the other in the right feeder. In the first 100 trials the food was delivered in the 2nd second of cue presentation in the appropriate feeder.

After that, a formal acquisition training began. The experimental session consisted of 34 non-correction trials separated by intervals of 35–45 s, the cue being presented only when the animal was at a center of the compartment facing its front wall. Cues were presented in a pseudo-random order, 17 times each during the session. The cue terminated when an instrumental response, correct or non-correct, had been performed. It lasted, however, for 5 s in the absence of response. The instrumental response consisted in approaching the appropriate feeder and placing the right paw on a lever located on that feeder. Food reward was given only when both components were correct. The training continued until the animal met a criterion of, a least, 90 correct res-
responses in 100 consecutive trials, 45 responses to each cue. The completion of training was followed by a 7 days’ rest interval, then by retention testing to criterion and surgery. Post-operative testing resumed after 7 days of recovery period was carried out till re-attaining the criterion.

Three types of tasks with different spatial relationships between cue and response were employed, each cat being trained on one of them. (i) Auditory frequency (F) differentiation. The tone of 700 Hz transmitted through the speaker located at the ceiling signalled food in the left feeder. The tone of 1000 Hz from the same speaker signaled food in the right feeder. (ii) Auditory location differentiation with cue-response spatial discontiguity (LspD) in which the tone of 1000 Hz was presented through either the left or right speaker (the left and right cue). The left cue signalled food in the right feeder and vice versa, the right cue signalled food in the left feeder. (iii) Auditory location differentiation with cue-response spatial contiguity (LspC): left cue — left feeder, right cue — right feeder.

The analysis of error distribution was done by means of Smirnov test.

RESULTS

Tasks performance. All lesioned cats appeared motorically and manually well-coordinated and no neurological symptoms were observed. One cat (V1) only exhibited transient enhanced motor activity.

The pre- and post-operative test scores are shown in Table I for the F and Table II for the LspD tasks. Consistent results were obtained for both tasks with about equal deficits by DL and DM lesion groups and much more persistent deficit by V-lesioned groups. During the first 100 post-operative trials impairments were found in every cat. Error differences between both retention tests (F and LspD) in this period of testing were not significant. The considerable overlap between scores among the lesioned groups and similar mean scores (Table I and II) indicated no differential lesion-effects on these measures. However, the scores for retraining to the task criterion (the total number of postoperative errors) showed more severe impairments in the V-lesioned cats. There was no overlap of error scores on either task between dorsal and ventral lesioned cats (P < 0.01). The retraining scores did not differ significantly between DL and DM groups, as far as errors are concerned. However, differences in tasks performance between DL and the other two groups (DM, V) are indicated by the incidence of differing types of errors (Fig. 2). The majority of errors consisted in
Table I

Performance on frequency differentiation task (F): Errors made before and after lesions to dorsolateral (DL) dorsomedial (DM) or ventral (V) segments of the head of the caudate nucleus

<table>
<thead>
<tr>
<th>CAT</th>
<th>Pre-operative</th>
<th>Post-operative</th>
<th>% of total nucleus damage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Acquisition</td>
<td>Retention*</td>
<td>Total</td>
</tr>
<tr>
<td>DL1</td>
<td>389</td>
<td>7</td>
<td>24</td>
</tr>
<tr>
<td>DL2</td>
<td>409</td>
<td>6</td>
<td>16</td>
</tr>
<tr>
<td>DL3</td>
<td>444</td>
<td>7</td>
<td>37</td>
</tr>
<tr>
<td>DL4</td>
<td>492</td>
<td>9</td>
<td>48</td>
</tr>
<tr>
<td>Mean number</td>
<td>433.5</td>
<td>7.2</td>
<td>31.2</td>
</tr>
<tr>
<td>DM1</td>
<td>346</td>
<td>4</td>
<td>39</td>
</tr>
<tr>
<td>DM2</td>
<td>425</td>
<td>10</td>
<td>36</td>
</tr>
<tr>
<td>DM3</td>
<td>444</td>
<td>10</td>
<td>24</td>
</tr>
<tr>
<td>DM4</td>
<td>678</td>
<td>6</td>
<td>19</td>
</tr>
<tr>
<td>Mean number</td>
<td>472.2</td>
<td>7.5</td>
<td>29.5</td>
</tr>
<tr>
<td>V1</td>
<td>338</td>
<td>7</td>
<td>24</td>
</tr>
<tr>
<td>V2</td>
<td>450</td>
<td>8</td>
<td>24</td>
</tr>
<tr>
<td>V3</td>
<td>458</td>
<td>6</td>
<td>35</td>
</tr>
<tr>
<td>V4</td>
<td>560</td>
<td>6</td>
<td>41</td>
</tr>
<tr>
<td>Mean number</td>
<td>452.0</td>
<td>6.8</td>
<td>32.0</td>
</tr>
</tbody>
</table>

