FUNCTION OF DOG'S AUDITORY CORTEX IN TESTS INVOLVING AUDITORY LOCATION CUES AND DIRECTIONAL INSTRUMENTAL RESPONSE

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Abstract. Twenty one dogs, distributed into four groups, were trained pre-operatively in differentiation of auditory location or frequency cues. In each group instrumental responses, reinforced by food consisted in placing by the animal its right paw on the side levers. The first differentiation, go-left, go-right task with two location cues, required the animal to place its paw on the lever located opposite to the source of the cue. The second differentiation task with the same location cues required placing the paw on the lever located close to the cue. The third task, involving 700 Hz vs. 1,000 Hz tone, required responding to one lever to the presentation of one tone and responding to the opposite lever to the presentation of the other. The last task was a symmetrically reinforced go, no-go differentiation with, again, auditory location cues: the animals were trained to place the paw on a lever to one location cue and to withhold this response to the other location cue. Bilateral ablation of the primary auditory cortex produced a considerable impairment of the performance of the two go-left, go-right tasks involving location cues. The go-left, go-right task employing frequency cues, and the symmetrically reinforced go, no-go task with location cues, were only slightly disturbed by this lesion.

INTRODUCTION

Since the first data concerning the location of the auditory cortex (3, 10) and its division into functional sections (1, 17) were obtained, a number of studies concerning the function of this particular cortical

1 We are grieved to inform that Irena Stepień died the last Summer. Correspondence should be addressed to W. Ławicka at the Nencki Institute.
area have been made. The results of some experiments indicated that the auditory cortex is crucial for sound localization. Consequently, an impairment of location tasks observed after auditory cortex lesions was considered as a sensory deficit (11, 13, 18). However, more recent data have shown that tasks based on sound location cues can be solved by the animals deprived of this particular cortex if testing is carried out under appropriate conditions. Ravizza and Masterton (15) found that a decorticated opossum was able to discriminate between the left and right sound burst if tested using conditioned suppression technique. Similarly, Heffner and Masterton (6) showed that monkeys deprived of the auditory cortex could discriminate between the left and right clicks if tested under conditioned suppression and without a delay between cue and response. On the other hand, Szwejkowska and Sychowa (19) reported that dogs with auditory cortex lesions were unable to discriminate between two sound locations (in front of and behind the animal) when tested on the go, no-go differentiation. The majority of investigations employed tasks which involved the animal's approaching the source of sound i.e. under conditions of cue-response spatial contiguity.

The present study was designed to explore the contribution of the auditory cortex in solving more complex tests differentiated by cue-response spatial relations. Two go-left, go-right tests were used involving either spatially contiguous, or discontiguous cue-response and the go, no-go differentiation task with location cues. Introducing the two former tasks offered a possibility to test the animal's ability to employ location cues as signals for two instrumental directional responses pointed either at the site of the sound source or at the opposite direction. Introducing the go, no-go test, on the other hand, offered a possibility to test the animal’s ability to use location cues as signal for non-directional response differentiation. Additionally, the go-left go-right task with frequency cues was used as a control test. Dogs were chosen for this experiment because they localize well the sound in space. In dogs, location cues prevail over quality auditory cues when both are available as stimuli guiding differential behavior requiring either locomotor (9) or manipulatory (2) response.

METHODS

Subjects

Twenty one experimentally naive male dogs were employed. They were mongrels about 1.5-2 years old, ranging in weight from 12 to 15 kg at the beginning of experiments. They were housed in individual chambers measuring 125×210 cm, with free access to water. They were fed once a day about 20-22 h before testing.
Experimental chamber

Testing was conducted in a standard CRs chamber (Fig. 1) with an elevated platform equipped with a feeder, three speakers and two levers. One speaker was situated on the left and the other (Fig. 1) on the right side of the platform, both close to the feeder and approximately at a level of the dog's head, 80 cm apart from each other. The third, middle speaker was located above the animal’s head. Close to each side speaker, there was a lever available to the animal. The feeder contained 21 wells situated on a disk, 20 of them hidden under the cover and one placed under a round opening in front of the dog. Each well with food (two pieces of bread with boiled meat and broth) could be moved and placed under the opening making food available to the dog. During and experimental session, the semirestrained animal was standing on the platform in front of the feeder. Auditory stimuli used as the cues for instrumental responses could be presented through either speaker and food could be delivered by remote control. The animal’s behavior could be watched on TV set.

Cues. The auditory location cues consisted of a 1,000 Hz tone delivered through either the left or right speaker (left and right cue). Frequency cues were two tones: either 700 Hz or 1,000 Hz delivered through the middle speaker.
Tests. Four auditory tests were presented with different cue-response spatial relations. In all four tests the animals were trained to use only the right paw for instrumental responding. Each dog was trained on a single test. (i) The go-left, go-right differentiation with cue-response spatially discontiguous (dogs Ecl-Ec5) required from the animal to respond by placing the paw on the right lever to the left cue or placing it on the left lever when the right cue was presented: left cue — right lever, right cue — left lever. (ii) The go-left, go-right differentiation with cue-response spatially contiguous (dogs Ec6-Ec10) required placing the paw on a lever located on the same side as the cue: left cue — left lever, right cue — right lever. (iii) The frequency differentiation (dogs Ecll-Ec15) required placing the paw on the left lever in response to the 700 Hz tone and placing it on the right lever to the presentation of 1.000 Hz tone: 700 Hz tone-left lever, 1.000 Hz-right lever. Both tones were delivered through the same speaker located in the middle above the dog's head. (iv) The go, no-go differentiation task with symmetrical reinforcement procedure (dogs Ec16-Ec21) required the animal to place the paw on the right lever to one location cue and to refrain from this response to another location cue. In three dogs (Ec16, Ec19, Ec21) the left cue signalled the placing of the paw, whereas the presentation of the right cue was a signal for withholding this response. In three other animals (Ec17, Ec18, Ec20) it was reversed. Both responses, limb placing and refraining from this response, were reinforced by food.

Behavioral procedure

Preliminary training. First, the animals were adapted to experimental conditions and learned to retrieve food from the wells. Then two either location or frequency cues were introduced, being presented in a pseudo-random order. The method of passive movements was used for instrumental response acquisition. A cue was presented, the paw was placed on an appropriate lever and food immediately delivered. During training the go, no-go task, in the no-go trials, food was delivered when the response was withhold for 5 s of the stimulus duration. When active responses of placing the paw on a lever appeared to stimuli presentation, the formal acquisition training began.

Acquisition training. Experimental sessions consisted of 20 trials. Both cues were delivered in a pseudorandom order, 10 times each, with intertrial intervals of 60 s. The cue terminated immediately after an instrumental response to a positive cue was performed, correct or non-correct, or it lasted for 5 s if the animal failed to respond to the cue. In the go, no-go test, the no-go cue always lasted 5 s and was reinforced
only when the animal's placing response was withhold. The non-correction method was used. The training continued until the animal reached criterion of at least 90 correct responses in a 100 consecutive trials, 45 to each cue. After the completion of preoperative training, the animals were given 14 days of rest followed by retention testing to criterion. Then they were subjected to surgery, followed by 14 days of recovery and postoperative retraining to criterion. After the completion of behavioral testing the animals were sacrificed and lesions identified.

_Surgical and histological procedure_

Each dog received one-stage bilateral ablation of the primary auditory cortex in aseptic conditions. Before surgery the animal was anesthetized with Nembutal (35 mg/kg) administered intramuscularly. Then the animal's head was shaved, washed and fixed in a special apparatus. The scalp was opened, temporal muscle dissected and retracted. The cranium bone, covering the auditory area removed, dura cut and cortical tissue removed by subpial aspiration. Bleeding was stopped with cautery; dura, muscles, underskin tissue and the skin itself was sewn. After the surgery, the dog was taken to a special care room and was given 150 µm of penicillin daily for a week. After the behavioral testing was completed, the animal was anesthetized with an overdose of Nembutal, perfused intracardially with saline and 10\% neutral formalin. Its brain was removed and embedded in paraffin for frozen sectioning, cut at 40 µm in frontal plane and alternate sections stained according to Nissl and Cluver-Barrera techniques in order to identify the lesion's location and extent.

**RESULTS**

_Anatomy_

The location and extent of representative damages are shown in Fig. 2. As it may be seen, the lesions were located in the intended area. They, however, did not cover the entire ectosylvian gyrus. Lesions were limited to the middle section of the gyrus in nine dogs (Ec3, Ec5, Ec7, Ec11, Ec14, Ec15, Ec16, Ec19, Ec20). They extended upon the rostral section of the gyrus in eight dogs, either unilaterally (Ec2, Ec8, Ec12, Ec13, Ec21) or bilaterally (Ec4, Ec9, Ec18). They included all three sections, rostral, middle and caudal, in four animals (Ec1, Ec6, Ec10, Ec17). Usually, damages were confined to ectosylvian area. In three animals, however, lesions invaded slightly either the sylvian (Ec6) or suprasylvian (Ec5, Ec11) cortex. Fibers underlying ectosylvian cortex were injured in five dogs (Ec2, Ec6, Ec12, Ec20, Ec21).
Fig. 2. Reconstructions of lesions in two representative animals for each test and selected cross sections at indicated section levels.
**Behavioral results**

Following bilateral ablations of primary auditory cortex, all dogs remained motorically well coordinated. Instrumental responses were performed efficiently and skillfully.