* Post-operative retention: errors performed in the first 100 trials

Table II

Performance on location task (LspD): Errors made before and after lesions to dorsolateral (DL) dorsomedial (DM) or ventral (V) segments of the head of the caudate nucleus

<table>
<thead>
<tr>
<th>CAT</th>
<th>Pre-operative</th>
<th>Post-operative</th>
<th>% of total nucleus damage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Acquisition</td>
<td>Retention*</td>
<td>Total</td>
</tr>
<tr>
<td>DL5</td>
<td>197</td>
<td>4</td>
<td>52</td>
</tr>
<tr>
<td>DL6</td>
<td>265</td>
<td>7</td>
<td>35</td>
</tr>
<tr>
<td>DL7</td>
<td>279</td>
<td>9</td>
<td>35</td>
</tr>
<tr>
<td>DL8</td>
<td>442</td>
<td>7</td>
<td>37</td>
</tr>
<tr>
<td>Mean number</td>
<td>294.5</td>
<td>6.7</td>
<td>39.7</td>
</tr>
<tr>
<td>DM5</td>
<td>182</td>
<td>4</td>
<td>30</td>
</tr>
<tr>
<td>DM6</td>
<td>194</td>
<td>5</td>
<td>27</td>
</tr>
<tr>
<td>DM7</td>
<td>247</td>
<td>7</td>
<td>36</td>
</tr>
<tr>
<td>DM8</td>
<td>348</td>
<td>4</td>
<td>46</td>
</tr>
<tr>
<td>Mean number</td>
<td>242.8</td>
<td>5.0</td>
<td>34.7</td>
</tr>
<tr>
<td>V5</td>
<td>190</td>
<td>7</td>
<td>45</td>
</tr>
<tr>
<td>V6</td>
<td>262</td>
<td>7</td>
<td>51</td>
</tr>
<tr>
<td>V7</td>
<td>350</td>
<td>8</td>
<td>40</td>
</tr>
<tr>
<td>V8</td>
<td>355</td>
<td>8</td>
<td>44</td>
</tr>
<tr>
<td>Mean number</td>
<td>289.3</td>
<td>7.5</td>
<td>45.0</td>
</tr>
</tbody>
</table>

* Post-operative retention: errors performed in first 100 trials.
approaching the wrong feeder and placing the right paw on that feeder's lever. These responses accounted in both tasks for about 90% of errors by normal (pre-operative), DM and V lesioned cats, but only for 50% and 70% of errors performed by DL cats, on F and LspD tasks, respectively (Fig. 2). The DL cats committed errors of withholding the response when they remained at the center of the compartment approaching neither feeder (24%, 10%) or of placing the right paw on the feeder instead on the lever (10%, 13%), or else withholding the placing response after approaching either feeder (7%, 5%), in F and LspD tasks, respectively. The left paw, however, had never been used for placing response. The postoperative errors occurred about equally to cues for the left or right responses.

In contrast to the above findings, the results in the LspC showed no performance impairments. All lesioned cats responded at least 90% correct in the first 100 post-operative trials on the task with spatial contiguity between cue and response.

Anatomy. As may be seen in Figs. 3–5, the lesions were located in the intended sections of the head of the caudate. However, not all of them were confined to this structure. All dorsal lesions (DL and DM) extended to the internal capsule fibers passing above the caudate, and some of them invaded an adjacent caudate segment within its head. Lesions in cats: DL5, DL6 and DL10 crossed to DM area, while two DM damages extended to either DL (DM3) or V (DM5) segment of the head of the caudate. Three V-lesions (V4, V6, V10) invaded the internal capsule fibers adjacent to this segment and one (V3) extended slightly

![Fig. 2. Patterns of errors performed by normal and lesioned cats with damage to dorsolateral (DL) dorsomedial (DM) or ventral (V) segment of the caudate's head. The left columns denote pre-operative errors. The right columns, post-operative errors. Approaching the wrong feeder and placing the right paw on its lever (1). Approaching either feeder and placing the paw on the feeder instead of a lever (2) or withholding the placing response (3) and, absence of approaching and placing response (4).](image-url)
Fig. 3. Selected cross-sections through the lesions of representative cats with damage to dorsolateral (DL) segment of the caudate's head.

to DM area. Seven V lesions, however, were confined to the ventral segment of the caudate's head.

As it is shown in Table I and II, the size of damage varied from 20/o to 150/o of the entire caudate nucleus. However, many lesions varied only from 50/o to 90/o and the size of ventral lesions was no larger than of orsal ones.

DISCUSSION

This study was designed to explore whether selective lesions within the head of the caudate nucleus in cat would produce an impairment on performance of tasks that involve (or not) spatial discontiguity between the location of cue and response.

The lesions placed either in the dorsal or ventral segment of the
caudate's head did not affect retention performance on the spatially contiguous task (LspC). They resulted, however, in impairments of the other tasks which involved a spatial discontiguity between the location of cue and response. For each lesion group the deficits were about equal for the F and LspD task. On both tasks the impairments were more severe after ventral than after dorsal lesions, DL or DM. A differential degree of deficit seems to depend more upon various location than different size of damages. All ventral lesions produced a more severe deficit than dorsal ones ($P < 0.01$) though the former damages were no larger than the latter. The ventral segment of the caudate's head seems to be more critically involved in solving tasks with cue-response spatial discontiguity than either dorsal segment.

Fig. 4. Selected cross-sections through the lesions of representative cats with damage to dorsomedial (DM) segment of the caudate's head.
On the other hand, a comparison of post-operative performance on the F and LspD tasks showed a striking similarity of impairments following lesions of the same localization. The question arose, which factor is responsible for the impairments. There would be either different information (frequency or location cues) or spatial discontiguity between the location of cue and response involved in both tasks. Though the former factor could not be excluded, the striking similarity of impairments on both tasks seems to indicate rather upon spatial discontiguity between the location of cue and response as a factor responsible for deficits.

The spatial problem is not new. It has been considered as one of the significant elements of the delayed response task (8, 10, 11, 22)

Fig. 5. Selected cross-sections through the lesions of representative cats with damage to ventral (V) segment of the caudate's head.
which could be responsible for a deficit on the delayed response performance caused by either prefrontal or anterior caudate lesions.

The significance of cue-response spatial factor has been demonstrated in this study by a dissociation of deficit: impairment on performance of the LspD task involving cue-response spatial discontiguity, and non-impairment on the LspC with cue-response spatial contiguity. Fundamental for orientation in space is an orienting response directed towards the source of cue. While in the spatially contiguous task the animal's orienting response to the cue guided its instrumental response, a more complex process is required for the solution of spatial discontiguity task. The orienting response elicits kinesthetic stimuli that serve for direction of the instrumental response signalled by cue. Problems of spatial discontiguity have been investigated in monkeys (5, 12) and in dogs (8, 9, 20, 21) following prefrontal lesions. The present findings show that the head of the caudate nucleus, especially its ventral segment in cat, performs an important function in the solution of these tasks.

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REFERENCES


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