Error scores are presented in Table I and II. The analysis of error distribution was done by means of mixed designed analysis of variance: type I (Table I) and type As (Table II), according to Linquist.

**Table I**

Number of errors in dogs trained in the go-left go-right tests. E, incorrect response; N, no response.

<table>
<thead>
<tr>
<th>Cue — lever relations</th>
<th>Dog</th>
<th>Acquisition</th>
<th>Retention (100 trials)</th>
<th>Post-op</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Pre-op</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Total E N</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Total</td>
<td>First 100 trials</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L — R</td>
<td>Ec1</td>
<td>59 49 10</td>
<td>6</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>Ec2</td>
<td>74 61 13</td>
<td>3</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>Ec3</td>
<td>87 85 2</td>
<td>3</td>
<td>79</td>
</tr>
<tr>
<td></td>
<td>Ec4</td>
<td>110 110 0</td>
<td>1</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td>Ec5</td>
<td>185 181 4</td>
<td>3</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>Ec6</td>
<td>8 5 3</td>
<td>2</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td>Ec7</td>
<td>10 8 2</td>
<td>2</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>Ec8</td>
<td>13 13 0</td>
<td>3</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Ec9</td>
<td>21 16 5</td>
<td>2</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>Ec10</td>
<td>26 21 5</td>
<td>0</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>Ec11</td>
<td>64 62 2</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Ec12</td>
<td>128 128 0</td>
<td>4</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Ec13</td>
<td>160 160 0</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Ec14</td>
<td>272 218 54</td>
<td>7</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>Ec15</td>
<td>293 285 8</td>
<td>3</td>
<td>27</td>
</tr>
</tbody>
</table>

Postoperative performance on the go-left, go-right differentiations to location cues (Table I) was considerably, although not equally, impaired. Especially severe deficit was found in the test which required performing the response at a direction opposite to the location of the cue: impairment was found in each animal of this group. During the first 100 postoperative trials all five dogs performed very poorly. Three of them (Ec2, Ec3, Ec4) made only 28, 21 and 47 correct responses, respectively. Two others responded correctly in 69 (Ec1) and 60 (Ec5) trials. Although all dogs improved in the course of postoperative testing and reached criterion, they required even more extensive retraining than the
training necessary for the original acquisition learning. Postoperative errors ranged from 158 to 328 in four dogs (Ec2-Ec5) and were 87 in one dog (Ec1). In all subjects, except one (Ec5), postoperative errors exceeded the preoperative number, which ranged from 59 to 87 in three dogs (Ec1-Ec3) and in two others was 110 (Ec4) and 185 (Ec5). The difference between preoperative and postoperative errors was statistically significant at $P < 0.001$, $(F_{(2,12)} = 14.65)$. Most preoperative and postoperative errors consisted in placing the paw on an incorrect lever. The other type of error, consisting in failing to perform instrumental response to the cue, accounted for only $6\%$ of preoperative and $28\%$ of postoperative number of errors. A decrease in instrumental responding during the postoperative testing was very pronounced in dog Ec2 ($70\%$), and less pronounced in Ec3 and Ec4 ($33\%$ and $20\%$). In two other animals (Ec1, Ec5), there was no decrease in responding.

**Table II**

Number of errors in dogs trained in the go, no-go symmetrically reinforced test

<table>
<thead>
<tr>
<th>Cue – lever relations</th>
<th>Dog</th>
<th>Pre-op acquisition</th>
<th>Post-op retention</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>Go</td>
</tr>
<tr>
<td><strong>L – R</strong></td>
<td>Ec16</td>
<td>25</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Ec19</td>
<td>57</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Ec21</td>
<td>99</td>
<td>42</td>
</tr>
<tr>
<td><strong>R – R</strong></td>
<td>Ec17</td>
<td>48</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>Ec18</td>
<td>48</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Ec20</td>
<td>87</td>
<td>47</td>
</tr>
</tbody>
</table>

Deficient performance in the second auditory location test, requiring placing the paw on the lever located close to the cue, occurred less often, although it was clearly pronounced. Postoperative errors which ranged from 23 to 45 in four animals (Ec7-Ec10) and were 68 for Ec6, exceeded the preoperative numbers ranging from 8 to 26, but the difference appeared not significant (Duncan tests). Most errors consisted in the choice of an incorrect lever. A failure to respond appeared only occasionally in four dogs and was more often ($13\%$) only in one dog (Ec6).

In contrast to the above findings, the performance of the two other tests was not impaired or was impaired only slightly. Postoperative errors were much less numerous than the preoperative ones $P < 0.001$, $(F_{(1,9)} = 15.25)$. In the performance of frequency differentiation the preoperative errors were 128-293 for four animals and 64 for one (Ec11), and the postoperative amounted to 14-29 for four dogs and 44 for one (Ec15). On the go, no-go postoperative differentiation (Table II) two animals
(Ec18, Ec21) solved the test at criterion level, two other (Ec16, Ec17) near criterion level making 14 and 15 errors, and two (Ec19, Ec20) made 20 and 18 errors, respectively.

DISCUSSION

The presented results show a dissociation of function following bilateral primary auditory cortex ablations. Dogs deprived of this cortical area were performing poorly these spatial differentiations which required the choice of one of the two side levers when the choice was guided by auditory location cues. On the other hand, lesioned animals performed well another test guided by the same pair of location cues, involved in the go, no-go test. They were also able to solve go-left go-right, differentiation when two instrumental responses were determined by auditory frequency cues.

The most severe impairment, measured by the number of postoperative errors, was found in the performance of go-left, go-right differentiation in which location cues and responses were spatially discontiguous. Postoperative number of errors in this task exceeded considerably the number of the preoperative ones, the difference being statistically significant. A less severe deficit was observed in the performance on the go-left, go-right differentiation with cues and responses spatially contiguous. A preponderance of postoperative number of errors over the preoperative ones in that task was statistically NS. On the other hand, the lesioned dogs were successful, or almost successful, in the performance of go, no-go differentiation with cue-response spatially contiguous (three dogs) or discontiguous (three other dogs) (see Table II). There was also only a very slight deficit, if any, in the performance of go-left, go-right task with frequency cues.

These data indicate that postoperatively the animals were able to discriminate two location cues (go-no go test) and to make differentiation between two directional responses (go-left, go-right with frequency cues). The deficit was present in these two differentiation tasks which involved two directional instrumental responses based on location cues. Earlier evidence indicated that animals deprived of the auditory cortex, such as opossum (15), cat (13, 16, 18), dog (4) or monkey (6) were able to solve some tests but unable to solve others, both test types being based on discrimination of location cues. Neff et al. (12) and Heffner (4) found that a crucial factor for the discrimination of location cues may be the distance between the animal and the source of sound. Animals deprived of the auditory cortex were unable to locate the source of a click from a long distance, but were still able to do it from a short
distance (4). I our experiments the distance between the animal and
the source of the cue was a short one.

Our finding concerning the postoperative decrease in the number of
instrumental responses, noticed in some operated dogs, had been observed
earlier (6, 12, 13) and interpreted as an effect of impairment of the
animal's ability to attend auditory stimuli. According to Heffner and
Masterton (6), however, the inattentiveness to sound stimuli may be
considered as the effect of the deficit rather than the cause of it. The
decrease in instrumental responding was found only in three operated
animals (Ec2, Ec3, Ec4) that failed to perform the response in 70, 33 and
20% of trials, respectively. Yet, like other dogs, they exhibited attentiveness manifested by head movements towards the cue.

The deficit in solving auditory location tests by animals deprived of
the auditory cortex was also interpreted as a result of separation between
structures involved in sound localization and motor structures involved
in the execution of particular motor responses (4, 5, 14, 15). This interpre-
tation could be, to some extent, applied to our results.

The deficit observed in two go-left, go-right tests with location cues
may indicate that kinesthetic stimuli generated by orienting responses
are no more associated with correct instrumental responses. Our data
suggest that postoperatively these stimuli could no more play a deter-
mining role (8). Lack of the deficit in the go, no-go test, in which the
orienting response signalled to the animal whether to perform or with-
hold the instrumental response, was possible because the stimulus in
the last task had only a releasing role (8).

The differential degree of deficit observed between the two go-left,
go-right tasks with location cues may be related to a different degree
doF test complexity. The animals in which the location cue signalled an
instrumental response on the lever opposite to the cue, manifested a more severe deficit than the animals trained to place the paw on the lever
close to the cue. The difference between these groups was also mani-
fested in the preoperative acquisition learning, in which the first group
with responses and cues spatially discontiguous, made more errors before
reaching criterion than the second group. Thus, the level of impairment
could be related to task difficulty. However, crucial for the differentia-
tion deficit were the determining properties of locations cues required
in these two tests and subsequently affected by ectosylvian lesion.

The question arises, whether similar impairment in tests with loca-
tion cues would be produced if motor requirements were changed to
nondirectional instrumental response, e.g. the left-paw, right-paw diffe-
rentiation. This will be the subject of the next study.
Changes suggested by referees were introduced by Waclawa Ławicka.

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REFERENCES


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